The butterfly community of a managed West African rainforest:

patterns of habitat specificity, diversity, stratification and movement

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CONTENTS

1. INTRODUCTION

Tropical forest ecosystems are under enormous pressure all over the world. Many forest areas in the tropics may only persist as production areas (Gomez-Pompa *et al.* 1991, Brown 1997, Rice *et al.* 1997, Hunter 1999), and pressure on unprotected forests is very likely to escalate (WIR 1985, Terborgh 1999, Lewis 2000). Despite the generally recognised importance for global diversity (e.g. Sutton and Collins 1991, ICBP 1992, World Conservation Monitoring Centre 1992), not more than 4% of all tropical forests are situated within the boundaries of reserves or national parks (Whitmore and Sayer 1992). Even the best protected areas might not be adequate to maintain the original ecosystems because of their small size and difficult political and social circumstances (Terborgh 1999). Recently, several ideas have been developed on the way to reach sustainability in and to slow down the rate of loss of tropical forests, e.g through ecotourism, sustainable use of nontimber products and natural forest management. Regardless of its function in actually maintaining diversity (see Johns 1992, Hunter 1999), natural forest management is generally considered a viable alternative to the continued mining of virgin forests (Terborgh 1999).

In West Africa, especially in Nigeria and Côte d’Ivoire where deforestation rates are extremely high (FAO 1988, Barnes 1990, Sayer *et al.*, 1992), silviculturalists experimented with natural forest regeneration and line planting during most of the first half of the twentieth century (Gomez-Pompa *et al.* 1991). More recently, thinning operations became an integral part of the forest management, promoting the growth of commercial timber species by freeing them from competition with climbers and non-crop tree species (Parren and de Graaf 1995). Thinning is becoming increasingly important for the natural forest management, and will be carried out over large areas of logged forests in Côte d’Ivoire (SODEFOR 1994). However, there still is a great need for studies testing the actual sustainability and economical profits of natural forest management techniques (Boyle and Sayer 1995, Dudley *et al.* 1995). Thinning operations in particular are often carried out over large forest areas, causing considerable changes in the vegetation structure and the distribution of forest interior birds (Waltert 2000).

Although the magnitude of biodiversity present on Earth is largely unknown (e.g. Dobson 1995) and its estimates remain highly controversial (Erwin 1982, May 1990, Stork 1988), it is generally accepted that much, if not most, of the global diversity in terms of numbers of species is represented by arthropods inhabiting tropical rainforests (e.g. Wilson 1988). Still, few data are available about the effects of forest disturbance upon these species-rich insect faunas (for the tropics e.g. Eggleton *et al.* 1995, Holloway 1987, Holloway *et al.* 1992, Klein 1989, Wolda 1987). Butterflies, however, are comparatively well-studied. Butterfly species composition in disturbed and undisturbed forests has been investigated for example in Southeast Asia (Spitzer *et al.* 1993, Hill *et al.* 1995, Beck and Schulze 2000), Madagascar

(Kremen 1992), and the Neotropics (Lovejoy *et al.* 1986, Brown 1991, Sparrow *et al.* 1994, DeVries *et al.* 1997, Wood and Gillman 1998).

Several studies showed that low disturbance levels have a positive effect on small-scale diversity and abundance of rainforest butterflies (Lovejoy *et al.* 1986, Brown 1991, Sparrow *et al.* 1994, Wood and Gillman 1998). These results are in accordance with the intermediate disturbance theory (Connell 1978) and have parallels in temperate forest habitats where the forest management providing a large range of shade levels, has been found to increase the number of habitats suitable to different butterfly species (Warren 1985). However, many studies also indicate adverse effects of disturbance on tropical butterfly communities (Bowman *et al.* 1990, Thomas 1991, Spitzer *et al.* 1993, 1997, Kremen 1994, Hamer and Hill 2000, Hill *et al.* 1995, 2001, Hill and Hamer 1998, Brown 1997, Lewis *et al.* 1998, Willott *et al.* 2000, Lewis 2000, Fermon *et al.* 2000, 2001), indicating an increase in diversity and/or abundance of widespread, common butterfly species and a decline in restricted range species after disturbance.

With few exceptions (e.g. DeVries *et al.* 1997, Wood and Gillman 1998, Hill *et al.* 2001), most of the previous mentioned forest disturbance studies focus on butterfly trapping or transect sampling at forest understorey level only, and do not consider changes at higher levels along the vertical strata. DeVries (1988) showed that differences in light from canopy to ground level maintain highly distinctive canopy and understorey butterfly assemblages. Wood and Gillman (1998) found a greater similarity between the understorey and canopy butterfly fauna in disturbed compared to undisturbed forest habitats. Hill *et al.* (2001) equally showed that the butterfly assemblage trapped at canopy level were more similar with those trapped in the understorey of forest gaps than those in closed-canopy sites. These findings indicate that differences in microclimate, caused by opening the forest canopy, can bias abundance and diversity data measured at understorey level due to a downward shift of higher strata species. Along with microclimatic changes, differences in vegetation structure and plant species composition can equally result from forest disturbance. In addition to differences in capture frequencies and butterfly richness parameters, these “architectural” changes are likely to influence butterfly behaviour. Butterfly movement patterns are known to depend on host plant distribution and resource availability (e.g. Baker 1984, Gilbert 1984), and habitat modification altering both of these is likely to cause different movement behaviour in butterflies.

Although deforestation rates are highest in several (West) African regions, little is known about the effects of forest disturbance on afrotropical butterflies (Larsen 1995a). In Madagascar, disturbed forest habitats and edges were equally found to be richer in species than undisturbed areas (Kremen 1992, 1994). Also in southern Nigeria, Larsen *et al.* (1979) found a surprisingly rich butterfly fauna in young secondary growth within the rainforest zone. In south-central Benin, overall butterfly species richness was higher in clearings than in closed forest, however, a high proportion of forest understorey species with a restricted geographic range were exclusively captured in closed forest patches (Fermon *et al*. 2001). Whereas there is still much work to do to describe the biodiversity of unmodified forest systems, questions concerning ecologically sound management plans cannot be answered without proper assessment in managed forest areas. Considering the high deforestation rates and the fact that a combination of ecology and economy is often the only strategy to protect the rich rainforest biodiversity in many developing countries (Brown 1997), these assessment studies will become increasingly important.

The present study mainly documents habitat specificity, diversity, movement and vertical stratification of fruit-feeding nymphalid butterflies in the over-logged, managed Bossematié Forest Reserve in south-eastern Côte d'Ivoire. The study took place within the framework of the management and biomonitoring programme developed for the region's seven forest reserves. In this programme, the Bossematié Reserve serves as a pilot forest for forest rehabilitation, in a cooperation between the German aid agency (GTZ) and the local forestry authorities (SODEFOR). The 75 ha study site included three management plots: a mono-dominant tree plantation, a thinned forest, and an regenerating plot as control forest. Within these three plots, nymphalid species abundance and diversity were assessed in different seasons, in different forest succession stages, as well as in different heights along the vertical strata. Furthermore, butterfly movement was analysed in relation to habitat differences due to the management regime applied, and the vegetation structure was compared between management sites.

First results concerning the impact of thinning operations on diversity and capture frequencies of nymphalid butterflies can be found in Fermon *et al*. (2000); results on movement and vertical stratification patterns can be found in Fermon *et al*. (in prep.).

2. BACKGROUND AND OBJECTIVES

On a world-wide scale, deforestation rates in Côte d'Ivoire are among the highest. The southern part of the country was once entirely forested, and consisted of an estimated 132,000 sq. km of moist forests (evergreen and semi-deciduous forest vegetation). By 1987, only 17 % of these remained (Sayer *et al.* 1992). Most forest reserves still covered by forest are over-logged, isolated fragments of variable size, mostly with a surface well below 200 sq. km (SODEFOR 1996). A high percentage of the forest reserves have been occupied illegally by farmers growing food and cash crops such as coffee and cocoa (Parren and de Graaf 1995). In addition, hunting is considered to be the major threat for many forest bird and mammal species (McGraw *et al.* 1998). As a response to the Biodiversity Conference in Rio, national governments world-wide started activities to stop uncontrolled exploitation of natural habitats and initiated the development of sustainable land-use and ecologically sound management plans. In 1990, a German sponsored development project started in eastern Côte d'Ivoire, aiming at the rehabilitation of the fragmented and timber-depleted forest reserves, the development of sound management techniques and the maintenance of biodiversity and the ecosystem's important ecological functions (Wöll 1992). The Bossematié Forest Reserve (22,000 ha) was selected as a pilot forest and a management plan was established to serve both economic as well as conservation purposes. To test the impact of the applied management plan and to describe the ecological status of the Bossematié and other forest reserves, long-term management effects on selected bird and mammal indicator species are being monitored (see Mühlenberg *et al.* 1995, 1999). The main monitoring programme is entirely community-based, but additional scientific studies were also designed (e.g. for birds see Waltert 2000, butterflies: this study). The principal objectives of this study were:

- ***to assess the potential of the butterfly fauna to survive in the secondary vegetation of a forest fragment of several 100 sq. km and to document the effects of further fragmentation.***

Hereby, the emphasis is put on the fruit- feeding butterfly community of a selected 75-ha study plot. Species abundance, richness, movement and vertical stratification patterns are the main aspects analysed. Results are considered both in different seasons and years as in different vegetation patches of the (secondary) forest mosaic. Furthermore, a comparison is made between nymphalid abundance and diversity patterns found on the study site within the 22,000 ha Bossematié Reserve and a 3 km distant, remnant 6 ha forest fragment;

and

- ***to document the effect of the forest management applied within the forest reserves on the butterfly community, particularly thinning operations and tree plantation.***

Butterfly habitat specificity, diversity, movement and vertical stratification patterns are studied and compared in terms of the management technique applied. Dry season patterns are compared to trends found during the wet season. Different assessment methods, in particular fruit trapping along different vertical strata, walk-and-captures on transects and point distance sampling, are analysed.

To study both aspects, the following questions were put:

Does the over-logged 22,000 ha large Bossematié Forest Reserve still represent a valuable ecosystem for true West African rainforest species? Or is there a shift in species composition towards savannah and ubiquitous species?

Larsen (1999) established a classification for West African butterfly species according to their preferred vegetation type (dry forests, moist/wet forests, savannah, ubiquitous, etc… see further) and geographical distribution (from Upper Guinean endemic to afrotropical). Larsen’s classification allows the analysis of the ecological composition of Bossematié’s butterfly fauna, in this study particularly of the nymphalid community.

An important related question is: *how do (nymphalid) species composition and diversity patterns found within the boundaries of the 22,000 ha Bossematié forest fragment differ from patterns found in a 3 km distant, isolated 6 ha forest fragment?*

The island biogeography model (MacArthur and Wilson 1967) has been used to predict number and percentage of species that would become extinct after fragmentation and habitat loss. A loss of 50% *resp*. 90% of the original habitat might result in a species loss of 10% *resp*. 50% (Simberloff 1992, Quammen 1996 cited in Primack 2000). Species similarity and composition might be expected to be largely different between both areas. Due to the large increase of edge effects and the lack of a real forest center, especially the sensitive “forest interior species” (Larsen 1999) might be affected.

What are the patterns of nymphalid species abundance and richness found on the 75 ha study plot of the secondary Bossematié Forest Reserve? Is there a pronounced seasonality? Are there essential differences in species abundance and/or diversity within the patchy forest mosaic? And, *how do the detected patterns differ from those reported for natural or less disturbed rainforest sites?*

Seasonal fluctuations in phytophagous insects are primarly linked to variations in rainfall (e.g. Wolda 1978), but seasonality in butterfly abundance and/or diversity has been poorly studied within the afrotropics. Libert (1994) indicated seasonal fluctuations in 23% of all butterfly species collected in a Cameroon rainforest, and variation seemed particularly high in nymphalid species. Owen (1977) also reported seasonal patterns in abundance of *Charaxes* species sampled in a savannah region in Northern Nigeria. Seasonality in nymphalid butterflies might therefore also be expected in the moist semi-deciduous Bossematié Forest Reserve, characterised by pronounced variations in rainfall from dry to wet season (Hetzel 1998).

Diversity and abundance structures in the over-logged Bossematié should differ significantly from natural or only moderately altered forest regions. Abundance distributions in disturbed habitats are known to follow a log-series rather than a log-normal pattern (Magurran 1988, for butterflies e.g. Hill *et al.* 1995), although several studies did not indicate differences in butterfly abundance distribution between disturbed and undisturbed forests (Willot *et al.* 2000, Lewis 2000). Due to the high habitat heterogeneity created by logging, overall species richness might still be high in (moderately) degraded forests, but due to the extreme ecological changes, some forest specialists, especially those belonging to the buffered forest understorey and with restricted geographical ranges, might already be or become extinct (e.g. Thomas 1991, Spitzer *et al.* 1993, 1997, Hill *et al.* 1995, 2001, Hill and Hamer 1998, Willott *et al.* 2000, Fermon *et al.* 2000, 2001). Eventual differences in species abundance, composition or richness between mature and young forest patches can indicate processes of local species extinction. A description of the vegetation structure and different succession stages within the mosaic-like 75 ha study plot was principally derived from Waltert (2000) and Fermon *et al.* (2000). A (tentative) comparison of nymphalid abundance and richness patterns is made with data from the equally large Bia and Kakum Forest Reserves in Ghana, as well as with data from other tropical forest regions (e.g. Larsen and Dall’Asta 1994, Schulze 1995, Larsen 1999, Lewis 2000, Willot *et al.* 2000, DeVries and Walla 2001, Hill *et al.* 2001).

What are the patterns of small-scale nymphalid (foraging) movements on the 75 ha study plot of the secondary Bossematié Forest Reserve? Are there interspecific differences and how do they relate to species habitat specificity and ecology?

In temperate regions, polyphagous butterfly species, the larvae of which feed on early successional plants and species characteristic of disturbed habitats are known to show further flights than single-brood species feeding on perennial trees or shrubs and species occupying permanent habitats (Scott 1975, Shreeve 1981). Tropical forest butterflies species can also be grouped according to their degree of host plant specialisation. We might therefore expect the more specialised species characteristic of a shaded forest floor and mature vegetation patches to be less mobile than the less sensitive, more polyphagous species present also in the younger forest succession stages of the study plot.

Is there a pronounced vertical stratification in the (adult) nymphalid species of the secondary Bossematié Forest Reserve?

Vertical stratification in butterflies has been shown for natural rainforest plots, e.g. in Poring, Malaysia (Schulze 1995), Costa Rica (DeVries 1988) and Equador (Beccaloni 1997, DeVries *et al.* 1997, 1999, DeVries and Walla 2001). Since forest disturbance, by opening the canopy, is likely to alter the original vegetation structure, microclimatic conditions, plant species composition and abundance, present under a closed canopy, the vertical distribution of butterflies might be less pronounced or even absent in the over-logged Bossematié Forest Reserve. The possible mechanisms of stratification are being discussed in the light of the patterns found on the 75 ha study plot.

What is the impact of the applied forest management on (various aspects of) the nymphalid butterfly community?

Thinning is a forest management technique to free economically important timber tree individuals from competition. Thinning operations produce a shift in the vegetation structure of the (already) over-logged Bossematié Forest Reserve (Waltert 2000), creating more gaps and reducing mature forest patches by increased treefall rates. Thinning and the establishment of plantations in the secondary forest reserve might be expected to further influence the nymphalid community in several ways. Although species richness parameters might even slightly increase after small-scale disturbance in tropical forests (Lovejoy *et al.* 1986, Brown 1991, Sparrow *et al.* 1994, Wood and Gillman 1998), local declines or even extinctions of sensitive forest species, especially those of the forest floor and those with limited geographical distributions, can be expected to occur after thinning and therefore lead to a significant loss in regional species richness.

Furthermore, thinning and the consequent changes in microclimate, vegetation structure and composition might be expected to affect nymphalid distribution along the vertical strata. Whereas vertical stratification patterns could still be somehow pronounced on the more closed, regenerating control forest, we might expect a disruption of stratification after thinning. Canopy species are know “to treat forest gaps and forest edges as if the canopy has come to the ground” (DeVries 1988). We might therefore expect more canopy flyers in understorey traps of the more disturbed (thinned) forest site. In a mature forest, canopy species might stay high up in the canopy and be less frequent at baits installed in the understorey. Although understorey data might indicate lower abundances, the overall abundance of canopy species (along the different vertical trap heights), particularly within the tree feeding taxa, might be expected to be highest in the less disturbed forest plot.

Generally, species movement patterns tend to be smaller in optimal compared to sub-optimal habitats. We might therefore expect species with a preference for mature forest to exhibit smaller movement parameters in the less disturbed forest site. Species for which younger succession stages offer the best habitat conditions, might display smaller movements in the more disturbed forest plot.

3. STUDY AREA

The Bossematié Forest is a forest reserve (*Forêt Classée*) covering 216 sq. km and is situated near Abengourou (6°35’ - 6°20’ N and 3°35‘ - 3°20‘ W) in the south-east of Côte d’Ivoire (Fig. 1), about 250 km north-east of Abidjan. The forest belongs to the seven *Forêts Classées* situated in eastern Côte d'Ivoire, covering 188,880 ha in total. Their essential function is to satisfy the country's industrial and traditional wood requirements. As a result of intensive exploitation and deforestation between the early 1960s and 1990, most of these *Forêts Classées* are timber-depleted and very degraded. Since 1990, a cooperation between the forest authority SODEFOR and the German aid agency GTZ attempts to apply a natural forest management regime and to maintain species diversity.

3.1 Climate, vegetation and soils

The Bossematié region receives an annual rainfall of *c.* 1300 mm. The long rainy season, from April to November with one peak in June (South West Monsoon) and a smaller in October, is interrupted by a short dry season between July and August. The long dry season stretches from December to March with predominantly North Easterly "Harmattan" winds. The rainy season is usually interrupted by a short dry period of some weeks from the end of July until mid August (Hetzel 1998). The comparison of rainfall data from 1920-1960 with that from 1961-1994 indicates an increase in rainfall variability after the deforestation period, resulting in longer periods without any rainfall during the months November to March (Hetzel 1998).

The Bossematié Forest belongs to the moist semi-deciduous forest zone (Hall and Swaine 1976) with *Celtis* spp. and *Triplochiton* spp. as most characteristic trees. This vegetation type, rich in commercial timber species (e.g. Utile *Entandrophragma utile* and African Mahogany *Khaya ivorensis*) is characteristic for West African lowland areas receiving an annual precipitation between 1200 and 1500 mm. The average tree species richness on 625 sq. m plots is 103 spp. (Hall and Swain 1976), and a total of 200 to 500 vascular plants can be found on one ha forest plots (Swaine and Hall 1986). The altitude of the area is 140 - 240 m and the relief is slightly hilly, with humid valleys, dry ridges, no permanent water but several small streams in the rainy season. The Bossematié Forest can be considered as an ecological island, totally surrounded by farmland without significant forest cover. The forest itself has been selectively logged five to six times from the early 1960s until 1990. Now, the upper storey is very open with less than eight stems over 60 cm diameter at breast height (dbh) per ha and a corresponding crown projection of less than 20 - 30 % of the total surface (Wöll 1992). As in other West African forests, the herb layer in gaps and larger clearings is now dominated by the invasive pioneer *Chromolaena odorata.* The African Forest Elephant *Loxodonta africana* *cyclotis* is present and might also be partly responsible for the status of the vegetation in the area (see Struhsaker 1997).

Near watersheds and on the higher slopes, there is a predominance of *ferralsols* with a high clay content (25-50%) in the subsoil and a humus-dependent but high nutrient content in the topsoil. Due to high compaction at depths below 30 cm, the subsoil is free of roots. In addition, high water percolation due to high skeletal content decreases soil water during the dry season, which is relatively unfavourable for plant growth (Hetzel 1998). However, this soil type covers *c.* 67 % of the total area of the Bossematié Forest. At mid- and down-slope levels, *cambisols* with only a small amount of skeletal material are predominant. Due to the more balanced water storage capacity, this soil type is best suited for root formation in the area. *Arenosols*, characterised by a high sand content, and *gleysols*, are predominant in the valleys of the Bossematié area. The *arenosols* show a considerable subsoil compaction due to the heavy machinery used for timber extraction, but generally they show a good root formation when undisturbed (Hetzel 1998). The *gleysols,* characteristic for the valley bottoms, show a poor soil water percolation due to considerable amounts of kaolin and a limited capacity for root growth.

Although, in general, the nutrient balance seems to be favourable for timber production, Hetzel (1998) concluded that unsustainable harvesting exceeding levels of more than 1 m^3 * ha^{-1} * $year^{-1}$ can result in severe imbalances in the water cycle which acts as important nutrient carrier. Heavy timber exploitation inside the Bossematié Forest already lead to a gradation of the heliophilous pioneer *Chromolaena odorata* (*Eupatorium odoratum,* Asteraceae), and resulted in a severe decrease in macro-nutrients in the topsoil and limited light conditions for saplings of pioneer tree species (Michler 1994).

3.2 Forest management and biomonitoring

Since 1992, scientific and management activities have been conducted in a co-operation between the German aid agency (GTZ) and the local forest authorities (SODEFOR). The implementation of the following management measures were initiated: establishment of three biological reserves covering 7,404 ha in total, planting of trees (mainly *Terminalia* spp.) on abandoned agricultural encroachments and larger clearings (1,076 ha), enrichment planting on other impoverished areas (2,034 ha) and liberation thinning, proposed to be carried out in the future on approximately 9522 ha (SODEFOR 1994). Thinning is a management method in favour of potential crop trees with 5 - 40 cm girth (PCTs) and will be carried out in compartments of the Bossematié Forest with a minimum stock of 60 PCTs/ha. It includes free cutting of lianas and climbers and killing of non-commercial trees, on average 1.5 m^2 / ha, representing about 10 % of the total basal area (Parren and De Graaf 1995). Trees are not directly felled to minimise initial vegetation damage, but intersected at their cambium and in this way ”devitalised”. A major objective is not to suppress the basal area below 50% of the original primary forest condition (Wöll 1992). Rare tree species and fruit trees important for birds and mammals are excluded from the treatment (see Waitkuwait 1992). Thinning is increasingly used in Côte d'Ivoire. The planned management activities will be conducted until 2014. Controlled exploitation of 1.3 trees per ha has been proposed for 2005-2014 on *c*. 4,515 ha. Although liberation thinning only kills a relatively minor proportion of the existing basal area, the operation changes vertical vegetation cover significantly by reducing foliage in the middle and increasing foliage in the lower strata of the forest (Bamba 1999) which can be explained by more light penetrating the understorey through defoliated crowns and an increased rate of treefalls. Besides this present study, the effects of the treatment on the forest fauna has only been studied for the understorey bird community (Waltert 2000).

To monitor the effects of the forest management, population monitoring of selected bird and mammal species has been carried out from permanent line transects using Distance Sampling methods (see Waitkuwait 1992, Mühlenberg *et al.* 1995, 1999). Although very degraded, the Bossematié Forest still possesses a high conservation potential. Comprehensive inventories for plants, mammals, birds (Waltert *et al.* 1999) and butterflies (data documented in Larsen 1999) revealed the presence of most forest species to be expected in the region. The Bossematié Forest forms part of the proposed trans-national Bia-Bossematié network area, containing the six areas in eastern Côte d’Ivoire/western Ghana where the African Forest Elephant *Loxodonta africana cyclotis* still occurs (Parren and de Graaf 1995). In addition to the Forest Elephant, the mammal fauna includes the Chimpanzee *Pan troglodytes verus*. However, the population densities of many forest animals have greatly declined, and particularly populations of the three resident large hornbills (*Ceratogymna* spp.) and primates (six species including Chimpanzee) seem very vulnerable to the existing high poaching levels (Mühlenberg *et al*. 1999). Only two of the primate species present in the forest, the guenons *Cercopithecus campbelli* and *C. petaurista*, may still live in viable populations (McGraw *et al.* 1998).

3.3 Study plot

Our 75 ha field site is part of a 1,982 ha experimental area, situated in the northern part of the Bossematié Forest (description in Parren and De Graaf 1995). It has been established to monitor the effects of the forest management on the growth of principal timber species. It includes a 30 ha regenerating forest plot or "control forest", a 30 ha liberation thinning plot or "thinned forest " and a five year old, 15 ha tree plantation (Figure 1). The control forest consisted of regenerating secondary forest and represented the true condition of the whole secondary Forêt Classée, which had been exploited all over until 1990 and in which no primary forest remained. The thinned forest had been treated three years before the present study started. Its vegetation structure has been described in Waltert (2000), who indicated a significant higher proportion of gap habitats in the thinned plot compared to a significant higher proportion of mature forest habitats in the control forest (Figure 2). The five year old tree plantation, consisting exclusively of *Terminalia ivorensis*, *T. superba*, and *Triplochiton scleroxylon*, possessed a strikingly more uniform vegetation structure compared to the more ”naturally managed” thinned compartment. Trees were regularly spaced at 6 - 9 m and were 10 - 12 m high. Due to the frequent manual cleaning of all regenerating understorey vegetation, only a herb layer dominated by *Chromolaena odorata* was present as an additional stratum.

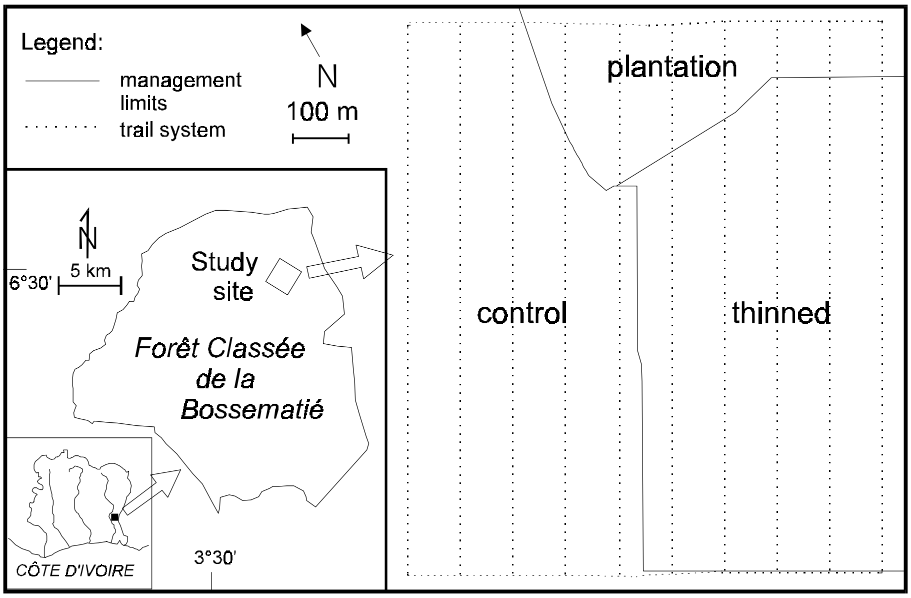


Figure 1: Location of the Bossematié Forest Reserve in Côte d’Ivoire and schematic map of the 30 ha thinned forest, the 30 ha regenerating control forest and the 15 ha plantation. Trails are indicated by dashed lines (after Waltert 2000).

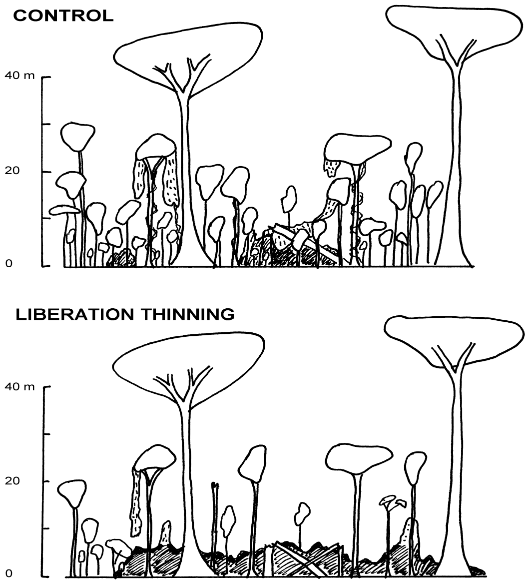


Figure 2: Differences in vegetation structure between the control and the thinned forests on the 75 ha plot within the over-logged Bossematié Forest Reserve (with kind permission of Waltert 2000).

4. METHODS

4.1 Vegetation analysis

The following structural characteristics of the vegetation were recorded (Waltert 1996, 2000): overstorey tree size (OTS), being the average diameter at breast height (dbh in cm) of the nearest overstorey tree (girth >10cm); overstorey tree dispersion (OTD), being the average distance from the sampling point to the nearest overstorey tree (girth >10 cm); and understorey tree dispersion (UTD), being the average distance from the sampling point to the nearest understorey tree (girth 5-10 cm). These parameters are often used to describe microhabitats of small mammals in tropical forests (e.g. Dueser and Shugart 1978, Ganzhorn *et al.* 1990). One measurement was taken for each quadrant (north-east / south-west divided) around sampling points situated every 25 m along the trails in the three studied forest plots: the regenerating or control forest, the thinned forest and the plantation plot. Means from the sampling points were calculated and compared between plots using Mann-Whitney U-tests and the Kruskal-Wallis ANOVA. Tests were run with the help of Statistica 5.1 (Statsoft 1995).

In addition, the successional status of the forest was recorded at each sampling point. Assuming that vegetation complexity increases with forest succession, four morphological succession stages were classified (see Table 1). The classification ranges from ”gap”, defined as a vertical hole in the vegetation down through all strata (Levey 1988), through ”S1” and ”S2”, both with a single-layered canopy at low levels but differing in overall understorey density, to ”S3” which includes all sampling points with a multi-layered canopy. For these succession stages, averages of the measured vegetation parameters as well as nymphalid capture frequencies were calculated and correlations analysed using the Gamma rank correlation for multiple ties (Statsoft 1995).

Table 1: Characterisation of four morphologically classified succession stages according to the criteria ”canopy layers” and ”understorey density”.

	Succession stage			
	Gap	**S1**	**S2**	**S3**
Canopy layers	Absent	Monolayered at low levels	monolayered at low levels	multilayered
Understorey	nearly absent	Dense	sparse	medium-open

4.2 Fruit trapping

All baiting reported in this study was done between 24th January 1996 and 18th August 1997 (see Table 2). Traps used were basically as in DeVries (1987, 1988) and Mühlenberg (1993) and the bait was a fermenting banana (see Appendix 7). Species from 4 out of the 7 African Nymphalidae subfamilies (Libytheinae, Danainae, Satyrinae, Charaxinae, Apaturinae, Nymphalinae and Acraeinae) use fermenting fruit as a resource: Nymphalinae, Satyrinae, Charaxinae and Apaturinae. In Africa, the following Nymphalinae genera feed consistently on fermenting fruit (see Owen 1971, Larsen 1994a): *Euphaedra*, *Bebearia*, *Euriphene*, *Euryphura*, *Cymothoe*, *Pseudacraea*, *Euptera* and *Pseudathyma*. Some other Nymphalinae such as *Hypolimnas*, *Salamis* and *Antanartia* are found on both flowers and fruit. Most tropical Satyrinae, especially within the *Bicyclus* and *Gnophodes*, are exclusively fruit-feeders. Furthermore, the Charaxinae and Apaturinae are attracted to both fruit and rotting animal matter and excrement.

4.2.1 Understorey

During the dry and the wet season 1996, 66 banana baited traps were installed at 1 m in the understorey within the 75 ha study site. All traps were located at higher slope level or near watersheds. A swampy area crossing the study site was excluded from the analysis. Traps were spaced by regular distances on a 100 x 100 m grid system. Twenty-eight traps were situated in the control, 28 in the thinned and 10 in the plantation plot. Traps were checked every 24 hours, and kept open for six consecutive days, amounting to a total of 168 trap days in the control and the thinned and 60 trap days in the plantation plot for both seasons. Thirteen of these traps were located in the forest habitat classified as S3, 23 in S2, 26 in S1 and three in gap habitats. Butterfly species, for which a 100 % positive identification was possible in the field, were released after marking using a permanent marker (Lumocolor 313) and data were included in an analysis on nymphalid movement patterns (see below).

In addition, five banana baited traps were installed in an isolated 6 ha forest fragment, located 3 km distant from the Bossematié Forest Reserve. Traps were equally installed at 1 m in the understorey and spaced by a regular distance of 100 m. Sampling was done during seven days between 27 July and 03 August 1997.

4.2.2 Higher vertical strata

During the wet season 1997, 12 banana baited traps were installed in trees at three different vertical heights: at 1 m, 12 m and 25 m. In the following, these trap heights are also referred to as understorey, midstorey and canopy trap level. Four traps were installed per height level, six traps were situated in the control and six in the thinned compartment on two locations each. Traps were equally checked every 24 hours, and kept open for 17 days, amounting to a total of 204 trap days in both the control and the thinned plot. In any comparison between seasons in different years, data were standardised for the four identical trap locations at trap height 1m and six sampling days only.

Table 2: Distribution of baiting activities in the 75 ha study site of the Bossematiè Forest Reserve. For the dry and wet season 1996, each date represents 22 trap locations sampled for six consecutive days (traps checked every 24 hours). Baiting was done at 66 single locations in total for both seasons 1996. During the wet season 1997, each date represents 4 trap locations, and three different heights were sampled on each location.

Year	**1996**					**1997**		
Season	**Dry**			**Wet**		**Wet**		
Month	**Jan**	**Feb**	**Mar**	**Sep**	**Oct**	**Jun**	**Jul**	**Aug**
Day	24 25 26 27 29 31	14 15 16 17 20 21 22 24 27 29	01 03 05	06 08 09 12 14 16 18 20 22 25 27 29	01 03 05 07 09 11	21 23 25	05 07 09 11 13 17 20 23 27	04 07 09 16 18
Days per month	6	9	3	12	6	3	9	5
Days per season	18			18		17		
Total number of traps	66			66		12		

4.3 Walk-and-capture

During the wet season 1997, walk-and-capture transect routes of 1 km each were surveyed during 28 days in total. Transects were walked between 09:00 and 12:00 in the morning and between 15:00 and 17:00 in the afternoon under sunny weather conditions, each for a duration of 1 hour. Three transects were situated in the control, another three in the thinned forest. A total of 28 person-hours was obtained for each plot (see Table 3). All butterflies seen 2.5 m either side of the transect route and up to 5 m in front were trapped or released after marking when positive identification was possible (after Pollard 1977, Hill *et al*. 1995).

4.4 Point distance sampling

Since differential visibility between habitats can influence encounter frequencies and produce biased results, distance theory was used to detect for density differences between the control and the thinned forest plots. Point transect data were collected using the Distance Sampling method, which extends conventional quadrat sampling methods (e.g. strip or point transects) by relaxing the assumption that all objects within the strip / point are counted. By measuring distances to the objects that are observed, the probability of observing an object within the strip or point can be estimated (Buckland *et al.*, 1993, Thomas *et al*. 2002).

Observations were pooled by point which was used as sampling unit. Objects of interest were single butterfly individuals and densities were calculated using the formula:

$$D = \frac{n}{k\pi w^2 P_a}$$

with n being the number of individuals observed, w the point width, k the number of points and P_a the probability that a randomly chosen individual within the survey area, $a = k\pi w^2$ is detected. An estimation of P_a is provided using a model that describes the recorded distances plotted in a histogram. Such analyses of perpendicular distances were run for each forest plot using the software Distance 3.5 (Thomas *et al.* 1998) during the wet season 1997. Point counts were carried out using random gridpoints along six transects in both the control and the thinned area. Sampling to only one side of each transect was carried out since it was found that only in this way re- (double-) counting of individuals was sufficiently avoided. Only non-moving individuals were recorded, since moving objects do not meet assumptions of the distance sampling theory (Buckland *et al.* 1993), and because transects can preferentially be used by some species to pass through otherwise dense understorey vegetation. Ten minutes were spent at each spot, before another spot 100 m away from the initial location was selected. A total of 20 spots were sampled in control, and 20 in the thinned area. Exact distances were noted in meters. Since 100% identification could not be guaranteed for every butterfly individual observed, especially in the furthest distance class, and false species identification could bias results, the analysis was mainly done at genus level only. Estimated were the encounter rate (n/K, with n = number of observations and K = number of sampling points), the proportion of individuals detected (p) and densities (as estimated number of individuals per hectare).

For analysis, right truncation was applied at $w = 7$ m. There was indication of slight evasive movement in response to the observer (slightly lower number of observations directly at 0 m), so that grouping of the first three meters to one distance classes (0-3 m) improved model fit and was applied throughout. Different models were fitted to the data, but since the halfnormal model was generally found to have a good fit, results presented in chapter 5.4.4 are derived from half-normal modelling.

Table 3: Walk-and-capture days during the wet season 1997 in the over-logged Bossematié Forest Reserve, Côte d'Ivoire. Each date represents 2 hrs of transect walking on one of a total of six transects.

Month	**June 97**	**July 97**	**August 97**
Day	08 19 25	09 10 14 15 16 21 22 23 27 28 29 30	02 04 05 06 07 08 09 11 12 13 14 16 19
Days per month	3	12	13
Total days	28 (56 hours)		

4.5 Butterfly identification and geographic range classification

Butterflies in the subfamily Nymphalinae were identified using D'Abrera (1980, 1997), Hecq (1988a, 1988b, 1990, 1992, 1994a, 1994b, 1997) and Hancock (1992). Charaxinae were identified using Henning (1989) and Satyrinae were identified using Condamin (1973). Butterflies which could be identified in the field were released after marking (to avoid pseudoreplicates), while others were collected and checked later at the Royal Museum for Central Africa, Tervuren. English names (additionally applied in the discussion), habitat associations (e.g. preference for certain forest types) and geographic distributions were adopted from Larsen (1991, 1994b, 1996a, 1996b, 1997, 1999) and Emmel and Larsen (1997). The geographic range was categorised on a scale of 1 - 7 (smallest to largest):

(1) Upper Guinean endemic;
(2) from western West Africa to the Nigeria-Cameroon border;
(3) from western West Africa to the Cameroon-Gabon-Congo zone;
(4) from western West Africa to Zaire;
(5) from western West Africa to Uganda or western Kenya;
(6) from western West Africa to east of Rift Valley;
(7) found throughout subsaharan Africa.

In order to avoid sampling artefacts distorting the real abundance/distribution relationship, analysed using the Gamma rank correlation for multiple ties (Statsoft 1995), species with less than 6 captures were excluded from the analysis (see Novotný 1991).

4.6 Butterfly abundance and movement

Differences in capture frequencies between samples (seasons, years, management plots, forest succession) were analysed using the Mann-Whitney *U*-statistics, Kruskal-Wallis ANOVA and chi-square or fisher's exact tests. Furthermore, the position of each adult capture and recapture was plotted on a map of the study site. Means of the following movement parameters where calculated for each recaptured individual (after Scott 1975, Warren 1987) and compared between sexes or species:

d_i**:** the minimum straight-line movement in metres between captures *i* and (*i*+1);
t_i**:** time in days between captures *i* and (*i*+1);
D: sum of d_is for each individual (minimum distance moved);
D_{max}: maximum D recorded;
T: sum of t_is for each individual (number of days between first and last capture)
R**:** Distance in metres of two furthest capture points for each individual (minimum range)

4.7 Calculation of community parameters

Butterfly diversity was analysed using EstimateS 5 (Colwell 1997). As comprehensive sampling of species richness is difficult in rich tropical communities, statistical methods have been established to estimate total species richness from single samples and randomisation of species turnover between them (see Colwell and Coddington 1994, 1995). For a research program on the arthropods of the La Selva forest, Costa Rica (Project ALAS), the calculation software EstimateS was developed by Colwell (1997). The program allows to compute richness estimators (as well as indexes of diversity and species similarity, if requested) based on the successive pooling of data from single samples. Using data (number of individuals per species) of one trap installed for an equal number of trap days as single samples, the following estimators were computed: Fisher’s alpha (alpha), Shannon and Simpson (1/D) diversity index (Magurran 1988), Evenness (E=Simpson/total species number S), as well as the size of the local species pools, as Abundance-Based (ACE) and Incidence-Based (ICE) Coverage Estimators of species richness (Colwell 1997). Sample order randomization with EstimateS (Colwell 1997) was set at 50 randomizations. Furthermore, differences in species richness and α-diversity were tested between the communities at each trap location for control, thinned and plantation comparing number of species (S), Simpson (1/D) diversity index and Evenness (E) with Mann-Whitney *U*-statistics.

Some information to the applied diversity indices is given in the following and principally derived from Magurran (1988).

A first group of diversity measures is called the diversity statistic indices. They are based on the idea that natural diversity can be measured as information contained in a theoretic code or message. Based on this rationale, theoretic diversity functions have been described. A frequently used diversity measure is the Shannon or Shannon-Weaver index.

The **Shannon or Shannon-Weaver index** is calculated as:

$$H_s = -\sum_{i=1}^{S} p_i \ln p_i$$

and $p_i = n_i / N$

and considers the proportion of individuals found in the ith species, p_i . This value is estimated as n_i / N (number of individuals in the ith species divided by the total number of individuals). Compared to other indices, the Shannon index is sensitive to changes in abundance of rare or intermediate abundant species. It appeared to have an only moderate discriminant ability and, since it is strongly influenced by changes in rare species, is sensitive to sample size. The index assumes that sampling is random and allows you to include all species present in the community.

The ratio of observed to maximum diversity can be taken as a measure of **Evenness**. Evenness is calculated as

$E = H'/ \ln S$

with H_{max} the „maximum diversity“ (all species equally abundant). Evenness E is constrained between 0 and 1.0, providing better opportunities for comparisons.

A second group of diversity measures are referred to as dominance measures since they particularly consider the abundances of the most common species rather than providing a measure of species richness. One of the most used dominance measures is **Simpson’s index**, which calculates the probability that any two individuals drawn at random from an infinitely large community belong to different species. It is calculated as:

$D = \Sigma p^2_i$ (reciprocal)
$1/D = 1/\Sigma p^2_i$
and $p^2_i = n_i(n_i-1) / N(N-1)$

In the formula, pi is the proportion of individuals in the ith species and is estimated from the relation of the number of individuals in the ith species to the total number of individuals. Simpson’s index especially takes into account the abundance of the most common species, and is less sensitive to species richness. It has a moderate discriminant ability and a low sensitivity to sample size, since it does not stress on changes in abundance of rare species, but of the commonest species. Since diversity decreases when D increases, mostly the reciprocal form of the index is used (1/D).

