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Effects of anthropogenic disturbance of Afromontane forest on fruit-feeding butterflies (*Lepidoptera, Nymphalidae*) in Amani Nature Reserve, Tanzania.

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Abstract

The majority of the world's biological diversity is located in the tropics, where forest is an essential biome. A healthy web of biodiversity is the foundation for ecosystem services humans depend on but it is currently under severe pressure due to anthropogenic disturbances. The result is a fragmented landscape of primary forest, secondary forest, plantations and agroforest. Conservation efforts have traditionally focused on preserving primary forest, but research on the response of different faunal groups to various anthropogenic disturbances has revealed incongruous results. Although still strongly disputed by some, many advocate the possible value of human-modified landscapes such as agroforest and secondary forest as alternative habitats, migration routes and buffer zones for biodiversity.

In this study, I sampled fruit-feeding butterflies (*Lepidoptera*, *Nymphalidae*) for 10 weeks in Amani Nature Reserve, Tanzania. Butterflies are frequently used as indicator species for biodiversity response to anthropogenic and environmental changes. Sampling occurred in six habitats with various degrees of anthropogenic disturbance; primary forest, moderately and heavily disturbed secondary forest, riverine forest, meadow and agroforest. 116 individuals of 19 species were collected. The effect of environmental variables and species traits on abundance, species richness and distribution was assessed. No morphological or ecological traits gave any clear trends as to the number of habitats a species was present. Canopy openness was the environmental variable most strongly correlated with abundance, with a positive relationship. Rain also significantly influenced butterfly abundance, with a negative relationship. Agroforest contained the majority of both abundance and species richness and also contained all sampled species which previously are known mainly to inhabit forests. There were no significant differences in either abundance or species richness between the closed-forest habitats in which also the species composition was similar. All though small-scale with a relatively low sample size, the findings of the present study support the view that agroforest may help maintain a high degree of biodiversity.

Heavy forest loss and poverty is closely related. Only a small fraction of the terrestrial tropical biome is within protected areas. Also, these protected areas attract human settlements due to increased employment opportunities, further increasing the pressure on the local biodiversity. With continued rates of population growth and resource exploitation, the long term viability of conservation strategies in these areas is dependent on the cooperation of local people. This emphasizes the need for further research to obtain adaptive management schemes which will maximize the conservation value of anthropogenic landscapes.

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List of acronyms

ANR	Amani Nature Reserve
SBA	Stand basal area
ZIP	Zero-inflated Poisson regression
A1	Agroforest, plot 1
A2	Agroforest, plot 2
A3	Agroforest, plot 3
H1	Heavily disturbed secondary forest, plot 1
H1O	Heavily disturbed secondary forest, original plot 1
H2	Heavily disturbed secondary forest, plot 2
H3	Heavily disturbed secondary forest, plot 3
Me	Meadow
M1	Moderately disturbed secondary forest, plot 1
M2	Moderately disturbed secondary forest, plot 2
M2O	Moderately disturbed secondary forest, original plot 2
M3	Moderately disturbed secondary forest, plot 3
M3O	Moderately disturbed secondary forest, original plot 3
P1	Primary forest, plot 1
P2	Primary forest, plot 2
P2O	Primary forest, original plot 2
P3	Primary forest, plot 3
P3O	Primary forest, original plot 3
R1	Riverine forest, plot 1
R2	Riverine forest, plot 2
R3	Riverine forest, plot 3
AGRO	Agroforest
HEAVY	Heavily disturbed secondary forest
MEADOW	Meadow
MODERATE	Moderately disturbed secondary forest
PRIMARY	Primary forest
RIVER	Riverine forest

1. Introduction

Biological diversity is the foundation for all ecosystem services the human population depends on, such as nutrient cycling, climate regulation and primary production (MEA 2005). Although biodiversity is difficult to quantify fully, the highest concentration is by far found in the tropics (Dirzo & Raven 2003). Tropical forests are a key biome to the biodiversity of the world (Gardner et al. 2009) but are subject to massive past and current degradation (Bradshaw et al. 2008).The dominant proximate driver of biodiversity losses and ecosystem service changes is human-induced habitat modifications (MEA 2005). The underlying causes for these changes is a complex web of socio-economic and ecological factors involving global, commercial agents as well as subsistence activities of rural people (Contreras-Hermosilla 2000). With the past and current pressures of human population densities and resource exploitation, the resulting landscape is a fragmented matrix of heterogeneous habitats (Chazdon et al. 2009). This has created a pressing concern for the future perseverance of the biodiversity associated with primary forests.