Another index which is very frequently used is **Fisher's alpha** diversity. It is calculated as:

$$\alpha = N(1 - x) / x$$

$$S/N = (1-x) / x - \ln(1/x)$$

and principally considers the total number of individuals N and x which is estimated from the iterative solution of $S/N = (1-x)/x[-\ln(1/x)]$. It does not take into account the relative abundance of the species. This means, in situations were the total number of species and individuals stay constant but the eveness of the community changes, alpha will not indicate a difference. However, the index appeared to have a very good discriminant ability between different samples and is not so sensitive to sample size. This attribute of alpha is a result of its dependence on the numbers of species of intermediate abundance, it is relatively unaffected by either rare or common species abundance changes. The index is based on the log-series species abundance model developed by Fisher, and is strictly speaking only appropriate when the community shows a log-series distribution. However, in practice it appeared to be a good diversity measure independent of the underlying abundance pattern.

To describe **species abundance distributions** of samples, species-abundance models were fitted to expected distributions (log-normal, log-series) by chi-square Goodness of fit tests. Expected distributions were calculated with the software LOGSERIE and LOGNORM, inserted in Krebs (1989). The majority of natural communities display a log-normal distribution which is believed to indicate a large, mature and varied community (Magurran 1988). A log-normal distribution of relative abundance implies a concave (logarithmic) abundance-rank diagram for the „lower"-ranking species (i.e. the most common ones) and a a convex curve for the „higher" ranking species. An extreme abundance form is the broken-stick abundance model, which reflects an even more equitable state being the biological correspondent of a uniform distribution. If a broken-stick distribution is found, there is incidence that an important ecological factor is shared more or less evenly between the species. The log-series distribution is often visible in immature or stressed communities, dominated by one or a few ecological factors, but can also be due to small sample sizes. In a (logarithmic) abundance-rank diagram, a logarithmic series distribution implies a straight line except for the „lower" ranking species.

The main estimator of total species richness used was the abundance-based coverage richness estimator **ACE** (Chao *et al.* 1993), based on functions of singletons and doubletons in the sample. For reference, the respective formulas are added (Colwell 1997). ACE is based on the fact

$$\mathbf{S_{obs} = S_{rare} + S_{abund}}$$

with S_{rare} being the number of of rare species, defined as those with 10 or fewer individuals when all samples are pooled and S_{abund} being the number of abundant species, defined as those with more than 10 individuals when all samples are pooled.

$C_{ace} = 1 - F_1/N_{rare}$

is a sample coverage estimate based on the numbers of singletons F_1 and the number of rare species N_{rare} which is calculated as

$N_{rare} = \Sigma^{10}{}_{i=1} iF_i$

So, this sample coverage estimate represents the proportion of all individuals in rare species that are not singletons. Then the ACE estimator of species richness is

$S_{ace} = S_{abund} + S_{rare}/C_{ace} + F_1/C_{ace}\, \gamma^2_{ace}$

and $\gamma^2_{\mathbf{ace}}$ estimates the coefficient of variation of the F_i's.

In addition, rarefaction methods were used to randomise species accumulation from sample to sample (Shinozaki 1963). The method is documented in Krebs (1989), who provides the software SHINO.

To compare the species composition between samples, the **Morisita Horn species similarity index** was used. The Morisita Horn index is found not being too much influenced by species richness or sample size and was calculated, with the help of EstimateS 5 (Colwell 1997), as:

$C_{mH} = 2\ \Sigma\ (an_i bn_i)\ /\ da+db)aN * bN$ and $da = \Sigma\ a\ n_i^2\ /\ aN^2$

Species similarity between different vertical strata were grouped using a matrix of dissimilarity (1 - Morisita Horn sample similarity index) and the single-linkage cluster dendrogramm produces using Statistica 5.1. (Statsoft 1995). The **species turnover-rate** along the vertical strata was calculated as:

$\mathbf{T = J + E / S_1 + S_2}$

with J being the number of species present at trap height 2 but not at trap height 1, E the number of species disappeared between trap height 1 and 2, S_1 the number of species at trap height 1 and S_2 the number of species at trap height 2.

The similarity between different sampling methods (fruit trapping *vs.* walk-and-capture, understorey *vs.* canopy, ...) was determined using the **DICE association index**:

$$M = J/\min.(A,B)$$

where J is the number of species shared in the comparison and min.(A,B) is the total number of species in the smaller of the two being compared (Wolda 1981). The DICE index does not assume similar sized samples and is therefore an appropriate index for comparing different sampling methods (Wood and Gillmann 1998).

5. RESULTS

5.1 The secondary vegetation structure of the Bossematié Forest Reserve

Figure 3 shows the composition of the habitat mosaic along sixteen 2 km transects within the Bossematié Reserve (after Waltert 1996, 2000b). In general, the Bossematié Forest is dominated by young secondary growth, with considerable proportions of gaps (13 %) and young secondary forest (S1 and S2 with 33 % and 28 %, respectively). 24 % of the sixteen 2 km transects was characterised by a multilayered canopy (S3). The mosaic character was very small-scaled, with patches changing mostly within distances of no more than 50 metres. This pattern of repeated alternation was similar for all sixteen transects, indicating that disturbance affected the entire forest and not just certain forest parts (Waltert 1996).

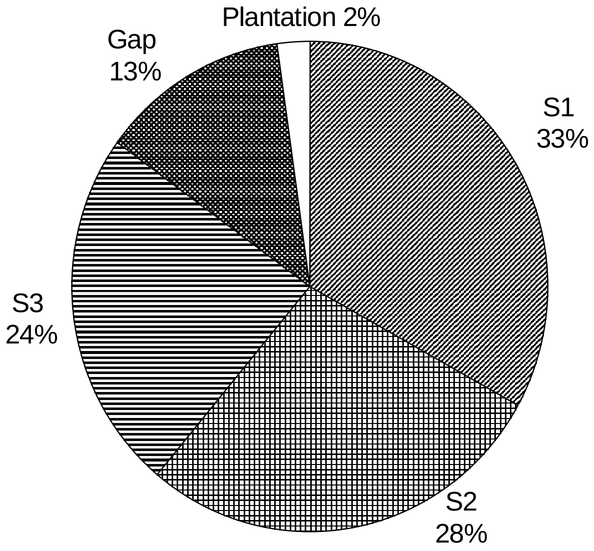


Figure 3: Composition of the habitat mosaic along sixteen 2-km transects in the over-logged Bossematié Forest, Côte d'Ivoire (after Waltert 1996, 2000b). Distribution of sampling points (n = 621) according to forest succession (gaps and three succession stages, for definition see Table 1). Plantations include recently abondoned agricultural encroachments.

The structural characteristics of the vegetation in the three different forest plots control, thinned and plantation on the 75 ha study site is shown in Table 4. Variance in vegetation parameters was very high in all forests (coefficient of variation > 55%). However, average understorey tree dispersion (UTD) was significantly lower in the thinned compared to the control forest (Mann-Whitney *U*-test, Z = 3.5, p < 0.001). Although not significant on the 5 % level, overstorey tree size (OTS) was smaller and overstorey tree dispersion (OTD) higher in thinned than control. Including values recorded in the *Terminalia* plantation, there was an overall significant increase in overstorey tree dispersion (OTD) from the control over the thinned area to plantation. (Kruskal-Wallis ANOVA, H = 16.45, p < 0.001). Overstorey tree size (OTS) was significantly higher in control (Mann-Whitney *U*-test, Z = -3.14, p < 0.01) but significantly lower in thinned (Mann-Whitney *U*-test, Z = -3.71, p < 0.001) compared to plantation. Again, understorey tree dispersion (UTD) differed most obviously between the areas: UTD was significantly higher in plantation (5.40) compared to control (4.00) or thinned (3.38) (Kruskall-Wallis ANOVA, Z = 50.54, p < 0.000).

Table 5 presents the structural characteristics of the vegetation in the four defined forest succession stages S1, S2, S3 and gap habitats within the 75 ha study site. Overstorey tree size (OTS) increased significantly with forest succession (gamma rank correlation for multiple ties, γ = 0.100, p < 0.05). Average overstorey tree dispersion (OTD) declined with habitat maturity, and average understorey tree dispersion (UTD) was largest at gap sites, but there were no significant correlations with forest maturity.

Table 4: Structural characteristics of the vegetation in three different forest plots: a regenerating forest (control), a liberation thinning (thinned) and a plantation plot (Fermon *et al.* 2000) of a 75 ha study site in the over-logged Bosematié Forest, Côte d'Ivoire. Since variables did not fit normal distribution, only means are listed and significance levels (p < values listed) are based on the Mann-Withney *U*-test (*) or Kruskal-Wallis ANOVA (**) (Statsoft 1995). Number of habitat descriptions at 25 m intervals along 1,000 m transects, for control = 416, for thinned = 232, for plantation = 89.

	CONTROL (1)	THINNED (2)	PLANTATION (3)	(1)-(2)*	(1)-(2)-(3)**
OTS (CM)	21.59	20.44	21.45	0.2	0.001
OTD (M)	4.29	4.66	5.40	0.4	0.001
UTD (M)	4.00	3.38	5.40	0.001	0.000

Table 5: Structural characteristics of the vegetation of representative samples in the four forest succession stages (Fermon *et al.* 2000) of a 75 ha study site in the over-logged Bossematié Forest, Côte d'Ivoire. Since variables did not fit normal distribution, only means are given and significance levels are based on gamma rank correlation for multiple ties (Statsoft, 1995). Number of habitat descriptions at 25 m intervals along 1,000 m transects, for gap = 121; S1 = 325; S2 = 206; S3 =103.

	SUCCESSION STAGE					
	GAP	S1	S2	S3	γ-RANK	p <
OTS (CM)	20.30	20.40	20.60	22.10	0.100	0.05
OTD (M)	4.60	4.50	4.30	4.20	-0.010	0.6
UTD (M)	4.13	3.72	3.69	3.89	-0.009	0.8

5.2 The butterfly fauna of the Bossematié Forest Reserve

A total of 263 butterfly species have been recorded within the Bossematié Forest Reserve (see Appendix 4). The species records included are partly own records obtained between May 1995 and August 1997, completed with recordings done by T.B. Larsen (Manila, The Phillipines) and U. Dall'Asta (Tervuren, Belgium) between October 1993 and May 1994 (Larsen and Dall'Asta 1994, Larsen 1999). Especially the Lycaenidae and Hesperiidae are under-represented, constituting only 15.5 % and 10.5 % of the total butterfly fauna. Due to the particular focus on the fruit-feeding butterfly community, the Nymphalidae family is well-represented and comprises 63.8 % of the butterfly fauna listed. The Papilionidae and Pieridae make up 3.3 % and 6.9 % respectively of the total records.

Based on intensive butterfly sampling with standardised effort all over the Bossematié area, the maximum butterfly richness can be estimated at 500 species in total (Larsen pers. comm.). According to this estimation, the Bossematié Forest would comprise 50% of all western West African species (between Sierra Leone and Togo). The estimated total species richness is comparable with that of the *c.* 22,000 ha large Bia and Kakum National Parks (both *c.* 600 species in total) in the moist semi-deciduous forest bloc in Ghana (Larsen, 1994b, 1995b). A relatively high number of species is shared between the Bossematié Forest and the Bia National Park, resulting in a Soerensen index of 71 %. The extreme dry semi-deciduous, 260 ha large Boabeng Fiema Sanctuary in Ghana (Larsen 1999), as well as the 4,777 ha large Noyau Central situated within the Dahomey Gap in south-central Benin (Fermon *et al.* 2001), both only represent half of the Bossematié's total species richness (see Table 6).

239 or 90.9 % of the recorded butterfly species belong to the ecological category forest species (Table 7), species centered on closed forests which do not usually colonise savannahs or other open habitats (Larsen 1994b, 1999, Emmel and Larsen 1997). Only a small fraction are either ubiquitous species (6.1 %) or habitat specialists linked to swampy zones (0.4 %) or belong to the savannah butterfly community (2.6 %). Half of all true forest species are species found generally distributed in all forest types, whereas 25 % are species centred on the moist semi-deciduous forests. 15 % of all forest species belong to the wet evergreen forest butterfly community, and only 5 % to the drier forests. Despite the significant presence of true forest species, only 30 % of all West African forest species have been recorded. Contrasted to that, 55 % of all West African ubiquitous species were present. As might have been expected, only 5 % of all West African savannah species were found (Table 7). The largest proportion of the recorded species (40 %) have a geographical distribution from western West Africa to Uganda/western Kenya (Table 8). 28 or 11 % of all species are Upper Guinean endemics. Twenty-two of these belong to the Nymphalidae, of which again 41 % belong to the genus Euphaedra. The other six Upper Guinean endemics are Lycaenidae.

Table 6: Known and estimated number of butterfly species in the Bossematié Forest Reserve compared with other West African regions (Larsen 1999). Estimated number of species after Larsen (1999, pers. comm.).

REGION	SPECIES KNOWN NUMBER	SPECIES ESTIMATED NUMBER
Afrotropical region	3,600	
West Africa	1,300	
West Africa west of Dahomey	996	
Ghana	870	
Bia National Park (Ghana, *c.* 22,000 ha)	330	max. 600
Kakum National Park (Ghana, *c.* 22,000 ha)	450	max. 600
Boabeng Fiema (Ghana, *c.* 260 ha)	252	max. 300
Noyau Central (Benin, *c.* 4,777 ha)	83	max. 250
Bossematié Forest (*c.* 21,600 ha)	263	max. 500

Table 7: The butterfly species collected in the Bossematié Forest (FCB) by ecological category (after Larsen 1991, 1994b, 1996a, 1996b, 1997, 1999 and Emmel and Larsen 1997), compared with the total fauna of West Africa (WA) west of the Dahomey Gap (data on the West African butterfly fauna after Larsen and Mei 1998).

ECOLOGICAL CATEGORY	SPECIES		% SPECIES	
	FCB	**WA**	**FCB**	**WA**
generally distributed in forests	126		47.9	
centred on the drier forests	12		4.6	
centred on moist evergreen and semi-deciduous forests	65		24.7	
centred on the wettest forest habitats	36		13.7	
forest species	**239**	**821**	**90.9**	**82.4**
centred on the Guinea Savannah and forest fringes	6		2.2	
centred on the Sudan Savannah	1		0.4	
savannah species	**7**	**141**	**2.6**	**14.2**
UBIQUITOUS SPECIES	**16**	**29**	**6.1**	**2.9**
SPECIES DEMANDING SPECIAL HABITATS	**1**	**5**	**0.4**	**0.5**
TOTAL	**263**	**996**	**100**	**100**

Table 8: The butterfly species by geographical range (geographical ranking after Larsen 1991, 1994b, 1996a, 1996b, 1997, 1999 and Emmel and Larsen 1997), collected in the over-logged Bossematié Forest, Côte d'Ivoire.

SPECIES DISTRIBUTION	SPECIES	% SPECIES
throughout Africa	42	16.0
from western West Africa to east of Rift Valley	23	8.7
from western West Africa to Uganda or western Kenya	102	38.8
from western West Africa to Zaire or Zaire-Uganda border	27	10.3
from western West Africa to Cameroon-Gabon-Congo zone	22	8.4
from western West Africa to Nigeria-Cameroon border	19	7.2
endemic to western West Africa	28	10.6
TOTAL	**263**	**100**

5.3 The baited butterfly community

5.3.1 Abundance

8,400 Nymphalidae individuals of the subfamilies Nymphalinae, Satyrinae, Charaxinae and Apaturinae were baited during the study period in total. The Satyrinae showed the highest proportional abundance (55 %), followed by the Nymphalinae (30 %) and the Charaxinae (15 %). The Apaturinae were only represented by one single individual and therefore not considered in the following. On genus level, the *Bicyclus* constituted 41 % of the total abundance, the *Euphaedra* 15 %, the *Charaxes* 13 % and both the *Bebearia* and *Gnophodes* 12 %. The genera *Euriphene* and *Palla* both only constituted 2 % of the total butterfly abundance.

5.3.1.1 Differences between seasons

The number of baited individuals amounted to 3,642 in the dry and 2,574 in the wet season 1996. During the wet season 1997, a total of 2,189 butterflies were baited, 1,425 of which at trap height 1 m and 764 at trap height 12 m and 25 m. The average number of individuals per sample was significantly higher in the dry compared to the wet season 1996 (55.3 *vs*. 39.8, Mann-Whitney *U*-test with 132 cases, Z = 3.8252, p = 0.000) but, standardised for four identical trap locations at trap height 1m and six sampling days in all seasons, highest in the wet season 1997 (Mann-Whitney *U*-test with 8 samples, p = 0.05 in both cases).

Subfamilies and genera. The dominance in proportional abundance of the subfamily Satyrinae was very pronounced during the dry season. During both wet seasons, however, the Nymphalinae were much more, the Satyrinae and Charaxinae far less abundant. In the wet season 1997, the Satyrinae and Charaxinae only constituted 26 % respectively 7 % of the total abundance, whereas the Nymphalinae largely dominated with 67 % (Figure 4). Twenty-four genera visited the banana baited traps during the total study period. The seven most abundant genera were: *Euphaedra*, *Bebearia*, *Euriphene* (Nymphalinae), *Bicyclus* and *Gnophodes* (Satyrinae) and *Charaxes* and *Palla* (Charaxinae). Other genera, baited much less frequently, were: *Ariadne*, *Aterica*, *Byblia*, *Catuna*, *Cymothoe*, *Eurytela*, *Harma*, *Hypolimnas*, *Junonia*, *Lachnoptera*, *Neptis*, *Pseudoneptis*, *Pseudacraea*, *Salamis* (Nymphalinae), *Melanitis*, *Hallelesis* and *Ypthima* (Satyrinae). The dominance of the subfamily Satyrinae during the dry season was mainly caused by the genera *Bicyclus* and *Gnophodes*, constituting 50 % and 16 % respectively of all baited individuals (Figure 5). The genus *Charaxes* (Charaxinae) constituted 17 % of the total abundance. Although still dominant, the *Bicyclus* were less abundant (42 %) during the wet season 1996. The same trend can be seen for *Gnophodes* (8 %) and *Charaxes* (12 %), whereas the proportional abundance of the three Nymphalinae genera *Euphaedra* (19 %), *Bebearia* (15 %) and *Euriphene* (1 %) were higher in the wet compared to the dry season 1996. This shift in proportional abundance is even more visible in the wet season 1997, with the Nymphalinae *Bebearia* (30 %) and *Euphaedra* (25 %) now as most dominant genera and the *Bicyclus* comprising only 17 % of the total abundance baited.

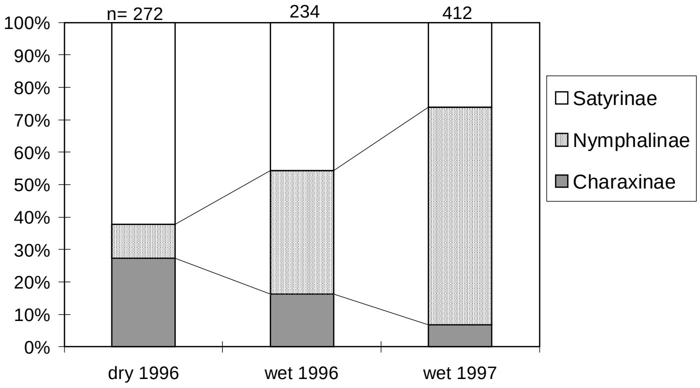


Figure 4: Proportional abundance of the baited Nymphalidae subfamilies during the dry and both wet seasons on a 75 ha study site in the over-logged Bossematié Forest, Côte d'Ivoire. Data were standardised for four identical trap locations at trap height 1 m and six sampling days in all seasons.

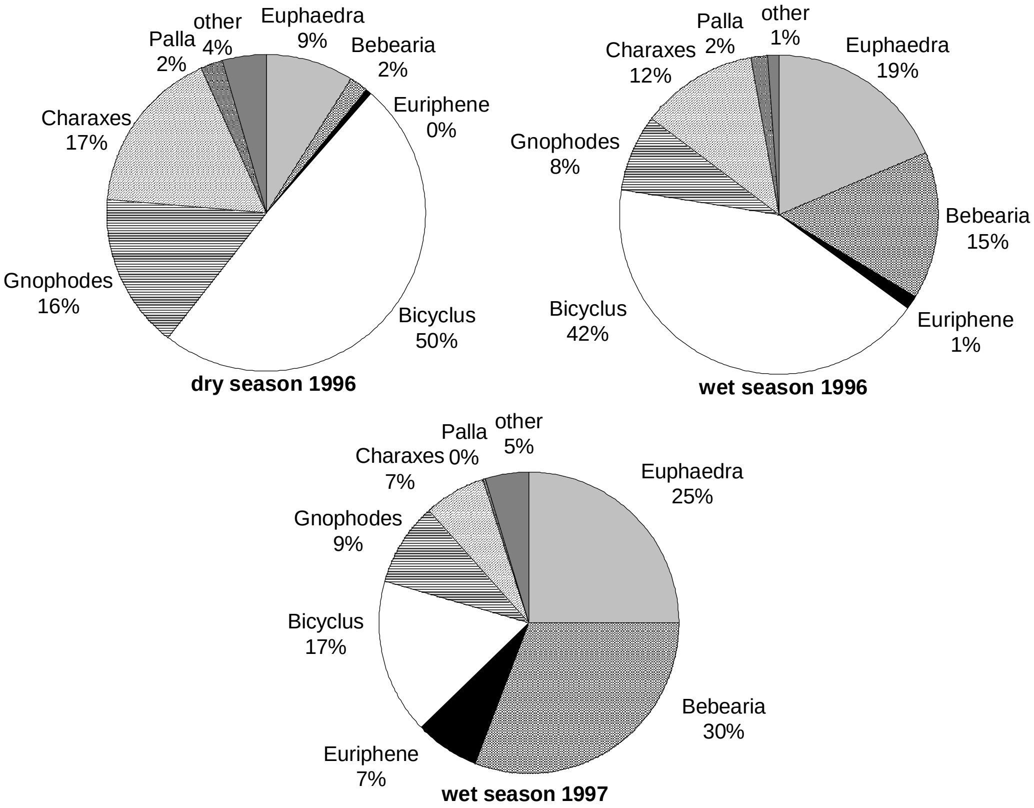


Figure 5: Proportional abundance of the seven most abundant genera sampled during three different seasons on a 75 ha study site in the over-logged Bossematié Forest, Côte d'Ivoire. For the wet season 1997, data from six sampling days and trap height 1m were considered only.

Species. Rank-abundance patterns (see Figure 6) did not differ significantly from a (truncated) log-normal distribution in any season (χ^2 Goodness of fit tests, $p > 0.6$ in all cases). The species abundance pattern for both dry and wet seasons 1996 differed significantly (or nearly significantly) from a log-series distribution (χ^2 Goodness of fit tests, $\chi^2_{8df} = 13.75$, $p = 0.08$ and $\chi^2_{9df} = 19.66$, $p = 0.02$, respectively). For the wet season 1997, no significant difference from a log-series distribution was found (χ^2 Goodness of fit tests, $\chi^2_{7df} = 4.82$, $p = 0.7$). During the dry season, the two most abundant species *Bicyclus funebris* and *Gnophodes chelys* were baited in 370 and 356 individuals respectively, followed by *B. vulgaris* (286 individuals), *B. zinebi* (241 individuals), *G. betsimena* (217 individuals) and *B. xeneas* (165 individuals), all members of the subfamily Satyrinae. During wet season 1996, the most abundant species, *B. zinebi*, was represented by no less than 634 individuals, followed by the Nymphalinae *Euphaedra phaetusa* (264 individuals), *Bebearia sophus* (218 individuals), the Satyrinae *G. chelys* (163 individuals), *B. sambulos* (116 individuals) and the Charaxinae *Charaxes protoclea* (104 individuals). The three most abundant species during the wet season 1996 were ranked fourth, eighth and twenty-third respectively during the dry season. The dominant species during the dry season, *B. funebris*, was not baited at all during the wet season of the same year. In both seasons, 26 species were represented by more than 20 individuals. The number of rare species (less than five individuals) was high: 40 rare species were found in the dry and 41 in the wet season 1996. During the wet season 1997, the two most abundant species at trap height 1 m were the Nymphalinae *Euphaedra phaetusa* (155 individuals) and *Bebearia tentyris* (197 individuals), followed by the Satyrinae *Bicyclus zinebi* (144 individuals), *Gnophodes chelys* (109 individuals), the Nymphalinae *Bebearia sophus* (83 individuals) and the Charaxinae *Charaxes protoclea* (58 individuals). Again, a high number of rare species (37) was found.

Four out of the six most abundant species in samples of the wet season 1996 were also ranked among the six most abundant species during the wet season 1997. The same comparison only reveals one identical species (*G. chelys*) between the dry season and the wet season 1997. Nine species baited in relevant abundances during the dry season were not present during the wet season 1996: *Bicyclus funebris*, *B. mandanes*, *Charaxes cedreatis*, *Cymothoe aubergeri*, *C. caenis*, *Euphaedra diffusa*, *E. sarcoptera*, *Harma theobene* and *Neptidopsis ophione*. Only 3 species baited in 4 individuals or more during the wet season were not found during the dry season 1996: *Bebearia arcadius*, *B. maledicta* and *Euphaedra eupale* (see Appendix 1).

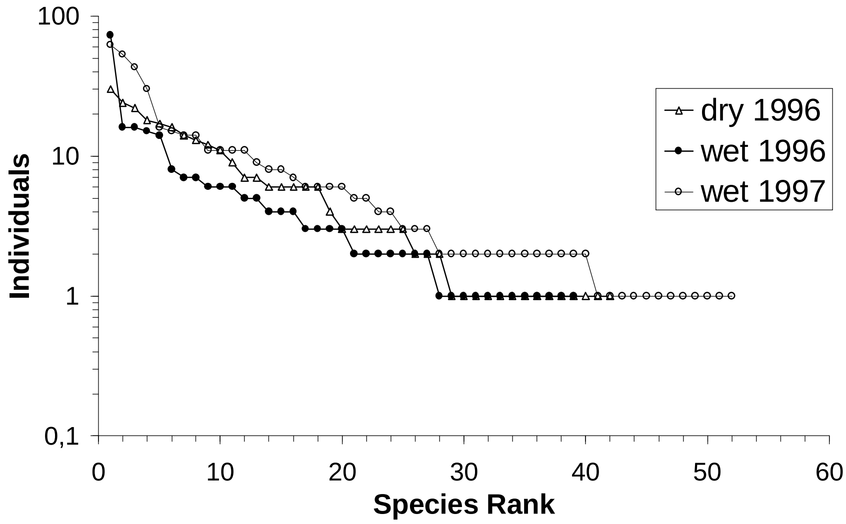


Figure 6: Rank-abundance distribution of Nymphalidae species in three different seasons on a 75 ha study site in the over-logged Bossematié Forest, Côte d'Ivoire. Data were standardised for four identical trap locations at trap height 1 m and six sampling days in all seasons.

Table 9 lists the 22 species with significant differences in abundance between the dry and the wet season in 1996. Almost all baited *Charaxes* and *Bicyclus* species were more abundant during the dry season, with significant results for *Charaxes cynthia* and *C. tiridates*, *Bicyclus abnormis*, *B. dorothea*, *B. vulgaris*, *B. xeneas*, *B. funebris*, *B. procora*, *B. taenias*, *Gnophodes chelys* and *G. betsimena*. However, two Satyrinae species, *B. zinebi* and *B. sambulos*, were significantly more abundant during the wet season. Within the subfamily Nymphalinae, nearly all *Bebearia* species showed higher abundances during the wet season, with significant results for *B. sophus*, *B. tentyris*, *B. mandinga* and *B. absolon*. Only one species of this genus, *B. zonara*, was more abundant during the dry season. A significant higher abundance during the wet compared to the dry season could also be found for *Euphaedra phaetusa*, *E. crockeri* and *E. ceres*. Only two Nymphalinae species, *Cymothoe egesta* and *Euphaedra harpalyce* were significantly more abundant in dry season samples.

Significant differences in proportional abundance were also found for species per ecological category (Larsen 1991, 1994b, 1996a, 1996b, 1997, 1999 and Emmel and Larsen 1997, see Figure 7). In the dry season, a significant higher proportion of species centred on the drier forests (DRF) was found (Mann-Whithey *U*-test with 132 cases, Z = 9.0113, p < 0.000), whereas the proportion of moist evergreen forest species (MEF) was significantly higher during the wet season (Mann-Whithey *U*-test with 132 cases, Z = -4.0278, p < 0.000).

Table 9: Nymphalidae species with marked differences in abundance between the dry and the wet season 1996. Values listed are absolute number of individuals calculated from q = 66 samples (sampling effort = 6 days each, highest values are bold); significance levels are based on the Mann-Whitney *U*-test (Statsoft 1995).

	DRY 1996	WET 1996	p <
CHARAXINAE			
Charaxes cynthia	**152**	59	0.001
C. tiridates	**108**	24	0.001
Palla violenitens	**45**	23	(0.06)
SATYRINAE			
Bicyclus abnormis	**138**	38	0.000
B. dorothea	**156**	38	0.000
B. vulgaris	**286**	9	0.000
B. xeneas	**165**	60	0.000
B. funebris	**370**	0	0.000
B. procora	**120**	49	0.01
B. taenias	**77**	25	0.01
Gnophodes chelys	**356**	163	0.000
Gnophodes betsimenas	**217**	36	0.000
Bicyclus zinebi	241	**634**	0.000
Bicyclus sambulos	58	**116**	0.001
NYMPHALINAE			
Cymothoe egesta	**58**	1	0.000
Euphaedra harpalyce	**58**	27	0.05
Euphaedra ceres	22	**61**	0.01
Euphaedra crockeri	14	**45**	0.001
Euphaedra phaetusa	151	**264**	0.000
Bebearia absolon	2	**21**	0.05
Bebearia mandinga	2	**23**	0.03
Bebearia sophus	24	**218**	0.000
Bebearia tentyris	9	**58**	0.000

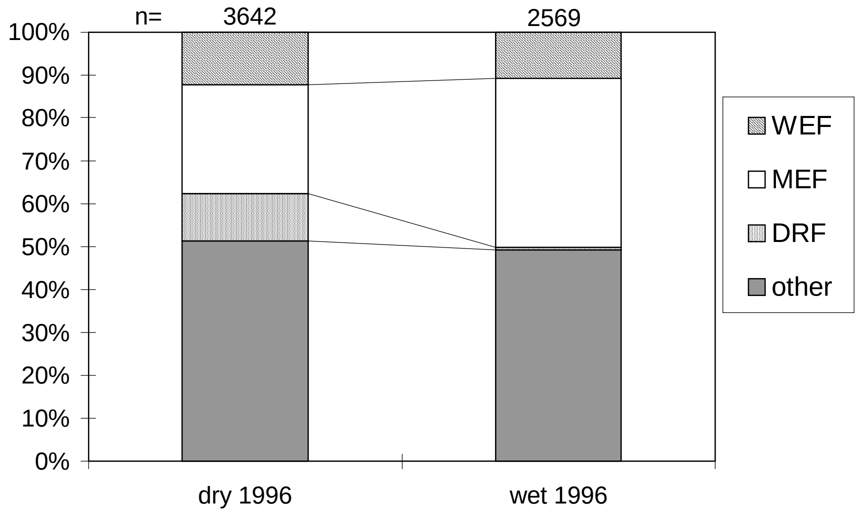


Figure 7: Proportional abundance of species by ecological categories during the dry and the wet season 1996. WEF=species centred on the wettest forest habitats; MEF=species centred on moist evergreen and semi-deciduous forests; DRF=species centred on the drier forests (ecological category after Larsen 1991, 1994b, 1996a, 1996b, 1997, 1999 and Emmel and Larsen 1997); n = individuals trapped.

5.3.1.2 Differences between succession stages

A total number of 4,863 butterfly individuals was baited in the four different forest succession stages gap habitats, young (S1), intermediate (S2) and old (S3) succession stages during the dry and the wet season 1996 (see 4.1 and 5.1).

131 *resp.* 120 butterflies were caught in traps installed in gap habitats (q=3), 1,000 *resp.* 970 in S1 (q=26), 899 *resp.* 799 in S2 (q=23) and 457 *resp.* 487 butterfly individuals were baited in S3 (q=13) for the dry *resp.* the wet season. A significant difference in average number of individuals baited per trap was found between S1 and S2 during the wet season, (Mann-Whitney *U*-test with 49 cases, $Z = -2.2622$, $p = 0.02$), indicating that butterfly abundance is likely to be slightly higher in younger and more open forest stages.

Analysing the habitat preference of the different species baited in relevant abundance, we find species with a higher abundance in traps installed in young succession stages (S1), whereas others show a higher abundance in older succession stages (S3). The gamma rank correlation between capture frequencies and succession indicates significant relationships for 33 species in all (Table 10).

Most *Charaxes* species showed a higher abundance in younger succession stages (gap/S1, $\gamma = -0.4168$, $n = 130$, $p < 0.000$). The relationship was significant for *Charaxes tiridates*, *C. cynthia* and *C. brutus* (both seasons), for *C. bipunctatus* and *C. virilis* (dry season) and *C. protoclea* (wet season). The Charaxinae *Palla violenitens* and *P. decius* also showed a higher abundance in traps of younger forest stages.

Most *Euphaedra* and *Euriphene* species were more abundant in the more closed, mature succession stages (S2/S3, $\gamma = 0.2853$, $n = 130$, $p < 0.001$ for the genus *Euphaedra*, but the pattern was not significant on genus level for the *Euriphene* with $\gamma = 0.1328$, $n = 130$, $p = 0.2$). On species level, there was a significantly positive correlation between abundance and habitat maturity in both seasons for the *Euphaedra*'s *E. crockeri* and *E. phaetusa*. During the wet season, the correlation was also significant for *E. gausape*, *E. eupale*, as well as for the two *Euriphene* species *E. gambiae* and *E. atossa*.

The abundance of two *Bebearia* species was negatively correlated with forest succession: *B. mardania* and *B. absolon* ($\gamma < -0.3246$, $p < 0.05$ in both cases). In other *Bebearia* species, this relationship was positive with significant results for *B. phantasina*, *B. demetra* and *B. abesa* ($\gamma > 0.4476$, $p < 0.05$ in all cases). During the dry season 1996, no significant results could be found for *Euriphene* or *Bebearia* species due to the low abundance.

Four more Nymphalinae showed a significant and negative correlation between abundance and habitat maturity ($\gamma < -0.5185$, $p < 0.05$ in all cases): *Harma theobene*, *Ariadne enotrea*, *Aterica galene* (dry season) and *Euphaedra ceres* (both seasons).

Table 10: Nymphalidae species with marked differences in capture frequencies between the four different succession stages during the dry and the wet season 1996 on a 75 ha study site in the over-logged Bossematié Forest, Côte d'Ivoire. Gap/S1 = young, S2/S3 = older sucession stages. Mean number of individuals calculated from q samples (each 6 sampling days) for gap (q = 3), S1 (q = 26), S2 (q = 23) and S3 (q = 13) are listed in Appendix 3; significance levels are based on γ rank correlation for multiple ties (Statsoft 1995) between abundance and the four forest succession stages separate. --- = not present / abundance < 4 individuals.

	MORE ABUNDANT IN	DRY 1996		WET 1996	
		γ	p <	γ	p <
CHARAXINAE					
Charaxes tiridates	**gap/S1**	-0.5539	0.000	-0.4947	0.01
C. cynthia	**gap/S1**	-0.3770	0.01	-0.3429	0.001
C. brutus	**gap/S1**	-0.7231	0.01	-0.7231	0.01
C. virilis	**gap/S1**	-0.8182	(0.09)	----	----
C. protoclea	**gap/S1**	-0.1917	(0.1)	-0.2488	0.05
C. bipunctatus	**gap/S1**	-0.4315	0.001	-0.0612	(0.7)
Palla violenitens	**gap/S1**	-0.3278	0.05	-0.4741	0.01
P. decius	**gap/S1**	----	----	-0.5862	0.05
SATYRINAE					
Bicyclus vulgaris	**gap/S1**	-0.3639	0.001	-0.5782	0.05
B. dorothea	**gap/S1**	-0.2421	0.05	-0.1094	(0.6)
B. sandace	**gap/S1**	-0.2293	(0.1)	-0.5835	0.000
B. xeneas	**gap/S1**	-0.2373	0.05	-0.0850	(0.5)
B. abnormis	**S2/S3**	0.2737	0.01	0.4132	0.000
B. nobilis	**S2/S3**	0.4335	0.01	----	----
B. zinebi	**S2/S3**	0.1983	(0.07)	0.2509	0.03
B. procora	**S2/S3**	0.0269	0.03	0.3500	0.01
B. sambulos	**S2/S3**	0.0618	(0.6)	0.2489	0.04
Gnophodes chelys	**S2/S3**	0.0954	(0.4)	0.2717	0.02
NYMPHALINAE					
Harma theobene	**gap/S1**	-0.7024	0.001	----	----
Ariadne enotrea	**gap/S1**	-0.6512	0.05	----	----
Aterica galene	**gap/S1**	-0.6105	0.05	-0.4584	0.02
Bebearia mardania	**gap/S1**	----	----	-0.4322	0.02
B. absolon	**gap/S1**	----	----	-0.3246	0.05
Euphaedra ceres	**gap/S1**	-0.5185	0.01	-0.2503	(0.06)
Bebearia phantasina	**S2/S3**	----	----	0.5200	0.01
B. demetra	**S2/S3**	----	----	0.4476	0.03
B. abesa	**S2/S3**	----	----	0.5702	0.05
Euriphene atossa	**S2/S3**	----	----	0.5714	0.04
E. gambiae	**S2/S3**	0.2308	(0.6)	0.4383	0.03
Euphaedra crockeri	**S2/S3**	0.8971	0.000	0.2980	0.03
E. phaetusa	**S2/S3**	0.2930	0.05	0.4404	0.001
E. gausape	**S2/S3**	0.3279	(0.1)	0.5230	0.01
E. eupalus	**S2/S3**	----	----	0.7647	0.04

Within the *Bicyclus*, the abundance of four species was negatively correlated with forest succession ($\gamma < -0.2373$, $p < 0.05$ in all cases): *B. vulgaris* (both seasons), *B. xeneas* and *B. dorothea* (dry season), and *B. sandace* (wet season). In five other *Bicyclus* species, this relationship was positive with significant results ($\gamma > 0.2489$, $p < 0.04$ in all cases) for *B. nobilis* (dry season), *B. zinebi* and *B. sambulos* (wet season), and for *B. abnormis* and *B. procora* (both seasons). One further Satyrinae, *Gnophodes chelys*, also showed a significant and positive correlation between abundance and forest succession ($\gamma = 0.2717$, $p < 0.02$).

5.3.2 Species richness and diversity

A total of 123 Nymphalidae species were baited in total. Almost 60 % of these belonged to the subfamily Nymphalinae. The Charaxinae comprised 24 % of the total species richness, followed by the Satyrinae (17 %), the subfamily with the highest proportional abundance. The subfamily Apaturinae was only represented by one single species. On the genus level, the highest proportion of species was found in the *Charaxes* (21 %), followed by the genera *Euphaedra* (15 %) and *Bicyclus* (12 %). The *Bebearia* represented 11 % of all species, the *Cymothoe* 5 %.

5.3.2.1 Differences between seasons

Of the 123 nymphalid species recorded, 99 were found during the dry season (q = 66 traps x 6 sampling days), 87 during the wet season 1996 (q = 66 traps x 6 sampling days) and 102 during the wet season 1997 (q = 4 traps x 3 trap heights x 17 sampling days). The comparison of the species distribution among different subfamilies (standardised for four identical trap locations at trap height 1 m and six sampling days), indicates a comparable proportion of Satyrinae species in all seasons (between 20.2 % and 23.5 %), but a higher proportion of Nymphalidae species during the wet season 1997 (62.3 %) compared to both dry (52.5 %) and wet (53.9 %) season 1996. The proportion of Charaxinae species was highest during the dry season (27.3 %), followed by the wet season 1996 (23.5 %) and lowest during wet season 1997 (16.9 %).

Dry and wet season samples shared 77 species in the year 1996, resulting in a similarity of 53 % (Morisita-Horn sample similarity index, Magurran 1988). The average number of species and Simpson diversity index calculated for each sample was significantly higher in the dry compared to the wet season 1996 (Mann-Whitney *U*-test with 132 cases, $p < 0.000$ in both cases). A significant higher Evenness per sample was also found for the dry season (Mann-Whitney *U*-test with 132 cases, $Z = 2.5987$, $p = 0.01$). The lower Evenness during the wet season 1996 is essentially caused by the dominance of the species *Bicyclus zinebi*. Excluding this species, a significant higher average Evenness per sample is found for the wet season (Mann-Whitney *U*-test with 132 samples, Z = -3.5179, $p < 0.000$), and only a near significant higher average Simpson diversity in the dry season (Mann-Whitney *U*-test with 132 samples, Z = 1.5268, $p < 0.1$). The average species richness and Simpson diversity index per sample was significantly higher in the wet season 1997 compared to both dry and wet seasons 1996 (Mann-Whitney *U*-test with 72 samples, $p < 0.01$ and $p < 0.05$ respectively in both cases, standardised for four identical trap locations at trap height 1 m and six sampling days), but the average Evenness per sample was lower during the wet season 1997 (Mann-Whitney *U*-test with 72 samples, $p < 0.04$ in both cases). Species similarity was highest (45 %) between both wet seasons, intermediate (43 %) between the dry and the wet season 1996 and lowest (40 %) between the dry season and the wet season 1997. Shinozaki curves, obtained from pooled data of traps during the three seasons are presented in Figure 8. Species accumulation curves show a higher expected number of species (ES [q]) for the dry compared to the wet season 1996, whereas the pattern of species accumulation at q = 4 still is comparable between the dry and the wet season 1997, but lower for the wet season 1996.

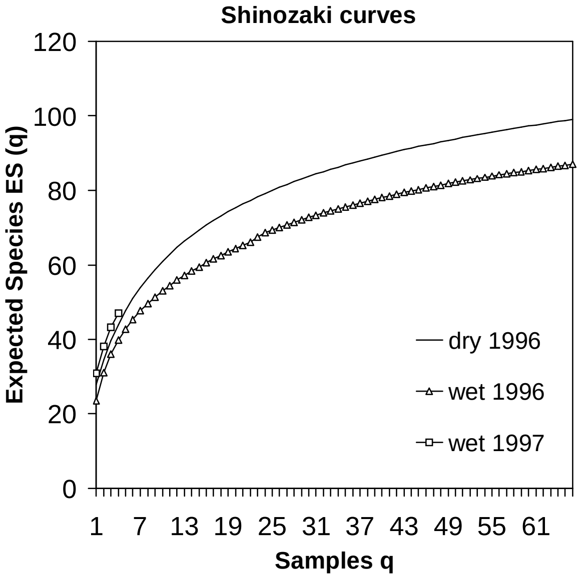


Figure 8: Expected number of Nymphalidae species (ES [q]) captured in banana traps installed in the understorey of a 75 ha study site during the dry season 1996 (q = 66 traps x 6 sampling days), the wet season 1996 (q = 66 traps x 6 sampling days) and the wet season 1997 (q = 4 traps x 6 sampling days) in the over-logged Bossematié Forest, Côte d'Ivoire. Expected means computed using Shinozaki rarefaction method (Shinozaki 1963).

The higher species richness during the dry compared to the wet season 1996 is also visible using Colwell's (1997) accumulation curves, which produce the highest Fisher's (alpha), Simpson and Shannon diversity index, as well as higher Evenness and estimators of total species richness (ICE and ACE) for the dry season (Table 11). Again, after leaving out *B. zinebi* for both seasons, Evenness is higher during the wet (0.214 ± 0.02) compared to the dry season 1996 (0.197 ± 0.01) and the difference in the dominance index (Simpson) between the two seasons far less important (19.47 *resp.* 17.91).

Table 11: Total number of individuals (I) and species (S), and diversity parameters of fruit-feeding nymphalid butterflies during the dry and the wet season 1996. Diversity indices and estimators of total species richness (ACE, ICE) calculated for q = 66 traps x 6 sampling days using EstimateS 5 (Colwell 1997). Evenness (E) calculated as E = D / S.

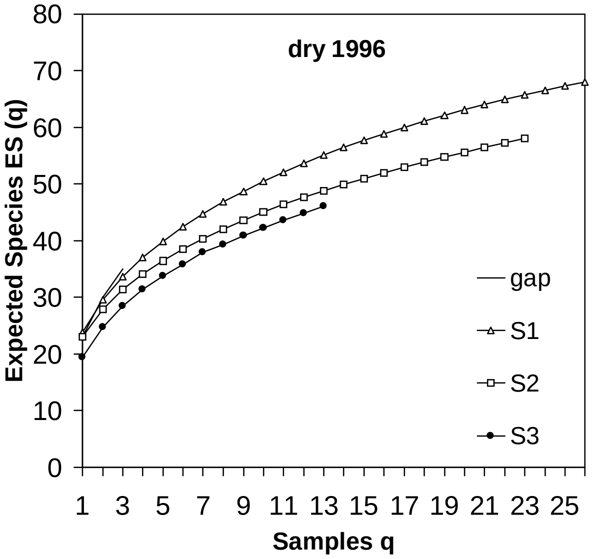
	DRY 1996	**WET 1996**
INDIVIDUALS (I)	3642	2569
SPECIES (S)	99	87
FISHER'S (ALPHA)	18.8	16.8
SIMPSON (1/D)	20.3	10.9
SHANNON	3.41	3.13
EVENNESS (E)	0.21	0.12
ACE	114.3	101.5
ICE	112.8	100.4

5.3.2.2 Differences between succession stages

The highest total number of species was baited in the young succession stage S1 (79, q=26), followed by S2 (78, q=23) and S3 (62, q=13). In the gap habitat (q=3), a total of 51 species was baited. In neither of both seasons, a significant difference could be found for the average number of species per sample between the different stages (Mann-Whitney *U*-test, $p < 0.9$ in all cases). However, a significant higher average Simpson diversity and Evenness was found per sample in both S1 and S2 compared to S3 during the wet season 1996 (Mann-Whitney *U*-test, $p = 0.05$ for both parameters and cases).

Species similarity (Morisita-Horn sample similarity index, Magguran 1988) for all samples pooled, as well as for both seasons 1996 separate, was highest between the two oldest succession stages S2 and S3 (97 %). Gap and S1, as well as S1 and S2 equally shared a high proportion of species (91 % and 94 %, respectively). Both gaps and S2, as well as S1 and S3 shared a slightly lower proportion of species (83 % and 89 %, respectively).

Species similarity was lowest, but still relatively high (73 %), between gaps and the oldest succession stage S3. The Morisita-Horn similarity between the different succession stages was generally higher during the wet compared to the dry season 1996 (ranging between 0.98 and 0.79 for the wet and 0.95 and 0.69 for the dry season), indicating that differences in species composition between succession stages were smaller during the wet than the dry season. The pattern of higher (α-)diversity in the younger succession stage S1 is even more pronounced when pooling the data of single traps by succession stage. Species accumulation curves (Figure 9) show a gradual decrease in species richness, with the highest richness in S1, the lowest in S3 and an intermediate species richness S2. This pattern is found for both seasons, although differences are less pronounced during the wet season 1996. To the contrary, species accumulation of the gap habitat is clearly higher than that of the different succession stages during the wet season 1996, whereas differences are less pronounced during the dry season 1996.



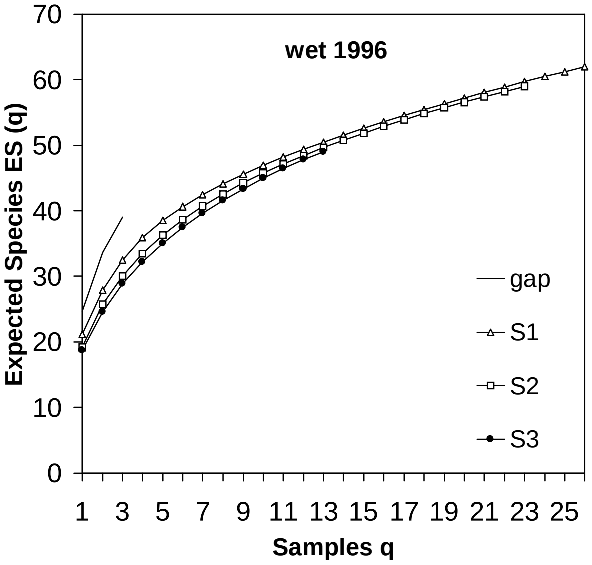


Figure 9: Expected number of Nymphalidae species (ES [q]) captured in banana traps in gaps (q = 3) and different forest succession stages S1 (q = 26), S2 (q = 23) and S3 (q = 13) during the dry and the wet season 1996 in the over-logged Bossematié Forest, Côte d'Ivoire. Expected means computed using Shinozaki rarefaction method (Shinozaki 1963).

5.3.3 Movement patterns

1,430 individuals of 37 Nymphalidae species were marked during the mark-recapture study, 678 females and 752 males. Of these, 416 individuals were recaptured in total. Including repeated recaptures of the same specimens, the total number of recaptures amounted to 540 with an equal number for males (269) and females (271). The nymphalid species with a number of recaptures ≥ 3 are listed in Table 12 .

Movement parameters were generally largest in species feeding on early successional larval host plants (grasses, forest gap and margin plant species) and smallest in species feeding on climbers and smaller shrubs characteristic of the forest understorey (Mann-Whitney *U*-test, Z > 2.44 and p < 0.01, see Table 12). The largest mean range (*R*) was found for females of the species *Bebearia sophus* (433 m). The smallest mean range was found in males of *Euphaedra ceres* (0 m) and the very similar species *Euphaedra phaetusa* (20 m), although maximum distances (D_{max}) ranging between 100 m and 160 m were seen in females of the same species. The mean range found for both *Bicyclus* species ranged between 77 m (males) and 361 m (females), for the *Gnophodes* species between 107 m (males) and 254 m (females). Within the genus *Charaxes*, largest mean ranges were found in females of *C. bipunctatus* and *C. tiridates* (340 m and 285 m, respectively), smallest ones in females of *C. zingha* (25 m) followed by *C. cynthia* and *C. protoclea* (79 m for females and 80 m for males, respectively).

For 7 species in total, significant sexual differences in movement parameters were found. The mean distance moved between captures (d_i), the mean minimum and maximum distance moved (*D*), as well as the mean minimum range (*R*) were significantly larger for females of the species *Bebearia sophus*, *Euphaedra phaetusa*, *E. ceres*, *Bicyclus dorothea*, *B. zinebi* and *Gnophodes chelys* (Mann-Whitney *U*-test, p <0.05 in all cases). Results indicate that females fly further than males, and also take longer to do so: in almost all species, time intervals between captures (t_i and *T*) were larger for females than for males. For most *Charaxes* species, movement parameters were similar in both males and females. However, contrasting with previous results, the mean distance moved between captures (d_i) was larger for males (200 m) than for females (25 m) in *Charaxes zingha* (Mann-Whitney *U*-test, Z = 2.9 and p < 0.05).

Table 12: Population movement data of selected Nymphalidae species captured in banana baited traps installed on a 75 ha study site in the over-logged Bossematié Forest, Côte d'Ivoire. Hostplant information after Larsen (1991, 1996b) and Hutchinson and Dalziel (1954). Total recaptures include recaptures of identical individuals; d_i: the minimum straight-line movement in metres between captures *i* and (*i*+1); t_i: time in days between captures *i* and (*i*+1); *D:* sum of d_is for each individual (minimum distance moved); D_{max}: maximum D recorded; *T*: sum of t_is for each individual (number of days between first and last capture); *R*: Distance in metres of two furthest capture points for each individual (minimum range).

	BEBEARIA SOPHUS		*EUPHAEDRA PHAETUSA*		*EUPHAEDRA CERES*		*EUPHAEDRA HARPALYCE*		*BICYCLUS DOROTHEA*		*GNOPHODES BETSIMENA*		*GNOPHODES CHELYS*	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Individuals marked	13	13	20	15	10	10	17	17	90	67	80	72	164	143
Individuals recaptured	7	3	10	8	3	3	5	7	35	28	24	23	31	36
Total recaptures	8	3	17	8	6	3	5	7	49	36	28	28	34	44
Mean *T* (days)	1.71	15.7	2.80	4.75	5.0	1.70	2.20	2.43	4.32	6.57	2.8	3.6	2.7	5.3
Mean t_i (days)	1.5	15.7	2.33	2.64	2.78	1.67	2.20	2.43	3.13	5.64	2.4	3.0	2.4	4.4
Mean *R* (m)	100.0	433.3	20.0	150.0	0.0	133.3	0.0	100.0	79.71	360.71	200.0	247.8	106.7	254.1
Mean *D* (m)	100.0	433.3	20.0	162.5	0.0	133.3	0.0	100.0	100.0	385.71	200.0	247.8	103.3	278.4
Mean d_i (m)	100.0	433.3	20.0	103.7	0.0	133.3	0.0	100.0	62.5	337.5	195.8	208.7	103.3	231.1
D_{max}	100.0	433.3	20.0	162.5	0.0	133.3	0.0	100.0	88.23	364.28	200.0	243.5	103.3	256.8
Known hostplants	climber species in forest margin/gaps (Apocynaceae)		climbers + smaller shrubs in forest understorey (Sapindaceae)		climbers + smaller shrubs in forest understorey (Sapindaceae)		Smaller forest understorey shrub species (Sapindaceae)		grass species (Poaceae)		grass species (Poaceae)		grass species (Poaceae)	

	BICYCLUS ZINEBI		*CHARAXES TIRIDATES*		*CHARAXES PROTOCLEA*		*CHARAXES ZINGHA*		*CHARAXES CYNTHIA*		*CHARAXES BIPUNCTATUS*	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Individuals marked	102	68	30	67	61	54	16	13	49	62	45	38
Individuals recaptured	44	28	4	13	25	23	3	4	15	14	11	5
Total recaptures	65	50	4	15	33	36	3	6	24	23	15	6
Mean *T* (days)	4.5	7.1	2.5	1.8	3.9	3.5	6.3	2.7	4.7	4.3	5.8	1.5
Mean t_i (days)	3.5	4.0	2.5	1.7	3.1	2.6	6.3	2.1	3.3	2.2	5.3	1.2
Mean *R* (m)	77.3	289.3	125.0	284.6	80.0	152.4	200.0	25.0	166.7	78.6	333.3	340.0
Mean *D* (m)	79.5	339.3	125.0	300.0	70.0	129.0	200.0	25.0	173.3	85.7	383.3	340.0
Mean d_i (m)	61.9	225.3	125.0	243.6	70.0	129.0	200.0	25.0	112.2	40.5	305.5	340.0
D_{max}	77.3	385.7	125.0	284.6	76.0	152.4	200.0	25.0	153.3	78.6	333.3	340.0
Known hostplants	Marantaceae and some ginger species (Zingiberaceae)		Tree species in several families		Tree species in several families		Tree species (Linaceae)		Tree species in several families		Tree species (Sapindaceae)	

5.3.4 Effects of further fragmentation

385 Nymphalidae belonging to 35 species were baited in the understorey of a 6 ha forest fragment during the wet season 1997. The subfamily Satyrinae dominated the samples, constituting 80 % of the total abundance. The two most abundant Satyrinae species were *Gnophodes chelys* (81 individuals) and *Bicyclus dorothea* (52 individuals), followed by *B. sandace*, *G. betsimena* and *B. vulgaris*. Both the Nymphalinae and the Charaxinae only constituted a small proportion of the total abundance baited (18.4 % and 1.6 % respectively). Sampling in the Bossematié Forest during the same period and with an equal sampling effort (4 traps and 7 sampling days) reveals a different abundance pattern, with the Nymphalinae constituting 56.2 % of the total abundance and the Satyrinae subfamily being less dominant (36.1 %). The lowest abundance was equally found in the Charaxinae subfamily, although they were comparatively more abundant constituting 7.7 % of the total butterfly number.

A significantly higher abundance was found for the genus *Bicyclus*, *Gnophodes* and *Melanitis* in the 6 ha forest fragment compared to the Bossematié Forest (Mann-Whitney *U*-test with 10 cases, $Z > 2.05$ and $p < 0.05$ in all cases). However, both *Bicyclus abnormis* and *B. procora*, present in samples from the Bossematié Forest, were never recorded in the nearby forest fragment. The abundance of *Charaxes* spp., *Bebearia* spp., *Euphaedra* spp. and *Euriphene* spp. was significantly lower in traps of the forest fragment compared to the Bossematié Forest (χ^2-test, $\chi^2_{1df} > 11.92$, $p < 0.005$ in all cases). However, three Nymphalinae species in particular were still relatively abundant in traps of the forest fragment: *Bebearia theognis*, *Euphaedra harpalyce* and *E. phaetusa*.

A comparison of diversity indices reveals a significant lower abundance, species number, species diversity and significant lower estimators of total species richness in the 6 ha forest fragment than the Bossematié Forest (Table 13). Both shared 28 species, resulting in a similarity of 33 % only (Morisita-Horn sample similarity index, Magurran 1988).

Table 13: Total number of individuals (I) and species (S), and diversity parameters of fruit-feeding nymphalid butterflies of a 6 ha forest fragment and a 6 ha study plot during the wet season 1997 in the Bossematié Forest, Côte d'Ivoire. Diversity indices and estimators of total species richness (ACE, ICE) calculated for q = 4 samples x 7 sampling days in both cases using EstimateS 5 (Colwell 1997).

	NEARBY FOREST FRAGMENT	BOSSEMATIÉ FOREST
Individuals (I)	288	405
Species (S)	30	56
Singletons	10	18
Fisher's (α)	8.43 ± 0.90	17.63 ± 1.50
Simpson (1/D)	9.23	14.34
Shannon	2.61	3.23
ACE	40.12 ± 1.43	71.18
ICE	39.45 ± 0.03	72.18 ± 0.02

5.4 Impact of the forest management

In the following, results on the impact of the forest management techniques applied in the over-logged Bossematié Forest, liberation thinning and tree plantation, on the butterfly community will be presented based on results from various sampling methods during a dry and two wet seasons in 1996 and 1997: fruit trapping in the understorey and at higher vertical strata, walk-and-capture along transects and point distance sampling.

5.4.1 Fruit trapping in the understorey

5.4.1.1 Abundance

The total butterfly abundance did not differ between the control, thinned and plantation plot during the dry season. The number of butterfly individuals per sample was not significantly different between the three management types (Kruskal-Wallis ANOVA with 66 cases, $H = 0.47$ and $p > 0.7$), although traps with highest numbers were situated in the regenerating control forest. During the wet season, however, the mean abundance per sample was higher in the control compared to both thinned and plantation plots (Mann-Whitney *U*-test with 56 resp. 38 cases, $Z > -2.82$ and $p < 0.01$ in both cases), but no difference was found between thinned and plantation (Mann-Whitney *U*-test with 38 cases, $Z = -1.351$ and $p = 0.2$).

On average, more individuals were caught per sample in control than thinned forests for the genera *Euphaedra*, *Euriphene* and *Gnophodes*. These differences were only marginally significant for dry season (Mann-Whitney *U*-test, $N = 56$, $p = 0.1$ in all 3 genera), but significant for wet season samples (Mann-Whitney *U*-test, $N = 56$, $p < 0.03$ in all 3 genera). On the species level (see Table 14), a significantly higher abundance in control was found for *Gnophodes chelys*, *Euphaedra phaetusa*, *E. crockeri* and, in the wet season only, for *E. harpalyce*. Although trends are comparable for the baited *Euriphene* species, the number of captures per species was too low for statistical comparison.

At the 5 % level, the abundance of the baited *Charaxes* was significantly higher in thinned than control (Mann-Whitney *U*-test, $N = 56$, $p < 0.01$). This trend is mainly caused by two species: *C. cynthia* and *C. tiridates*. For one *Charaxes* species, *C. bipunctatus,* a significantly higher abundance was found in the conrol plot during the wet season.
Within the genus *Bicyclus*, three species showed a significantly higher abundance in the thinned area: *B. vulgaris*, *B. sandace* and *B. dorothea*. Another four *Bicyclus* species were significantly more abundant in control traps: *B. abnormis*, *B. zinebi*, *B. funebris* and *B. sambulos*. Consequently, there were no significant differences in abundance between control and thinned plots on the genus level (Mann-Whitney *U*-test, $N = 56$, $p > 0.6$ in both seasons).

For *Bebearia*, no differences could be detected during the dry season, neither on genus (Mann-Whitney *U*-test, N = 56, p > 0.8), nor on species levels. In the wet season, however, *B. sophus* showed a significantly higher abundance in the control forest.

Table 14: Species with marked differences in capture frequencies in a 30 ha regenerating forest (control) and a 30 ha thinned forest plot during the dry and the wet season 1996 in the over-logged Bossematié Forest, Côte d'Ivoire,. Values are absolute number of individuals (highest numbers are bold); significance levels are based on the Mann-Whitney *U*-test.

	CONTROL (q=28)	THINNED (q=28)	Z	p <
DRY SEASON 1996				
CHARAXINAE				
Charaxes cynthia	46	**85**	-2.658	0.05
C. tiridates	23	**46**	-1.979	0.01
SATYRINAE				
Bicyclus vulgaris	78	**134**	-2.267	0.02
B. dorothea	49	**60**	-2.155	0.03
B. abnormis	**101**	36	3.416	0.001
B. zinebi	**148**	91	2.034	0.05
B. funebris	**148**	106	2.283	0.02
Gnophodes chelys	**188**	148	2.251	0.02
NYMPHALINAE				
Euphaedra crockeri	**12**	2	2.309	0.02
E. phaetusa	**89**	62	2.029	0.05
WET SEASON 1996				
CHARAXINAE				
Charaxes cynthia	22	**32**	-2.654	0.05
Charaxes bipunctatus	**25**	11	3.081	0.002
SATYRINAE				
Bicyclus sandace	8	**21**	-2.067	0.05
B. dorothea	5	**23**	-2.235	0.02
B. sambulos	**72**	39	3.153	0.001
B. abnormis	**32**	6	2.570	0.01
B. zinebi	**331**	273	2.023	0.05
Gnophodes chelys	**93**	57	2.291	0.02
NYMPHALINAE				
Bebearia sophus	**137**	74	3.081	0.002
Euphaedra crockeri	**34**	11	2.761	0.006
E. harpalyce	**20**	7	2.378	0.02
E. phaetusa	**193**	71	3.560	0.001

Most striking differences in individual numbers were visible between traps located in the forest (control or thinned) compared to the plantation. The abundance of the baited *Euphaedra*, *Euriphene*, *Bebearia* and *Gnophodes* individuals was higher in traps of the control (Mann-Whitney *U*-test, N = 38, p < 0.05 in all 4 genera for both seasons) compared to the plantation, whereas the numbers of *Charaxes* individuals was highest in the plantation for both seasons (Mann-Whitney *U*-test, N = 38, p = 0.05). The comparison plantation to thinned indicated a significant higher abundance in the thinned zone for the genera *Bebearia*, *Euphaedra* and *Euriphene* (Mann-Whitney *U*-test, N = 38, $p < 0.05$ in all 3 genera and both seasons). No significant difference in abundance between thinned and plantation could be found for the baited *Charaxes* and *Gnophodes* (Mann-Whitney *U*-test, N = 38, $p > 0.05$ in both genera).

During the dry season, eight species showed a significantly higher abundance in plantation traps compared to traps installed in both control and thinned pooled. Three of them were *Charaxes* species: *C. lucretius* (Fisher's exact test, $p < 0.05$), *C. anticlea* (Fisher's exact test, $p < 0.01$) and *C. castor* (Fisher's exact test, $p < 0.01$). The other five species were *Ariadne enotrea* ($\chi^2_{(1)}$=124.45, $p < 0.000$), *Eurytela dryope* (Fisher's exact test $p < 0.01$), *Bicyclus safitza* (Fisher's exact test, $p < 0.01$), *Salamis cacta* (Fisher's exact test, $p < 0.01$), and *Byblia anvatara* (Fisher's exact test, $p < 0.05$). Seventeen species belonging to the genera *Euphaedra*, *Bicyclus*, *Gnophodes* and *Charaxes* were significantly more abundant in forest (thinned and control) compared to plantation traps ($\chi^2_{(1)} > 3.7$, $p < 0.05$, in all cases). During wet season, only two *Charaxes* species, *C. etheocles* and *C. brutus* were significantly more abundant in the plantation (Fisher's exact test, $p < 0.05$ in both cases). Nine species belonging to the genera *Euphaedra*, *Bicyclus*, *Gnophodes* and *Charaxes* were significantly more abundant in forest (thinned and control) compared to plantation traps ($\chi^2_{(1)} > 3.7$, $p < 0.05$, in all cases). *Euriphene* and *Euphaedra* species were never seen in the plantation. *Bebearia* species did not show marked differences in abundance between plantation and forest traps in any season.

5.4.1.2 Species richness and diversity

The average number of species and the Simpson diversity index calculated for each sample were significantly higher for both the control and the thinned area compared to the plantation (Mann-Whitney *U*-tests with 38 cases; $p < 0.05$ in both cases and seasons), but no significant differences could be found for Evenness. Between the control and the thinned plots, there were no significant differences in number of species and Simpson diversity index per sample (Mann-Whitney *U*-tests with 56 traps; $p > 0.05$ in both cases and seasons). Shinozaki curves, obtained from pooled data of traps for control, thinned and plantation areas during the dry season are presented in Figure 10 (Shinozaki 1963). In contrast to the lack of significant difference in α-diversity between single traps located in either control or thinned forest, species accumulation curves showed a higher expected number of species (ES [q]) for thinned compared to control. Standard deviations derived from rarefaction analysis (Achtziger *et al.* 1995) confirm these results, as they do not show overlap in the number of expected species between the control and the thinned area after 1,000 collected individuals. The higher species richness in the thinned compared to the control forest is also visible using Colwell's (1997) accumulation curves, which produce a much higher Simpson index, higher Evenness and considerably higher estimators of total species richness (ICE and ACE) for the thinned compared to the control forest. Similarly, Fisher's alpha index (Magurran 1988) was higher in thinned than control, but standard deviations overlapped (see Table 15). During the wet season, diversity differences were less pronounced between areas. Although (Fisher's) alpha diversity, Simpson diversity, Shannon index and Evenness were all slightly higher in the thinned area, standard deviations still overlapped at q = 28 samples pooled. The size of the local species pool (ACE) for control is estimated to be 85 - 86, and in thinned 95 - 105 species for the dry season. During wet season, values were lower and estimated at 73 and 86 - 90 for the control and thinned areas respectively.

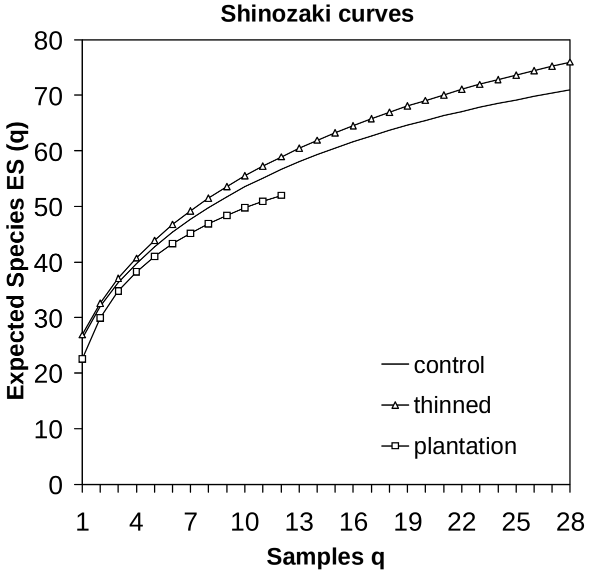


Figure 10: Expected number of Nymphalidae species (ES [q]) captured in banana baited traps in a regenerating forest (control), a liberation thinning (thinned) and a plantation plot during the dry season 1996 in the over-logged Bossematié Forest, Côte d'Ivoire. Expected means computed using Shinozaki rarefaction method (Shinozaki 1963).

The control and the thinned forest shared 54 and 50 species during the dry and the wet season respectively, resulting in a similarity of 92 % respectively 89 % between the two areas (Morisita-Horn sample similarity index, Magurran 1988). In both seasons, species similarity standardised at q = 10 samples was highest (86 % respectively 80 %) between control and thinned, intermediate (64 % respectively 60 %) between thinned and plantation and lowest between control and plantation (56 % respectively 51 %). In the plantation, species richness and diversity was lower than in both forest plots during both seasons. During the dry season, a total of 52 species were captured after q = 12 samples, while 55 were recorded in both control and thinned forests. The local species pool for q = 12 samples (approximate area covered 15 ha) is estimated at 62 (ACE) to 70 (ICE) species; in the control these values ranged from 76 to 78 species, in thinned from 77 to 78 species. Differences between the plantation and both forest plots followed the same pattern during the wet season.

Table 15: Total number of individuals (I) and species (S), and diversity parameters of fruit-feeding nymphalid butterflies of a regenerating forest (control) compared to a liberation thinning (thinned) plot (each approximatly 30 ha) during the dry and the wet season 1996 in the over-logged Boseematié Forest, Côte d'Ivoire. Diversity indices and estimators of total species richness (ACE, ICE) calculated for q=28 samples using EstimateS 5 (Colwell 1997). Evenness (E) calculated as E = D / S. Standard deviations in parentheses.

	DRY SEASON 1996		WET SEASON 1996	
	CONTROL	THINNED	CONTROL	THINNED
Individuals (I)	1,574	1,503	1,388	966
Species (S)	71	76	66	63
Fisher's (alpha)	15.3 (±0.9)	16.6 (±1.0)	14.42 (±0.87)	15.16 (±1.02)
Simpson (1/D)	17.9 (±0.2)	20.6 (±0.2)	10.11 (±0.0)	10.01 (±0.27)
Shannon	3.25 (±0.0)	3.35 (±0.0)	2.98 (±0.0)	3.00 (±0.02)
Evenness (E)	0.252 (± 0.003)	0.271 (±0.003)	0.153 (±0.000)	0.159 (±0.008)
ACE	85.4 (±3.7)	95.1 (±2.5)	72.79 (±0.0)	90.37 (±4.13)
ICE	85.8 (±3.4)	105.2 (±3.6)	72.84 (±0.0)	86.14 (±2.88)

5.4.1.3 Habitat specificity and geographical range

A significant negative correlation between geographic range and preference for control traps (expressed as % of individuals trapped in control as compared to thinned forest) was visible in the 43 species present with 6 or more captures during the dry season (Gamma rank correlation for multiple ties, $\gamma = -0.5782$, n = 43 spp., $p < 0.000$, see Figure 11). This relationship was significant for the Nymphalinae species separately ($\gamma = -0.8448$, n = 16 spp., $p < 0.000$), as well as for the genus *Euphaedra* ($\gamma = -0.7059$, n = 10 spp., p = 0.01). It was not significant for *Bebearia*, neither for the Satyrinae or *Bicyclus* species separately. The Charaxinae showed a reverse trend: a significant increase in abundance in control traps with extent of geographic range ($\gamma = 0.5517$, n = 11 spp., p = 0.03). The habitat preference for control compared to plantation (standardised for q = 12 samples) showed a significant negative relation with increasing geographic range (Gamma rank correlation for multiple ties, $\gamma = -0.5323$, n = 41 spp., $p < 0.001$).

During the wet season, trends were similar. A significant negative correlation between geographic range and preference for control traps was found in the 39 species present with 6 or more captures (Gamma rank correlation for multiple ties, $\gamma = -0.4370$, n = 39 spp., $p < 0.000$). Again, this relationship was significant for the Nymphalinae species separately ($\gamma = -0.6000$, n = 18 spp., $p < 0.01$), as well as for the genus *Euphaedra* ($\gamma = -0.7647$, n = 7 spp., p = 0.03) and *Bebearia* ($\gamma = -0.6842$, n = 8 spp., p = 0.05). It was not significant for the Satyrinae or *Bicyclus* and *Gnophodes* species separately, neither for the Charaxinae ($\gamma = 0.1429$, n = 9 spp., p = 0.7). The habitat preference for control compared to plantation (standardised for q=10 samples) equally showed a significant negative relation with increasing geographic range (Gamma rank correlation for multiple ties, $\gamma = -0.4721$, n = 35 spp., $p < 0.000$).

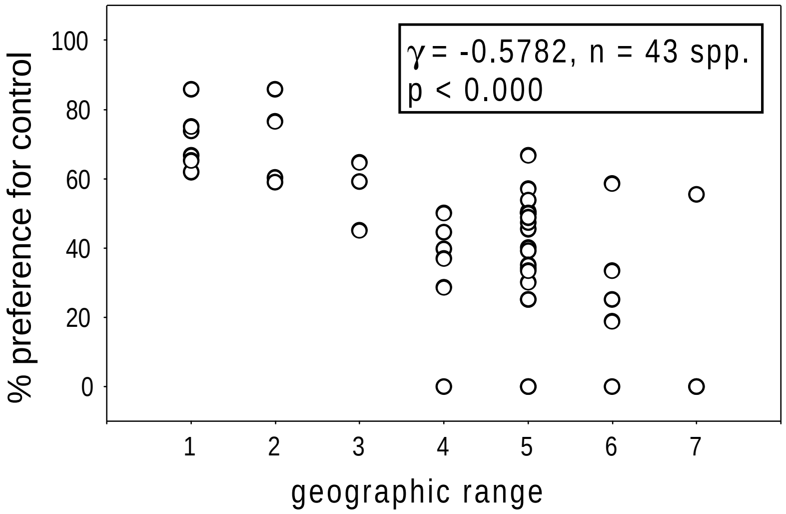


Figure 11: Relationship between geographic range and habitat specificity (% individuals in the regenerating forest (control) in 43 Nymphalidae species captured in 6 individuals or more. The gamma rank correlation coefficient γ (Statsoft 1995) indicates a significant decrease in habitat specificity with increasing geographic range.

5.4.1.4 Movement patterns in different management plots

Of the 1,430 marked individuals, 490 were found in the control, 630 in the thinned and 135 in the plantation plot. In total, 448 individuals were recaptured in the three management zones. The percentage of recaptured individuals was comparable between the control and the thinned plot (36 % and 38 %, respectively). The recapture rate in the plantation was slightly lower (24 %), most probably due to the smaller area studied (15 ha compared to both 30 ha plots). These recaptures were all from original capture sites, no flights between the three studied plots were found. The comparison of movement parameters between plots reveals (in all species with adequate data) largest average movement parameters for the plantation and smallest for the control forest (see Table 16). Species characteristic of the forest understorey, within the *Euphaedra*, *Bebearia* and *Gnophodes* (Larsen 1991, 1996b, 1999), as well as canopy flying species of the *Charaxes* group, which feed on trees, (Larsen 1991, 1996b, 1999), all tended to move larger distances between captures in the thinned compared to the control forest (Mann-Whitney *U*-test, $Z > 1.99$ and $p < 0.05$ for all measured distance parameters). On the other hand, species in the genus *Bicyclus*, also flying at forest understorey level and feeding on grasses, Marantaceae and gingers as larvae (Larsen 1991, 1996b, 1999), showed significant smaller movement parameters in the thinned compared to the control forest (Mann-Whitney *U*-test, $Z > 2.51$ and $p < 0.01$).

Table 16: Population movement data of selected Nymphalidae species captured in banana baited traps installed in a regenerating forest (control, C), a thinned forest (T) and a plantation (P) site on a 75 ha study site of the over-logged Bossematié Forest, Côte d'Ivoire. *Bebearia sophus* and *Bicyclus zinebi* were captured but never recaptured in the plantation, *Euphaedra* species were never captured in the plantation. -- = not enough data for analysis. Vertical stratum after Larsen and Dall'Asta (1994) and Larsen (1999). Total recaptures: includes recaptures of identical individuals; d_i: the minimum straight-line movement in metres between captures *i* and (*i*+1); t_i: time in days between captures *i* and (*i*+1); *D:* sum of d_is for each individual (minimum distance moved); D_{max}: maximum D recorded; *T*: sum of t_is for each individual (number of days between first and last capture); *R*: Distance in metres of two furthest capture points for each individual (minimum range).

	BEBEARIA SOPHUS		***EUPHAEDRA PHAETUSA***		***EUPHAEDRA CERES***		***EUPHAEDRA HARPALYCE***		***BICYCLUS DOROTHEA***			***GNOPHODES BETSIMENA***			***GNOPHODES CHELYS***		
	C	**T**	**C**	**T**	**C**	**T**	**C**	**T**	**C**	**T**	**P**	**C**	**T**	**P**	**C**	**T**	**P**
Individuals marked	8	12	23	9	6	12	23	12	27	51	31	53	69	22	129	133	10
Individuals recaptured	3	4	10	7	23	3	7	1	12	25	6	15	15	3	22	31	2
Total recaptures	3	5	21	8	2	6	7	1	14	28	7	19	16	3	25	38	2
Mean *T* (days)	2.6	9.2	4.4	2.6	3.0	3.5	2.5	--	6.6	4.0	5.2	4.3	2.5	2.7	3.7	4.5	2.5
Mean t_i (days)	2.6	8.9	2.4	2.6	3.0	1.8	2.5	--	5.4	2.9	4.8	3.2	2.3	2.7	3.4	3.6	2.5
Mean *R* (m)	20.0	240.0	59.1	114.3	0.0	105.0	63.6	--	217.0	177.8	300.0	116.7	283.3	320.0	118.5	226.3	400.0
Mean *D* (m)	20.0	240.0	50.0	100.0	0.0	105.0	63.6	--	260.0	181.5	300.0	116.7	283.3	320.0	118.5	247.4	400.0
Mean d_i (m)	20.0	240.0	66.4	100.0	0.0	105.0	63.6	--	196.7	156.5	290.0	75.0	272.9	320.0	112.9	205.3	400.0
D_{max}	20.0	240.0	66.4	100.0	0.0	105.0	63.6	--	236.7	170.4	300.0	116.7	279.2	320.0	118.5	226.3	400.0
Vertical stratum	understorey		Understorey		Understorey		Understorey		Understorey			Understorey			understorey		

	BICYCLUS ZINEBI		***CHARAXES TIRIDATES***			***CHARAXES PROTOCLEA***			***CHARAXES ZINGHA***			***CHARAXES CYNTHIA***			***CHARAXES BIPUNCTATUS***		
	C	**T**	**C**	**T**	**P**	**C**	**T**	**P**	**C**	**T**	**P**	**C**	**T**	**P**	**C**	**T**	**P**
Individuals marked	88	78	37	27	20	40	59	5	9	10	4	15	61	13	18	47	13
Individuals recaptured	28	32	4	5	3	23	18	2	1	6	1	9	14	4	3	5	3
Total recaptures	41	61	4	6	3	31	29	2	1	6	3	13	25	5	3	5	4
Mean *T* (days)	6.1	4.6	2.1	1.5	2.1	4.0	3.5	--	--	2.8	4.0	3.4	5.4	2.3	1.7	6.3	5.5
Mean t_i (days)	4.8	2.8	2.1	1.5	1.8	3.0	2.7	--	--	2.8	1.3	2.2	3.2	1.7	1.5	6.2	4.3
Mean *R* (m)	200.0	119.0	200.0	233.3	287.5	68.0	175.0	--	--	20.0	100.0	37.5	155.6	166.7	166.7	385.7	500.0
Mean *D* (m)	223.5	137.8	200.0	233.0	312.5	68.0	175.0	--	--	20.0	100.0	37.5	166.7	166.7	166.7	385.7	650.0
Mean d_i (m)	150.2	98.0	200.0	233.3	220.8	52.7	157.1	--	--	20.0	100.0	18.7	102.8	150.5	166.7	371.4	441.6
D_{max}	191.2	124.3	200.0	233.3	287.5	64.0	175.0	--	--	20.0	100.0	37.5	150.0	195.6	166.7	385.7	500.0
Vertical stratum	Understorey		Higher strata			Higher strata			Higher strata			Higher strata			Higher strata		

5.4.2 Fruit trapping in different vertical strata

During the wet season 1997, fruit trapping was done along the vertical gradient on the 75 ha study site in the over-logged Bossematié Forest. Based on the pooled data set, the patterns of vertical stratification of the fruit feeding butterfly community were analysed. In addition, the impact of thinning operations on the patterns of vertical stratification were assessed, as well as the differences in capture frequencies at all trap heights due to the forest management.

5.4.2.1 General

2,189 individuals belonging to 103 species were captured in twelve banana baited traps installed in the three different trap heights 1 m, 12 m and 25 m. There was a significant, negative correlation between trap height and both number of individuals (Gamma rank correlation for multiple ties, $\gamma = -0.46$, $n = 12$, $p = 0.04$) and number of species (Gamma rank correlation for multiple ties, $\gamma = -0.45$, $n = 12$, $p = 0.04$), with a decrease in abundance from 1,425 (1 m) to 359 (25 m) individuals and in number of species from 77 (1 m) to 52 (25 m).

Species richness was highest at trap height 1 m, but no difference in species richness could be found between trap height 12 m and 25 m (see Figure 12). Fisher's α-diversity (Magguran 1988) was highest at trap height 1 m (17.4) and lowest at both trap heights 12 m and 25 m (16.5 and 16.7, respectively). Simpson's α-diversity (Magguran 1988) was lowest for the species spectrum recorded at trap height 25 m (14.4), but equal at lower trap heights 1 m and 12 m (17.0 and 16.9, respectively).

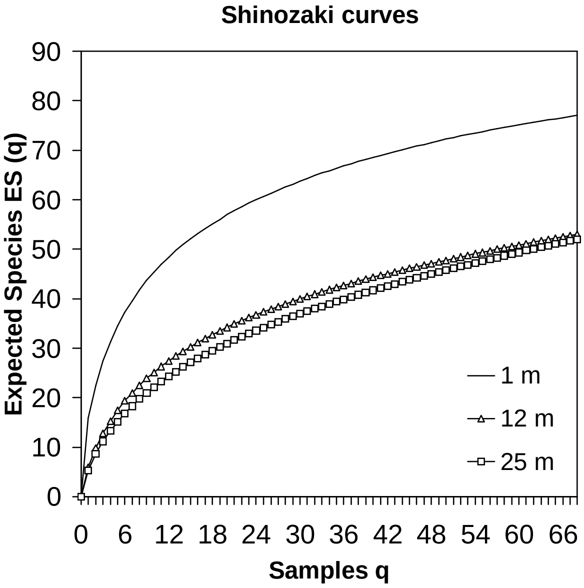


Figure 12: Expected number of Nymphalidae species (ES [q]) captured in banana baited traps installed in three different vertical heights (1 m, 12 m and 25 m, q = 4 traps x 17 sampling days) in the over-logged Bossematié Forest during the wet season 1997. Expected means computed using Shinozaki rarefaction method (Shinozaki 1963).

To analyse the similarity of species assemblages at different trap heights, a cluster analysis was done based on the Morisita-Horn index (Figure 13). Single samples (four per vertical height level) were compared and their dissimilarity (1–Morisita-Horn) plotted. The single-linkage cluster indicates that samples cluster according to trap height. Principally, two distinct species spectra can be separated. Traps at 1 m (Figure 12: 1A, 1B, 1C, 1D) constitute the first group, and differ clearly from those at 12 m (12A, 12B, 12C, 12D) and 25 m (25A, 25B, 25C, 25D) forming the second group. Figure 13 also shows that affinities between the species assemblage at 1 m and 12 m were slightly higher than those at 1 m and 25 m traps. One sample location at 12 m (12C), however, deviates from this general pattern and does not cluster together with the other sample locations at trap height 12 m but with those at 25 m. In contrary to the other 12 m traps, this particular trap location was more exposed, located in low vegetation cover, almost without surrounding foliage.

The species turnover-rate along the vertical gradient indicates the largest shift in species composition between trap heights 1 m and 25 m, with a species turnover-rate T = 0.52. An equally large species turnover-rate was found between the trap heights 1 m and 12 m (T = 0.48), whereas the turnover-rate between 12 m and 25 m was only half as large (T = 0.26). This illustrates once again the clear shift in species composition between understorey and midstorey / canopy level.