Conservation efforts have traditionally been focused on protecting large tracts of primary forest (Bhagwat et al. 2008) as they have been found to contain significantly higher biodiversity than secondary forest, particularly for threatened and restricted range species (Barlow et al. 2007; Kudavidanage et al. 2012; Sundufu & Dumbuya 2008). However, protected areas often attract human settlements as seen in increased human growth rates in the edges and adjacent areas of protected areas across the world. This has been linked to the park-related funding by governmental and international donors, which produce a range of employment opportunities (Wittemyer et al. 2008). Within this lie potentially adverse effects on the associated biodiversity, particularly through increased land conversion and introduction of exotic species (Luck 2007). The protected tropical forests of the world have been increasingly isolated over the past twenty years (DeFries et al. 2005). Additionally, over 90 % of the terrestrial tropical biome is still found outside of protected areas (Chazdon et al. 2009; Gardner et al. 2009). Therefore, while protection of primary forest is irrefutably an essential part of biodiversity conservation, it is becoming clear that it is not a viable strategy on its own (Dent & Wright 2009; Gardner et al. 2009).

For most species living in distinct habitats, meta-population processes with local deaths replaced by immigration from other populations are crucial for the long time survival of the species within an area (Primack 2010). For the meta-population structure to function

between protected areas, it is vital that the intermittent transit landscape is permeable and can be utilized as migration routes (Vandermeer & Perfecto 2007). There is an increasing amount of empirical studies on the responses of various animal groups to land use changes - from mammals (Wu et al. 1996) and birds (Beukema et al. 2007; Bobo & Waltert 2011; Waltert et al. 2005), to invertebrates such as ants and beetles (Bos et al. 2007), and butterflies (Koh 2007; Mas & Dietsch 2004; Munyuli 2012). The outcome of these studies is often highly divided between the groups; while some report positive or negative relationships, others find no relationship at all (Ewers & Didham 2006). These contradictory results can partly be explained by methodological factors of the surveys such as spatial and temporal scale and sampling effort (Ewers & Didham 2006; Gardner et al. 2009; Koh 2007). At the same time, they also relate to differences in species life history traits evoking divergent disturbance response patterns and complications by the synergistic effects of habitat fragmentation and, for example, climate change (Ewers & Didham 2006). As a result, the allotted conservation value of human-modified landscapes is highly contentious (Barlow et al. 2007). However, with the future prospect of continued fragmentation and human-expansion, the necessity of adaptive management schemes and landscape connectivity is evident (Chazdon et al. 2009). Thus, there is an increasing focus on the potential conservation value of the surrounding matrix of human modified landscapes such as secondary forests and agroforests (Chazdon et al. 2009; Gardner et al. 2009; Sodhi et al. 2010). These habitats are less hostile transit habitats for forest species and may thus facilitate dispersal or function as a replacement habitat.

Small scale agroforestry systems, generally referred to as agroforests, is a widely applied land use practice in the tropics. There are few, if any, universal aspects defining the practice which can include slash-and-burn farming, home gardens, monocultures and complex multi-stratified communities of crop plants and retained forest trees (Scales & Marsden 2008). Secondary forest is also a highly heterogeneous classification with forests which vary in the type of land use previously applied as well as age since abandonment and regrowth (Dent & Wright 2009). Amani Nature Reserve (ANR), Tanzania, is a nature reserve with a heterogeneous landscape comprised of primary forest, secondary forest, botanical gardens, agroforestry, infrastructure and various settlements and also nests several tea plantations which are not part of the reserve (Conte 2004; Frontier Tanzania 2001). It is part of the Eastern Arc Mountains, and as such, included in the world's top 35 biodiversity hotspots (Mittermeier et al. 2011). ANR supports a high degree of biological diversity, including a great number of endemic and restricted range species, particularly birds and amphibians (Frontier Tanzania 2001). Another speciose group within ANR is butterflies (*Lepidoptera*).