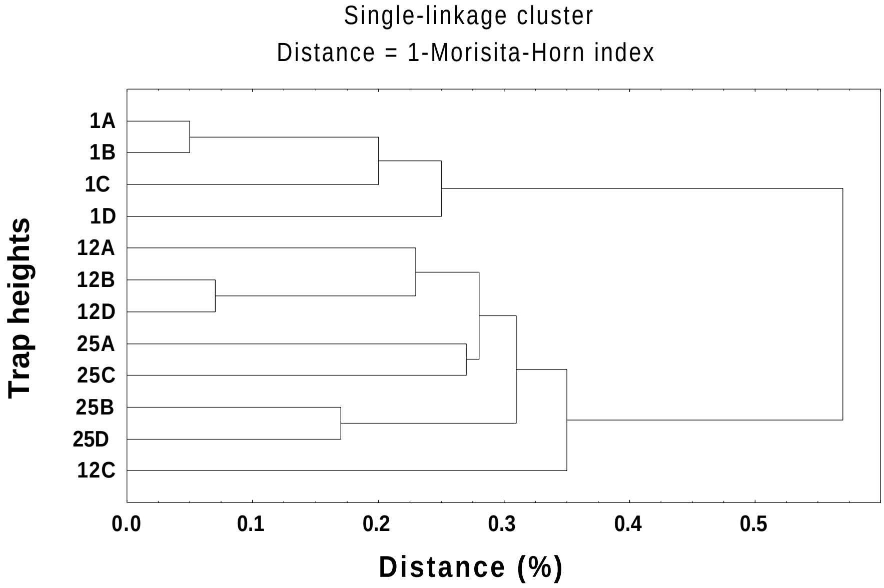


Figure 13: Dendrogramm of dissimilarities (distance = 1–Morisita-Horn) between the different trap heights 1 m, 12 m and 25 m. A, B, C, D represent the four different trap locations. Single-linkage cluster produced using Statistica 5.1. (Statsoft 1995).

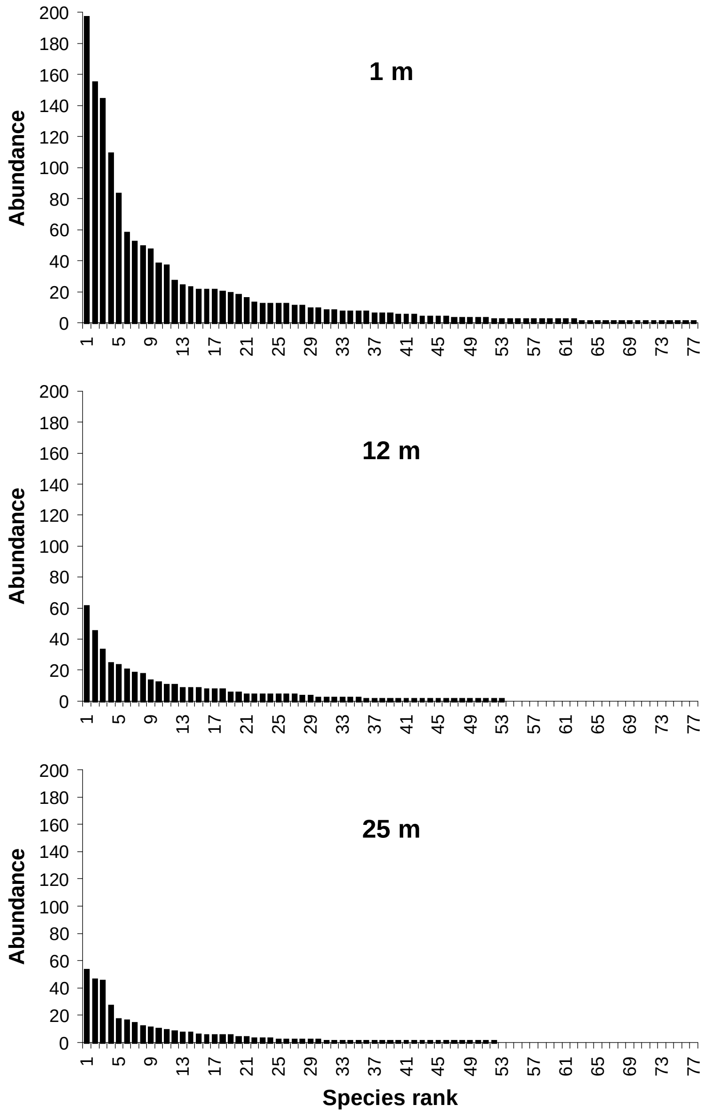


Figure 14: Rank-abundance pattern of the species spectra baited at three different trap heights during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

Figure 14 represents the abundance pattern of the species spectra at different trap heights. At 12 m and 25 m, no species was baited in more that 65 individuals. At 1 m, however, five species were still baited in 80 individuals and more. Furthermore, we can see that the proportion of rare species (< 5 individuals) increases with trap height. Whereas the proportion of rare species in the species assemblage is 45.5 % at trap height = 1m, it reaches 62.3 % and 63.5 % for traps installed at 12 m and 25 m respectively.

Patterns in subfamilies. As for the number of baited individuals, the Nymphalinae were clearly dominating at trap height 1 m (Figure 15), constituting 67.2 % of the total butterfly abundance. At 12 m and 25 m, the Nymphalinae only represented 25 % and 39.5 % respectively of the total sample. Although never dominant at any height level, the Satyrinae were also most abundant at trap height 1 m, constituting 26.1 % of the total abundance. At 12 m and 25 m trap height, the Satyrinae were represented by 19.3 % and 9.4 %, respectively. For both trap heights 12 m and 25 m, the

Charaxinae were visibly dominant, with a maximum proportion of 55.8 % at 12 m. At 1 m height, the Charaxinae only constituted 6.7 % of the total butterfly individuals baited.

Also in terms of species richness, the Nymphalinae represented the dominant subfamily at trap height 1 m (Figure 16). Here, a maximum proportion of 62.3 % was found. At trap height 12 m and 25 m, the Nymphalinae were also dominating (41.6 % and 47.6 % of the species number respectively), however, the Charaxinae constituted an almost comparable proportion of the total species number baited at both trap heights (37.7 % and 39.2 %, respectively). For the Charaxinae, the proportion of baited species at 1 m represented only half of that found at higher height levels (16.9 %). The proportion of baited Satyrinae species was comparable at 1 m and 12 m trap heights (20.8 % and 20. 7 % respectively), and lowest at 25 m (13.7 %).

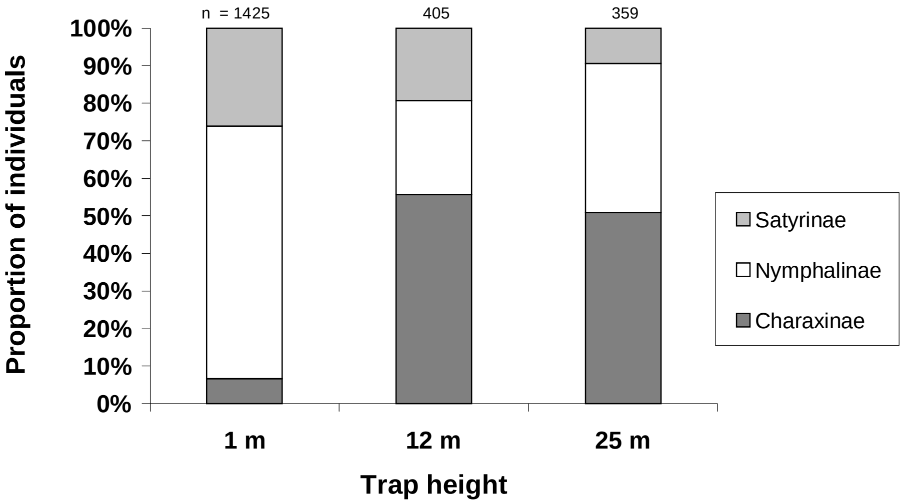


Figure 15: Proportion of Nymphalidae individuals per subfamily baited in three different trap heights during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

Analysing the absolute individual and species numbers along the vertical gradient, we can see clear patterns for two of the three fruit-feeding Nymphalidae subfamilies. The number of baited Satyrinae species decreased significantly with increasing trap height from 16 spp. at 1 m to 7 spp. at 25 m ($r_s = -0.860$, $N = 12$, $p = 0.000$), the number of baited individuals decreases significantly from 372 at 1 m to 34 at 25 m ($r_s = -0.887$, $N = 12$, $p = 0.000$). The same trend could be found for the Nymphalinae: a significantly negative correlation between both the number of species and the abundance with trap height ($r_s = -0.757$, $N = 12$, $p = 0.004$ and $r_s = -0.591$, $N = 12$, $p = 0.04$, respectively). For the Charaxinae, the positive correlation between both number of baited Charaxinae species and individuals and trap height was not significant ($r_s = 0.447$, $N = 12$, $p = 0.1$ and $r_s = 0.384$, $N = 12$, $p = 0.2$ respectively).

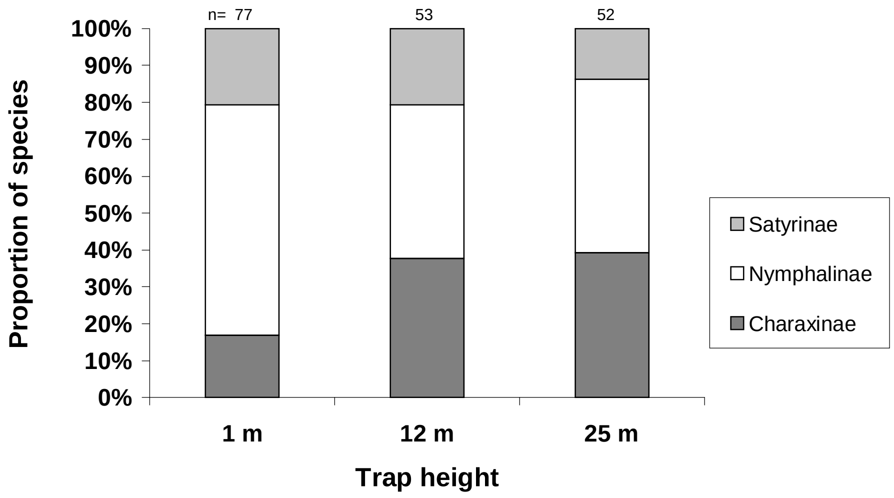


Figure 16: Proportion of Nymphalidae species per subfamily baited in three different trap heights during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

Patterns in species. To characterise the patterns of vertical stratification on species level, species abundance of species baited in six individuals and more was correlated with trap height. Six different groups could be separated:

- True understorey species:

33 species in total were classified as true understorey species. Most of them were exclusively baited at trap height 1 m or showed a strong significantly negative correlation (Spearman-rank correlation coefficient r_s<-0.6, N = 12, p < 0.05 in all cases) between abundance and trap height. These were: *Bicyclus vulgaris*, *B. sambulos*, *B. martius*, *B. zinebi*, *B. dorothea*, *B. procora*, *B. sandace*, *Euphaedra xypete*, *E. eburnensis*, *E. gausape*, *E. harpalyce*, *E. janetta*, *E. medon*, *E. ceres*, *E. crockeri*, *E. phaetusa*, *Euriphene simplex*, *E. gambiae*, *E. barombina*, *Bebearia cocalia*, *B. zonara*, *B. sophus*, *B. mandinga*, *B. abesa*, *B. absolon*, *B. tentyris*, *B. demetra*, *B. oxione*, *Aterica galene* and *Harma theobene*.

- True canopy species:

The following eight species were classified as true canopy species. They all showed a strong, significantly positive correlation (Spearman-rank correlation coefficient r_s >0.6, N = 12, p < 0.05 in all cases) between abundance and trap height: *Charaxes lucretius*, *C. eupale*, *C. cedreatis*, *C. etheocles*, *C. anticlea*, *Euryphura chalcis*, *Cymothoe caenis* and *Pseudacrea lucretia*.

- Understorey/midstorey species:

In this third group, species were classified which were equally abundant at trap height 1 m and 12 m, but significantly less abundant or abscent at trap height 25 m. They all showed a modest, significantly negative correlation between trap height and abundance (Spearman-rank correlation coefficient $r_s > -0.6$, $N = 12$ and $p < 0.05$). These were: *Charaxes protoclea*, *Cymothoe aubergeri*, *C. egesta*, *Hypolimnas salmacis*, *Gnophodes betsimena*, *G. chelys* and *Bicyclus xeneas*.

- Midstorey species:

Two species were classified as true midstorey species. A significant higher abundance was found at trap height 12 m compared to both other trap heights 1 m and 25 m (χ^2-test, $\chi^2_{2df} > 6.00$ and $p<0.05$): *Charaxes zingha* and *C. cynthia*.

- Midstorey/canopy species:

In this fifth group, species were classified which were equally abundant at trap height 12 m and 25 m, but significantly less abundant or abscent at trap height 1 m. They all showed a modest, significantly positive correlation between trap height and abundance (Spearman-rank correlation coefficient $r_s < 0.6$ and $p < 0.05$). These were: *Charaxes pleione*, *C. virilis*, *C. tiridates*, *C. bipunctatus*

- Species for which no clear stratification pattern could be detected:

For 4 species in total, no clear stratification pattern was found. They were baited equally abundant at all trap heights: *Euphaedra sarcoptera*, *E. cyparissa*, *Bicyclus abnormis*, *Melanitis leda*.

5.4.2.2 Differences between management plots

The abundance distribution of higher strata species differed along the vertical trap height between the control and the thinned forest (see Table 17). *Charaxes* species, most of them inhabitants of the forest canopy and only coming downward to feed at baits in the understorey (Larsen 1991, 1996b, 1999), showed a significant difference in vertical abundance distribution between forest plots. They were more abundant at trap height 1 m and 12 m, but less abundant at trap height 25 m in the thinned compared to the control forest (cross-tables, $\chi^2_{2df} = 63.52$, $p < 0.000$). For the species *Cymothoe caenis* (the Common Migrant Glider), equally flying at higher vertical levels in the forest (Larsen 1999, DeVries 2001), a similar trend was found. *Cymothoe caenis* was absent at trap height 1 m in both plots, however, the species was significantly more abundant at trap height 12 m than at trap height 25 m in the thinned compared to the control plot (cross-tables, $\chi^2_{2df} = 69.66$, $p < 0.000$). Although comparing data from lower trap levels only might indicate the opposite (see also Fermon *et al*. 2000), abundance data from all vertical trap levels pooled reveal a higher abundance of *Charaxes* spp. in the control site ($\chi^2_{1df} = 4.03$, $p < 0.04$). *Charaxes* spp. were even three times as abundant in canopy traps of the control compared to those of the thinned forest.

Table 17: Numbers of individuals captured in banana baited traps installed in three different height levels (1 m, 12 m and 25 m, q = 68) in a regenerating forest (control), a thinned forest on a 75 ha study site of the Bossematié Forest Reserve, Côte d'Ivoire.

	Charaxes spp.		*Cymothoe caenis*	
	control	**thinned**	**control**	**thinned**
understorey	23	70	0	0
midstorey	107	112	8	23
Canopy	144	47	16	6

As expected, species most abundant in understorey traps (see 5.4.2.1) did not show any difference in abundance distribution along the three trap heights between forest plots (cross-tables, $\chi^2{}_{2df} < 2.029$, $p < 0.05$ in all cases). However, comparable to the results of understorey fruit trapping during the dry and the wet season 1996, differences in relative abundance between the control and the thinned forest were present at understorey level for several species during the wet season 1997. *Euphaedra crockeri*, *E. phaetusa*, *E. harpalyce*, *Euriphene barombina*, *E. gambiae*, *Bebearia absolon* and *B. sophus* were all more abundant at trap height 1 m in the regenerating control forest (Mann-Whitney *U*-test, $Z > 2.07$ and $p < 0.05$ in all cases). One *Charaxes* species, *C. cynthia*, was more abundant in traps at 1 m height of the thinned compared to the control plot (Mann-Whitney *U*-test, $Z = - 2.28$ and $p = 0.02$). For the species *Bicyclus abnormis,* found equally abundant in traps of all three vertical strata, the highest abundance was again found in traps of the control compared to the thinned plot at any trap height ($\chi^2{}_{2df} > 6.23$, $p < 0.01$ in all 3 cases).

Also at trap height 12 m and 25 m, significant differences in capture frequencies between control and thinned were found. The species *Charaxes etheocles, C. anticlea* and *C. bipunctatus* were more abundant in 12 m and 25 m traps of the control forest ($\chi^2{}_{2df} > 4.76$, $p < 0.03$ in all cases). For no other *Charaxes* species, however, significant differences between forest plots could be found at higher trap levels ($\chi^2{}_{2df} < 2.55$, $p < 0.05$ in all cases). For all trap heights 25 m pooled, the species *Cymothoe caenis* also showed a significantly higher abundance in the control than the thinned forest ($\chi^2{}_{2df} = 13.37$, $p = 0.0003$). One more nymphalid species, *Pseudacraea lucretia,* was also significantly more abundant in 25 m traps of the control compared to the thinned forest ($\chi^2{}_{2df} = 4.75$, $p = 0.03$).

5.4.3 Walk-and-capture

5.4.3.1 General

On the six 1 km transects walked during 28 days in the wet season 1997, an average of 13.6 individuals per two hours belonging to a total of 52 species were captured (Figure 17). The size of the total species pool on the six transects is estimated at ACE = 68.0 ± 0.0 and ICE = 71. 4 ± 0.0 species.

The subfamily Nymphalinae were clearly dominant, constituting 73 % of the total of 367 butterflies and 92 % of all species encountered. The Satyrinae only represented 7 % of the total abundance and 23 % of the total species spectrum. The subfamily Pierinae consituted 1 % and 4 % of all captured individuals and species, respectively. The families Papilionidae, Lycaenidae and Hesperiidae, as well as the nymphalid subfamilies Danainae, Acraeinae, Libytheinae, Apaturinae and Charaxinae and the pierid subfamilies Pseudopontinae and Coliadinae were never netted during transect walks.

Species of the genus *Bebearia* were most frequently netted on the six transects and constitute 51 % and 19 % of the total abundance and species number respectively. Second most abundant were the genera *Euriphene* (13 %) and *Euphaedra* (11 %), followed by the genus *Catuna* (8 %). The *Bicyclus* only represented 5 % of the total butterfly abundance netted, however, they constituted with 17 % the second most species-rich genus (Figure 17).

Only 10 of the 52 species were represented by more than 10 individuals, all belonging to the Nymphalinae subfamily. The most abundant species was *Bebearia tentyris* (95 individuals), followed by *Euriphene barombina*, *Bebearia absolon*, *Bebearia zonara* and *Euphaedra crockeri* (between 30 and 22 individuals), *Euphaedra phaetusa*, *Bebearia mandinga*, *Euriphene gambiae*, *Bebearia abesa* and *Catuna angustata* (between 14 and 11 individuals). The proportion of rare species (< 5 captured individuals), 69.2 %, was very large.

The rank-abundance pattern for the netted butterfly community during the wet season 1997 did not differ significantly from a (truncated) log-normal (χ^2 Goodness of fit tests, $\chi^2_{14df} = 3.0606$, $p < 0.9$), nor from a log-series distribution (χ^2 Goodness of fit tests, $\chi^2_{10df} = 3.1052$, $p < 0.9$). As expected from the species dominance pattern, the mean Simpson diversity index of all transect data pooled was rather low (10.7 ± 0.0), whereas Fisher's alpha was relatively higher (16.1 ± 1.4).

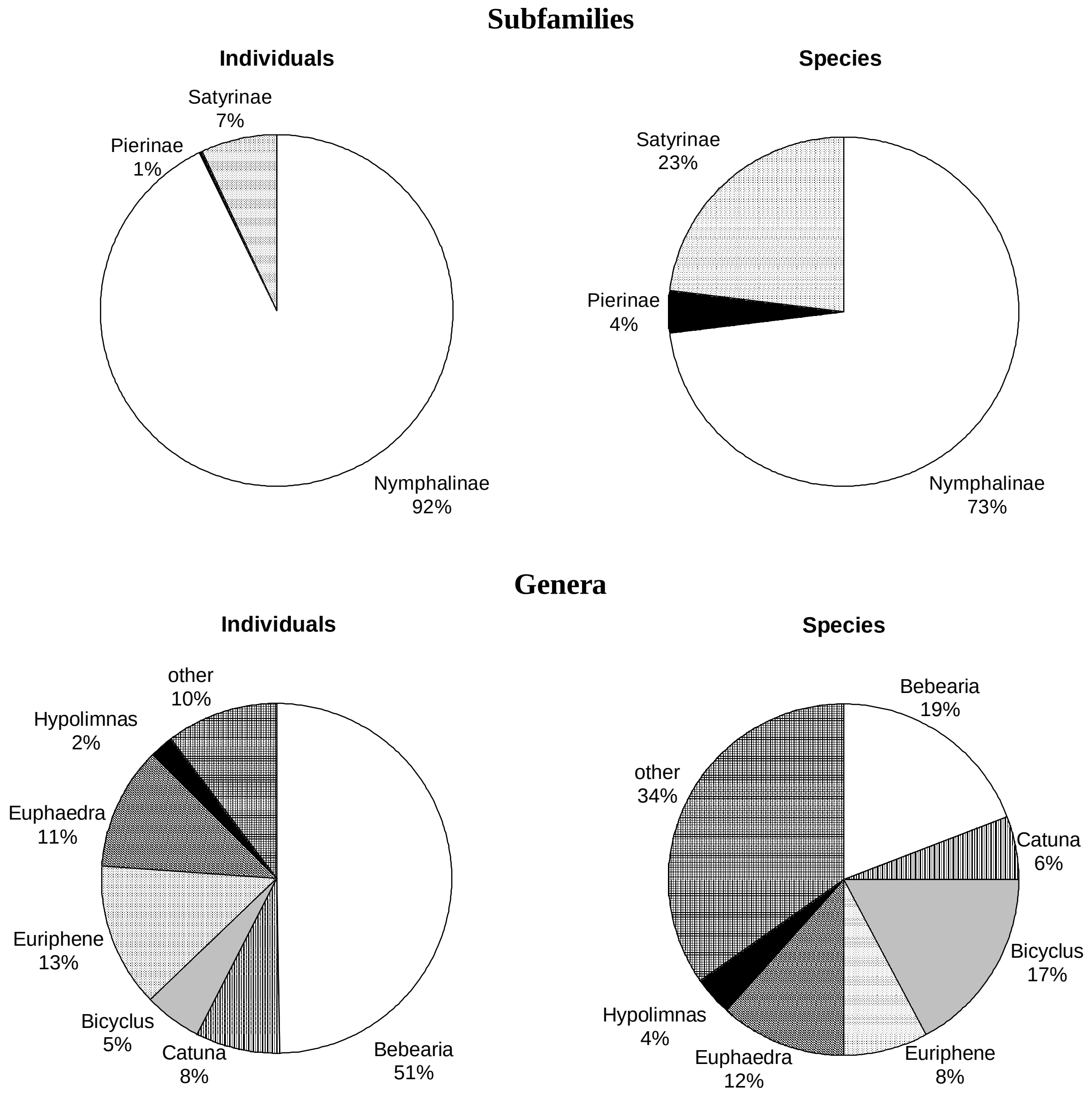


Figure 17: Procentual distribution of butterfly individuals and species per subfamily and genus on a total of six 1 km transects during 28 capture days in the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

5.4.3.2 Differences between management plots

During the wet season 1997, the impact of the thinning operations was assessed by walk-and-capture on a total of six 1 km transects during 56 hrs each. Three transects were situated in the regenerating forest (control) and three in the thinned forest.

No significant difference was found in average number of butterfly individuals, species, alpha diversity (Simpson index) or Evenness per sample between the control and the thinned forest (Mann-Whitney *U*-test with 29 samples, $Z < 1.27$ and $p > 0.2$ in all cases). Equally, no differences in species richness, diversity indices or estimators of total species richness were visible using Colwell's (1997) accumulation curves.

Abundances were significantly higher in the control compared to the thinned area for the genera *Euphaedra*, *Euriphene*, *Bebearia* and *Catuna* (χ^2-tests, $\chi^2_{1df} > 6.75$, $p > 0.01$ in all cases). On the species level, a significantly higher abundance in control was found for *Euphaedra crockeri* (χ^2-tests, $\chi^2_{1df} = 14.72$, $p = 0.0001$), *Euriphene barombina* (χ^2-tests, $\chi^2_{1df} = 4.80$, $p = 0.02$) and *Catuna angustatum* (Fisher's exact test, $p < 0.01$). For one single species, *Aterica galena*, the abundance was significantly higher in traps of the thinned compared to the control forest (Fisher's exact test, $p < 0.05$).

5.4.3.3 Walk-and-capture* vs*. fruit trapping

In the analysis of differences between walk-and-capture and fruit trapping, data from the wet season 1997 were considered exclusively, and only walk-and-capture data from the 4 transects where fruit trapping was done were included.

The comparison of walk-and-capture and fruit trapping at understorey level shows a similar α-diversity and only slightly different Evenness in both species assemblages. The walk-and-capture data pooled after 28 sampling days (sampling during both 1 hour in the morning and afternoon) reveal an α-diversity of 16.11 ± 1.44 and an Evenness of 0.21 ± 0.00. Fruit trapping data from traps installed in the understorey during the same sampling period and equally pooled after 28 trap days indicate an α-diversity of 17.71 ± 1.51 and an Evenness of 0.29 ± 0.05. Fruit trapping data from higher vertical strata still indicate a comparable α-diversity between the walk-and-capture and both midstorey and canopy species assemblages, however, Evenness is found to be significantly larger for the species spectrum baited at higher strata than those baited and netted at understorey level (Table 18).

Of the total species spectrum baited, 37 species were equally recorded by walk-and-capture. This means that 36 % of the species recorded by fruit trapping were also found by walk-and-capture. Within the four Nymphalidae subfamilies Nymphalinae, Satyrinae, Charaxinae and Apaturinae recorded by fruit trapping, the following percentage of species can also be detected by walk-and-capture: Nymphalinae 46 %, Satyrinae 53 %, Charaxinae and Apaturinae both 0 %. Considering the DICE-index, which takes into account methodical differences of the census and variation in sample size, a similarity of 0.71 is found between the species assemblages recorded by walk-and-capture and fruit trapping in the understorey. The DICE similarity between the walk-and-capture data and the fruit trapping data, however, decreases with trap height. Similarity between the netted and the baited butterfly species assemblage found in the midstorey and the canopy amounts to 0.35 and 0.31 respectively (Table 19).

Table 18: Total number of individuals (I) and species (S), and diversity parameters of the butterfly assemblages found on six transects with two different sampling methods during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire. Diversity indices calculated for q = 28 sampling days x 2 hrs for walk-and-capture and q = 28 sampling days x 24 hrs for fruit trapping using EstimateS 5 (Colwell 1997). Evenness (E) calculated as E = D / S.

	WALK-AND-CAPTURE	FRUIT TRAPPING			
		UNDERSTOR	MIDSTOREY	CANOPY	COMBINED
Individuals (I)	305	406	107	118	450
Species (S)	52	56	32	31	70
Fisher's alpha	16.11 (±1.44)	17.71(±1.51)	16.03 (±2.49)	14.23 (±2.10)	23.44 (±1.87)
Evenness	0.21 (±0.00)	0.29 (±0.05)	0.53 (±0.10)	0.44 (±0.10)	0.37 (±0.06)

Table 19: Number of shared species and similarity values, using the DICE association index, of butterfly species assemblages found between walk-and-capture transects and bait trapping in the understorey, midstorey, canopy and the three elevation heights combined in the over-logged Bossematié Forest, Côte d'Ivoire.

	SHARED SPECIES	DICE-INDEX
UNDERSTOREY (1 M)	34	0.71
MIDSTOREY (12 M)	17	0.35
CANOPY (> 25 M)	15	0.31
COMBINED	37	0.77

Already on family level, we can see a shift in sex ratio for the baited nymphalids. In all seasons, males appeared significantly more often in the fruit-baited traps than females ($\chi^2_{1df} = 78.64$, $p < 0.000$). Although less pronounced and only nearly significant, the species spectrum recorded during walk-and-capture was also dominated by males compared to females. For the nymphalid species spectrum recorded by fruit trapping, a sex ratio males to females of 1.24:1 was found, whereas the walk-and-capture data revealed a males to females ratio of 1.16:1.

The analysis on subfamily level indicates a significant shift in sex ratio in favour of males for the baited Nymphalinae, Charaxinae and Satyrinae ($\chi^2_{1df} > 12.31$, $p < 0.000$ in all cases). The disproportion in captured males to females is largest for the Nymphalinae but smallest for the Satyrinae recorded by baiting (male:female ratio = 1.34:1 for the Nymphalinae and 1.14:1 for the Satyrinae) and walk-and-capture (1.17:1 for the Nymphalinae and 1.08:1 for the Satyrinae). For the Pierinae, only males were recorded during walk-and-capture, but their abundance was too small to permit comparison.

Comparing the abundance of sexes on species level, we find a large spectrum of different sex ratios. In most of the baited species, males were baited more frequently than females. This difference was significant for 20 species in total: *Bebearia abesa* (male:female = 2.22:1), *B. mandinga* (2.3:1), *B. tentyris* (1.7:1), *B. zonara* (1.9:1), *Pseudacrea lucretia*, *Bicyclus abnormis* (3.9:1), *B. dorothea* (1.3:1), *Charaxes bipunctatus* (1.7:1), *C. castor* (8:0), *C. etheocles* (6.1:1), *C. eupale* (8:0), *C. lucretius* (7.5:1), *C. protoclea* (1.4:1), *Cymothoe aubergeri* (3.3:1), *Harma theobene* (5:1), *Euphaedra crockeri* (1.9:2), *E. cyparissa* (2.3:1), *E. phaetusa* (1.6:1), *Euryphura chalcis* (1.9:1) and

Euriphene simplex (4.3:1), (χ^2_{1df} > 4.17, $p < 0.04$ in all cases). In two species only, females were significantly more abundant in traps than males: *Bicyclus martius* (1:3.4) and *Charaxes tiridates* (1:1.9).

Although males of most species were also more frequently recorded compared to females during walk-and-capture, data do not reveal significant difference. A near significant result was found for the Nymphalinae species *Euriphene barombina*, for which a male:female ratio of 2:1 was found ($\chi^2_{1df} = 3.33$, $p = 0.07$). The distribution of the baited males and females over the different vertical strata indicates that, for the entire Nymphalidae species spectrum, males were significantly more frequent in the higher compared to the lower strata, whereas females were more frequent in the understorey compared to the canopy (cross-tables, $\chi^2_{2df} = 10.03$, $p = 0.01$). This trend, (more males higher up, more females further down) is also visible for two of the three baited Nymphalidae subfamilies: the Charaxinae and the Satyrinae (Figure 18). Charaxinae males were slightly more abundant (or females less abundant) in the upper compared to the lower strata, but no significant difference was found (cross-tables, $\chi^2_{2df} = 1.88$, $p = 0.4$). In the Satyrinae, a similar trend was visible and nearly significant (cross-tables, $\chi^2_{2df} = 4.89$, $p = 0.09$). For the Nymphalinae, however, both males and females were equally distributed over the different vertical strata.

For 30 species, the abundance of both males and females was large enough to permit a comparison between different strata. Since 7 species were only baited in the understorey for both males and females, differences can only be expected in 23 species. However, the comparison of the distribution of males and females did not reveal significant results for any of these. For two species, *Bicyclus xeneas* and *Charaxes tiridates*, only a near significant trend (more males higher up, more females further down) was found (cross-tables, $\chi^2_{2df} < 4.45$, $p > 0.1$).

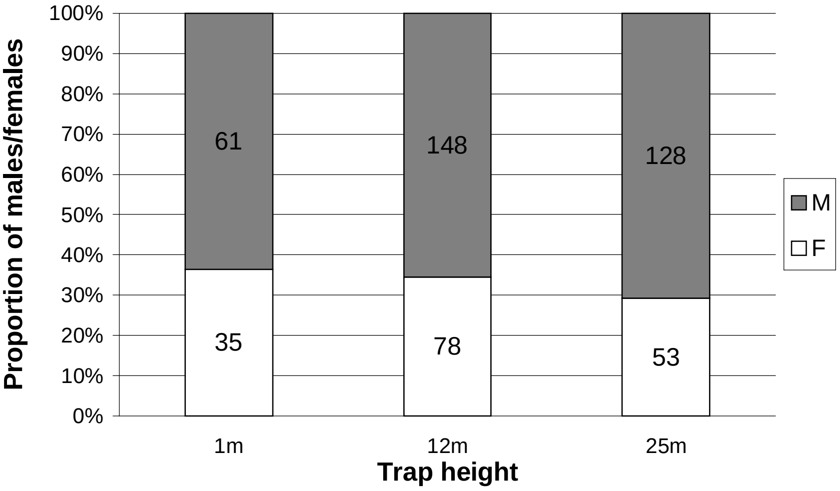


Figure 18: Comparison of the proportion of Nymphalidae males to females baited at three different trap heights during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

The comparison of the number of butterflies obtained by fruit trapping *vs.* walk-and-capture indicates that differences in butterfly abundance found between the control and the thinned forest are consistent between methods. Genera, as well as species, which were baited more frequently in either the control or the thinned area were also encountered more frequently during walk-and-captures in that patricular forest plot (Table 20). However, although similar patterns can be detected in most genera or species, both methods do reveal complementary information. Species of the genus *Catuna*, for instance, were baited much less frequently than netted during the same study period and, although trends were comparable, significant differences in abundance of *Catuna* spp. between the forest plots could only be detected by walk-and-capture. On the other hand, no *Charaxes* spp. was ever netted during the 28 days of walk-and-capture, whereas they did enter the banana baited traps in high numbers. Furthermore, fruit trapping at higher vertical strata reveal additional trends which remain undetected by walk-and-capture. Although equally abundant on transects of the control and thinned area, fruit traping at higher levels did reveal significant differences in abundance between forest plots for both the *Cymothoe* spp. and *Pseudacrea* spp.

Table 21 shows the DICE association index between the walk-and-capture and the fruit trapping methods. In every comparison made between the similarity of butterfly assemblages found using walk-and-capture and fruit trapping in different heights, the greater similarity values were found in the thinned rather than the control forest and in the understorey rather than the canopy (Table 21).

Table 20: Number of Nymphalidae butterflies baited in the understorey (q = 4 traps and 17 sampling days, trap height = 1m) and higher strata (q = 8 traps and 17 sampling days, trap heights 12 m and 25 m) compared to the number of butterflies obtained by walk-and-capture (q = 6 * 1 km transects and 56 walking hrs) during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

	FRUIT TRAPPING IN THE UNDERSTOREY		**FRUIT TRAPPING AT HIGHER STRATA**		**WALK-AND-CAPTURE**	
	CONTROL	THINNED	CONTROL	THINNED	CONTROL	THINNED
BEBEARIA	376	64	8	2	105	68
BICYCLUS	136	103	45	16	9	6
CATUNA	4	1	0	0	25	4
CHARAXES	23	70	251	159	0	0
EUPHAEDRA	256	100	18	26	32	10
EURIPHENE	91	6	0	0	33	15
CYMOTHOE	10	9	49	22	2	2
PSEUDACREA	1	1	16	7	1	1

Table 21: Similarity values, using the DICE association index, of butterfly species assemblages found between walk-and-capture transects and bait trapping at 1m, 12m and 25m height and the three elevation heights combined in the over-logged Bossematié Forest, Côte d'Ivoire.

	CONTROL	**THINNED**
FRUIT TRAPS AT 1M	0.65	0.81
FRUIT TRAPS AT 12M	0.24	0.29
FRUIT TRAPS AT 25 M	0.19	0.20
ALL HEIGHTS COMBINED	0.70	0.84

5.4.4 Point distance sampling

During the wet season 1997, point distance sampling was done at 40 random points situated in the regenerating forest (control) and the thinned forest to obtain densities of selected butterflies on genus and species level. Since Distance Sampling does not attract the species and allows for compensation of differences in detectabilities between habitats, the method has been selected to complement other abundance data. In total, observations were sufficient for the three genera: *Bebearia* spp. ($n_{thinned}$ = 71, $n_{control}$ = 196) , *Euphaedra* spp. ($n_{thinned}$ = 9, $n_{control}$ = 38) and *Euriphene* spp. ($n_{thinned}$ = 11, $n_{control}$ = 35) (Table 22). All three genera belong to the forest understorey butterfly fauna, and highest densities as well as encounter rates were found in the control compared to the thinned forest. On species level, reliable results on densities were obtained for *Bebearia tentyris* ($n_{thinned}$ = 30, $n_{control}$ = 112) and *Euriphene barombina* ($n_{thinned}$ = 10, $n_{control}$ = 19 observations). For both, encounter rates and densities were higher in the control plot. Densities of *Bebearia tentyris* (95 % confidence interval) were calculated reaching 388 - 1,373 individuals / hectare for the thinned (% CV = 22, df = 15), and 2,936 - 7,603 individuals / hectare in control (% CV = 17, df = 23). *Euriphene barombina* densities were only slightly higher in the control reaching 436 - 2,290 individuals / hectare (% CV = 43, df = 36) opposed to 59 - 572 (% CV = 59, df = 20) in the thinned forest.

Point distance sampling data on the three selected nymphalid genera and the above mentioned species all confirm results found during walk-and-capture as well as fruit trapping. None of the three methods produced contradictory trends in habitat preference, underlining the validity of fruit trapping as an unbiased sampling method. Furthermore, in the case of a high general abundance (e.g. as in *Bebearia* spp.), fruit trapping most probably reflects the actual numbers more acurately than walk-and-capture. Point distance sampling indicates relevant differences in the proportion of individuals detected (p) between forest plots: in all analysis, p was higher in the thinned than control forest (see Appendix 6). The actual differences in abundance obtained through direct observations therefore are less pronounced than they should be without this “detectability bias”. Fruit trapping indeed indicated more pronounced differences in abundance between forest plots (see Table 20).

Table 22: Densities (individuals per hectare) of three Nymphalidae genera obtained by point distance sampling compared to the capture frequencies obtained by fruit trapping at understorey level during the wet season 1997 in the over-logged Bossematié Forest, Côte d'Ivoire.

	FRUIT TRAPPING		**POINT DISTANCE SAMPLING (95 % CONFIDENCE INTERVAL)**	
	CONTROL	THINNED	CONTROL	THINNED
BEBEARIA	376	64	5,433 – 12,386	1,513 - 5,270
EUPHAEDRA	256	100	306 - 1,275	19 - 288
EURIPHENE	91	6	730 - 3,079	82 - 653

6. DISCUSSION

6.1. Composition of the Bossematié's butterfly fauna

6.1.1 General

Until now, no published butterfly records were available for the Bossematié Forest Reserve. Apart from the under-representation of both the Lycaenidae and Hesperiidae in the species list (Appendix 4), the overall butterfly species composition found in the Bossematié Forest is quite similar to the butterfly community described by Larsen and Dall'Asta (1996) and Larsen (1999) for the less than 30 km distant *c.* 22,000 ha large Bia Reserve in Ghana. Situated in the same vegetation belt and biogeographic area, the moist semi-deciduous Bia Forest can be regarded as a reference area and allows faunal comparisons. However, the Bia Reserve has equally been subject to intensive logging operations in the past (Hawthorne 1993), and does not represent a large unfragmented and unlogged forest area. 263 species were recorded during our study in the Bossematié Reserve, and the maximum estimated species number is 500, 100 less than the estimated 600 butterfly species assumed to be present in the Bia Reserve (Larsen 1999, pers. comm.). One nymphalid species, *Bebearia dallastai*, has been discovered only recently as new species and is endemic to the Bossematié area (Larsen and Dall'Asta 1994). The majority of the butterfly species recorded in the Bossematié are true rainforest species, and data suggest that there is almost no faunal change at all (Fermon *et al.* 2000), e.g. by an increase of savannah forms, which only constitute 2.6 % of the fauna. These findings are in line with results found on the bird community of the Bossematié Forest Reserve. A comparison of the bird community between the Bia and Bossematié forests did also not reveal any important difference in species composition (Waltert 2000b). However, 4 butterfly species characteristic of mature forests and collected quite frequently at Bia were never observed in the Bossematié Forest Reserve: *Pentila hewitsoni* (Lycaenidae), *Katreus hollandi*, *Calleagris lacteus* and *Sarangese tricerata* (Hesperiidae). As equally discussed by Larsen and Dall'Asta (1994), it seems probable that, although a significant number of true forest species are still able to survive locally in the less disturbed forest parts of the Bossematié, a large number of specialised forest species might already have entirely disappeared from the region.

6.1.2 The nymphalid community

A total of 123 nymphalid species were recorded during the present study. Most African butterfly species tend to be restricted to one or a limited number of ecological zones and are found in specific habitats (Larsen 1995a). 119 of the 123 nymphalid species trapped belong to the African rainforest zone, with 65 species present in all forest types (ALF), 28 species concentrated in moist evergreen forest (MEF), 18 in wet evergreen forest (WEF) and eight in dry forest (DRF). Only two species are classified as Guinea savannah centred (GUI) and another two are ubiquitous (UBQ) (Larsen 1994b, Emmel and Larsen 1997, Larsen 1999, see Appendix 1). Species dominance structure and composition are different from those reported by Condamin and Vuattoux (1972) for *Bicyclus* observed at Lamto, Côte d'Ivoire. Lamto is situated in the Guinea Savannah, on the border of the forest zone with stretches of riverine and transitional forest; 60 % of the total *Bicyclus* specimens collected (between 1962 and 1969) are strictly savannah species not present in our samples. However, the Bossematié butterfly community might be more similar to the fauna in Freetown gardens (Sierra Leone), where *Charaxes* have been studied (Owen and Chanter 1972). There was a large species overlap of 18 *Charaxes* species between Freetown and the Bossematié plots. Only eight of 26 *Charaxes* species caught in Freetown were not trapped on our study site, but six of these were savannah species and the remaining two are forest species which are everywhere very rare (Larsen 1999). Four of five common *Charaxes* species at Freetown were rare in our samples. However, these species also showed a lower abundance during one or both dry season sampling periods reported in Owen and Chanter (1972).

6.1.3 The nymphalid community of a nearby remnant forest fragment

The most characteristic difference in species composition between the 6 ha forest fragment and a similar sized plot within the Bossematié Forest Reserve was the clear shift in species dominance structure. Whereas samples from the forest fragment were dominated by species of the subfamily Satyrinae, simultaneous sampling inside (a 6 ha plot of) the Bossematié Forest revealed the Nymphalinae as dominant subfamily. In the forest fragment, both Nymphalinae and Charaxinae only constituted but a small proportion of the total abundance of the fruit-feeding butterflies. Satyrinae generally feed on grasses and, in contrast to many of the relatively more specialised Nymphalinae understorey species, they should be more capable of dispersing into the matrix of the cultural landscape. For many Nymphalinae species, several of them feeding on plant species of a mature forest understorey (Larsen 1999), this matrix might constitute a real barrier (Fermon *et al.* 2000). Consequently, species similarity between both sampling locations was very low.

Species richness and diversity also differed significantly between the Bossematié and the forest fragment. For the forest fragment, overall species richness was only estimated being half of the overall species richness found for a similar sized study plot in the Bossematié Forest. Although published comparisons of butterfly diversity between ecologically similar forests of different size are lacking, the lower overall species richness and diversity parameters found in the forest fragment are in accordance with general theories on the species-area relationship (MacArthur and Wilson 1964). The Bossematié Forest itself represents a small "leftover" fragment compared to the once unbroken Upper Guinean forest block. Although biodiversity studies, especially in the aftrotropics, started only recently and comparative data from original forest faunas are not available, species losses must already have been enormous. A 90 % loss in habitat is estimated to imply a 50 % loss in original species (Primack 2000). In this study, the small fragment only represented 1 % of the

22,000 ha Bossematié Forest, and a 50 % loss in species was estimated. The findings correspond with those in Rogo and Odulaja (2001), who investigated two small coastal forest remnants near the Arabuko-Sokoke Forest Reserve in Kenya.

6.2 Patterns of nymphalid abundance and diversity

Most striking when analysing results on nymphalid abundance found for the 75 ha study site in the Bossematié Forest is the extremely high daily number of butterfly individuals baited per trap. On average, 8.3 nymphalid butterflies were baited per day and trap during the total study period in both years. These very high abundance of the fruit-feeding butterflies species still present in the over-logged Bossematié Reserve can be explained by the overall secondary status of the vegetation, and contrasts with the comparatively low abundance reported by several authors for natural or undisturbed forest plots in other tropical regions. Schulze (1995) found an average number of fruit-feeding nymphalids between 0.5 and 1.2 per day and trap in a natural forest plot in the lowland region of Mount Kinabalu (East-Malaysia). During a 5-years sampling period in intact floodplain forest without any signs of human disturbance at the La Selva Lodge (Ecuador), Devries and Walla (2001) found an average number of baited nymphalids per day and per trap of 0.8. Hill *et al*. (2001) found an equally low nymphalid capture rate of 0.9 individuals per trap day in an unlogged forest plot in Sabah (Malaysia). A somewhat higher average capture rate of 2.9 nymphalids was reported by Shahabuddin and Terborgh (1999), from a set of forested islands in Venezuela. Comparable findings were reported for birds equally sampled in the Bossematié Forest Reserve on the same study site. Although several endemic birds were reported absent, Waltert (2000a) found a much higher overall understorey bird density in the heavily logged Bossematié Forest in comparison to values illustrated in bird studies in primary or natural forest plots.

Although direct comparisons are lacking, it is very likely that those butterfly species less vulnerable to habitat disturbance show considerably increased densities in the Bossematié study site in comparison to unbroken (or less disturbed) African rainforests. In contrast to the very high overall abundance of fruit-feeding butterflies, the abundance in several more specialised species typical of the forest understorey community, especially within the genera *Euriphene* and *Euphaedra,* were rather low. The Upper Guinea endemics *Euphaedra laguerrei*, *E. perseis, E. modesta* and *E. eupalus*, for example, were only baited in one, four, six and eight specimens respectively on a total of 996 trap days in both years. Both *E. modesta* and *E. perseis* are known as “present in mature, undisturbed forest but generally rather scarce” (Larsen 1999), however, both *E. laguerrei* and *E. eupalus* are classified as common and abundant by the same author. At least for these two more specialised nymphalid species, the present study might already indicate a serious decline in abundance.

As found for the majority of natural communities, the log-normal distribution, characteristic of a large, mature and varied community (Magurran 1988), seemed to be the best fit for the nymphalid community sampled on the 75 ha study site of the Bossematié Forest. This finding is somewhat contradictory to those in Hill *et al*. (1995), where log-series were found to be the best fit for the butterfly community of a disturbed forest plot, whereas log-normal best fitted the community of an unlogged plot in Buru, Indonesia. DeVries and Walla (2001) also found the sampled nymphalid community of an undisturbed forest site in Equador to be best fitted by a log-normal distribution. However, Willott *et al*. (2000) did not find any difference in rank-abundance patterns between a disturbed and a primary forest plot in Borneo, reporting a log-normal-like distribution for both. In the second year of the study, both the log-series and log-normal fitted the data. Lewis (2000) equally found both log-series and log-normal to fit the nymphalid community of both a logged and an unlogged forest site in Belize. Unfortunately, until present no comparable butterfly diversity studies have been made in Afrotropical forests.

Comparing the overall butterfly richness estimated for the Bossematié Forest to estimations made for forests in the same vegetation belt (data documented in Larsen 1999), we can carefully conclude that the species richness of the Bossematié might be similar to that from the equally large Bia and Kakum Forests in Ghana. The same can be concluded when comparing the Bossematié's nymphalid species list to a species list developed by Prof. J. Bossart from fruit trapping activities in Kakum National Park, Ghana (for a comparison of species lists, see http://bossart.intrasun.tcnj.edu/Ghana/SpeciesChecklists.htm). The Kakum National Park is an impressive example of largely intact forest, and although overall species numbers might be similar to those found in the Bossematié Forest, several of the more specialised forest floor species present at Kakum were not observed in the Bossematié Forest.

A (rough) comparison with the baited butterfly community of a Central American rainforest (DeVries 1988), indicates strong differences in species richness. DeVries (1988) baited a total of 46 species in 10 canopy and understorey traps, whereas on the Bossematié study site, a total of 103 species was baited in 12 traps installed at different heights in the wet season 1997. The Nymphalidae of Costa Rica are represented by 356 species in total (after DeVries 1987), a comparable number of 320 nymphalids are listed on a provisional checklist of the butterflies of Ghana and of Africa West of the Dahomey Gap (Larsen 1994b). However, contrary to the present study, DeVries (1988) did not sample at midstorey level, which could partly explain the lower species richness. Schulze (1995) baited a total of 53 species in 12 traps during his two years trapping study at different vertical heights in Poring (Malaysia). Nymphalid species diversity of the West African secondary Bossematié Forest seems to be much higher, compared to both more undisturbed rainforests in Central American and especially in Borneo. It should be considered, that geographical and climatic barriers have enabled the development of more or less distinct, regional West African faunas. On Borneo, geographical barriers do practically not exist (Schulze 1995), therefore most species might have an island-wide distribution and there should be a relatively smaller γ-diversity in comparison to Côte d'Ivoire.

6.2.1 Findings in different seasons

In tropical environments, seasonality is primarily driven by variations in rainfall (e.g. Wolda 1978). Because timing and availability of rain exerts a major influence on plant growth and reproduction, phytophagous insects can be expected to show some adaptive behaviour, e.g. by synchronising larval feeding with food availability (Ehrlich and Raven 1964, Braby 1995). The average overall abundance in baited nymphalid individuals found during this study differed significantly between seasons and years. Average overall abundance was highest during dry compared to wet season 1996, however, highest during the wet season 1997. DeVries and Walla (2001) reported larger differences between months (in different seasons) than years for both abundance and diversity of baited nymphalids in Ecuador. The abundance structure found in this study was equally more comparable between both wet seasons in different years (1996 and 1997) than between the two seasons of the same year (1996). During the dry season, representing the late dry season during this study, the Satyrinae were most abundant, especially within the grass feeding genera *Bicyclus* and *Gnophodes*. Although the comparison dry to wet season is based on one sampling pair only, differences are very marked and suggest strong seasonal patterns. Many herbaceous plant species such as grasses frequently dry off during dry periods (e.g. Vickery 1984, Lieberman and Lieberman 1984), implying that reproductive dormancy might have occurred in the adult stage in satyrines (see also Spitzer 1983, Brakefield and Larsen 1984, Larsen 1987, Brakefield 1987). Alternatively, satyrine species may be breeding even in the unfavourable dry season by choosing more persistent food plants or specialised microhabitats where resources tend to be more predictable (Braby 1995). Braby (1995) equally indicated that tropical satyrines surpass the dry season as adults, and most breed throughout the year by selecting favourable habitats or microenvironments, a tactic which undoubtedly reflects the sedentary nature of this group of butterflies as a whole. Hill (1999) found that Satyrinae butterflies are more confined to areas with high cover of host-plants during dry conditions, whereas during wet season they are more scattered. In this study, species similarity between different forest succession stages was found to be higher during the wet compared to the dry season. This equally indicates that, under drier conditions, butterfly species might be more sedentary within their habitat of preference. During the wet season, they might be more equally distributed among different habitat types. Especially spending the late dry season as an adult within favourable habitats, either in diapause or with mature eggs, may improve the capacity to utilise new growth of grasses in a wider range of habitats at the start of the wetter season (Braby 1995). It may also provide additional flexibility to encounter the temporal uncertainty of the dry season. One satyrine species, *Bicyclus funebris*, was totally absent from wet season samples in both years, but very abundant during the dry season. *B. funebris* is classified as “a species centred on the drier forests” (e.g. Emmel and Larsen 1997). In the wetter forests, they can apparently be found during drier periods. Since adults of *B. funebris* are totally lacking in both wet seasons, it seems probable that local dispersal or migration might be the species strategy to continue breeding in more favourable conditions. Contrasting to the general trend found in most Satyrinae, two *Bicyclus* species seemed to be significantly more abundant as imago during wet than dry season. Both originally belong to the moist or wet evergreen forest regions (Emmel and Larsen 1997), and their low abundance during the late dry season might indicate that the species' imago only emerge under wetter conditions. This trend is in line with findings on the ecological composition of the baited species during either dry or wet season. Whereas dry season samples showed a very high proportion of species centred on the drier forests, species of this ecological group were practically totally absent from wet season samples and "replaced" by species centred on moist forest regions (Larsen 1991, 1994b, 1996a, 1996b, 1997, 1999, Emmel and Larsen 1997). Similar to most of the Satyrinae, the Charaxinae also showed higher abundance in dry season samples. A possible explanation could be that, since many trees were leafless during dry season sampling, it might have been more easy for the canopy flying *Charaxes* spp. to reach the understorey traps. During wet season, leaves might have somehow limited this downward movement. At Freetown, no major evidence for seasonal changes in abundance of the *Charaxes* (Nymphalidae, Charaxinae) species was found. The area experiences a heavier rainfall during the rainy season than the Bossematié area (Owen and Chanter 1972), and the dry season is less pronounced. At both Bossematié and Freetown sites, the *Charaxes* species dominance structure is comparable and more balanced compared to a savannah region in Northern Nigeria. There, a single species represents 65 % of the abundance, and seasonal fluctuation of *Charaxes* diversity and abundance is evident (Owen 1977). Being far less numerous during dry season, the subfamily Nymphalinae represented the most abundant group in the wet season samples, especially within the genera *Euphaedra*, *Bebearia* and *Euriphene*. Dormancy during dry periods have been reported for several nymphaline species (e.g. Owen 1971), and the low abundance during dry season might indicate that several nymphaline species rather survive the unfavourable conditions through diapause as non-adults. Information on seasonal variations in nymphalines from other West African forests, however, are scarce. Whereas in temperate regions, all butterfly species show marked seasonal patterns in their life cycles, seasonality in tropical butterflies is rather poorly known. Libert (1994) indicated a seasonal phenology for 23% of the 228 butterfly species collected during a seven years study at two different forest sites in Yaoundé, Cameroon.

During a six year survey of the butterfly fauna of a secondary bush locality in Southern Nigeria, Larsen (1979) found a ”lack of defined seasonality” in butterfly diversity. At Freetown, Owen and Chanter (1972) equally did not find any seasonal fluctuations in *Charaxes* diversity. However, seasonal differences in diversity were again reported by Owen (1977) for a savannah region in Northern Nigeria. This seems to confirm that seasonal fluctuations in phytophagous insects are indeed primarily linked to variations in rainfall. Regions with higher rainfall variations seem to show higher variance in butterfly diversity and abundance. During sampling in the moist semi-deciduous Bossematié Forest, seasonal differences in nymphalid diversity were also present. Within the same year, a species similarity of 53% only was found between dry and wet seasons. Accumulated nymphalid diversity indices and estimators of total species richness were significantly higher in the dry compared to the wet season 1996. These differences can be largely explained by the dominance of one *Bicyclus* species during the wet season. Accumulated diversity parameters for wet season samples from 1997, calculated after standardising sampling effort, seemed to be comparable with those found for the dry season 1996. Species richness and Simpson diversity calculated per sample (representing spot diversity), however, was highest for the wet season 1997. Samples taken during the wet season 1997 indicated a significant higher proportion of nymphalid species compared to the wet season 1996. In 1996, sampling was done during September and October, rather representing the late wet season. In 1997, sampling took place at the peak of the rainy season in June, July and August, a period which might coincide more with “population bursts” in many nymphalid species. Species similarity was generally low, however, highest between both wet seasons, lowest between the dry and wet season in different years.

As for the effectiveness of the traps themselves, it has been discussed that baiting might be more efficient during dry compared to wet seasons, which could partly explain the higher overall abundance in that season. Owen and Chanter (1972) found that most *Charaxes* spp. will not fly when the weather is overcast and wet, and traps are less effective when more fallen fruit is available as an alternative food source. On the other hand, some species are less active and more sedentary during the dry than wet season. This was found for instance for *Bicyclus safitza* by Brakefield and Reitsma (1991) in Malawi. Birket-Smith (1970) also indicated that a lower relative humidity causes inactivity in some *Euphaedra* spp.

Seasonal differences in both nymphalid abundance and diversity found during this study were evident, and since data sets were large enough to permit a separate statistically sound analysis, results were presented for each season separately.

6.2.2 Findings in different succession stages

Both nymphalid abundance and diversity indices were on average higher in fruit traps of younger and more open forest habitats than in mature succession stages. Also, accumulated species richness was highest in gap habitats, and gradually decreased with habitat maturity. Since there was no important shift in ecological composition of the Bossematié's butterfly fauna, e.g. by an increased presence of savannah butterflies (see above) in the open habitats, this increased diversity could be due to canopy species turning up in gaps rather than in mature, closed forest sites. Indeed, both the canopy flying *Charaxes* spp. and *Palla* spp. (Larsen 1999) showed a significantly higher abundance in gap and open forest habitats compared to the more closed-canopy understorey sites. Similar findings were reported by Hill *et al.* (2001), who illustrated the notion of a divers and distinctive gap butterfly fauna, comprising more widespread, mobile species. Higher butterfly abundance and/or diversity in open forest habitats were equally illustrated for tropical forests by several other authors (e.g. Sparrow *et al.* 1994, Kremen 1994, DeVries *et al.* 1997, 1999 Wood and Gillman 1998, Willott *et al.* 2000, Fermon *et al.* 2000, 2001). Species similarity between the different forest succession stages was generally high, lowest between gaps and the most mature succession stage (S3) and highest between the two eldest succession stages present on the study site (S2 and S3, see 4.1.). In addition to a high abundance of canopy flyers, gaps and open habitats were characterised by high numbers of more widespread Nymphalinae and Satyrinae species. The six nymphalines significantly more abundant in open forest sites, are all classified by Larsen (1999) as "species generally distributed in all types of forests (ALF)". The four satyrines characteristic for gaps and open habitats are classified as "species surviving in most types of forest habitats, often penetrating agricultural lands" (Larsen 1999). To the contrary, six of the nine species with a significant preference for the more closed, mature forest habitats are described as "species centred on the wetter or moist forest zones", indicating that they are more confined to a "buffered" closed forest understorey with a more stable microclimate. Especially the genera *Euphaedra* and *Euriphene* were more abundant in closed habitats. Both genera are characteristic of a mature understorey and belong to the more sensitive forest floor butterfly fauna.

6.3 Patterns of nymphalid movement

Recent studies on butterfly movement, both in tropical and temperate species, principally deal with biomechanics and kinematics of flight (e.g. Betts and Wootton 1988, Dudley 1991, Kingsolver 1999, Kingsolver and Srygley 2000), flight behaviour such as antipredator defence (Chai and Srygley 1990), territorial defence (Benson *et al.* 1989), hilltopping (e.g. Turchin *et al.* 1991), or foraging and oviposition (Thomas and Cheverton 1983). Other more recent studies on butterfly movement focus on modelling and quantifying flight patterns (Turchin *et al.* 1991, Turchin 1991), discuss the relationship between movement, landscape mosaics (Haddad 1999) and local butterfly diversity (Debinski *et al.* 2001), population size (Roland *et al.* 2000) or structure (Knutson *et al.*

1999) or illustrate the role of movement and migration for the persistence of selected butterfly species in fragmented habitats (e.g. Schultz 1996, Baguette *et al*. 2000, Gutierrez and Thomas 2000, Shahabuddin *et al*. 2000). Trapping has been done in several other studies on vertical stratification (e.g. DeVries 1988, DeVries *et al*. 1997, 1999; see also above) or effects of forest disturbance (e.g. Daily and Ehrlich 1995, Wood and Gillman 1998, Shahabuddin and Terborgh 1999, Fermon *et al*. 2000; see also above), but small-scale movements of tropical butterflies have rarely been assessed using baits (but see Lewis 2000).

The pro's and contra's of baiting in comparison to netting and other sampling methods have been extensively discussed in Daily and Ehrlich (1995) and DeVries *et al*. (1997). However, it could be that baiting biases movement patterns due to a possible "learning effect" in all or some of the butterflies species. Learning might be expected to reduce flights in species capable of memorising foraging locations (see Keller *et al*. 1966, Ehrlich and Gilbert 1973, Benson and Emmel 1973). During the movement study, we rebaited traps continuously every 48 hrs. To compensate for the eventual learning effect, a timely interruption between the sampling days, leaving traps unbaited, could be advisable. However, the matrix of 66 traps covering an area of 75 ha most might have helped avoiding butterfly aggregation at single trap locations.

We found very limited movement in *Euphaedra* species, and this mainly concerned males. Birket-Smith (1970) illustrated that a lower relative humidity can cause inactivity in some *Euphaedra* species, as might have been the case during the dry season, but did not find any sexual differences in flight behaviour. The trend of smaller movement in males was found in all of the sampled Nymphalinae (*Bebearia* spp., *Euphaedra* spp.) and Satyrinae (*Bicyclus* spp. and *Gnophodes* spp.). No differences in movement between males and females, or even a reverse trend, smaller movement in females (*Charaxes zingha*), was seen in the Charaxinae. Warren (1987) also found similar distances covered by males and females in a European Nymphalidae and reported mean adult ranges of 84 – 214 m. Lortscher *et al*. (1997) found similar movement in males and females of two European Lycaenidae and Satyridae species. Shreeve (1981) found both similar, longer or shorter flights between males and females in 20 European woodland species. Other studies reported longer flights in females compared to males (e.g. Scott 1975, Roer 1959 and Shapiro 1970 in Scott 1975). Scott (1975) related these findings to mate-locating behaviour and stated that males of both perching and patrolling species tend to be concentrated at the most favourable mating sites, while females tend to disperse more. Our movement data principally illustrate adult foraging flights. Longer flights and time intervals between two recaptures in females might also indicate that females spent less time on foraging than males.

Both *Euphaedra ceres* and *E. phaetusa* showed the shortest flights. They are generally confined to the forest understorey, and are host-specific to one or a few lower forest plants (Larsen 1991, 1996b, 1999). The largest movement parameters were found in the species *Bebearia sophus*, the larvae of which amongst others feed on *Landolphia* species of the family Apocynaceae (Larsen

1991, 1996b, 1999), characteristic of forest gaps and marginal habitats. The satyrid *Bicyclus dorothea*, feeding on Poaceae, also showed relatively large movement considering its small size. Scott (1975) equally found that single-brood species feeding as larvae on perennial trees or shrubs showed shorter flights, whereas multibrood polyphagous species feeding on early successional plants showed farthest flights. The same was reported by Shreeve (1981), who found lowest mobility in European woodland species occupying permanent habitats and highest mobility in butterfly species characteristic of disturbed habitats or with early successional larval host plants.

Movement parameters found in this study are comparable with those found in other tropical fruit-feeding butterflies ranging (with only two exceptions) between 20 m and 412 m (Lewis 2000), and fall into the flight pattern category "strong flying but relatively sedentary" characteristic of the Nymphalidae familial association (Miller 1994). Movement distances were generally small in all recorded species, a trend which has been found in other studies as well. Mobility in most non-migratory butterfly species is usually less than their possible agility (e.g. Scott 1975, Shreeve 1981). Thomas and Cheverton (1983) also found foraging flights to be very short compared to oviposition or displacement flights in *Anartia fatima*, a neotropical Nymphalinae species.

6.4 Patterns of nymphalid stratification

For tropical rainforests, differences between species communities of different strata have already been shown for many taxa, e.g. for birds (e.g. Terborgh 1980), mammals (Bourliere 1989, Whitmore 1984) and insects (Davis 1944, Basset *et al*. 2001, Birket-Smith 1956, 1960, Intachat and Holloway 2000, Sutton 1979, 1983, 1989, Sutton and Collins 1980, Wolda 1978, 1987). In contrast to most other studies on butterfly stratification (DeVries 1988, DeVries *et al*. 1999, DeVries and Walla 2001, Hill *et al*. 1992, Hill *et al*. 2001, Jackson 1961, but see Schulze 1995), this study does not only compare understorey to canopy traps, but equally considers traps installed at midstorey height levels. There were clear patterns of vertical stratification in the fruit-feeding nymphalid butterflies on the 75 ha study site.

Both the number of nymphalid species and individuals decreased with increasing trap height. This primarily reflects the availability of rotting fruits, which may be most likely to fall to the ground (Hill *et al*. 2001). The probability that rotting fruits stay high up in the vegetation decreases with vegetation height, since both vegetation density and number of fruits present per area size decline towards the canopy (see Schulze 1995). At canopy height, overall nymphalid abundance was only one fourth of that trapped in the understorey.

The decrease in species richness from understorey to canopy, however, was less important. The stronger decrease in individual numbers implies that, at the end of the gradient (i.e. canopy), where the species community reaches its minimum richness and abundance, species are generally more rare. A significant increase in proportion of rare species with trap height was actually found for the fruit-feeding nymphalid community trapped. Schulze (1995) equally found an increase in rare fruit-feeding species with stratum height, whereas for nectar-feeding species the inverse trend was shown. This indicates that, in contrary to the nectar-feeding guild, fruit-feeding butterfly species seem to be less resource-limited at lower strata than higher up.

A clear shift in species similarity could be found between understorey and midstorey traps. The single-linkage cluster clearly showed a defined understorey fruit-feeding community, different from a distinct midstorey / canopy nymphalid assemblage. The species turnover rate between the nymphalid community trapped at understorey and midstorey level was indeed large, whereas differences between both higher strata were far less important. The large species turnover between understorey and midstorey could possibly be explained by the low number of species which seem to have specialised on fruit-feeding at midstorey level only. 70 % of all species included in the analysis were either clearly limited to the understorey or to the canopy stratum and rarely surpassed these. 20 % of the fruit-feeding spectrum was equally represented in two strata (understorey and midstorey or midstorey and canopy), and 7 % did not seem to have a defined clear feeding stratum. The clear shift in species similarity of the fruit-feeding community between the different strata indicates two main groups of specialised species: forest understorey species and canopy flyers. In both groups, there were species exclusively found in the preferred stratum, a small proportion of species seem to expand their range down- or upward beyond the preferred stratum. A proper, midstorey group could not be detected, there were only two *Charaxes* species with a (weak) preference for this mid stratum (*Charaxes zingha* and *C. cynthia*).

Patterns of vertical stratification could be found on any taxonomical level analysed, from subfamily to species. Both the Nymphalinae and Satyrinae subfamilies showed a decreasing abundance and species number with trap height. However, several canopy species were not or rarely recorded in 1 m traps. Already at subfamily level, both abundance and species richness of the Charaxinae were dominant both at midstorey and canopy trap height. They were relatively uncommon at understorey trap level. These findings are in accordance with Schulze (1995), who found nymphalines and satyrines dominant at understorey and charaxines dominant at higher trap levels in a rainforest in Poring, Borneo.

True canopy species were especially found among the genus *Charaxes*, but also adults of *Euryphura chalcis*, *Pseudacrea lucretia* and *Cymothoe caenis* seemed to prefer feeding at canopy level. Except for *P. lucretia*, which was netted on one single occasion, none of these canopy species have been observed or captured during the walk-and-capture study (see Appendix 5). Also in East-Malaysia, *Charaxes* were found to be most abundant at canopy level (Schulze 1995). Typical understorey species on the 75 ha plot were found within the genera *Euphaedra*, *Euriphene*, *Bebearia*, *Bicyclus*, *Aterica* and *Harma*. Four species were equally abundant at any trap height: *Euphaedra sarcoptera*, *E. cyparissa*, *B. abnormis* and *Melanitis leda*.

The principle factors which might be responsible for vertical stratification patterns in butterflies have been discussed by several authors (e.g. DeVries 1988, Schulze 1995, Beccaloni 1997, Hill *et al*. 2001). In the following, some possible determining factors, other than fruit availability (see above) related to stratification are being discussed in the light of the patterns found on the 75 ha plot of the Bossematié Forest Reserve. In general, butterfly stratification is considered as a result of a combination of different factors, their "selective pressure" depending on the characteristics of each separate species or higher taxon. Gilbert (1984) discussed the following factors important in determining the possible niches occupied by butterfly species: microhabitat, larval hostplants (which plant taxa *resp*. parts/growth forms are used for larval development), adult resources, time and avoidance of predators.

Beccaloni (1997) studied vertical stratification of ithomiine butterflies and found adult flight height to be positively correlated with the height of their larval hostplants. Female butterflies spend most of their total flight time searching for host-plants (Benson 1978), and they probably fly at the height of their hosts because this maximises the probability of encountering plants of the correct species and growth stage. Males spend much of their time attempting to find conspecific females with which to mate. In species where females spend most of their adult life in a particular stratum, natural selection should favour males which fly in the same stratum (Beccaloni 1997). Since, with few exceptions, both species host-plant information and host-plant growth forms are not very well known (Larsen 1999 and pers. comm.), a similar correlation between host-plant height and flight height was not possible in this study. However, separate observations on adult flight and perching behaviour in several African nymphalid species do also indicate a strong connection between vertical stratification and larval host-plant height and are discussed in the following.

All host-plant seeking behaviour described for the genus *Euphaedra* did indeed never occur above the one meter level close to the forest floor (see Larsen 1991, 1996b, 1999, Hecq pers. comm.). This corresponds with the stratification pattern found for most of the *Euphaedra* species, which seem to be confined to the buffered forest floor. Two *Euphaedra*'s, however, were equally flying at all trap heights. Exclusively within the genus, both the species *E. sarcoptera* and *E. cyparissa* feed on Annonaceae, whereas all other *Euphaedra*'s are know to feed on Sapindaceae. In the Bossematié Forest Reserve, a large proportion of Annonaceae are classified as meso- and megaphanerophytes (Trees and shrubs of 5–50 m and above 50 m height, respectively), whereas within the Sapindaceae most species are classified as nano- and microphanerophytes (Trees and shrubs of 2–5 m and below 2 m height, respectively; classification after an unpublished plant species list of Prof. Dr. Stefan Porembski, University Rostock). This illustrates again that interspecific differences in vertical stratification might be related to differences in host plant use. Furthermore, both *E. sarcoptera* and *E. cyparissa* are relatively small and have very falcate forewings. Males and females in both species were frequently observed flying and perching relatively high, at three to five meters or more above the ground (Larsen 1999). The canopy flying species *Euryphura chalcis, Pseudacrea lucretia* and *Cymothoe caenis* equally show relatively falcate forewings. DeVries (1988), Schulze (1995) and

Hill *et al.* (2001) indicate changes in nymphalid phenotype with stratum height: nymphalids trapped at higher stratum levels show a smaller wing size and a more “sturdy” body shape (i.e. low body length/thorax diameter ratio). However, in the Papilionidae of a Costa Rican rainforest, the opposite was found (DeVries 1988): larger species were found more abundant at canopy level.

The exclusive use of the host plant family Poaceae by most of the Satyrinae butterflies (e.g. Corbet and Pendlebury 1992, Fiedler 1998, Larsen 1999) also illustrates the relation between butterfly stratification and host plant height. Satyrinae generally showed higher capture rates at lower trap heights, and plant species within the Poaceae family are equally most common at lower strata in the forest. For several Satyrinae species, crepuscular flights are known to occur (Larsen 1999). This behaviour could already indicate a possible adaptation to the “darker”, less sunny and cooler understorey stratum.

Charaxes mainly feed on tree species (Larsen 1999) and were equally trapped at higher strata. The canopy flying *Euryphura chalcis* is rather polyphagous, but many of the host plant records are from *Celtis* trees. *Cymothoe caenis*, found significantly more abundant at canopy height, feeds on Flacourtiaceae, a family consisting uniquely of tree and shrub species (Hutchinson and Dalziel 1972). Furthermore, *Pseudacrea lucretia*, equally classified as canopy species, feeds on members of the Sapotaceae family, representing trees, shrubs and rarely climbers (Hutchinson and Dalziel 1972).

However, oviposition habitats do not necessarily always correspond with strata visited for feeding (DeVries 1988). In Asia, many swallowtail species of higher strata seem to oviposit low down (Larsen pers. comm.), and oviposition in many canopy flying *Charaxes* species are also often seen at lower strata (Larsen 1999). DeVries (1986, 1987) found females of some rarer canopy species in a Costa Rican rainforest to oviposit on hostplants in gaps near ground level, whereas in certain understorey species, males can spend much time patrolling in the canopy. Also for many palearctic butterfly species, feeding habitats are known to differ from oviposition habitats (e.g. Ebert and Rennwald 1991a, 1991b).

DeVries (1988) suggests that differences in light regime along a vertical gradient in the forest might be the most important microclimatic factor for explaining patterns of vertical stratification in diurnal butterflies. This study also indicates a disruption of distinct stratification patterns in the thinned forest plot (see also chapter 6.7.3), characterised by a more open vegetation structure, with less changes in light intensity from canopy to forest floor (Waltert 2000a, 2000b). The canopy species of the *Charaxes* group were indeed significantly more abundant in the understorey of the more disturbed forest without pronounced differences in light levels. In the regenerating control forest, they remained more in the upper strata. The understorey species within the *Euphaedra* and *Euriphene*, on the other hand, were never observed in the plantation only 100 meters away from both forest plots. Species in both groups are known to stay in the shaded parts of the forest understorey (Larsen 1999) and do not often visit baits placed in open areas. Their habitat specificity seems to be highly correlated with the presence of “light” or “shade” (Birket-Smith 1970, see also chapter 6.7.2.). These findings confirms DeVries’ assumption that differences in light regime are an important factor in maintaining stratification of fruit-feeding butterflies in tropical rainforests (e.g. DeVries 1988).

Other important microclimatic factors related to stratification patterns in nymphalids could be temperature and wind intensity. The increase in body size in fruit-feeding nymphalids towards the lower forest strata, as indicated in DeVries (1988), Schulze (1995), might probably be connected with the lower temperatures found in the understorey compared to the canopy. A favourable surface/volume ratio, by increasing body size, could be more useful for thermoregulation in the lower than in the upper strata. In the sunny and warmer canopy, overheating could possibly pose a problem for the larger nymphalid species.

A larger wind speed in the upper compared to the lower strata, on the other hand, might be partly responsible for the higher abundance of more robust “stocky” species with larger and broader thoraxes, adapted for faster flight, at canopy level (Schulze 1995). *Charaxes* species are indeed known as fast flying butterflies (e.g. Larsen 1999), with a strong, robust body and well developed musculature. A smaller wing surface could also be favourable under windy conditions, so that both temperature and wind speed can selectively favour the presence of smaller nymphalid species in higher strata.

The vegetation structure can also directly influence the vertical stratification of mobile butterflies. Wing morphology in insectivorous birds and bats is known to be adapted to the spatial structure of the habitat (Norberg 1986). Hill *et al*. (2001) found that butterflies characteristic for open gap habitats generally had broader thoraxes, indicating a flight morphology adapted for faster flight. In denser forest habitats, butterflies are characterised by broader, shorter wings, which favour slow, manoeuvrable flight (Betts and Wootton 1988). This indicates that stocky species, adapted for faster flights (as e.g. the *Charaxes*, see above), will be more adapted to the vegetation structure of the canopy, characterised by many free and open spaces. Slower but more manoeuvrable species might be more adapted to flying in the denser lower strata, as shown for several larger Morphinae (Schulze and Fiedler 1998) and Satyrinae species (Schulze 1995).

Could predation be an additional factor influencing nymphalid stratification patterns? A butterfly undergoes predation pressure in any development stage. The most important predators are birds, bats, other small mammals, reptilia, predating insects and spiders. Birds can be considered the most important predators on adult, mobile butterflies. Schulze (1995) indicated an increase in abundance of insectivore birds with stratum height in Borneo. A higher predation pressure at higher stratum levels is therefore plausible. This higher predation pressure towards the canopy could possibly select for differences in butterfly (flight) morphology along the vertical gradient.

Although for most species or higher taxonomic groups, the patterns of vertical stratification found can be discussed, the stratification pattern in two Satyrinae species *Melanitis leda* and *Bicyclus abnormis* remains difficult to clarify (Larsen pers. comm.). The general absence of a distinct stratification pattern in the widespread *Melanitis leda* has equally been shown in Schulze (1995), where the species was found to be present in comparable numbers at all trap heights in a rainforest in Poring, Borneo. In most studies based on understorey data, *Bicyclus abnormis* is described as a very rare species (Larsen 1999), possibly an indication for the species broad distribution along the vertical strata. Furthermore, a very weak trend of sexual differences in stratification patterns was found: males were slightly more abundant in the higher strata than females. However, this possible difference in vertical distribution between males and females, found in other stratification studies (see Schulze 1995, DeVries 1988), was not significant in the present data.

6.5 Influence of the forest management

6.5.1 Microclimate, vegetation structure and the nymphalid community

It is known that microclimatic conditions such as light intensity, temperature, humidity and wind, evaporation and insolation can differ significantly along the vertical gradient from forest floor to the upper canopy of closed tropical rain forests (see Allee 1926, Kiltie 1993, Smith *et al*. 1992, Whitmore 1993, Yoda 1992). These parameters stay remarkably constant at forest floor level, whereas variation is high in tree-tops (Allee 1926). In a rain forest in Cameroon, for example, the canopy surface characteristics are more similar to chaparral shrub vegetation than to familiar rain forest understorey vegetation (Bell *et al*. 1999). Especially light conditions can alter dramatically: average light availability decreases up to two orders of magnitude over short distances from the external surface to a few centimetres inside the canopy (Mulkey *et al*. 1996). Allee (1926) showed that only 0,25 % of the light intensity present in the canopy reaches the forest floor. Fluctuations of relative humidity and temperature, solar energy and wind speed are all notably higher in the upper canopy than in the understorey (e.g. Blanc 1990). Changes in forest vegetation structure (e.g. by logging or thinning operations), not only imply changes in abiotic characteristics at different vertical levels; they also alter important biotic factors such as vegetation density, plant species composition and dominance structure, predators, etc. (Terborgh 1980).

It seems obvious that changes to any of the previous mentioned factors can influence nymphalid species composition, abundance and diversity, movement patterns, as well as their natural stratification along the vertical gradient from forest floor to canopy (e.g. DeVries 1988, Kremen 1994, Schulze 1995, Lewis *et al*. 1998, Wood and Gillman 1998). Microclimatic conditions influence the diversity and abundance of butterfly food plants. Local changes in foodplant availability can have important consequences for the persistence of local butterfly populations (e.g.

Gilbert 1984). Butterflies highly depend on light e.g. as energy for reaching the ideal body temperature for flying (e.g. Scoble 1992). Furthermore, larval development is highly dependent on certain microclimatic conditions, and possibly also on parasitisation rates. In contrast, an increased production of plant biomass may partly compensate for negative effects and the availability of fruits for butterfly adults is certainly not reduced to critical levels, as shown by the presence of many frugivorous birds in the thinned forest plot (Waltert 2000a).

The overall vegetation structure of the Bossematié Forest Reserve can be considered as “mostly degraded” according to a scaling developed by Hawthorne and Abu-Juam (1995, see also Waltert 2000b). The vegetation structure of the 75-ha study site reflects this status and appears as a mosaic of patches of variable structure. Most characteristic for the site was the high proportion of early successional forest patches. This status results from repeated over-logging during the last decades, leading to a critical overall forest condition (2000b). Within the 75-ha study site, there were significant differences in vegetation structure between the three management plots. As expected, the mono-dominant tree plantation showed a much lower vegetation density at both overstorey and understorey level. The most characteristic difference between the thinned and the control forest was the much higher density of understorey vegetation in the thinned plot. Thinning alters the structural characteristics of the forest, creating more open, degraded patches and a dense understorey (Waltert 1996, 2000b). In the control forest, a larger overstorey tree size (OTS), a significantly larger understorey tree distance (UTD), and a smaller overstorey tree distance (OTD) was found, implicating a higher proportion of more mature succession stages. The contrary was found for the thinned forest site, reflecting the dominance of younger succession stages. However, it is important to stress that the control plot may certainly not be viewed as a primary-like forest plot. It represents the overall status of the Bossematié Forest Reserve, and should be regarded as a regenerating secondary forest plot, differing from the thinned plot only in the fact that no thinning operation were carried out three years before this study.

6.5.2 Habitat specificity

As discussed above, changes in the vegetation structure and the consequences for the microclimatic conditions along the vertical gradient of a tropical rain forest, are known to influence sensitive species of the buffered forest floor zone. The present results also indicate that the understorey nymphalid butterfly community of the Bossematié Forest is sensitive to small-scale disturbance. At our study site, thinning was carried out three years before this study started and treefalls still occurred as a consequence of the management. Although traps of the control and the thinned forest were separated by 200 meters only and butterflies were attracted by bait, there were considerable differences between the compartments. The more specialised, closed canopy species with smaller geographic ranges seemed to be the most affected group.

Most species with significantly lower capture frequency in the thinned forest showed a significant preference for older succession stages of the type S2 / S3 (for a comparison, see Tables 10 and 14). *Bicyclus abnormis* (the Western White-Tipped Bush Brown) and *B. sambulos* (The Tailed Bush Brown) are classified as wet evergreen forest species, *B. zinebi* (the Western Large Bush Brown) and *Euphaedra crockeri* (Crocker's Forester) as moist evergreen forest species, generally flying in mature, dense forest and rarely out in the open (Emmel and Larsen 1997, Larsen 1994b, 1999). They are host-specific to one or a few low forest plants. *E. crockeri* exclusively breeds on a few species of Sapindaceae (Hecq and Vuattoux 1989). *B. zinebi* breeds mainly on *Afromomum* (Zingiberaceae; Larsen 1999). While these species are still present in the degraded secondary semi-deciduous Bossematié Forest, they seem to depend on relicts of mature succession stages. Both *E. phaetusa* (The Common Ceres Forester) and *E. harpalyce* (The Common Blue-Banded Forester) are known to visit disturbed areas and are very common and abundant (Larsen 1999). However, they also prefer the more mature patches inside the secondary Bossematié Forest. It's preferred flight activity towards the evening could explain the habitat specificity in the moist evergreen species *Gnophodes chelys* (The Lobed Evening Brown), which was more abundant in the overall more canopy-closed (and consequently darker) control forest. One Charaxes species, *C. bipunctatus* (the Two-Spot Blue Charaxes) equally preferred the more mature control forest. It is a true rain forest canopy species, centred on the wet evergreen forests (Larsen 1999), with host plant records of two genera within one family only. Blandin *et al.* (1975) classified the species as rather uncommon and exclusively living in forests.

Both *Euphaedra* (The Foresters) and *Euriphene* (The Nymphs) species were exclusively found inside the forest, never in plantation traps only 100 meters away from traps in control and liberation thinned forest. This strongly indicates that they do not easily migrate over non-forested areas. Spitzer *et al.* (1993) found a higher overall degree of habitat specificity within forest understorey species. Birket-Smith (1970) tested the behaviour of *Euphaedra* spp. in relation to temperature, humidity and light and found that a lower relative humidity and higher temperature (as in plantations) causes heliophobia and makes species return to the shade after a few minutes. In Bia

National Park of Ghana, Larsen (*personal observation*) recorded just a few *Euphaedra* spp. and *Bebearia* spp. (The Bebearia's) visiting huge numbers of mango fruits in an open compound around a ranger station, just 25 meters away from mature forest. The same mangoes, placed on tracks in the forest, attracted virtually every species of *Bebearia*, *Euphaedra* and *Euriphene* recorded in Ghana.

For *Euriphene spp*., baiting did not reveal differences between successional stages or between the control and the thinned forest site, and only one *Bebearia* spp. was found more abundant in traps of the control forest during the wet season. It should be noted that especially *Bebearia* and *Euriphene* species are probably under-represented in traps, since they are known to fly very low near the forest floor and probably do not fly up into the trap when leaving the bait (Larsen pers. comm.). Escape rates however are not relevant for our comparison.

Most species with significant lower capture frequency in the control forest showed a significant preference for early succession stages of the type gap / S1 (for a comparison, see Tables 10 and 14). *Bicyclus vulgaris* (the Vulgar Bush Brown), *B. sandace* (the Dark Vulgar Bush Brown) and *B. dorothea* (The Light Bush Brown) are Bush Browns classified as ”species surviving in most types of forest habitats, often penetrating the Guinea Savannah and agricultural lands” (Larsen 1999). They are known to fly also in open country, and especially the Vulgar Bush Brown seems to adapt more and more to agricultural areas.

In the Nymphalinae, only 5 species were significantly more abundant in plantation traps. All five species are seen regularly flying in disturbed forest areas, clearings, farmland or shifting cultivation near villages and rarely inside intact forest (Larsen 1999). *A. enotrea* (the African Castor) as well as *B. safitza* (the Common Savannah Bush Brown), *E. dryope* (the Golden Piper), and *Byblia anvatara* (the African Joker) are species of the savannah / dry forest zone, breed on plants of disturbed, somewhat open habitats in degraded forest parts (Emmel and Larsen 1997, Larsen 1999). *S. cacta* (the Lilac Beauty) is a widely distributed forest edge species feeding in Côte d'Ivoire on an Urticaceae species (Vuattoux and Blandin 1979).