Butterflies is a well-studied taxonomic group due to their conspicuous morphology and ease of sampling (DeVries 1997), particularly members of the family *Nymphalidae* (Bobo et al. 2006). Many butterflies are forest dwelling or forest dependent and can be negatively affected by logging (Hill & Hamer 2004) but many are also light loving and diversity can increase in canopy gaps (Hill et al. 2001) or regenerating secondary forest (Bobo et al. 2006). They are sensitive to microclimatic changes and light availability (Murphy et al. 1990) and as such can show distinct habitat preferences (Barlow et al. 2007; Sundufu & Dumbuya 2008). They provide important ecosystem services such as pollination as well as having intrinsic value (Bonebrake et al. 2010). Perhaps more importantly, they are valued for their function as indicators of biodiversity and ecosystem-response to environmental changes (Brown & Freitas 2000). However, as with many other groups, studies on butterflies reveal great variation in disturbance response patterns (Ghazoul 2002). Studies show variation in butterfly responses in relation to temporal and spatial scale and between geographical locations of the sites (Barlow et al. 2007).

The aim of the present study is to add to the knowledge of the effect of human disturbances on the biological diversity by using the fruit-feeding guild of nymphalid butterflies as study group. In this thesis I assess their understorey species richness, abundance and composition in habitats with various grades of anthropogenic disturbance in or adjacent to Amani Nature Reserve, Tanzania. The effect of four environmental variables on abundance is investigated. Additionally, the ecology and morphological traits of the sampled species are discussed in relation to the observed habitat distributions of the species.

2. Materials and methods

2.1 Study area

Amani Nature Reserve (ANR) (4˚58' - 5˚13' S and 38˚32'– 38˚48' E) is located in the southern part of the East Usambara Mountains, Tanga Region, Tanzania (Frontier Tanzania 2001) (Figure 2.1a,b). The East Usambara Mountains are part of the Eastern Arc mountain chain running from southern Kenya down through eastern Tanzania (Burgess et al. 2007; Moreau 1935). This mountain chain is an ancient rock formation (Moreau 1935) consisting of 13 separate mountain blocks (Burgess et al. 2007). It is considered one of the world's top 34 biodiversity hotspots due to its characteristics of having exceptionally high endemism combined with an extremely high risk of habitat loss (Mittermier et al. 2004) in addition to high levels of biodiversity in general (Burgess et al. 2007). The Eastern Arc has lost 70 % of its estimated original forest cover (Burgess et al. 2007).

Of the 13 forest blocks East Usambara is one of the most biologically important (Burgess et al. 2007). Originally, the East Usambara Mountains were mostly covered by a continuous forest (Moreau 1935) but particularly since the 1950's they have been suffering from intense timber harvesting leaving only smaller patches of remaining forest (Kielland 1990). Amani Nature Reserve covers 8380 ha and is thus the largest single block of forest remaining in the East Usambara Mountains (Frontier Tanzania 2001). However, from the 1890's, European colonizers have heavily influenced the Amani area through logging activity and the establishment of a botanical garden containing both indigenous and exotic species (Conte 2004; Frontier Tanzania 2001). A combination of logging and invasive pioneer species has resulted in large areas with a great change in vegetation composition. The invasive tree species causing the greatest impact is *Maesopsis eminii* (Cordeiro et al. 2004; Frontier Tanzania 2001). In addition, two tea plantations are located within the nature reserve (Frontier Tanzania 2001) causing further disruption to the ecosystem. Canopy height of the remaining intact forest within ANR ranges from 20 to > 30 m (Frontier Tanzania 2001). The annual precipitation pattern is bimodally distributed with the highest peak lasting from March through May and another lower peak from October through December. Rainfall ranges from 1200 – 2200 mm/year, depending on altitude (Frontier Tanzania 2001). Elevations range from approximately 190 – 1130 m above sea level, thus the nature reserve contains both lowland forest and submontane forest (Frontier Tanzania 2001).