Capture frequencies of most *Charaxes* species were also highest in the understorey of younger succession stages and in the thinned forest plot. Five *Charaxes* species even showed a significantly higher abundance in plantation traps. The genus *Charaxes* (and probably also *Palla*), are believed to be principally inhabitants of middle and higher strata (Larsen 1991, 1999) and were also found more frequently in canopy traps during the present study. Birket-Smith (1956, 1960) demonstrated that the African rain forest in the Cameroons, when fully developed, contains at least three, more or less continuous bioclimatical strata, each of which has its own rather well defined insect fauna. DeVries (1988) indicated that disturbance can disrupt this stratification, and Wood and Gillman (1998) found a greater similarity of the butterfly fauna between understorey and canopy traps in disturbed than in undisturbed forest habitats in Trinidad. The higher capture frequencies of *Charaxes* spp. in the understorey of the thinned forest indicates that stratification is less pronounced in this more open forest plot compared to the more canopy-closed control forest site. Both *Charaxes cynthia* (the Western Red Charaxes) and *C. tiridates* (the Common Blue Charaxes) are more common species. Although species of the African forest belt, they have adapted also to gardens and savannah and are highly polyphagous, with host plant records within several plant families and genera (Blandin *et al.* 1975, Vuattoux 1988, Larsen 1999). The higher capture frequencies of the *Charaxes* spp. and *Palla* spp. in the plantation, the thinned forest and the younger succession stages might rather be explained as an effect of the distortion of distinct stratification. A more detailed discussion of differences in stratification patterns between the thinned and the control forest is given below.

6.5.3 Geographic range and habitat specificity

This study supports other findings (see Thomas and Mallorie 1985, Lepš and Spitzer 1990, Thomas 1991, Novotný 1991, Holloway *et al.* 1992, Spitzer *et al.* 1993, 1997, Hill *et al.* 1995, Hamer *et al.* 1997, Owen *et al.* 1998) that forest disturbance is more likely to affect species with narrow geographic ranges. A significant decrease of the species' habitat specificity with increasing geographic range was visible, indicating that least widespread species are most vulnerable to human disturbance. Analyses on the species level showed that 50 % of the species with a significantly higher abundance in the control plots are endemic to western West Africa or western West Africa to the Nigeria-Cameroon border (geographical range 1 and 2). Six of nine species with lower capture frequencies in the thinned forest showed preference for mature succession stages and most were ranked Upper Guinean endemics or Guinea-Congolian-restricted species (geographic range rank 1 to 3). To the contrary, all species more abundant in traps of the thinned forest were geographically widespread, ranging from western West Africa to the Zaire-Uganda border (range 4; e.g. *Bicyclus sandace*) or living throughout all Africa in suitable habitats (range 7; e.g. *B. vulgaris*, *B. dorothea*). 80 % of the species with a significantly higher capture frequency in the younger succession stages are widely distributed (geographic range 4 to 7). Only two species with a small geographic range (1 to 2) were more abundant in the gap / S1 habitats.

6.5.4 Species richness and diversity

Species richness and diversity indexes did not differ between single samples (spot diversity) in the control and the thinned forests, but species accumulation and rarefaction methods from all samples pooled did indicate a somewhat richer nymphalid community in the thinned site (approximately 30 ha). Thinning seems to create a higher habitat heterogeneity with a variety of young and old succession stages. In the control forest, older succession stages predominate. However, species richness was not strikingly different and the higher richness in the thinned understorey zone was due to the shift in vertical stratification in canopy species. Excluding canopy species of the genus *Charaxes* from the analysis (Figure 19) indicates an equal accumulated species richness in both control and thinned forest plots. Figure 19 even reveals a slightly higher accumulated species richness for the control forest. Considering that species with narrow geographical ranges are more likely to decline in numbers with disturbance, it can be assumed that thinning increases their local extinction risk. Therefore, biodiversity is more likely to decrease on a regional scale instead of being augmented.

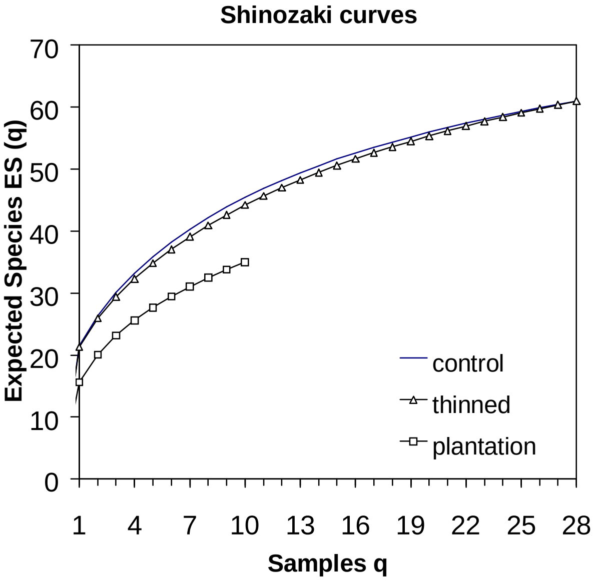


Figure 19: Expected number of Nymphalidae species (ES [q]) captured in banana baited traps in a regenerating forest (control), a liberation thinning (thinned) and a plantation plot during the dry season 1996 in the over-logged Bossematié Forest, Côte d'Ivoire. Canopy species (*Charaxes* spp.) were excluded from the analysis. Expected means computed using Shinozaki rarefaction method (Shinozaki 1963).

Apparently, the nymphalid community of the plantation is limited to an association of open habitat specialists of low diversity. Although the plantation was situated adjacent to the more ”natural” forest plots (control and thinned), a considerable avoidance of this habitat type was documented in many forest species. Obviously, this is caused by a reduced complexity of the vegetation and ground coverage. Human disturbance on a larger scale, such as conversion to plantation, will most probably result in a significant loss of both local and regional nymphalid species richness, as already shown by Holloway *et al.* (1992) for moths sampled in four plantations in East Malaysia.

6.5.5 Movement and stratification

The comparison of movement parameters between different management sites reveals the largest average movement for the plantation. Although the area size sampled in the plantation was only half that of the control and thinned sites, these larger movement parameters could also reflect the larger homerange sizes in the mono-dominant habitat compared to both natural forest sites.

The results discussed above (and see also Fermon *et al*. 2000) indicated differences in abundance between the control and the thinned forest for several Nymphalinae (especially the *Euphaedra*), Satyrinae (*Bicyclus*) and Charaxinae (*Charaxes*) species. These abundance data showed that the control forest constitutes the habitat of preference for several *Euphaedra* species. Our movement data confirm this finding, assuming that home-ranges tend to be smaller in more optimal (control) compared to the less optimal (thinned) forest.

As discussed above, most *Euphaedra* species are characteristic of a mature forest understorey, are sensitive to changes in microclimate and are relatively host-specific to a few plant species of the shaded forest understorey (Larsen 1999). We assume that both the buffered microclimatic conditions and suitable hostplants are more patchily distributed within the thinned area, causing *Euphaedra* species to move larger distances.

The Satyrinae *Bicyclus dorothea*, the larvae of which mainly feed on grasses (e.g. Larsen 1999), was more abundant (see Table 14 and Fermon *et al*. 2000) and generally showed smaller movement parameters in the thinned compared to the control forest. The satyrid *B. zinebi*, feeding on Marantaceae and gingers (e.g. Larsen 1999), equally showed smaller movement in the thinned forest. However, this moist evergreen species, known to fly in mature forest patches, was more abundant in the control forest. Thinning additionally creates canopy gaps (Waltert 2000b), most probably enhancing the growth of the *Bicyclus* hostplants (Marantaceae, grasses and gingers). This increase in resource availability can explain the shorter flights found in the thinned forest for both studied *Bicyclus* species. For two other satyrids within the genus *Gnophodes*, however, longer flights were found in the thinned than the control forest. Although equally feeding on grasses, both *G. betsimena* and *G. chelys* are classified as cryptic forest understorey species, rarely seen flying in open habitats (Larsen 1991, 1996b). This may possibly explain their shorter flights in the more closed and darker control forest. *Gnophodes* species were equally more abundant in the control forest

Higher strata species (*Charaxes*) also moved smaller distances in the control compared to the thinned forest. Their overall abundance, sampled along different vertical heights in both plots, was equally higher in the control plot. *Charaxes* caterpillars mainly feed on trees as larvae. Since thinning gradually causes non-crop trees to fall, decreasing overall tree density, their larval resources are likely to be more scarce in the thinned than in the control forest. However, data based on understorey sampling alone (see above and Fermon *et al.* 2000) indicated a significant lower abundance of *Charaxes* sp. in understorey traps of the control compared to the thinned forest. What could be the reason for the higher *Charaxes* abundance in the understorey traps of the thinned forest site? DeVries (1988) stated that forest disturbance, changing distinct light levels, is most likely to disrupt distinct vertical stratification, causing canopy flyers to visit the forest ground more frequently. We might therefore expect canopy species to fly more abundantly in thinned areas, because of the decreased canopy coverage (Waltert 2000a, Hill *et al.* 2001). The comparison of the vertical stratification patterns between the control and thinned forest show that the abundance distribution of the trapped *Charaxes* species along the vertical strata differed significantly between both sites. *Charaxes* were more abundant in canopy traps and less abundant in midstorey and understorey traps installed in the control site. Although *Charaxes* species were trapped less frequently in understorey traps of the control compared to the thinned site, they are not less abundant there but stay in the upper strata. In the thinned forest, they are more likely to fly down in the understorey traps. Except for the species *C. bipunctatus*, a true rainforest canopy species (Larsen 1999) with host plant records of two genera within one family only, the *Charaxes* species analysed in this study are common and polyphagous (Blandin *et al.* 1975, Vuattoux 1988, Larsen 1999). They can occasionally or frequently be seen in gardens and savannahs, but originally belong to the forest canopy fauna. However, the comparison of abundance data from higher trap levels indicate that *Charaxes* spp. were more abundant in the control than in the thinned forest. Disruption of vertical stratification was also found for the canopy species *Cymothoe caenis* (the Common Migrant Glider). This species seemed more abundant at lower trap level in the thinned than in the control forest. But, comparing only traps installed at canopy level between sites reveals a higher abundance of *C. caenis* in the control forest. The species has been described as “very common in very open forests” (Larsen 1991, 1996b, 1999). Our present data suggest that *C. caenis* seems to visit lower strata more frequently where the canopy is opened. In closed canopy forests, this species might rather stay in the upper strata and therefore be less observed at understorey level.

Miller (1994) stated that behavioural observations on butterflies, with respect to habitat and resource partitioning, are needed to explain ecological patterns found in butterflies and for the evaluation of conservation and management efforts. This study discusses foraging flights and stratification in relation to tropical forest management, and confirms previous results, indicating that thinning affects the more specialised species, which are likely to have small geographical ranges (Fermon *et al.* 2000). The more specialised forest understorey species showed shorter flights in the control forest, whereas species feeding on early successional larval hostplants had shorter flights in the thinned forest. In addition, our data on movement and vertical stratification clarify trends found in higher strata species. Thinning techniques might also negatively affect the abundance of several canopy species, some of which are more common and widespread. However, due to a clear disruption of vertical stratification after thinning, causing a downward shift in higher strata species, this trend cannot be detected when sampling at understorey level only.

6.5.6 Comparison of assessment methods

Assessment methods, which can be used to study butterfly communities in a standardised way, and with a manageable sampling effort, are bait trapping and direct observations. In this study, fruit trapping has been used as main tool to analyse different aspects of the (nymphalid) butterfly community and to assess the impact of the forest management. Additional methods used were walk-and-capture and point distance sampling on semi-permanent transects. Additional methods were principally applied to look for complementary trends, especially in those adult butterfly species not using fermenting fruits as primary resource, and to test for eventual contradictory or parallel trends between baiting and direct observations.

A large disadvantage of direct observations is that sampling methods highly depend on and vary with vegetation structure. A comparable "detection probability" should be given independent of habitat structure, however, it is obvious that observations can bias highly with vegetation density. Furthermore, topography and vegetation structure might influence behaviour or activity patterns in species (Vane-Wright pers. comm.). As in baiting, direct observations only comprehend certain groups of organisms. Certain criteria should be fulfilled before an experienced butterfly specialist can collect relevant data: the community should contain species which are highly active during daytime, and many characteristic species, easy to identify in the field, i.e. large enough and showing specific colour or other clear morphological characteristics, should be present. Furthermore, identification in the field needs years and years of taxonomic experience. For many (Afrotropical) butterfly species, comparison with (a series of) museum specimens is absolutely necessary, especially in rare species, often showing the most interesting patterns. In the field, particularly those patterns can be highly biased by misidentification (Larsen pers. comm., Walpole and Sheldon 1999).

Baiting using traps can be applied to study several groups of arthropods and certain small mammal species (e.g. O'Farrell *et al*. 1977, 1978). Because in fruit trapping, a "natural" olfactorical attractant is used, we can assume that the distribution of the (nymphalid) butterflies, both horizontally and vertically, is not influenced or changed by sampling methods. Especially when using a grid trapping system, the collected species are not expected to visit baits in locations which they would not frequent naturally for feeding. Attraction of species outside the borders of their "preferred vegetation patch" could, in the worst case, mean that certain differences in e.g. capture frequencies between patches are missed. Since in this study, 66 traps were installed only 100 m apart, this possible bias is considered to be minimal. Patterns (in adult feeding behaviour) which are actually found, do in each case reflect the natural situation. Fruit baiting allows relatively uncomplicated sampling at different vertical heights, aspects which can only be studied by direct observation after establishing special infrastructures (canopy walkways) or climbing trees. In this way, additional patterns of the community structure can be studied and eventual biases in understorey trapping detected (see above).

Moderately similar butterfly assemblages and comparable diversity values were found when comparing walk-and-capture and baiting. However, since the very species-rich family of Lycaenidae, as well as species of the Papilionidae and Hesperiidae, were not collected at all during the walk-and-capture study period, a fairly higher species richness can be expected for this collecting method with considerably higher effort. Overall, collecting could reveal a total of *ca*. 500 butterfly species in the Bossematié Forest Reserve (Larsen pers. comm.). The generally known trend that males seem to visit baits more frequently than females was also found during this study. The walk-and-capture data indicated a comparable trend: males were more frequently netted than females. Transect data generally confirmed patterns of habitat specificity found during fruit trapping. And, as expected, walk-and-capture revealed some complementary information within certain groups, especially in species which were rare or never present at baits (e.g. The Pathfinders or *Catuna* spp. and some *Euriphene* spp.). Some species (all *Charaxes* spp.), very abundant in traps, were never collected during transect walks. Species similarity between fruit trapping and data from direct observations was largest for the thinned (more disturbed) than for the control forest, indicating that the control area still contains a more stratified butterfly assemblage, whereas differences in stratification are more disrupted in the thinned area (Wood and Gillman 1998). Another factor is the possible lower detectability of butterflies on transects in the dark understorey of the less disturbed (control) vegetation. Differences in detectability between the study pots can also result from the higher overall abundance in forest understorey species (e.g. *Bebearia*, *Euphaedra*) in the control compared to the thinned forest. The standardised walk-and-capture method most probably revealed a smaller proportion of the total number of individuals present in the control than in the thinned plot, and differences between plots were indeed much less pronounced in walk-and-capture than in fruit trapping data.

Point Distance Sampling again confirmed patterns found using both fruit trapping and walk-and-capture: higher abundance in forest understorey species in the control than thinned forest. Interestingly, over the distance category analysed (0 m to 7 m), the lower butterfly density in the thinned area allowed for a significantly higher proportion of individuals detected in comparison to the control forest. This was, however, due to the fact that encounter rates (overall number of observations at each point) were higher in the control forest, and that the time spent counting was largely determined by the high number of identifications to be made at zero distance in control. In other words: in the thinned area, the observer had more time to search for animals at larger distances, due to an overall lower number of individuals to note. Also, the darker habitat conditions in the control forest seemed to inhibit detection at larger distances (e.g. > 4 m) than the more light-penetrated thinned forest area.

6.6 Implications for the forest management

The Upper Guinean forests of Côte d'Ivoire and Ghana have been designated as global priority areas of conservation because of the extreme vulnerability and biological uniqueness (Larsen 1999, Primack 2000; see Figure 20). Although Afrotropical forest loss has far exceeded that occurring in the rest of the world, these vulnerable ecosystems have received scant research attention relative to their Neotropical and Indo-Malayan counterparts. Many developing countries in the tropics maintain a considerable proportion of their forest area as production forests. Also the forests in eastern Côte d'Ivoire are and will be production forests. To maintain biodiversity in these areas, management plans should ideally combine economy *and* ecology (see also Brown 1997). Ecologically sound management techniques are therefore highly needed.

The conversion of natural forests, even though degraded, to monodominant and homogenous tree plantations, composed of few tree species and manually cleared understorey, is certainly a less favourable alternative than natural forest management. Due to frequent manual clearing of the regenerating vegetation, the *Terminalia* plantation of the study plot did not show major understorey succession. A monolayered canopy and a lack of a diverse understorey vegetation were characteristic. Although some fruit producing trees were left, especially at the plantation border (e.g. *Musanga* spp. and *Trema* spp.), and the plantation does still offer valuable feeding resources for some ubiquitous and less sensitive nymphalid species (e.g. *Ariadne enotrea*, *Eurytela dryope*, *Bicyclus safitza*, *Salamis cacta*, *Byblia anvatara*), it is hardly imaginable that this mono-structured vegetation type can play a role in maintaining the forest interior butterfly fauna. Some studies indicate that shade coffee plantations still represent an important diversity of birds and insects (e.g. Roberts *et al*. 2000). But these diversity parameters would certainly be much lower in more isolated plantations, not neighbouring undisturbed mature forest patches. Although the (also shade-offering) *Terminalia* plantation was bordering the less disturbed control forest, species richness was considerably lower and specialised forest floor species were lacking. As is foreseen in the Bossematié Forest, plantations should be limited to areas with low regeneration potential (SODEFOR 1994), and manual clearing should be reduced to a minimum (Waltert 2000b).

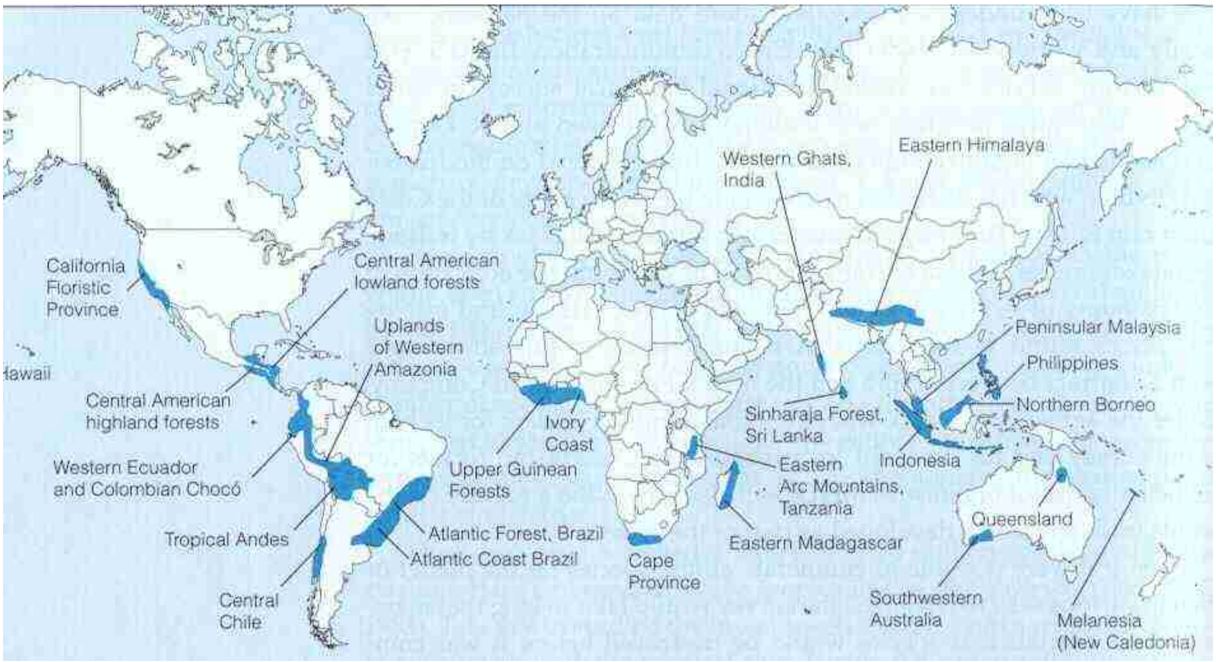


Figure 20: Hotspots of diversity throughout the world (with kind permission of J. Bossart, drawn from http://bossart.intrasun.tcnj.edu/Ghana/SpeciesChecklists.htm)

The present study illustrates that thinning operations cannot be regarded as valid “alternatives” to biological reserves. As stated previously (Waltert 2000a, Fermon *et al*. 2000), thinning cannot be regarded as an imitation of the natural forest dynamics. Especially in already highly degraded forests, such as the Bossematié Forest Reserve, the scale at which thinning operations can be applied should be considered, since it creates even more gaps and decreases the availability of mature patches. The general assumption that management impacts can be regarded as an imitation of the natural dynamic of gap formation and forest succession should be viewed critically. It certainly does not match in forests where younger succession stages are already dominating the habitat mosaic. The special danger of initial damage caused by liberation thinning techniques in a forest where Forest Elephants (*Loxodonta africana cyclotis*) are present (see Struhsaker 1997) should be taken in particular consideration. Liberation thinning increases the vegetative ground cover, which according to experiences of Struhsaker (1997) increases utilisation by elephants and as a result greatly hinders or possibly suspends forest regeneration. Compensation for the impact by liberation thinning is necessary.

As natural forest management also aims at the maintenance of biodiversity, forest patches of considerable sizes should be gazetted as biological reserves without any management for timber. In the Bossematié Forest, three biological reserves covering one third (7404 ha) of the total area have been established. At the time of the study, these areas did not yet represent a different (more mature) forest type. However, they certainly played a role for the conservation of biodiversity, and generally play an important role inside production forests (Johns 1966, 1997 cited in Waltert 2000b). They serve as recolonisation areas from which forest interior species can disperse and recolonise regenerating habitats. In the Bossematié Forest, the reserves are located at the centre, and have been shown to be important for large hornbills (*Ceratogymna* spp.), probably because of the reduced poaching pressure in the core area (Mühlenberg *et al*. 1997, 1999, 2000).

In the remaining forests of south-eastern Côte d'Ivoire, where poaching certainly is one of the most important threats to the mammal and bird fauna (McGraw *et al.* 1998), the ecological impacts of the forest management should not be neglected. A consistent and long-term monitoring of the liberation thinning impact is necessary to adjust activities in space and time, as impacts seem to be considerable and management will be carried out on larger scales (e.g. in the Bossematié Forest: on more than one third of its surface). At present, bird and mammal species are monitored in the south-east of Côte d'Ivoire by local staff. However, the effects of ecological changes on vertebrate populations appear with long time-lags (see results in Struhsaker 1997) and are not as easily and rapidly detected as in invertebrates (Murphy and Wilcox 1986).

The need for including insects in tropical (forest) habitat assessments is extensively discussed in Janzen (1987). Our results indicate that monitoring butterflies could guide management on a smaller scale and over shorter periods. Terrestrial arthropods have been considered useful in conservation planning by e.g. Kremen *et al*. (1993). Mendez (1995) found several butterfly species to react very sensitive to tropical deforestation, and proposed a multitaxonomic monitoring to provide a broad measure of management impacts on biodiversity in Guatemala and Costa Rica. Nymphalid butterflies seem to provide a good indicator tool (see also Beccaloni and Gaston 1995, New 1997). During the study, nymphalid abundance differed considerably between management sites and, although at the time of the study no replicates of experimental plots were available, results correspond well with general information on life history and adult behaviour. Attracting nymphalid butterflies by fermenting banana could even provide a better indicator system than attracting moths with light traps. Whereas moth diversity in a plantation in Borneo was high due to the presence of species which flew in from adjacent forest (Holloway *et al.* 1992), this study indicates that several fruit-feeding butterflies are purely restricted to the forest and do not enter the plantation even when attracted. Furthermore, baiting allows the detection of vertical stratification patterns or the disruptions of it, again in contrast to results found for (geometroid) moths sampled by light attraction in Malaysian lowland rainforest (Intachat and Holloway 2000).

Our results showed that species richness and diversity do not represent very powerful indicators for monitoring degrees of forest disturbance on the scale considered. The abundance of species of conservation concern, such as restricted range species, is of a much more indicative value. Ranking of the species conservation value according to their geographic range is applied in other animal groups such as birds (see Stattersfield *et al.* 1998). Changes in relative abundance of selected nymphalid species of small geographic range can give us a quick impression of the management impact, allowing adjustment options in space or time.

7. SUMMARY

Fruit trapping, standardised transect walks and point distance sampling were used to study the butterfly fauna of a managed, over-logged rainforest in south-eastern Côte d'Ivoire, West Africa. The study site within the 22,000 ha large Bossematié Forest Reserve included three different forest plots: a 15 ha tree plantation, a 30 ha thinned forest and a 30 ha regenerating control forest. The impact of the local forest management on the butterfly community was tested. The main emphasis was put on the fruit-feeding Nymphalidae, trapped with a standardised, fermenting fruit bait.

263 butterfly species are reported for the over-logged Bossematié Forest Reserve, and the estimated total species richness amounts to *c*. 500. The Bossematié's butterfly community still mainly consists of true rainforest species, with only a small fraction of savannah species, and is very similar to that of the less disturbed, but equally logged Bia National Park. 28 Upper Guinean Endemics were found, as well as one nymphalid species (*Bebearia dallastai*) endemic to the Bossematié Region. Four butterfly species, characteristic of mature forests and abundant in the nearby Bia Reserve, were not found in the Bossematié Forest. Daily nymphalid capture rates were high compared to those known from other studies, however, the abundance of several range-restricted hostplant specialists feeding on understorey shrubs and climbers and common in other forest locations, was found to be relatively low. This implicates the (ongoing) local decline and potential loss in specialised forest species due to disturbance. The (nymphalid) species richness of a 3 km distant, 6 ha small forest remnant was only half of that found in a similar sized plot within the Bossematié's Reserve: in this small isolated fragment, the grass-feeding species of the Satyrinae subfamily were dominating, several Nymphalinae species using understorey shrubs as hostplants, as well as Charaxinae species, were lacking.

A total of 8,400 nymphalid individuals, representing 123 species, were baited during 996 trap days in a dry and two wet seasons on the 75 ha studied. There were pronounced variations in nymphalid abundance and diversity between years and seasons, with a shift in dominance from the Satyrinae in the dry to the Nymphalinae in both wet seasons. Alpha diversity was highest during wet season 1997, slightly lower during dry season 1996, and lowest during wet season 1996. Accumulated species richness seemed highest in, and comparable between, the dry season 1996 and the wet season 1997. Species similarity was highest between both wet seasons and lowest between different seasons in different years. Variation in nymphalid abundance and diversity was equally related to micro-scale variation in vegetation structure at each trap location (i.e. the four succession stages). Accumulated species richness and overall abundance seemed to decrease with habitat maturity, and differences were more pronounced during the dry season. In 33 nymphalid species, there was a significant relationship between forest maturity and capture frequency. Canopy flyers (especially among the Charaxinae), as well as understorey nymphaline and satyrine species with a wider geographical range found in various forest types (from wet evergreen to dry forests) were more abundant in gaps and early successional forest patches. In contrast, those nymphaline understorey species, centred on the wetter or moist forest zones and with a more restricted distribution, were more abundant in canopy-closed forest patches.

In a mark-recapture study during 396 trap days in the dry season, 1,430 *resp*. 540 nymphalid individuals were marked *resp*. recaptured in total. In most species, females seemed to fly further than males. Average movement values ranged between 0 m and 433 m. Movement parameters were generally largest in species feeding on early successional larval hostplants characterteristic of gap and margin habitats and smaller in species characteristic of the darker forest understorey, feeding on climbers and smaller shrubs.

Vertical stratification of the nymphalid community on the 75 ha study site, studied during 204 trap days of the wet season 1997, was pronounced at different taxonomic levels. Species richness and abundance decreased with increasing trap height. A defined understorey community could be separated from a distinct midstorey / canopy fruit-feeding butterfly assemblage. The increase in percentage of rare nymphalid species towards the canopy indicates that resources (rotting fruits) are more limited at higher strata than towards the forest floor. In several species, stratification patterns seemed to correlate with information on larval host-plant height or oviposition behaviour and sensitivity to light regime changes.

Accumulated nymphalid species richness and diversity indices were lower in the control compared to the thinned forest, but lowest in the plantation. However, there was a significant, negative correlation between the species' preference for the control forest and the size of the species geographical range. Six out of the nine species with a lower capture frequency in the thinned forest showed preferences for mature succession stages and most of these were either Upper Guinean endemics or Guinea-Congolian-restricted species. The five species with higher capture frequencies in the thinned plot were all geographically more widespread and showed higher frequencies in younger forest succession stages. Ten species, mainly canopy specialists, ubiquitous species or species centred on the Guinea savannah / dry forests, were most abundant in understorey traps of the plantation. Seventeen more nymphalid species avoided the plantation forest. Thinning seems to affect hostplant and wet/moist forest specialists with smaller geographic ranges, thus risking loss of regional diversity. Patterns of habitat specificity and or diversity were largely consistent between sampling methods. Walk-and-capture revealed additional information in species which were not or less frequently baited but, as shown with point distance sampling data, differences in detectability between different forest vegetation structure might account for differences in encounter probabilities.

Movement and stratification data confirm the (negative) impact of thinning on restricted range species of the forest understorey, and clarify trends found in higher strata species. In all species, movement parameters were largest in the plantation. Species feeding on early successional larval host-plants characteristic of gap and margin habitats showed shorter flights, whereas species feeding on climbers and smaller shrubs of the forest understorey showed larger movement in the thinned compared to the control forest. Higher strata species (e.g. within the Charaxinae) equally showed smaller movement in the control plot. Including samples taken at higher vertical strata, they also showed higher overall abundance in the control forest, although understorey sampling alone indicated the contrary. A comparison of nymphalid vertical distribution patterns between the thinned and the control forest indicated a clear disruption of stratification after thinning. Canopy species seemed to stay in the upper strata of the less disturbed control forest, and are more likely to fly down to the forest floor in the more open thinned forest. Their higher abundance in understorey traps of the early succession stages, and the thinned forest site, illustrates a sampling bias rather than a true habitat preference. Thinning might therefore not only affect the range-restricted understorey butterfly fauna, but also several more widespread species belonging to the forest canopy community.

8. REFERENCES

Achtziger, R., Nigmann, U., Zwölfer, H. (1992) Rarefaction-Methoden und ihre Einsatzmöglichkeiten bei der zooökologischen Zustandsanalyse und Bewertung von Biotopen. *Z. Ökologie u. Naturschutz* **1**, 89-105.

Ackery, P. R., Smith, C. R., Vane-Wright, R. I. (1995) *Carcasson's African Butterflies.* Australia: CSIRO.

Allee, W. C. (1926) Measurement of environmental factors in a tropical rain forest of Panama. *Ecology* **7**, 273-301.

Baguette, M., Petit, S, Queva, F. (2000) Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology* **37**, 100-108.

Baker, R. R. (1984) The Dilemma: When and How to Go or Stay. In *The Biology of Butterflies* (Vane-Wright, R. I., Ackery, P. R., eds.), pp.279-296. Princeton: Princeton University Press.

Bamba, S. (1999) Evaluation des Forêts Classées de l'Est de la Côte d'Ivoire sur la base de l'evolution des populations de quatres espèces d'oiseaux (Période Mars 1994 à Mars 1999) et des données sur la stratification verticale. Master thesis, University of Göttingen, Germany.

Barnes, R. F. W. (1990) Deforestation trends in tropical Africa. *African Journal of Ecology* **28**, 161-173.

Basset, Y, Aberlenc, H.-P., Barrios, H., Curletti, F, Bérenger, J.-M., Vesco, J.-P., Causse, P., Haug, A., Hennion, A.-P., Lesobre, L., Marquès, F., O'Meara, R. (2001) Stratification and diel activity of arthropods in a lowland rainforest in Gabon. *Biological Journal of the Linnean Society* **72**, 585-607.

Beccaloni, G. W., Gaston, K. J. (1995) Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera:Nymphalidae) as indicators. *Biological Conservation* **71**, 77-86.

Beccaloni, G. W. (1997) Vertical stratification of ithomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: the relationship between adult flight height and larval host-plant height. *Biological Journal of the Linnean Society* **62**, 313-341.

Beck, J., Schulze, C. (2000) Diversity of fruit-feeding butterflies (Nymphalidae) along a gradient of tropical rainforest succession in Borneo with some remarks on the problem of ‘pseudoreplicates’. *Trans. Lep. Soc. Japan* **51**, 89-98.

Bell, A. D., Bell, A., Dines, T. D. (1999) Branch construction and bud defence status at the canopy surface of a West African rainforest. *Biological Journal of the Linnean Society* **66**, 481-499.

Benson, W. W., Emmel, T. C. (1973) Demography of gregariously roosting populations of the nymphaline butterfly *Marpesia berania* in Costa Rica. *Ecology* **54**, 326-335.

Benson, W. W. (1978) Resource partitioning in passion vine butterflies. *Evolution* **32**, 493-518.

Benson, W. W., Haddad, C. F., Zikan, M. (1989) Territorial behavior and dominance in some Heliconiine butterflies (Nymphalidae). *Journal of the Lepidopterists‘ Society* **43**, 33-49.

Betts, C. R., Wootton, R. J. (1988) Wing shape and flight behaviour in butterflies (Lepidoptera: Papilionoidea and Hesperioidea): a preliminary analysis. *Journal of experimental Biology* **138**, 271-288.

Birket-Smith, J. (1956) Remarks on the environment. *Bull. Inst. fr. Afr. noire A* **18**, 569-82.

Birket-Smith, J. (1960) Lepidoptera III. *Ibid.* **22**, 1259-84.

Birket-Smith, J. (1970) The behaviour of *Euphaedra* spp. in relation to temperature, relative humidity and light (Lep. Rhopalocera). *Entomol. Scand.* **1**, 123-6.

Blanc, P. (1990) Bioclimatologie comparée de la canopée et du sous-bois. In *Biologie d’une canopée de forêt équatoriale* (Hallé, F., Blanc, P. eds.), pp 42-43. Paris: Montpellier II et CNRS-Paris VI.

Blandin, P., Vuattoux, R, Plantrou, J. (1975) Les Lépidoptères Charaxinae (Nymphalidae) récoltés à la Station d’Écologie tropicale de Lamto (Côte d’Ivoire). I. Inventaire systématique et remarques faunistiques. *Bull. Inst. Fond. Afr. noire A* **37**, 840-58.

Bourlière, F. (1989) Mammalian species richness in tropical rainforests. In *Vertebrates in complex tropical ecosystems* (Harnelin-Vivien, M. J., Bourlière, F., eds.). New York, Berlin, Heidelberg, London, Paris, Tokyo: Springer-Verlag.

Bowman, D. M. J. S., Woinarski, P. O., 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. *Journal of Biogeography* **17**, 227-239.

Boyle, T. J. B., Sayer, J. A. (1995) Measuring monitoring and conserving biodiversity in managed tropical forests. *Commonwealth Forestry Review* **74**, 20-25.

Braby, M. F. (1995) Reproductive seasonality in tropical satyrine butterflies: strategies for the dry season. *Ecological Entomology* **20**, 5-17.

Brakefield, P. M, Larsen, T. B. (1984) The evolutionary significance of dry and wet season forms in some tropical butterflies. *Biological Journal of the Linnean Society* **22**, 1-12.

Brakefield, P. M. (1987) Tropical dry and wet season polyphenism in the butterfly *Melanitis leda* (Satyrinae): phenotypic plasticity and climatic correlations. *Biological Journal of the Linnean Society* **31**, 175-191.

Brown, K. S. (1991) Conservation of Neotropical environments: insects as indicators. In *The Conservation of Insects and their Habitats. 15th Symposium of the Royal Entomological Society of London, September 1989* (Collins, N. M., Thomas, J. A., eds.), pp. 405-24. London: Academic Press.

Brown, K. S. Jr. (1997) Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation* **1**, 25-42.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L. (1993) *Distance sampling. Estimating abundance of biological populations.* London: Chapman and Hall.

Chai, P., Srygley, R. B. (1990) Predation and flight, morphology and temperature of neotropical rain-forest butterflies. *The American Naturalist* **135**, 748-765.

Chao, A., Ma, M.-C., Yang, M. C .K. (1993) Stopping rules and estimations for recapture debugging with unequal failure rates. *Biometrika* **80**, 193-201.

Collwell, R. K., Coddington, J. A. (1994) Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. Royal Soc. B* **345**, 101-118.

Collwell, R. K., Coddington, J. A. (1995) Estimating terrestrial biodiversity through extrapolation. In *Biodiversity measurement and estimation* (Hawksworth, D. L., ed.), pp. 101-118, London: Chapman and Hall.

Collwell, R. K. (1997) *EstimateS: Statistical estimation of species richness and shared species from samples. Version 5*. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Condamin, M, Vuattoux R. (1972) Les Lépidoptères Satyridae des environs de Lamto (Côte d'Ivoire). *Ann. Univ. d'Abidjan E* **5**, 31-57.

Condamin, M. (1973) Monographie du genre *Bicyclus* (Lepidoptera Satyridae). *Mém. Inst. Fond. Afr. noire* **88**, 1-324.

Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs: high diversity of trees and corals maintained only in a non-equilibrium state. *Science* **199**, 1302-10.

Corbet, A.S., Pendlebury, H.M. 1992. *The butterflies of the Malay Archipelago, 4th edition.* Kuala Lumpur: Malayan Nature Society.

D'Abrera, B. (1980) *Butterflies of the Afrotropical Region*. Melbourne: Lansdowne Editions.

D'Abrera, B. (1997) *Butterflies of the Afrotropical Region, Part I*. Melbourne and London: Hill House Publishers.

Daily, G. C., Ehrlich, P. R. (1995) Preservation of biodiversity in small rain-forest patches: rapid evaluations using butterfly trapping. *Biodiversity and Conservation* **4**, 35-55.

Davis, D. E. (1944) A comparison of mosquitos captured with avial bait at different vegetation levels. *Animal Behaviour* **26**, 138-147.

Debinski, D. M., Ray, C., Saveraid, E. H. (2001) Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? *Biological Conservation* **98**, 179-190.

DeVries, P. J. 1986. Hostplant records and natural history notes on Costa Rican butterflies (Papilionidae, Pieridae and Nymphalidae). *J. Res. Lep*. **4**, 290-333.

DeVries, P. J. (1987) *The butterflies of Costa Rica and their natural history (Papilionidae, Pieridae, Nymphalidae)*. Princeton University, Princeton, New Jersey.

DeVries, P. J. (1988) Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera* **26**, 98-108.

DeVries, P. J., Murray, D., Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.* **62**, 343-64.

Devries, P. J., Walla, T. R., Greeney, H. F. (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society* **68**, 333-353.

DeVries, P. J., Walla, T. R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society* **74**, 1-15.

DeVries, P. J. (2001) Butterflies. In *Encyclopedia of Biodiversity* (Levin, S., ed.), pp. 559-573. New York: Academic Press.

Dobson, A. P. (1995) *Conservation and biodiversity*. New York: Scientific American Library.

Dudley, R. (1991) Biomechanics of flight in neotropical butterflies: aerodynamics and mechanical power requirements. *The journal of experimental biology* **159**, 335-357.

Dueser, R. D., Shugart, H. H. (1978) Microhabitats in a forest-floor small mammal fauna. *Ecology* **59**, 89-98.

Dudley, N., Jeanrenaud, J. P., Sullivan, F. (1995) *Bad harvest? The timber trade and the degradation of the world’s forests*. London: Earthscan Publications.

Ebert, G., Rennwald, E. (1991a) *Die Schmetterlinge Baden-Württembergs, Part 1*. Stuttgart: Verlag Eugen Ulmer.

Ebert, G., Rennwald, E. (1991b) *Die Schmetterlinge Baden-Württembergs, Part 2*. Stuttgart: Verlag Eugen Ulmer.

Eggleton, P., Bignell, D. E., Sands, W. A., Waite, B., Wood, T. G., Lawton, J. H. (1995) The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forets Reserve, southern Cameroon. *J. Trop. Ecol.* **11**, 85-98.

Ehrlich, P. R., Gilbert, L. E. (1973) Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* **5**, 69-82.

Ehrlich, P. R., Raven, P. H (1964) Butterflies and plants: a study in coevolution. *Evolution* **18**, 586-608.

Emmel, T. C., Larsen, T. B. (1997) Butterfly diversity in Ghana, West Africa. *Trop. Lepid.* **8**, 1-13.

Erwin, T. L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36**, 74-75.

FAO (1988) *An interim report on the state of forest resources in the developing countries*. Rome: FAO.

Fermon, H., Waltert, M., Larsen, T. B., Dall'Asta, U., Mühlenberg, M. (2000) Effects of forest management on diversity and abundance of fruit-feeding nymphalid butterflies in south-eastern Côte d'Ivoire. *Journal of Insect Conservation* **4**, 173-189.

Fermon, H., Schulze, C. H., Waltert, M., Mühlenberg, M.(2001) The butterfly community of the Noyau Central, Lama Forest (Republic of Benin), with notes on its ecological composition and geographic distribution. *African Entomology* **9**, 177-185.

Fermon, H., Waltert, M., Mühlenberg, M. (in prep.) Movement and vertical stratification in tropical fruit feeding butterflies. Submitted to the *Journal of Insect Conservation*.

Fiedler, K. (1998) Dieth breath and host plant diversity of tropical vs. temperate zone herbivores: South-East Asian and West Palearctic butterflies as a case study. *Ecol. Entomol.* **23**, 285-297.