The first detailed biodiversity survey of the nature reserve was not undertaken until 1999-2000 through the East Usambara Conservation Area Management Programme (Frontier Tanzania 2001). The survey recorded 112 butterfly species representing 9 families, including one endemic and seven near-endemic species.
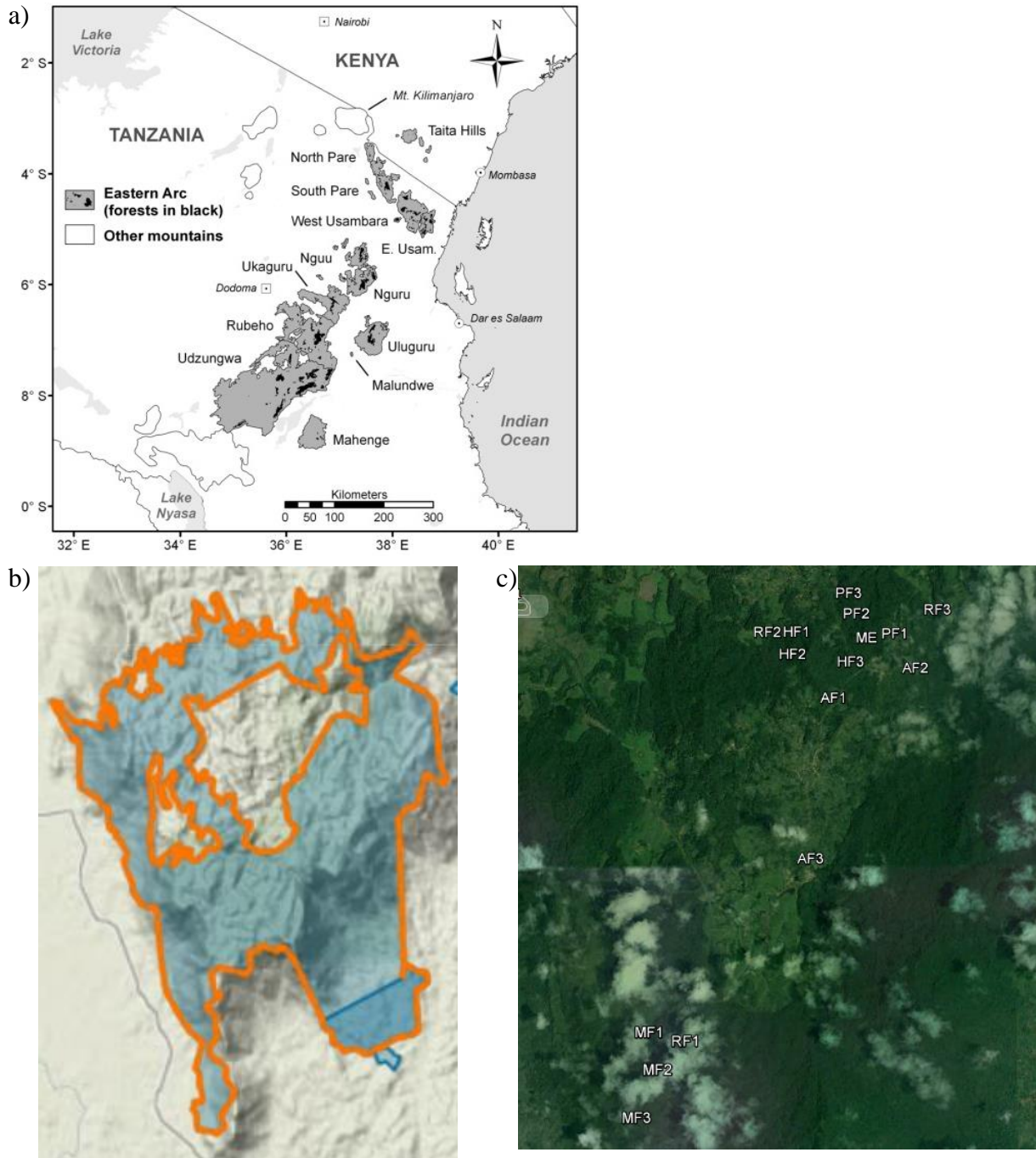
Figure 2.1 a) Map of Eastern Tanzania. Red circle indicates area of Amani Nature Reserve (Maps by Valuing the Arc Project: http://www.valuingthearc.org/eastern_arc_mountains/index.html), b) Outline of Amani Nature Reserve (blue area) and the nested tea plantations (grey areas). Dark blue area in bottom right corner is forest not yet included in the reserve. http://www.protectedplanet.net/sites/Amani_Nature_Reserve, c) Plot locations within or around Amani Nature Reserve, Google Earth.

2.2 Study plots

Plots within six habitats were selected for butterfly sampling; primary forest, moderately disturbed secondary forest, heavily disturbed secondary forest, riverine forest, agroforest and meadow (Figure 2.1c). All habitats were represented by three separate plots except meadow which was only represented by one plot. Depending on the size of the forest and access to it, the distribution of the plots differed somewhat between habitats. For primary forest and moderately disturbed secondary forest all plots were selected within one continuous forest. For heavily disturbed secondary forest the three plots were located in two separate forests. All agroforestry plots and riverine forest plots were placed in separate locations. Plots located within continuous forest were placed with a straight line distance of 200 m to 600 m between them to reduce the risk of pseudo replication (Ghazoul 2002), except H1 and H2 which due to the small size of the forest had <200 m between them. Plots as representatives of each habitat type were chosen based on botanical and historical information from the guides employed by ANR Conservation Centre. All plots were selected within an elevational range of 300 meters since elevation can have an effect on butterfly composition (Axmacher & Fiedler 2009; Brehm et al. 2007; Pyrcz et al. 2009).

Primary forest

Primary forests are characterized by the composition of the mature stand consisting of many endemic or indigenous tree species such as *Allanblackia stuhlmannii*, *Cephalosphaera usambarensis* and *Annickia kummeriae*. All three plots were placed within one continuous forest by following small animal or human tracks or simply going directly through the forest. Due to initial low capture rates, two traps (P2 and P3) were moved in an attempt to stimulate trap visits. The traps were moved to locations with larger gaps in the canopy as gaps may support a higher diversity of butterfly species (Hill et al. 2001). The move occurred on the second bait day of cycle 2; 10.10.13.

Moderately disturbed secondary forest

I define moderately disturbed secondary forest as forest which has experienced moderate logging during the 20th century (Frontier Tanzania 2001; Newmark 2002). As a result, the mature stand is composed of a mix of indigenous and exotic species but lacking large old trees. All plots were placed within one continuous forest approximately 200 m from a wide path going through the forest. The traps were accessed by following three separate entrance

points leading from the road into the forest to the plots. Due to initial low capture rates, two of the traps were moved in an attempt to stimulate trap visits. The two traps were moved to locations with larger gaps in the canopy. The moves occurred on the first bait day of cycle 2; 09.10.13. The gaps were closer to the road by approximately 100 m.

Heavily disturbed secondary forest

I define heavily disturbed secondary forest as forest which has experienced heavy logging during the 20th century (Frontier Tanzania 2001; Newmark 2002). As a result, the mature stand is heavily dominated by exotic tree species, particularly *Maesopsis eminii*. The three plots are divided between two forest sites of similar characteristics because none of the sites were large enough to contain all three plots with a minimum straight line distance of 200 m between them. The site with two plots was still too small to allow a minimum straight line distance of 200 m to any road or edge. The plots were placed ca 170 m from a small path going through the forest as well as the edge. H3 was placed in a different site but this was also small. Therefore it was difficult to place the trap far enough from any road or opening due to many of these passing through the forest. As a result, it was placed < 100 m from the closest road as well as the forest edge. H1 was initially placed by the side of a canopy gap but due to low capture rates it was moved to the middle of the gap in an attempt to stimulate trap visits. The move occurred on bait day 2 in cycle 2; 10.10.13.

Agroforest

The three agroforest plots were placed in three different locations which were chosen as representing the average agroforest within ANR. The characteristics of the three plots were similar. Main crop plants in all locations were banana (*Musa* genus), cardamom (*Elettaria* or *Amomum* genus), clove (*Syzygium aromaticum*), yam (*Dioscorea* genus), cassava (*Manihot esculenta*), elephant grass (*Pennisetum purpureum*), jackfruit (*Artocarpus heterophyllus*) and guava (*Psidium* genus). However, the crop composition varied slightly between plots. All three plots were adjacent to heavily trafficked dirt roads as well as being close to human settlements.