Ganzhorn, J. U., Ganzhorn, A. W., Abraham, J.-P., Andriamanarivo, L., Ramananjatavo, A. (1990) The impact of selective logging on forest structure and tenrec populations in western Madagascar. *Oecologia* **84**, 126-33.

Gilbert, L. E. (1984) The biology of butterfly communities. In *The Biology of Butterflies.* (Vane-Wright, R. I, Ackery, P. R., eds.), pp. 41-54. Princeton: Princeton University Press.

Gomez-Pompa, A., Whitmore, T. C., Hadley, M. (1991) *Rain Forest Regeneration and Management*. Paris: Unesco.

Gutierrez, D., Thomas, C. D. (2000) Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni*. *Ecological Entomology* **25**, 165-170.

Haddad, N. M. (1999) Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* **9**, 612-622.

Hall, J. B., Swain, M.D. (1976) Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology* **64**, 913-951.

Hancock, D. L. (1992) The *Bebearia mardania* complex (Nymphalidae). *Journal of the Lepidopterists' Society* **46**, 54-69.

Hamer, K .C., Hill, J. K., Lace, L. A., Langan, A. M. (1997) Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *J. Biogeo.* **24**, 67-75.

Hamer, K. C., Hill, J. K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology* **14**, 1435-1440.

Hawthorne, W. D., Abu-Juam, M. (1995) *Forest protection in Ghana. With particular reference to vegetation and plant species*. IUCN/ODA/Ghana Forest Department, Gland: IUCN.

Hawthorne, W. D. 1993. *Forest regeneration after logging*. London: ODA Forestry Series No. 3.

Hecq, J. (1988a) Etude des *Bebearia*, groupe *mardania*. *Lambillionea* **88**, 119-24.

Hecq, J. (1988b) Remarques sur les *Catuna* du groupe *crithea* (Lepidopt. Nymph.). *Lambillionea* **88**, 151.

Hecq, J., Vuattoux, R. (1989) Biologie des Euphaedra (Nymphalidae Africains). *Lambillionea* **89**, 44-50.

Hecq, J. (1990) Les *Bebearia*. *Révue d'Entomologie Génerale (Lambillionea - fascicule hors série)* **1**, 1-46.

Hecq, J. (1992) *Euryphura* et *Euryphurana* (nymphalides Africains). *Révue d'Entomologie Générale (Lambillionea -fascicule hors série)* **6**, 1-26.

Hecq, J. (1994a) Remarques sur quelques espèces de Nymphalidae Africains des genres *Euphaedra*, *Bebearia* et *Euriphene*. *Lambillionea* **94**, 437-9.

Hecq, J. (1994b) *Euriphene (Nymphalidae Africains).* Bruxelles: Revue d'Entomologie Générale.

Hecq, J. (1997) *Euphaedra.* Tervuren: Lambillionea, Union des Entomologistes belges.

Henning, S. F. (1989) *The Charaxinae butterflies of Africa*. Johannesburg: Aloe Books.

Hetzel, F. (1998) *The nutrient and water cycle in a tropical rain forest and a cocoa plantation in Côte d'Ivoire*. PhD thesis, University of Göttingen, Germany.

Hill, C. J., Gillison, A. N., Jones, R. E (1992) The spatial distribution of the rain forest butterflies at three sites in North Queensland. *Journal of Tropical Ecology* **8**, 37-46.

Hill, J. K., Kramer, K. C., Lace, L. A., Banham, W. M. T. (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *J. Appl. Ecol.* **32**, 754-60.

Hill, J. K., Hamer, K. C. (1998) Using species abundance models as indicators of habitat disturbance in tropical forests. *Journal of Applied Ecology* **35**, 458-460.

Hill, J. K. (1999) Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *J. Appl. Ecol.* **36**, 564-72.

Hill, J. K., Hamer, K. C. , Tangah, J., Dawood, M. (2001) Ecology of tropical butterflies in rainforest gaps. *Oecologia* **128**, 294-302.

Holloway, J. D., (1987) *The moths of Borneo, Part 3.* Kuala Lumpur: Southdene Sdn. Bhd.

Holloway, J. D., Kirk-Spriggs, A. H., Khen, C. V. (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Phil. Trans. R. Soc. London B.* **335**, 425-36.

Hunter, M. L. (1999) *Maintaining biodiversity in forest ecosystems*. Cambridge: Cambridge University Press.

Hutchinson, J., Dalziel, J. M. (1954) *Flora of West Tropical Africa*. London: The Whitefriars Press.

ICBP (1992) *Putting biodiversity on the map: priority areas for global conservation*. Cambridge: International Council for Bird Conservation.

Intachat, J., Holloway, J. D. (2000) Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropcical forest? *Biodiversity and Conservation* **9**, 1417-1439.

Jackson, T. H. E. (1961) Entomological studies from a high tower in Mpanga Forest, Uganda. IX Observations on Lepidoptera (Rhopalocera). *Trans. R. Ent. Soc. Lond.* **113,** 346-350.

Janzen, D.H. (1987) Insect diversity of a Costa Rican dry forest: why keep it, and how? *Biological Journal of the Linnean Society* **30**, 343-356.

Johns, A.D. (1992) Species conservation in managed tropical forests. In *Tropical deforestation and species extinction* (Whitemore, T. C., Sayer, J. A., eds.), pp. 15-33. London: Chapman and Hall.

Keller, E. C., Mattoni, H. T., Sieger, M. S. B. (1966) Preferential return of artificially displaced butterflies. *Animal Behavior* **14**, 197-200.

Kiltie, R. A. (1993) New light on forest shade. *Trends Ecol. Evol.* **8**, 39-40.

Kingsolver, J.G. (1999) Experimental analyses of wing size, flight, and survival in the western white butterfly. *Evolution* **53**, 1479-1490.

Kingsolver, J. G., Srygley, R. B. (2000) Experimental analyses of body size, flight and survival in pierid butterflies. *Evolutionary Ecology Research* **2**, 593-612.

Klein, B. C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* **70**, 1715-1725.

Knutson, R. L., Kwilosz, J. R. (1999) Movement Patterns and Population Characteristics of the Karner Blue Butterfly (Lycaeides melissa samuelis) at Indiana Dunes National Lakeshore. *Natural Areas Journal* **19**, 109-120.

Krebs, C. J. (1989) *Ecological Methodology*. New York: Harper and Row Publishers.

Kremen, C. (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Appl.* **2**, 203-17.

Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R.F., Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**, 796-808.

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

Larsen, T. B., Riley, J., Cornes, M. A. (1979) The butterfly fauna of a secondary bush locality in Nigeria. *J. Res. Lepid.* **18**, 4-23.

Larsen, T. B. (1987) Seasonal variation among tropical butterflies. *Naturens Verden* **4**, 118-122.

Larsen, T. B. (1991) *The butterflies of Kenya and their natural history*. Oxford: Oxford University Press.

Larsen T. B., Dall'Asta U. (1994) *Liste provisoire commentée des papillons (Lepidoptera Rhopalocera & Grypocera) de la Forêt Classée de la Bossematié (Est de la Côte d'Ivoire)*. GTZ-Project 88.2522.6-01.100. dallasta@africamuseum.ac.be

Larsen, T. B. (1994a) Fruit-feeding butterflies in large numbers on flowers. *Entomologists' Rec. J. Var.* **106**, 157-8.

Larsen, T. B. (1994b) *The butterflies of Ghana - their implications for conservation and sustainable use*. Report to IUCN and Dept. of Game and Wildlife, Ghana. torben.larsen@hotmail.com

Larsen, T.B. (1995a) Butterfly biodiversity and conservation in the Afrotropical region. In *Ecology and Conservation of Butterflies* (Pullin, A.S., ed.), pp. 290-303. London: Chapman and Hall.

Larsen, T. B. (1995b) Butterflies in Kakum National Park, Ghana. *Metamorphosis* **6**, 138-145.

Larsen, T. B. (1996a) Butterflies as indicator species in Africa - Presidential address. *Trop. Lepid. News* **3**, 1-4.

Larsen, T. B. (1996b) *The butterflies of Kenya and their natural history (2nd edition)*. Oxford: OUP.

Larsen, T. B. (1997) An overview of the distribution patterns of afrotropical rainforest butterflies (Lepidoptera: Rhopalocera). Proceedings of the inaugural conference on African Lepidoptera, Nairobi, 1997. *Metam. Occ. Suppl.* **3**, 183-8.

Larsen, T. B., Mei, M. (1998) Butterflies from a Guinea transition area, the Parc National de Haut Niger (Republic of Guinea), with description of a new subspecies of *Platylesches robusta* (Lepidoptera Hesperiidae). *Bollettino della Societa Entomologica Italiana* **130**, 255-272.

Larsen, T. B. (1999) *Butterflies of West Africa - origins, natural history, diversity and conservation*. Manila: Larsen CD-ROM. torben.larsen@hotmail.com

Lepš, J., Spitzer, K. (1990) Ecological determinants of butterfly communities (Lepidoptera, Papilionoidea) in the Tam Dao Mountains. Vietnam. *Acta Entomol. Bohemoslov.* **87**, 182-94.

Levey, D. J. (1988) Tropical wet forest treefall gaps and distributions of understorey birds and plants. *Ecology* **69**, 1076-89.

Lewis, O. T., Wilson, R. J., Harper, C. H. (1998) Endemic butterflies on Grande Comore: habitat preferences and conservation priorities. *Biological Conservation* **85**, 113-121.

Lewis, O. T. (2000) Effects of experimental selective logging on tropical butterflies. *Conservation Biology* **15**, 389-400.

Libert, M. (1994) Évolution temporelle des populations de Rhopalocères de deux collines boisées des environs de Yaoundé (Cameroun). *Rev. Écol.: la terre et la vie* **49**, 151-75.

Lieberman, D., Lieberman, M. (1984) The causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica* **16**, 193-201.

Lortscher, M., Erhardt, A., Zettel, J. (1997) Local movement patterns of three common grassland butterflies in a traditionally managed landscape. *Bulletin de la Société Entomologique Suisse* **70**, 43-55.

Lovejoy, T. E., Bierregaard, R. O. Jr., Rylands, A. B. (1986) Edge and other effects of isolation on Amazon forest fragments. In *Conservation Biology: The Science of Scarcity and Diversity* (Soulé, M. E., ed.), pp. 257-85. Massachusetts: Sinauer Associates Inc.

MacArthur, R. H., Wilson, E .O. (1967) *The theory of island biogeography*. Princeton: Princeton University Press.

Magurran, A. E. (1988) *Ecological diversity and its measurement*. Princeton: Princeton University Press.

May, R. M. (1990) How many species? *Philosophical Transactions of the Royal Society of London B* **330**, 293-304.

McGraw, W. S., Monah, I. T., Abedi-Lartey, M. (1998) Survey of endangered primates in the forest reserves of eastern Côte d'Ivoire. *African Primates* **3**, 22-25.

Mendez, C. A., Sisk, T. D., Haddad, N. M. (1995) Beyond birds: multitaxonomic monitoring programs provide a broad measure of tropical biodiversity. In *The International Wildlife Management Congress* (Bissonnette, J. A., Krausman, P. R., eds), pp. 451-456. Bethesda: The Wildlife Society.

Michler, H. (1994) Bodenqualität und Nährstoffumsatz im Forêt Classée de la Bossematié. Ein Vergleich von Regenwald, landwirtschaftlicher Nutzfläche und Chromolaena-Brache. Diploma thesis, University of Göttingen, Germany.

Miller J. Y. (1994) Behavior in butterflies as a means of conservation: comparison of insular and continental fauna. *Florida Entomol.* **77**, 74-4.

Mühlenberg, M. (1993) *Freilandökologie*. 3rd edition. Heidelberg: Quelle and Meyer.

Mühlenberg, M., Slowik, J., Wöll, H., Waitkuwait, W. E. (1995): Strategies for restoration of tropical forests that incorporate wildlife protection: an example from the Côte d'Ivoire, West Africa. In *Integrating people and wildlife for a sustainable future. Proc. 1st Internat. Wildl. Management Congr.* (Bissonnette, J. A., Krausman, P. R., eds), pp. 413-17. Bethesda: The Wildlife Society.

Mühlenberg, M., Slowik, J., Waltert, M., Fermon, H., Singho, B., Waitkuwait, W. E. (1997) *Présentation des données du biomonitoring dans les forêts classées de l'est de la Côte d'Ivoire.* Report on population developments of monitoring species from four Forêts Classées to SODEFOR/GTZ, Zentrum für Naturschutz, Universität Göttingen: mmuehle@gwdg.de

Mühlenberg, M., Slowik, J., Waltert, M., Fermon, H., Singho, B., Waitkuwait, W. E. (1999) Biomonitoring in Tropenwäldern. Ein Beitrag zur Bewertung von Sustainable Use. *Göttinger Beitr. Land- u. Forstwirtsch. Tropen u. Subtropen* **133**, 220-5.

Mühlenberg, M., Waltert, M. (2000) Der Einfluß des Verhaltens von Wirbeltieren auf die Anwendung von Monitoringmethoden. Beispiele aus Westafrika. In *Internationales Symposium Naturschutz und Verhalten, Göttingen 1999* (Gottschalk, E., Mühlenberg, M., Barkow, A., Settele, J., eds.) Leipzig: UFZ-Berichte.

Mulkey, S. S., Kitajima, K., Wright, S. J. (1996) Plant physiological ecology in tropical forest canopies. *Trends in Ecology and Evolution* **11**, 408-412.

Murphy, D. D., Wilcox, B. A. (1986) Butterfly diversity in natural habitat fragments: A test of the validity of vertebrate-based management. In *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates,* (Verner, J., Morrison, M. L., Ralph, C. J., eds). Wisconsin: University of Wisconsin Press.

New, T. R. (1997) Are Lepidoptera an effective 'umbrella group' for biodiversity conservation? *J. Insect Conserv.* **1**, 5-12.

Norberg, U. M. (1986) Evolutionary convergence of foraging niche and flight morphology in insectivorous aerial-hawking birds and bats. *Ornis Scand.* **17**, 253-532.

Novotný, V. (1991) Effects of habitat persistence on the relationship between geographic distribution and local abundance. *Oikos* **61**, 431-3.

O'Farrell, M., Kaufman, D. W., Lundahl, D. W. (1977) Use of live-trapping with the assessment line method for density estimation. *Journal of Mammology* **58**, 575-582.

O'Farrell, M., Austin, G. T. (1978) A comparison of different trapping configurations with the assessment line technique for density estimations. *Journal of Mammology* **59**, 866-868.

Owen, D. F. (1971) *Tropical Butterflies*. Oxford: University Press.

Owen, D. F., Chanter, D. O. (1972) Species diversity and seasonal abundance in *Charaxes* butterflies (Nymphalidae). *J. Entomol.* **46**, 135-43.

Owen, D. F. (1977) Species diversity and seasonal abundance in Charaxes butterflies (Nymphalidae) in a garden in Northern Nigeria. *Bull. Inst. Fond. Afr. noire A* **39**, 346-50.

Owen, T. L., Wilson, R. J, Harper, C. H. (1998) Endemic butterflies on Grande Comore: habitat preferences and conservation priorities. *Biol. Conserv.* **85**, 113-21.

Parren, M. P. E., de Graaf, N. R. (1995) *The quest for natural forest management in Ghana, Côte d'Ivoire and Liberia*. Tropenbos Series 13. Wageningen: Tropenbos Foundation.

Pollard, E. (1977) A method for assessing changes in the abundance of butterflies. *Biological Conservation* **12**, 116-134.

Pomeroy, D. E., Service, M. W. (1986) *Tropical Ecology*. Harlow: Longman Scientific and Technical.

Primack, R.B. (2000) *A Primer of Conservation Biology, Second Edition*. Massachusetts: Sinauer Associates.

Rice, R. E., Gullison, R. E., Reid, J. W. (1997) Can sustainable management save tropical forests? *Scientific American* **276**, 44-49.

Rogo, L., Odulaja, A. (2001) Butterfly popultaions in two forest fragments at the Kenya coast. *African Journal of Ecology* **39**, 266-275.

Roland, J., Keyghobadi, N., Fownes S. (2000) Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* **81**, 1642-1653.

Sayer, J. A., Harcourt, C. S., Collins, N. M. (1992) *The Conservation Atlas of Tropical Forests. Africa.* New York: IUCN.

Schultz, C. B. (1996) Dispersal Behavior and Its Implications for Reserve design in a rare Oregon Butterfly. *Conservation Biology* **12**, 284-292.

Schulze, C. H. (1995) Die Tagfalterzönose eines südostasiatischen Regenwaldes. Muster und Mechanismen der Stratifikation. Diploma thesis, University of Würzburg, Germany.

Schulze, C. H., Fiedler, K. (1998) Habitat preference and flight activity of Morphinae butterflies in a Bornean rainforest, with a note on sound production by adult *Zeuxidia* (Lepidoptera: Nymphalidae). *Malay. Nat. J.* **52**, 191-193.

Scoble, M. J. (1992) *The Lepidoptera: form, function and diversity*. Oxford, New York, Toronto: Oxford University Press.

Scott, J. A. (1975) Flight patterns among eleven species of diurnal Lepidoptera. *Ecology* **53**, 1367-1377.

Shahabuddin, G., Terborgh, J. W. (1999) Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and effects of isolation. *Journal of Tropical Ecology* **15**, 703-722.

Shahabuddin, G., Herzner, G. A., Aponte, R. C., Del C. Gomez, M. (2000) Persistence of a frugivorous butterfly species in Venezuelan forest fragments: the role of movement and habitat quality. *Biodiversity and Conservation* **9**, 1623-1641.

Shinozaki (1963) Note on the species-area curve. *Proceedings 10th Annual Meeting, Ecol. Soc. Japan* **10**, p 5.

Shreeve, T. G. (1981) Flight Patterns of Butterfly Species in Woodlands. *Oecologia* **51**, 289-293.

Smith, A. P., Hogan, K. P., Idol, J. R. (1992) Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* **24**, 503-11.

Stattersfield, A. J., Crosby, N. J., Long, A. J., Wege, D. C. (1998) *Priorities for Bird Conservation*. Cambridge: Birdlife International.

Struhsaker, T. T. (1997) *Ecology of an African Rain Forest: logging in Kibale and the conflict between conservation and exploitation.* Gainesville: University Press of Florida.

SODEFOR (1994) Plan d'Aménagement de la Forêt Classée de la Bossematié (22 200 ha). Unpublished Report for the GTZ-KfW-SODEFOR, **PN 88.2522.6-01.00**.

Sparrow, H. R., Sisk, T. D., Ehrlich, P. R., Murphy, D. D. (1994) Techniques and guidelines for monitoring neotropical butterflies. *Conserv. Biol.* **8**, 800-9.

Spitzer, K. (1983) Seasonality of the butterfly fauna in southeastern Vietnam (Papilionidae. *Journal of Research of the Lepidoptera* **22**, 126-130.

Spitzer, K., Novotný, V., Tonner, M., Lepš, J. (1993) Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionidae) in a montane tropical rain forest, Vietnam. *J. Biogeo.* **20**, 109-21.

Spitzer, K., Jaroš J., Havelka, J., Lepš, J. (1997) Effects of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation* **80**, 9-15.

Statsoft (1995) *Statistica 5.1. Vol. I.* Oklahoma: Tulsa

Stork, N. E. (1988) Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35**, 321-337.

Sutton, S. L. (1979) The vertical distribution of flying insects in the lowland rainforest of Brunei: preliminary report. *Brunei Museum Journal* **4**, 161-173.

Sutton, S. L. (1983) The spatial distribution of flying insects in tropical rainforests. In *Tropical Rain Forest: ecology and Management* (Sutton, S. L., Whitmore, T. C., Chadwick, A. C., eds.). Oxford: Blackwell Scientific Publications.

Sutton, S. L. (1989) The spatial distribution of flying insects. In *Tropcial Rain Forest Ecosystems. Biogeographical and ecological Studies.* Amsterdam: Elsevier.

Sutton, S. L., Collins, N. M. (1991) Insects and tropical forest conservation. In *The Conservation of Insects and their Habitats. 15th Symposium of the Royal Entomological Society of London, September* 1989 (Collins, N. M., Thomas, J. A., eds), pp. 405-24. London: Academic Press.

Swaine, M. D., Hall, J. B. (1986) Forest structure and dynamics. In *Plant ecology in West Africa. Patterns and processes* (Lawson, G. W., ed.), pp. 273-307. Chichester: John Wiley and Sons.

Terborgh, J. (1980) *Vertical stratification of a neotropical forest bird community*. Symposium on habitat utilisation. Proceedings of the 17th International Ornithological Congress, pp. 1005-1012.

Terborgh, J. (1999) *Requiem for Nature*. Washington: Island Press.

Thomas, C. D., Cheverton, M. R. (1983) On the behaviour and flight pattern of the neotropical butterfly *Anartia fatima* Fabricius (Nymphalinae). *Journal of Research on the Lepidoptera* **21**, 202-204.

Thomas, C. D., Mallorie, H. C. (1985) Rarity, species richness and conservation: butterflies of the Atlas Mountains in Morocco. *Biol. Conserv.* **33**, 95-117.

Thomas, C. D. (1991) Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biol. Conserv.* **55**, 269-81.

Thomas, L., Laake, J.L., Derry, J.F., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Strindberg, S., Hedley, S.L., Burt, M.L., Marques, F., Pollard, J.H., Fewster, R.M. (1998) *Distance 3.5*. Research Unit for Wildlife Population Assessment. UK: University of St. Andrews.

Thomas, L., Buckland, S.T., Burnham, K.P., Anderson, D.R., Laake, J.L., Borchers, D.L., Strindberg, S. (2002) Distance Sampling. In *Encyclopedia of Environmetrics Volume 1* (El-Shaarawi, A.H., Piegorsch, W.W., eds.), pp 544-552. Chichester: John Wiley & Sons, Ltd.

Turchin, P. (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**, 1253-1266.

Turchin, P., Odendaal, F. J., Rausher, M. D. (1991) Quanitifying Insect Movement in the Field. *Environmental Entomology* **20**, 955-963.

Vickery, M. L. (1984) *Ecology of tropical plants*. New York: John Wiley and Sons.

Vuattoux, R., Blandin, P. (1979) Les lépidoptères Nymphalides de Lamto. *Ann. Univ. D'Abidjan E* **12**, 141-158.

Vuattoux, R. (1988) Les lepidoptères de la station d'écologie de Lamto: Nouvelles données sur les Charaxinae. *Ann. Univ. d'Abidjan E* **20**, 31-41.

Waitkuwait, W. E. (1992) Restauration d'un écosystème forestier: contribution à l'amenagement de la faune. In *Compte rendu séminaire sur l'aménagement intégré des forêts denses humides et des zones agricoles périphériques* (Vooren, A. P., Schork, W., Blokhuis, W. A., Spijkerman, A. J. C., eds), pp. 203-14. Wageningen: La Foundation Tropenbos. Tropenbos Series 1.

Walpole, M. J., Sheldon, I. R. (1999) Sampling butterflies in tropical rainforest: an evaluation of a transect walk method. *Biological Conservation* **87**, 85-91.

Waltert, M. (1996) Unterholzstruktur und Habitatpräferenzen von Unterholzvögeln im Forêt Classée de la Bossematié – Erste Ergebnisse aus dem Zeitraum Dezember 1995 – März 1996. Report to the GTZ, Eschborn, SODEFOR, Abengourou, pp. 39. mwalter@gwdg.de

Waltert, M., Yaokokore Beibro, K. H., Mühlenberg, M., Waitkuwait, W. E. (1999) Preliminary check-list of the birds of the Bossematié area, Côte d'Ivoire. *Malimbus* **21**, 93-109.

Waltert, M. (2000a) Forest management and the distribution of understorey birds in the Bossematié forest, eastern Côte d'Ivoire. *Ostrich* **71**, 295-299.

Waltert, M. (2000b) Diversity and structure of a bird community in a logged forest in south-east Côte d'Ivoire. PhD thesis, University of Göttingen, Germany.

Warren, M. S. (1985) The influence of shade on butterfly numbers in woodland rides to the wood white *Leptidea sinapsis*. *Biol. Cons.* **33**, 147-164.

Warren, M. S., (1987) The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia* II. Adult population structure and mobility. *Journal of Applied Ecology* **24**, 483-498.

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

Whitmore, T. C. (1993) *Tropische Regenwälder*. Heidelberg, Berlin, New York: Spektrum Akademischer Verlag.

Willott, S. J., Lim, D. C., Compton, S. G., Sutton, S. L. (2000) Effects of Selective Logging on the Butterflies of a Bornean Rainforest. *Conservation Biology* **14**, 1055-1065.

Wilson, E. O. 1988. The current state of biological diversity. In *Biodiversity* (Wilson, E.O. ed.), pp. 3-18. Washington: National Academic Press.

WIR (1985). *Tropical Forests: A Call to Action*. Washington: World Resources Institute.

Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* **47**, 369-381.

Wolda, H. (1981) Similarity indices, sample size and diversity. *Oecologia* **50**, 296-302.

Wolda, H. (1987) Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* **30**, 313-323.

Wood, B., Gillman, M. P. (1998) The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. *Biodivers. and Conserv.* **7**, 597-616.

World Conservation Monitoring Centre (1992) *Global biodiversity: status of the Earth's living resources*.London: Chapman and Hall.

Wöll, H. J. (1992) Le projet ”Rehabilitation de la Forêt Classée de Bossematié”, Côte d'Ivoire, Region d'Abengourou. In *Compte rendu séminaire sur l'aménagement intégré des forêts denses humides et des zones agricoles périphériques* (Vooren, A. P., Schork, W., Blokhuis, W. A., Spijkerman, A. J. C., eds), pp. 163-79. Wageningen: La Foundation Tropenbos. Tropenbos Series 1.

Yoda, K.(1992) Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Jap. Jour. Ecol.* **24**, 247-54.

Appendices

Appendix 1 Baited butterfly species within the different management zones of the study plot

Individual numbers of Nymphalidae species trapped in a regenerating control plot (C) compared to an adjacent, three year old thinned forest plot (T) and a tree plantation (P) during the dry and the wet season 1996 and in three different vertical heights 1m, 12m and 25m during the wet season 1997 in a 75 ha study site in the heavily logged Bossematié Forest, south-east Côte d'Ivoire. p=samples x sampling days. Authorities and dates can be found in the Afrotropical catalogue (Ackery et al. 1995).

	DRY SEASON 96			WET SEASON 96			WET SEASON 97			TOTAL
	C	T	P	C	T	P	1m	12m	25m	
	p=168	p=168	p=60	p=168	p=168	p=60	p=68	p=68	p=68	
Apaturinae										
Apaturopsis cleochares	0	0	0	0	0	0	0	0	2	2
Nymphalinae										
Ariadne enotrea	2	3	29	0	0	1	0	0	0	35
Aterica galene	1	3	0	4	11	0	22	0	1	42
Bebearia abesa	2	0	0	2	1	0	24	0	1	30
B. absolon	2	0	0	6	0	15	37	0	0	60
B. arcadius	0	0	0	3	2	0	4	0	0	9
B. cocalia	3	7	0	3	11	0	7	0	0	31
B. demetra	1	0	0	10	3	0	7	0	0	21
B. laetitia	0	0	0	1	1	0	0	0	0	1
B. maledicta	0	0	0	2	1	0	2	0	0	6
B. mandinga	0	2	0	13	9	1	21	0	0	46
B. oxione	0	0	0	0	0	0	8	0	0	8
B. phantasina	2	0	0	10	1	0	0	0	0	13
B. sophus	9	14	1	137	74	7	83	2	1	328
B. tentyris	4	5	0	24	32	2	197	1	1	266
B. theognis	3	1	0	11	7	2	1	0	0	24
B. zonara	4	2	0	3	0	0	49	0	0	58
Byblia anvatara	0	2	6	0	0	0	0	0	0	8
Catuna angustatum	0	0	0	0	0	0	1	0	0	1
C. crithea	1	0	0	0	0	0	4	0	0	5
Cymothoe aubergeri	4	1	0	0	0	0	5	5	0	16
C. caenis	4	0	1	0	0	0	0	31	22	60
C. coccinata	0	0	0	0	0	0	1	0	0	2
C. egesta	26	29	3	0	1	1	11	10	0	80
C. fumana	0	1	0	0	0	1	1	0	0	2
C. jodutta	0	0	0	0	0	1	0	1	0	1
C. mabillei	0	0	2	0	0	1	0	1	0	3
Euphaedra albocoerulea	1	4	0	1	1	0	2	0	0	9
E. ceres	13	9	0	35	26	0	38	0	0	121
E. crockeri	12	2	0	34	11	0	47	0	0	106
E. cyparissa	6	1	0	0	1	0	16	2	17	43
E. eburnensis	4	2	0	1	2	0	7	0	0	16
E. edwardsi	0	1	0	0	0	0	0	0	0	1
E. eleus	0	0	0	1	0	0	1	0	0	2
E. eupalus	0	0	0	3	1	0	4	0	0	8
E. gausape	6	2	0	11	3	0	9	0	0	31
E. harpalyce	35	23	0	20	7	0	18	0	0	103
E. janetta	14	4	0	12	10	0	21	2	1	64
E. laguerrei	1	0	0	0	0	0	0	0	0	1
E. medon	5	5	0	4	3	0	23	0	0	41
E. modesta	0	1	0	2	0	0	3	0	0	6
E. perseis	1	1	0	2	0	0	0	0	0	4
E. phaetusa	89	62	0	193	71	0	155	8	0	578

Appendix 1 (continued)

	DRY SEASON 96			**WET SEASON 96**			**WET SEASON 97**			***TOTAL***
	C	**T**	**P**	**C**	**T**	**P**	**1 m**	**12 m**	**25 m**	
Nymphalinae (cont.)										
E. sarcoptera	3	3	0	0	0	0	3	7	5	21
E. themis	0	1	0	2	0	0	3	0	0	6
E. xypete	0	0	0	3	0	0	6	0	0	9
Euptera zowa	0	0	0	0	0	0	0	0	1	1
Euriphene ampedusa	2	0	0	2	1	0	2	0	0	7
E. aridatha	0	0	0	1	0	0	5	0	0	6
E. attosa	1	0	0	4	0	0	2	0	0	7
E. barombina	4	1	0	1	1	0	52	0	0	59
E. gambiae	2	3	0	8	2	0	27	0	0	42
E. simplex	2	0	0	5	1	0	9	0	0	17
Euryphura chalcis	0	0	1	0	0	1	1	17	51	70
Eurytela dryope	0	1	9	0	0	1	0	1	0	12
E. hiarbas	0	0	0	0	0	0	0	2	3	5
Harma theobene	3	13	0	0	0	0	8	1	1	26
Hypolimnas anthedon	0	0	0	0	0	0	0	1	1	2
H. dubius	0	0	0	0	0	0	0	0	1	1
H. salmacis	0	1	1	1	0	0	7	3	2	15
Junonia terea	0	0	0	0	0	1	1	0	0	2
Lachnoptera anticlea	2	2	1	2	0	0	0	0	1	8
Neptis agouale	0	0	0	0	0	0	0	1	0	1
N. metella	1	0	0	0	0	0	0	0	0	1
N. nysiades	0	0	0	0	0	0	0	1	1	2
N. strigata	0	1	0	0	0	0	0	1	1	3
Pseudoneptis bugandensis	1	0	0	0	0	0	0	0	0	1
Pseudacraea eurytus	0	0	0	0	0	0	1	0	1	2
P. lucretia	0	0	1	0	1	0	1	1	16	20
P. warburgi	0	0	0	0	0	0	0	2	1	3
Salamis cacta	1	3	9	0	1	0	0	0	0	14
Satyrinae										
Bicyclus abnormis	101	36	1	32	6	0	12	13	12	213
B. dorothea	49	60	47	5	23	10	12	1	0	207
B. evadne	2	0	0	1	0	0	0	0	0	3
B. funebris	148	106	116	0	0	0	3	0	0	373
B. madetes	1	1	1	7	0	7	0	0	0	17
B. mandanes	3	3	5	0	0	0	1	1	0	13
B. martius	51	50	8	36	23	12	6	1	1	188
B. nobilis	11	6	0	2	1	0	0	0	0	20
B. procora	59	59	2	29	16	4	12	1	0	182
B. safitza	0	1	5	0	1	0	3	0	1	11
B. sambulos	35	23	0	72	39	5	11	1	0	186
B. sandace	10	25	16	8	21	17	13	0	0	110
B. taenias	29	44	4	11	9	5	4	0	0	106
B. vulgaris	78	134	74	3	2	4	6	0	0	301
B. xeneas	58	99	8	28	29	3	12	18	7	262
B. zinebi	148	91	2	331	273	30	144	4	0	1023
Elymnias bammakoo	1	0	0	0	0	0	0	0	0	1
Gnophodes betsimena	94	78	46	9	12	15	19	10	2	284
G. chelys	188	148	20	93	57	13	109	20	1	649
Hallelesis halyma	0	2	0	0	1	0	0	0	0	4
Melanitis leda	5	4	1	2	0	0	5	8	6	31
Charaxinae										
Charaxes ameliae	0	1	1	0	1	0	0	1	2	6

Appendix 1 (continued)

	DRY SEASON 96			WET SEASON 96			WET SEASON 97			TOTAL
	C	**T**	**P**	**C**	**T**	**P**	**1 m**	**12 m**	**25 m**	
Charaxinae (cont.)										
C. anticlea	0	1	8	2	0	1	2	33	48	95
C. bipunctatus	24	46	13	25	11	4	2	23	19	167
C. brutus	2	4	6	0	1	4	2	7	5	31
C. candiope	2	1	2	0	0	0	0	0	0	4
C. castor	0	0	6	0	1	1	0	0	0	8
C. cedreatis	0	2	1	0	0	0	2	4	13	23
C. cynthia	46	85	21	22	32	5	20	61	10	302
C. dreuxi	0	0	0	0	0	0	0	0	1	1
C. etesipe	0	0	2	0	0	0	0	0	1	3
C. etheocles	0	0	4	0	1	2	0	12	47	66
C. eupale	0	1	3	1	0	1	0	2	7	15
C. fulvescens	0	1	0	0	0	0	2	0	0	3
C. imperalis	0	1	0	0	0	1	0	0	0	2
C. lucretius	2	2	6	0	1	1	0	3	6	21
C. lycurgus	0	1	0	0	0	0	0	1	0	2
C. numenes	5	6	2	1	7	2	1	2	1	27
C. paphianus	0	0	0	0	0	0	0	0	1	1
C. petersi	0	0	0	0	0	0	0	1	2	3
C. pleione	0	6	6	1	2	2	0	5	4	29
C. pollux	3	0	1	0	0	0	0	0	0	1
C. protoclea	79	56	9	50	42	12	58	45	8	359
C. tiridates	23	46	39	8	8	8	2	7	9	150
C. virilis	0	5	3	0	2	0	0	4	5	20
C. zelica	1	0	1	0	0	0	0	0	0	1
C. zingha	14	12	5	15	17	12	2	8	2	87
Euxanthe eurinome	0	0	0	0	1	0	0	0	0	1
Palla decius	0	2	1	3	1	0	1	0	0	7
P. publius	0	7	1	4	4	2	1	4	0	23
P. ussheri	3	9	2	4	9	0	1	2	0	31
P. violenitens	21	22	2	6	15	2	0	1	1	70
Acraeidae										
Acraea vestalis	0	0	0	0	0	0	0	0	1	1
Lycaenidae										
Oxylides faunes	1	0	0	0	0	0	0	0	0	1
Total individuals	**1574**	**1503**	**565**	**1388**	**966**	**220**	**1425**	**405**	**359**	**8400**

Appendix 2 Baited butterflies within the different succession stages of the study plot

Individual numbers of Nymphalidae species trapped in the different succession stages S1 (q = 26), S2 (q = 23), S3 (q = 13) and gap habitats (q = 3) during the dry and wet season 1996 (each sampled during 6 consecutive days) in a 75 ha study site in the heavily logged Bossematié Forest, south-east Côte d'Ivoire. Authorities and dates can be found in the Afrotropical catalogue (Ackery *et al*. 1995).

	DRY SEASON 96				WET SEASON 96				TOTAL
	Gap	S1	S2	S3	Gap	S1	S2	S3	
Nymphalinae									
Ariadne enotrea	1	2	1	0	0	0	0	0	4
Aterica galene	0	4	1	0	2	9	2	2	20
Bebearia abesa	0	1	0	0	0	1	0	2	4
B. absolon	0	0	1	0	2	13	1	5	22
B. arcadius	0	0	0	0	0	3	2	0	5
B. cocalia	0	5	0	3	1	10	2	1	22
B. demetra	0	0	1	0	0	3	4	6	14
B. laetitia	0	0	0	0	0	0	0	1	1
B. maledicta	0	0	0	0	0	3	1	0	4
B. mandinga	0	1	0	1	1	10	5	6	24
B. phantasina	0	0	0	2	0	2	6	3	13
B. sophus	1	7	7	2	11	75	79	46	228
B. tentyris	0	2	4	1	5	25	14	12	63
B. theognis	0	1	2	0	1	11	6	0	21
B. zonara	0	2	1	1	0	1	1	1	7
Byblia anvatara	2	0	0	0	0	0	0	0	2
Catuna crithea	0	0	1	0	0	0	0	0	1
Cymothoe aubergeri	0	1	0	2	0	0	0	0	3
C. caenis	0	0	4	0	0	0	0	0	4
C. egesta	4	16	16	6	0	1	0	0	43
C. fumana	1	0	0	0	0	0	0	0	1
C. mabillei	0	2	1	0	0	0	0	0	3
Euphaedra ceres	1	12	4	1	4	24	18	15	79
E. crockeri	0	0	3	14	2	13	18	12	62
E. cyparissa	1	0	3	2	0	1	0	0	7
E. eburnensis	0	2	2	1	0	1	2	0	8
E. edwardsi	0	1	1	0	0	0	0	0	2
E. eleus	0	0	0	0	0	0	1	0	1
E. eupale	0	0	0	0	0	0	2	1	3
E. diffusa	1	0	0	1	2	0	0	1	5
E. gausape	0	3	4	2	0	3	4	7	23
E. harpalyce	2	25	14	7	2	8	9	8	75
E. janetta	1	5	6	6	2	10	8	2	40
E. medon	0	4	3	3	0	2	4	1	17
E. modesta	0	0	0	0	0	0	1	1	2
E. perseis	0	0	0	1	0	1	0	1	3
E. phaetusa	0	12	65	60	2	83	96	83	401
E. sarcoptera	0	0	3	1	0	0	0	0	4
E. themis	0	0	1	0	0	0	1	1	3
E. xypete	0	0	0	0	0	1	0	2	3
Euriphene ampedusa	0	0	1	0	0	1	0	2	4
E. aridatha	0	0	0	0	0	0	1	0	1
E. attosa	0	1	0	0	0	1	1	3	6
E. barombina	0	3	1	0	0	2	0	0	6
E. gambiae	0	4	0	1	0	3	4	3	15
E. simplex	0	0	0	2	2	1	0	3	8
Euryphura chalcis	0	0	1	0	0	0	0	0	1
Eurytela dryope	0	0	1	0	0	0	0	0	1

Appendix 2 (continued)

	DRY SEASON 96				**WET SEASON 96**				**TOTAL**
	Gap	S1	S2	S3	Gap	S1	S2	S3	
Harma theobene	4	8	2	0	0	0	0	0	14
Hypolimnas salmacis	0	2	0	0	0	0	1	0	3
Lachnoptera anticlea	0	1	0	1	0	1	1	0	4
Pseudoneptis bugandensis	0	1	1	0	0	0	0	0	2
Pseudacraea lucretia	0	0	0	0	0	0	1	0	1
Salamis cacta	0	4	0	0	0	1	0	0	5
Satyrinae									
Bicyclus abnormis	3	24	51	28	1	8	19	10	144
B. dorothea	9	45	42	7	0	8	19	1	131
B. evadne	0	1	0	0	0	0	1	0	2
B. funebris	17	63	86	40	0	0	0	0	206
B. madetes	0	1	1	0	0	5	7	2	16
B. mandanes	0	2	2	1	0	0	0	0	5
B. martius	0	34	24	23	1	27	18	13	140
B. nobilis	0	4	10	5	0	1	2	0	22
B. procora	1	36	28	31	1	14	20	10	141
B. safitza	0	1	0	0	0	1	0	0	2
B. sambulosus	2	22	14	10	4	46	37	24	159
B. sandace	1	20	10	4	3	19	7	0	64
B. taenias	1	15	30	8	4	8	7	1	74
B. vulgaris	11	109	57	14	1	3	1	0	196
B. xeneas	13	64	31	16	2	28	20	7	181
B. zinebi	4	60	55	34	22	258	199	125	757
Elymnias bammakoo	0	0	0	1	0	0	0	0	1
Gnophodes betsimena	7	51	50	32	2	9	6	4	161
G. chelys	12	91	95	52	8	50	63	29	400
Hallelesis halyma	0	2	1	0	0	1	0	0	4
Melanitis leda	1	2	4	1	0	0	1	1	10
Charaxinae									
Charaxes ameliae	1	0	0	0	1	0	0	0	2
C. anticlea	1	0	0	0	0	0	2	0	3
C. bipunctatus	4	36	22	4	4	14	13	5	102
C. brutus	2	1	1	0	0	0	1	0	5
C. candiope	0	1	1	0	0	0	0	0	2
C. castor	0	1	0	0	1	0	0	0	2
C. cedreatis	1	1	0	0	0	0	0	0	2
C. cynthia	5	57	26	8	7	34	9	4	150
C. etheocles	0	1	0	0	1	0	0	0	2
C. eupale	0	0	0	0	0	1	0	0	1
C. lucretius	1	1	0	0	1	0	0	0	3
C. lycurgus	0	0	1	0	0	0	0	0	1
C. numenes	2	4	3	1	1	3	3	1	18
C. pleione	0	2	0	1	0	2	1	0	6
C. protoclea	7	45	50	8	5	53	21	13	202
C. tiridates	4	30	20	1	2	10	4	0	71
C. virilis	0	2	0	0	1	1	0	0	4
C. zelica	0	1	0	0	0	0	0	0	1
C. zingha	0	9	15	3	2	15	13	2	59
Palla decius	0	0	0	0	1	2	1	0	4
P. publius	0	3	0	0	0	6	1	1	11
P. ussheri	0	9	2	1	1	7	4	1	25
P. violenitens	2	17	11	2	4	12	3	2	53
Total individuals	131	1000	899	457	120	970	799	487	4863

Appendix 3 Species with marked differences in capture frequencies between different succession stages of the Bossematié Forest Reserve

Table 1: dry season 96. Values listed are mean number of individuals calculated from q samples (each 6 days, higher values are bold by pairs of stages gap/S1 versus S2/S3); significance levels are based on gamma rank correlation for multiple ties (Statsoft, 1995).

	Succession stage					
	gap (q=3)	S1 (q=26)	S2 (q=23)	S3 (q=13)	γ	p <
CHARAXINAE						
Charaxes tiridates	**1.33**	**1.15**	0.87	0.08	-0.5539	0.000
C. bipunctatus	**1.33**	**1.38**	0.96	0.31	-0.4315	0.001
C. cynthia	**1.67**	**2.19**	1.13	0.61	-0.3770	0.01
C. brutus	**0.67**	**0.04**	0.04	0.00	-0.7231	0.01
Palla violenitens	**0.67**	**0.65**	0.48	0.15	-0.3278	0.05
SATYRINAE						
Bicyclus vulgaris	**3.67**	**4.19**	2.48	1.08	-0.3639	0.001
B. xeneas	**4.33**	**2.46**	1.35	1.23	-0.2373	0.05
B. dorothea	**3.00**	**1.73**	1.83	0.54	-0.2421	0.05
B. abnormis	1.00	0.92	**2.22**	**2.15**	0.2737	0.01
B. nobilis	0.00	0.15	**0.43**	**0.38**	0.4335	0.01
B. zinebi	1.33	2.31	**2.39**	**2.62**	0.1983	(0.07)
NYMPHALINAE						
Harma theobene	**1.33**	**0.31**	0.09	0.00	-0.7024	0.001
Euphaedra ceres	**0.33**	**0.46**	0.17	0.08	-0.5185	0.01
Ariadne enotrea	**0.33**	**0.10**	0.04	0.00	-0.6512	0.05
Aterica galene	**0.00**	**0.20**	0.04	0.00	-0.6105	0.05
E. crockeri	0.00	0.00	**0.13**	**1.10**	0.8971	0.000
E. phaetusa	0.00	0.46	**2.83**	**4.62**	0.2930	0.05

Table 2: wet season 96. Values listed are mean number of individuals calculated from q samples (each 6 days, higher values are bold by pairs of stages gap/S1 versus S2/S3); significance levels are based on gamma rank correlation for multiple ties (Statsoft, 1995).

	Succession stage					
	gap (q=3)	S1 (q=26)	S2 (q=23)	S3 (q=13)	γ	p <
CHARAXINAE						
Charaxes cynthia	**2.33**	**1.31**	0.39	0.31	-0.3429	0.001
C. tiridates	**0.67**	**0.38**	0.17	0.00	-0.4947	0.01
C. protoclea	**1.67**	**2.04**	0.91	1.00	-0.2488	0.05
Palla violenitens	**1.33**	**0.46**	0.13	0.15	-0.4741	0.01
P. decius	**0.33**	**0.08**	0.04	0.00	-0.5862	0.05
SATYRINAE						
Bicyclus sandace	**1.00**	**0.73**	0.30	0.00	-0.5835	0.000
B. vulgaris	**0.33**	**0.11**	0.04	0.00	-0.5782	0.05
B. abnormis	0.33	0.31	**0.83**	**0.77**	0.4132	0.000
B. procora	0.33	0.54	**0.87**	**0.77**	0.3500	0.01
B. zinebi	7.33	9.92	**8.65**	**9.61**	0.2509	0.03
B. sambulos	1.33	1.77	**1.61**	**1.85**	0.2489	0.04
Gnophodes chelys	2.67	1.93	**2.74**	**2.23**	0.2717	0.02
Melanitis leda	0.00	0.00	**0.04**	**0.08**	0.7857	0.03
NYMPHALINAE						
Aterica galene	**0.67**	**0.35**	0.09	0.15	-0.4584	0.02
Bebearia mardania	**0.33**	**0.42**	0.26	0.00	-0.4322	0.02
Bebearia absolon	**0.67**	**0.50**	0.04	0.38	-0.3246	0.05
Euphaedra ceres	**1.33**	**0.92**	0.78	1.15	-0.2503	(0.06)

Appendix 3 (continued)

	Succession stage					
	gap (q=3)	S1 (q=26)	S2 (q=23)	S3 (q=13)	γ	p <
NYMPHALINAE (cont.)						
Bebearia phantasina	0.00	0.08	**0.26**	**0.23**	0.520	0.01
Bebearia demetra	0.00	0.11	**0.17**	**0.46**	0.4476	0.03
Bebearia abesa	0.00	0.04	**0.00**	**0.16**	0.5702	(0.07)
Euriphene gambiae	0.00	0.12	**0.17**	**0.23**	0.4383	0.03
E. attossa	0.00	0.04	**0.04**	**0.15**	0.5714	0.04
Euphaedra. phaetusa	0.67	3.19	**4.17**	**6.38**	0.4404	0.001
E. gausape	0.00	0.11	**0.17**	**0.54**	0.5230	0.01
E. crockeri	0.67	0.50	**0.78**	**0.92**	0.2980	0.03
E. eupale	0.00	0.00	**0.09**	**0.08**	0.7647	0.04

Appendix 4 Systematic list of the butterflies (Rhopalocera) of the Bossematié Forest Reserve

The preliminary check-list of butterfly species recorded from the Bossematié Forest Reserve is presented in systematic order. The list is based on own records obtained between May 1995 and August 1997, completed with records by T.B. Larsen (Manila, The Phillipines) and U. Dall'Asta (Tervuren, Belgium) between October 1993 and May 1994 (data illustrated in Larsen 1999). Authorities and dates were derived from the Afrotropical catalogue of Ackery *et al.* (1995). Species are arranged by family, subfamily, tribes and genus and listed in alphabetic order. For each species, ecological category and geographical distribution (see Larsen, 1991, 1994b, 1996a, 1996b, 1997, 1999; Emmel & Larsen 1997) is given. The following abbreviations are used:

Ecological category

ALF = generally distributed in forests.
DRF = centred on the drier forests.
MEF = centred on moist evergreen and semi-deciduous forests.
WEF = centred on the wettest forest habitats, the true rainforests.
GUI = centred on the Guinea savannah and forest fringes.
SUD = centred on the Sudan savannah.
UBQ = ubiquitous or widespread (usually not in virgin forest).
SPE = special habitat requirements such as swamps

Geographical distribution

GEQ = found from Ghana to Zaïre-Uganda.
WWE = found only in western West Africa.
WWN = from western West Africa to Nigeria-Cameroon border.
WWC = from western West Africa to Cameroun-Gabon-Congo zone.
WWZ = from western West Africa to Zaire or Zaire-Uganda border.
WWU = from western West Africa to Uganda or western Kenya.
WWT = from western West Africa to east of Rift Valley.
AAF = throughout Africa.

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
FAMILY PAPILIONIDAE		
SUBFAMILY PAPILIONINAE		
Genus *Graphium* SCOPOLI 1777		
Graphium illyris HEWITSON 1873	WEF	WWZ
Graphium leonidas leonidas FABRICIUS 1793	UBQ	AAF
Graphium policenes CRAMER 1775	ALF	AAF
Genus *Papilio* LINNAEUS 1758		
Papilio dardanus dardanus BROWN 1776	ALF	WWT
Papilio bromius bromius DOUBLEDAY 1845	ALF	WWT
Papilio nireus nireus LINNAEUS 1758	UBQ	AAF
Papilio menestheus menestheus DRURY 1773	ALF	WWN
Papilio cyproeofila cyproeofila BUTLER 1868	MEF	WWC
Papilio cynorta cynorta FABRICIUS 1793	ALF	WWU

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
FAMILY PIERIDAE		
SUBFAMILY COLIADINAE		
Genus *Catopsilia* HÜBNER 1819		
Catopsilia florella FABRICIUS 1793	UBQ	AAF
Genus *Eurema* HÜBNER 1819		
Eurema brigitta brigitta STOLL 1770	UBQ	AAF
Eurema hecabe solifera BUTLER 1875	UBQ	AAF
Eurema senegalensis BOISDUVAL 1836	ALF	WWU
SUBFAMILY PIERINAE		
Genus *Appias* HÜBNER 1819		
Appias epaphia epaphia BOISDUVAL 1833	UBQ	AAF
Appias sylvia sylvia FABRICIUS 1775	ALF	WWU
Genus *Belenois* HÜBNER 1819		
Belenois calypso calypso DRURY 1773	ALF	WWU
Belenois hedyle CRAMER 1777	DRF	WWN
Belenois theora theora DOUBLEDAY 1846	ALF	WWU
Genus *Dixeia* TALBOT 1932		
Dixeia capricornus capricornus WESTWOOD 1871	DRF	WWC
Dixeia cebron WESTWOOD 1871	DRF	WWC
Genus *Leptosia* HÜBNER 1818		
Leptosia alcesta alcesta STOLL 1781	ALF	AAF
Leptosia hybrida hybrida BERNARDI 1952	MEF	WWT
Genus *Nepheronia* BUTLER 1870		
Nepheronia thalassina thalassina BOISDUVAL 1836	ALF	AAF
Nepheronia argia argia FABRICIUS 1775	ALF	AAF
FAMILY NYMPHALIDAE		
SUBFAMILY ACRAEINAE		
Genus *Acraea* FABRICIUS 1807		
Acraea alciope HEWITSON 1852	ALF	WWU
Acraea circeis DRURY 1782	ALF	WWC
Acraea egina egina CRAMER 1775	ALF	WWT
Acraea endoscota LE DOUX 1928	ALF	WWU
Acraea epaea epaea CRAMER 1779	ALF	WWT
Acraea eponina CRAMER 1780	UBQ	AAF
Acraea jodutta jodutta FABRICIUS 1793	ALF	WWU
Acraea lycoa lycoa GODART 1819	ALF	WWU
Acraea pentapolis pentapolis WARD 1871	MEF	WWZ
Acraea pseudegina WESTWOOD 1852	UBQ	WWU
Acraea quirina quirina FABRICIUS 1781	ALF	WWT
Acraea umbra umbra DRURY 1782	UBQ	WWU
Acraea vestalis vestalis FELDER 1865	ALF	WWU
SUBFAMILY APATURINAE		
Genus *Apaturopsis* AURIVILLIUS 1898		
Apaturopsis cleochares cleochares HEWITSON 1873	MEF	WWT
SUBFAMILY DANAINAE		
Genus *Amauris* HÜBNER 1816		
Amauris niavius niavius LINNAEUS 1758	GUI	AAF
Genus *Danaus* KLUK 1802		
Danaus chrysippus LINNAEUS 1758	UBQ	AAF
SUBFAMILY LIBYTHEINAE		
Genus Libythea FABRICIUS 1807		
Libythea labdaca labdaca WESTWOOD 1851	ALF	AAF

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
SUBFAMILY SATYRINAE		
Tribe Biini		
Genus *Gnophodes* WESTWOOD 1851		
Gnophodes betsimena parmeno DOUBLEDAY 1849	ALF	AAF
Gnophodes chelys FABRICIUS 1793	MEF	WWT
Genus *Melanitis* FABRICIUS 1807		
Melanitis leda helena LINNAEUS 1758	UBQ	AAF
Tribe Elymniini		
Genus *Elymnias* HÜBNER 1818		
Elymnias bammakoo bammakoo DOUBLEDAY 1849	MEF	WWZ
Tribe Mycalesini		
Genus Bicyclus KIRBY 1871		
Bicyclus abnormis DUDGEON 1909	WEF	WWE
Bicyclus dorothea dorothea CRAMER 1779	ALF	WWC
Bicyclus evadne CRAMER 1779	WEF	WWZ
Bicyclus funebris GUERIN-MEN EVILLE 1844	DRF	WWU
Bicyclus madetes HEWITSON 1874	WEF	WWZ
Bicyclus mandanes HEWITSON 1873	ALF	WWU
Bicyclus martius melas CONDAMIN 1965	MEF	WWU
Bicyclus nobilis AURIVILLIUS 1893	WEF	WWC
Bicyclus procora KARSH 1893	WEF	WWU
Bicyclus safitza safitza HEWITSON 1851	GUI	AAF
Bicyclus sambulos unicolor CONDAMIN 1971	WEF	WWU
Bicyclus sandace HEWITSON 1877	ALF	WWZ
Bicyclus taenias HEWITSON 1877	MEF	WWZ
Bicyclus vulgaris BUTLER 1868	ALF	AAF
Bicyclus xeneas occidentalis CONDAMIN 1965	ALF	WWZ
Bicyclus zinebi BUTLER 1869	MEF	WWE
Genus *Hallelesis* CONDAMIN 1963		
Hallelesis halyma FABRICIUS 1793	MEF	WWE
Tribe Ypthimini		
Genus *Ypthima* VAN SON 1955		
Ypthima doleta KIRBY 1880	ALF	WWU
SUBFAMILY NYMPHALINAE		
Tribe Argynnini		
Genus *Lachnoptera* HORSFIELD 1829		
Lachnoptera anticlea HÜBNER 1819	MEF	WWU
Genus *Phalanta* HORSFIELD 1829		
Phalanta phalanta aethiopica ROTHSCHILD & JORDAN 1903	DRF	AAF
Phalanta eurytis eurytis DOUBLEDAY & HEWITSON 1848	ALF	AAF
Tribe Biblini (Eurytelini)		
Genus *Ariadne* HORSFIELD 1829		
Ariadne enotrea enotrea CRAMER 1779	ALF	WWU
Ariadne albifascia JOICEY & TALBOT 1921	ALF	WWU
Genus *Byblia* HÜBNER 1819		
Byblia anvatara crameri AURIVILLIUS 1894	UBQ	AAF
Byblia ilithyia Drury 1773	SUD	SAA
Genus *Eurytela* BOISDUVAL 1833		
Eurytela dryope dryope CRAMER 1775	DRF	WWT
Eurytela hiarbas hiarbas DRURY 1770	ALF	WWT
Genus *Neptidopsis* AURIVILLIUS 1898		
Neptidopsis ophione ophione CRAMER 1779	ALF	WWT

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
Tribe Cyrestini (Marpesiini)		
Genus *Cyrestis* BOISDUVAL 1832		
Cyrestis camillus camillus FABRICIUS 1832	ALF	WWT
Tribe Limenitini		
Genus *Aterica* BOISDUVAL 1833		
Aterica galene BROWN 1776	ALF	WWT
Genus *Bebearia* HEMMING 1960		
Bebearia abesa abesa HEWITSON 1869	MEF	WWU
Bebearia absolon absolon FABRICIUS 1793	ALF	WWE
Bebearia arcadius FABRICIUS 1793	WEF	WWE
Bebearia barce barce DOUBLEDAY 1847	WEF	WWU
Bebearia carshena Hewitson 1870	MEF	WWU
Bebearia cocalia FELDER & FELDER 1867	ALF	WWU
Bebearia dallastai HECQ 1994	ALF	WWE
Bebearia demetra GODART 1819	MEF	WWN
Bebearia laetitia laetitia PLÖTZ 1880	WEF	WWZ
Bebearia maledicta Strand 1912	WEF	WWN
Bebearia mandinga mandinga FELDER 1860	ALF	WWU
Bebearia mardania FABRICIUS 1793	ALF	WWN
Bebearia oxione oxione HEWITSON 1866	ALF	WWU
Bebearia phantasina STAUDINGER 1891	ALF	WWN
Bebearia sophus phreone FEISTHAMEL 1850	ALF	WWU
Bebearia tentyris HEWITSON 1866	ALF	GEQ
Bebearia zonara BUTLER 1871	DRF	WWU
Genus *Catuna* KIRBY 1871		
Catuna angustatum FELDER 1867	MEF	WWU
Catuna crithea crithea DRURY 1773	ALF	WWU
Catuna oberthueri KARSCH 1894	ALF	WWZ
Genus *Cymothoe* HÜBNER 1819		
Cymothoe adela STAUDINGER 1889	WEF	WWE
Cymothoe aubergeri PLANTROU 1977	WEF	WWE
Cymothoe caenis DRURY 1773	ALF	WWU
Cymothoe coccinata coccinata HEWISTON 1874	ALF	WWZ
Cymothoe egesta egesta CRAMER 1775	MEF	WWU
Cymothoe fumana fumana WESTWOOD 1850	MEF	WWZ
Cymothoe jodutta jodutta WESTWOOD 1850	ALF	WWU
Cymothoe mabillei OVERLAET 1944	MEF	WWC
Genus *Euphaedra* HÜBNER 1819		
Euphaedra albocoerulea ROTHSCHILD 1918	DRF	WWC
Euphaedra ceres FABRICIUS 1775	ALF	WWC
Euphaedra crockeri BUTLER 1869	MEF	WWE
Euphaedra cyparissa CRAMER 1775	ALF	WWN
Euphaedra eburnensis HECQ 1979	WEF	WWE
Euphaedra edwardsi VAN DER HOEVEN 1845	ALF	WWZ
Euphaedra eleus DRURY 1782	ALF	WWU
Euphaedra eupalus FABRICIUS 1781	MEF	WWE
Euphaedra francina GODART 1821	WEF	WWE
Euphaedra gausape BUTLER 1865	ALF	WWE
Euphaedra harpalyce CRAMER 1777	ALF	WWN
Euphaedra janetta BUTLER 1871	ALF	WWN
Euphaedra laguerrei HECQ 1979	MEF	WWE
Euphaedra medon LINNAEUS 1763	DRF	WWU
Euphaedra modesta HECQ 1982	WEF	WWE
Euphaedra perseis DRURY 1773	WEF	WWE

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
Euphaedra phaetusa BUTLER 1865	ALF	WWN
Euphaedra sarcoptera BUTLER 1871	MEF	WWZ
Euphaedra themis HÜBNER 1806	ALF	WWC
Euphaedra xypete HEWISTON 1865	ALF	WWN
Euphaedra zampa WESTWOOD 1850	WEF	WWE
Genus *Euptera* STAUDINGER 1891		
Euptera zowa FOX 1965	MEF	WWE
Genus *Euriphene* BOISDUVAL 1847		
Euriphene ampedusa HEWITSON 1866	ALF	WWN
Euriphene aridatha HEWISTON 1866	MEF	WWC
Euriphene attosa attosa HEWITSON 1865	MEF	WWU
Euriphene barombina AURIVILLIUS 1894	ALF	WWZ
Euriphene gambiae FEISTHAMEL 1850	ALF	WWZ
Euriphene simplex STAUDINGER 1891	MEF	WWN
Genus *Euryphura* STAUDINGER 1891		
Euryphura chalcis chalcis FELDER 1860	ALF	WWU
Euryphura togoensis SUFFERT 1904	WEF	WWE
Genus *Harma* Doubleday 1848		
Harma theobene theobene Doubleday 1848	ALF	WWT
Genus *Pseudacraea* WESTWOOD 1850		
Pseudacraea eurytus LINNAEUS 1758	ALF	WWU
Pseudacraea fulvaria BUTLER 1869	ALF	WWU
Pseudacraea lucretia lucretia CRAMER 1775	ALF	WWT
Pseudacraea semire CRAMER 1775	ALF	WWU
Pseudacraea striata BUTLER 1874	ALF	WWU
Pseudacraea warburgi AURIVILLIUS 1892	MEF	WWU
Genus *Pseudathyma* STAUDINGER 1891		
Pseudathyma sibyllina STAUDINGER 1890	MEF	WWU
Genus *Pseudoneptis* SNELLEN 1882		
Pseudoneptis bugandensis ianthe HEMMING 1964	MEF	WWZ
Tribe Neptini		
Genus *Neptis* FABRICIUS 1807		
Neptis agouale agouale PIERRE-BALTUS 1978	ALF	WWU
Neptis alta OVERLAET 1955	MEF	WWU
Neptis melicerta melicerta DRURY 1773	ALF	WWU
Neptis metella metella DOUBLEDAY & HEWITSON 1850	ALF	WWU
Neptis nemetes nemetes HEWITSON 1868	ALF	WWU
Neptis nicomedes HEWITSON 1874	ALF	WWU
Neptis nicoteles HEWITSON 1874	ALF	WWU
Neptis nysiades HEWITSON 1868	ALF	WWU
Neptis strigata AURIVILLIUS 1894	WEF	WWU
Neptis trigonophora melicertula STRAUDINGER 1912	ALF	WWT
Neptis troundi PIERRE-BALTUS 1978	MEF	WWC
Tribe Nymphalini		
Genus *Hypolimnas* HÜBNER 1821		
Hypolimnas anthedon anthedon DOUBLEDAY 1845	ALF	AAF
Hypolimnas dinarcha liberiensis BERNARDI 1959	WEF	WWU
Hypolimnas misippus LINNAEUS 1767	UBQ	AAF
Hypolimnas salmacis salmacis DRURY 1773	ALF	WWU
Genus *Junonia* HÜBNER 1819		
Junonia oenone oenone LINNAEUS 1758	UBQ	AAF
Junonia sophia sophia FABRICIUS 1793	ALF	WWU
Junonia stygia stygia AURIVILLIUS 1894	ALF	WWU
Junonia terea terea DRURY 1773	ALF	WWT

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
Genus *Salamis* BOISDUVAL 1833		
Salamis cacta cacta FABRICIUS 1793	ALF	WWU
Salamis parhassus parhassus DRURY 1782	ALF	AAF
SUBFAMILY CHARAXINAE		
Genus *Charaxes* OCHSENHEIMER 1816		
Charaxes ameliae doumeti PLANTROU 1984	ALF	WWZ
Charaxes angelae MINIG 1975	MEF	WWE
Charaxes anticlea anticlea DRURY 1782	ALF	WWU
Charaxes bipunctatus bipunctatus ROTHSCHILD 1894	WEF	WWU
Charaxes brutus brutus CRAMER 1779	ALF	WWT
Charaxes candiope candiope GODART 1824	GUI	AAF
Charaxes castor castor CRAMER 1775	DRF	WWT
Charaxes cedreatis HEWITSON 1874	ALF	WWU
Charaxes cynthia cynthia BUTLER 1865	ALF	WWU
Charaxes dreuxi BOUCHE & MINIG 1977	WEF	WWE
Charaxes etesipe etesipe GODART 1824	DRF	AAF
Charaxes etheocles etheocles CRAMER 1777	ALF	WWU
Charaxes eupale eupale DRURY 1782	ALF	WWU
Charaxes fulvescens AURIVILLIUS 1891	ALF	WWT
Charaxes imperialis imperialis BUTLER 1874	DRF	WWU
Charaxes lucretius lucretius CRAMER 1775	MEF	WWU
Charaxes lycurgus lycurgus FABRICIUS 1793	ALF	WWU
Charaxes numenes numenes HEWITSON 1859	ALF	WWU
Charaxes paphianus falcata BUTLER 1872	WEF	WWU
Charaxes petersi VAN SOMMEREN 1968	MEF	WWE
Charaxes pleione pleione GODART 1824	ALF	WWT
Charaxes pollux pollux CRAMER 1775	MEF	WWT
Charaxes protoclea protoclea FEISTHAMEL 1850	ALF	WWT
Charaxes tiridates tiridates CRAMER 1777	ALF	WWU
Charaxes varanes vologeses MABILLE 1876	GUI	AAF
Charaxes virilis virilis VAN SOMMEREN & JACKSON 1952	ALF	WWU
Charaxes zelica zelica BUTLER 1869	WEF	WWU
Charaxes zingha STOLL 1780	ALF	WWU
Tribe Euxanthini		
Genus *Euxanthe* HÜBBNER		
Euxanthe eurinome eurinome CRAMER 1775	ALF	WWU
Tribe Pallini		
Genus *Palla* HÜBBNER 1819		
Palla decius CRAMER 1777	MEF	WWZ
Palla publius publius STAUDINGER 1892	MEF	WWZ
Palla ussheri ussheri BUTLER 1870	MEF	WWZ
Palla violinitens violinitens CROWLEY 1890	ALF	WWU
SUBFAMILY LIBYTHEINAE		
Genus *Libythea* FABRICIUS 1807		
Libythea labdaca WESTWOOD 1851	ALF	AAF
FAMILY LYCAENIDAE		
SUBFAMILY LIPTENINAE		
Tribe Epitolini		
Genus *Hypophytala* CLENCH 1965		
Hypophytala hyettoides AURIVILLIUS 1895	MEF	WWC
Tribe Liptenini		
Genus *Citrinophila* KIRBY 1887		
Citrinophila marginalis KIRBY 1887	MEF	WWN

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
Genus *Falcuna* STEMPFFER & BENNETT 1963		
Falcuna campinus STEMPFFER & BENNETT 1965	WEF	WWE
Falcuna leonensis HOLLAND 1890	WEF	WWC
Genus *Larinopoda* BUTLER 1871		
Larinopoda eurema PLÖTZ 1880	MEF	WWE
Genus *Liptena* WESTWOOD 1866		
Liptena simplicia MÖSCHLER 1888	MEF	WWN
Genus *Micropentila* AURIVILLIUS 1895		
Micropentila adelgitha HEWITSON 1874	MEF	WWZ
Genus *Mimeresia* STEMPFFER 1961		
Mimeresia libentina HEWITSON 1866	ALF	WWC
Mimeresia semirufa GROSE-SMITH 1902	WEF	WWE
Genus *Tetrarhanis* KARSCH 1893		
Tetrarhanis symplocus CLENCH 1965	MEF	WWN
Tribe Pentilini		
Genus *Ornipholidotos* BETHUNE-BAKER 1914		
Ornipholidotos ornitshae STEMPFFER 1964	WEF	WWC
Genus *Pentila* WESTWOOD 1852		
Pentila condamini STEMPFFER 1963	MEF	WWE
Pentila petreia HEWITSON 1874	ALF	WWN
Pentila phidia HEWITSON 1874	MEF	WWE
Pentila picena picena HEWITSON 1874	MEF	WWN
Genus *Ptelina* WESTWOOD 1852		
Ptelina carnuta HEWITSON 1873	MEF	WWU
Genus *Telipna* AURIVILLIUS 1895		
Telipna acraea HEWITSON 1851	MEF	WWZ
Telipna semirufa GROSE-SMITH & KIRBY 1889	WEF	WWE
SUBFAMILY MILETINAE		
Tribe Miletini		
Genus *Megalopalpus* RÖBER 1886		
Megalopalpus metaleucus KARSCH 1893	MEF	WWU
Megalopalpus zymna zymna HEWITSON 1852	MEF	WWU
SUBFAMILY POLYOMMATINAE		
Tribe Lycaenesthini		
Genus *Anthene* DOUBLEDAY 1847		
Anthene lachares lachares HEWITSON 1878	MEF	WWU
Anthene larydas CRAMER 1780	ALF	WWU
Anthene liodes liodes HEWITSON 1874	ALF	AAF
Anthene princeps princeps BUTLER 1876	GUI	AAF
Anthene sylvanus sylvanus DRURY 1773	ALF	WWU
Anthene rubricintus rubricintus HOLLAND 1891	MEF	WWZ
Genus *Neurellipes* BETHUNE-BAKER 1910		
Neurellipes chryseostictus BETHUNE-BAKER 1910	WEF	WWU
Genus *Neurypexina* BETHUNE-BAKER 1910		
Neurypexina lyzianus HEWITSON 1874	WEF	WWZ
Tribe Polyommatini		
Genus *Azanus* MOORE 1881		
Azanus mirza PLÖTZ 1880	GUI	AAF
Genus *Eicochrysops* BETHUNE-BAKER 1924		
Eicochrysops hippocrates FABRICIUS 1793	SPE	AAF
Genus *Euchrysops* BUTLER 1900		
Euchrysops malathana BOISDUVAL 1833	UBQ	AAF
Genus *Oboronia* KARSCH 1893		
Oboronia ornata ornata MABILLE 1890	ALF	WWU

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
Genus *Thermoniphas* KARSCH 1893		
Thermoniphas micylus CRAMER 1780	MEF	WWC
Genus *Tuxentius* LARSEN 1982		
Tuxentius carana kontu KARSCH 1893	ALF	WWZ
Genus *Uranothauma* BUTLER 1895		
Uranothauma falkensteini DEWITZ 1879	ALF	AAF
Genus *Zizeeria* CHAPMAN 1910		
Zizeeria knysna TRIMEN 1862	UBQ	AAF
SUBFAMILY THECLINAE		
Tribe Deudorigini		
Genus *Hypokopelates* DRUCE 1891		
Hypokopelates viridis STEMPFFER 1964	WEF	WWN
Tribe Hypolycaenini		
Genus *Hypolycaena* FELDER 1862		
Hypolycaena antifaunas antifaunas DOUBLEDAY & HEWITSON 1852	MEF	WWZ
Hypolycaena dubia AURIVILLIUS 1895	MEF	WWU
Tribe Iolaini		
Genus *Iolaus* FABRICIUS 1807		
Iolaus iasis iasis HEWITSON 1865	ALF	WWU
Tribe Oxylidini		
Genus *Oxylides* HÜBNER 1819		
Oxylides faunas faunas DRURY 1773	MEF	WWU
FAMILY HESPERIIDAE		
SUBFAMILY PYRGINAE		
Genus *Acleros* MABILLE 1887		
Acleros nigrapex STRAND 1912	MEF	WWU
Genus *Andronymus* HOLLAND 1896		
Andronymus caesar caesar FABRICIUS 1793	ALF	AAF
Genus *Borbo* EVANS 1883		
Borbo fatuellus fatuellus HOPFFER 1855	ALF	AAF
Genus *Ceratrichia* BUTLER 1869		
Ceratrichia argyrosticta argyrosticta PLÖTZ 1879	WEF	WWU
Ceratrichia nothus nothus FABRICIUS 1787	WEF	WWC
Genus *Caenides* HOLLAND 1896		
Caenides dacela HEWITSON 1876	ALF	WWU
Caenides dacena HEWITSON 1876	MEF	WWU
Genus *Gretna* EVANS 1937		
Gretna waga PLÖTZ 1886	ALF	WWC
Genus *Hypoleucis* MABILLE 1891		1937
Hypoleucis ophiusa ophiusa HEWITSON 1866	ALF	WWU
Genus *Melphina* EVANS 1937		
Melphina noctula DRUCE 1909	MEF	WWU
Melphina unistriga HOLLAND 1894	MEF	WWU
Genus *Meza* HEMMING 1939		
Meza mabillei HOLLAND 1894	MEF	WWC
Genus *Monza* EVANS 1937		
Monza alberti HOLLAND 1896	ALF	WWU
Monza cretacea SNELLEN 1872	ALF	WWU
Genus *Osmodes* HOLLAND 1892		
Osmodes laronia HEWITSON 1868	ALF	WWU
Osmodes thora PLÖTZ 1884	ALF	WWU
Genus *Paracleros* BERGER 1978		
Paracleros placidus PLÖTZ 1879	MEF	WWU
Paracleros overlaeti BERGER 1978	MEF	WWU

	ECOLOGICAL CATEGORY	GEOGRAPHICAL DISTRIBUTION
Genus *Pardaleodes* BUTLER 1870		
Pardaleodes edipus STOLL 1781	ALF	WWU
Genus *Platylesches* HOLLAND 1896		
Platylesches galesa HEWITSON 1877	ALF	AAF
Platylesches picanini HOLLAND 1894	ALF	AAF
Genus *Pteroteinon* WATSON 1893		
Pteroteinon iricolor HOLLAND 1890	WEF	WWC
Pteroteinon laufella HEWITSON 1868	ALF	WWC
Genus *Rhabdomantis* HOLLAND 1896		
Rhabdomantis galatia HEWITSON 1868	MEF	WWU
Genus *Xanthodisca* AURIVILLIUS 1925		
Xanthodisca astrape HOLLAND 1896	ALF	WWU

Appendix 5 Butterflies recorded during walk-and capture on the study plot of the Bossematié Forest Reserve

Individual numbers of butterfly species recorded during walk-and-capture in a regenerating control plot and a thinned forest plot during the wet season 1997 on six 1 km transects in the heavily logged Bossematié Forest Reserve, south-east Côte d'Ivoire. Authorities and dates can be found in the Afrotropical catalogue (Ackery et al. 1995).

	control **t=28hrs**	**thinned** **t=28hrs**	**total** **t=56hrs**
Nymphalinae			
Aterica galene	0	8	8
Bebearia abesa	7	4	11
B. absolon	8	14	22
B. carshena	2	0	2
B. mandinga	5	9	14
B. oxione	4	1	5
B. phantasina	1	0	1
B. sophus	2	1	3
B. tentyris	62	31	93
B. zonara	14	8	22
Catuna angustatum	11	0	11
C. crithea	7	1	8
C. oberthueri	7	3	10
Cymothoe coccinata	1	0	1
C. egesta	0	1	1
C. fumana	1	1	2
Euphaedra crockeri	20	2	22
E. janetta	1	0	1
E. medon	0	1	1
E. perseis	1	0	1
E. phaetusa	8	6	14
Euptera zowa	0	0	0
E. xypete	2	1	3
Euriphene aridatha	1	0	1
E. barombina	21	9	30
E. gambiae	8	4	12
E. simplex	3	2	5
Harma theobene	2	1	3
Hypolimnas dubius	2	1	3
H. salmacis	2	3	5
Junonia stygia	1	0	1
Lachnoptera anticlea	2	0	2
Neptis agouale	2	0	2
Pseudoneptis bugandensis	3	0	3
Pseudacraea lucretia	1	0	1
P. warburgi	0	1	1
Salamis cacta	2	1	3
S. parrhassus	1	1	2
Satyrinae			
Bicyclus abnormis	3	1	4
B. dorothea	2	0	2
B. martius	1	1	2
B. procora	1	0	1
B. sambulos	1	0	1
B. sandace	0	1	1
B. taenias	1	0	1

Appendix 5 (continued)

	control **t=28hrs**	**thinned** **t=28hrs**	**total** **t=56hrs**
Satyrinae (cont.)			
B. xeneas	0	1	1
B. zinebi	0	2	2
Gnophodes betsimena	0	1	1
G. chelys	1	3	4
Ypthyma doleta	1	0	1
Pieridae			
Belenois calypso	1	0	1
Nepheronia thalassina	2	0	2
Total individuals	**228**	**125**	**353**

Appendix 6 Point Distance Sampling of selected butterfly species recorded on the 75 ha plot of the Bossematié Forest Reserve

Abbreviations:	
n:	number of observations
K:	number of sampling points
p:	proportion of individuals actually detected
D:	density in individulas per hectare

A. Genus *Bebearia* (data grouped, truncated at 7 m)

	control forest				**thinned forest**			
	mean	**% CV**	**df**	**95 % C.I.**	**mean**	**% CV**	**df**	**95 % C.I.**
Encounter rate (n/K)	8.2	16.6	23	5.8 – 11.5	4.4	15.9	15	3.2 – 6.2
Proportion detected (p)	0.1	12.5	194	0.1 – 0.2	0.2	27.9	69	0.1 – 0.3
Density (Ind./ha)	8,203.5	20.8	54	5,433 – 12,386	2,824	32.2	82	1,513 – 5,270

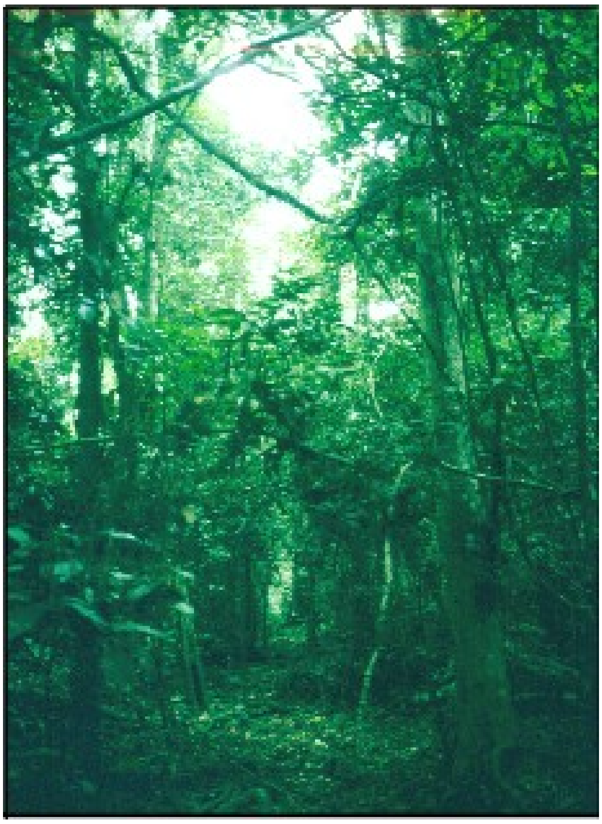
B. ***Euphaedra*** **spp.** (data ungrouped, untruncated)

	Control forest				**thinned forest**			
	mean	**% CV**	**df**	**95 % C.I.**	**mean**	**% CV**	**df**	**95 % C.I.**
Encounter rate (n/K)	1.6	29.9	23	0.9 – 2.9	0.6	28.0	15	0.3 – 1.0
Proportion detected (p)	0.3	20.9	37	0.2 – 0.5	1.0	62.9	8	0.3 – 1.0
Density (Ind./ha)	624.7	36.5	44	306 – 1,275	73.0	68.9	11	19 - 288

C. Genus ***Euriphene*** **spp.** (data grouped, truncated at 7 m)

	control forest				**thinned forest**			
	mean	**% CV**	**df**	**95 % C.I.**	**mean**	**% CV**	**df**	**95 % C.I.**
Encounter rate (n/K)	1.5	21.8	23	0.9 – 2.3	0.7	34.4	15	0.3 – 1.4
Proportion detected (p)	0.1	23.7	33	0.07 – 0.18	0.4	40.6	10	0.2 – 0.9
Density (Ind./ha)	1,755	32.3	55	730 – 3,079	234.1	53.2	22	82 - 653

Appendix 7 *Photographic Section*

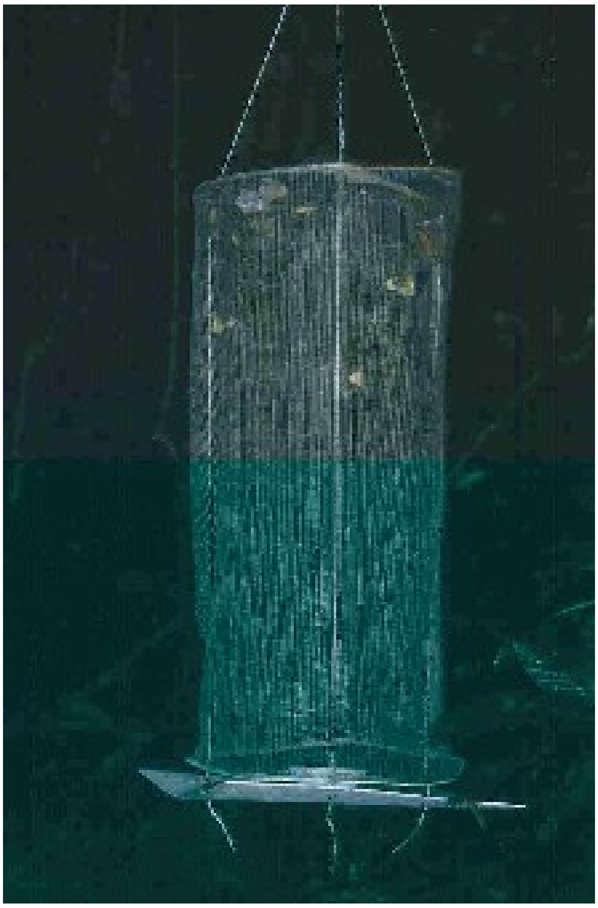


Regenerating control forest

Thinned forest

***Terminalia* plantation**

Fruit trapping at different vertical heights



Fruit-trapping in canopy-closed understorey

Fruit trapping in gap habitats

Mark-recapture

Euphaedra crockeri

Euphaedra perseis

Cymothoe caenis

Charaxes varanes

Aterica galene

Salamis cacta

Lebenslauf

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Publikationen:

Fermon, H. and Flémal, J. (1995) Les ennemis du café – Les principales maladies des caféiers. In *Kawa. Les secrets du café: du caféier à la tasse* (E. Robbrecht, ed.), pp. 71-80. Meise: Jardin Botanique National de Belgique.

Schrijvers, J., Fermon, H. and Vincx, M. (1996) Resource competition between macrobenthic epifauna and infauna in a Kenyan *Avicennia marina* mangrove forest. Marine Ecology Progress Series 136: 123-135.

Mühlenberg, M., Slowik, J., Waltert, M., Fermon, H., Singo, B. and Waitkuwait, W.E. (1997) Présentation des données du biomonitoring dans les forêts classées de l'est de la Côte d'Ivoire. Report on population developments of monitor species from four Forêts Classées to SODEFOR/GTZ, Zentrum für Naturschutz, Universität Göttingen, Germany. zfn1@gwdg.de

Fermon, H., Dall'Asta, U. and Mühlenberg, M. (1997) Baited butterflies (Nymphalidae) as a tool for the development of inexpensive and easily implemented monitoring programs in West-African rainforests. – Abstract, The SEL Xith European Congress of Lepidopterology, Malle, Belgium.

Mühlenberg, M., Slowik, J., Waltert, M., Fermon, H., Singo, B. and Waitkuwait, W.E. (1999) Biomonitoring in Tropenwäldern. Ein Beitrag zur Bewertung von Sustainable Use. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen 133: 220-225.

Fermon, H., Waltert, M., Larsen, T.B., Dall'Asta, U. and Mühlenberg, M. (2000) Effects of forest management on diversity and abundance of fruit feeding nymphalid butterflies in south-eastern Côte d'Ivoire. Journal of Insect Conservation 4:173-189.

Fermon, H., Schulze, H. C., Waltert, M. and Mühlenberg, M. (2001) The butterfly fauna of the Noyau Central, Lama Forest, Republic of Benin, with notes on ecological composition and geographic distribution. African Entomology 9: 177-185.

Vane-Wright, R.I. and Fermon, H. (in press) Taxonomy and identification of *Lohora* Moore (Lepidoptera: Satyrinae), the Sulawesi bush-browns. *Invertebrate Taxonomy*.

Fermon, H., Waltert, M., Mühlenberg, M. (in prep.) Movement and vertical stratification in tropical fruit feeding butterflies. Submitted to the Journal of Insect Conservation.