Riverine forest

The three riverine forest plots were placed in three different locations which were chosen mainly for their spatial accessibility. The characteristics of the individual rivers vary. R1 is by a small waterfall of ca 3 m. The river is approximately 4 m wide. R2 is by a wetland with a

small stream. R3 is by a quite strong river approximately 5 m wide near a very large and steep waterfall. The species composition of the mature stand was relatively similar between sites, consisting of a mix of indigenous and invasive species. All plots were located ca 100 m from any road as it was difficult to find suitable places any further away.

Meadow

The meadow is a ca 2500 m^2 open area surrounded by primary forest, but with a few trees on the meadow. This habitat is only represented by one plot because of a lack of similar habitats found within appropriate distance. The plot was not established until cycle 2.

2.3 Study organism

Butterflies are well-studied in general because they are relatively easy to sample and have a rather large body size and conspicuous morphology (DeVries et al. 1997). Adult tropical butterflies obtain nutrients from a range of substrates but can be divided into two main feeding guilds regarding where they attain the majority of their nutritional requirements. The first guild feed mainly on flower nectar while the second feed mainly on the juices of rotting fruits or plant sap (DeVries 1988). The *Nymphalidae* is a highly speciose family with many fruit-feeding species that are attracted to fermented fruits which can be used easily in baited traps (Larsen 1994). Therefore, the focus of the present study has been on this taxon only. Additionally, many nymphalid butterflies show distinct habitat preferences in terms of both forest type and vertical stratification (Sundufu & Dumbuya 2008) and are sensitive to structural and microclimatic changes (Meyer & Sisk 2001). As a result, they are regularly used as indicators of ecological dynamics and effects of human disturbance (Bobo et al. 2006).

Lack of knowledge about the phylogeny of *Nymphalidae* has resulted in a highly contentious classification (De Jong et al. 1996). However, the subject matter is under current revision and thanks to contributions by recent molecular and morphological studies a clearer picture evolves. Particularly in regards to the status of *Acraeidae*, *Satyridae*, *Libytheinae*, *Satyrinae* and *Danainae* as families of their own or as subfamilies within *Nymphalidae* (Brower 2000; Freitas & Brown 2004; Larsen 1991; Monteiro & Pierce 2001; Peña et al. 2006; Wahlberg et al. 2003). I have applied the taxonomy of Kielland (1990) where they are separate families.

2.4 Sampling period

The butterfly sampling was conducted between October 1st and November 22nd 2013. The intent was to cover the period from dry season through an intermittent season and into the wet season as this has an effect on species distribution and occurrence (DeVries et al. 1997; DeVries et al. 1999). However, the weather was not as expected, with irregular periods of heavy rain and dry weather throughout the whole period. Trapping was conducted in six cycles (Table 2.1). The first two days in each cycle were bait days where half the traps were baited on day one and the other half baited on day two. The subsequent six days were sampling days. Each trap was sampled every other day; half the traps on one day and the other half on the next day. The combination of the two days completing the sampling of all plots once is termed sampling round. The first three cycles consisted of eight days, with each trap being sampled three times (three sampling rounds). Due to practical difficulties, the last three cycles were reduced to six days; with each trap being sampled twice (two sampling rounds). All traps were sampled between 09:00 and 17:00 hours. I alternated the daily order in which the traps were sampled to reduce systematic bias (Hughes et al. 1998), as far as it was logistically possible.

Table 2.1 Cycle schedule. Gray squares represent the plots A1, A3, H3, M1, M2, M3 and R3. Green squares represent A2, H1, H2, R2, R3, P1, P2, P3 and Me (Me was not established until Cycle 2). Sampling days 5 and 6 in Cycles 4, 5 and 6 are marked N/A as these cycles were reduced to contain only four sampling days each. Sampling was not completed on sampling day 6 in Cycle 3 and the un-sampled plots (P1, P2, P3 and Me) were sampled on the next day; 27.10.

	CYCLE 1	CYCLE 2	CYCLE 3	CYCLE 4	CYCLE 5	CYCLE 6
Bait day 1	29.09.	09.10.	19.10.	30.10.	08.11.	17.11.
Bait day 2	30.09.	10.10.	20.10.	31.10.	09.11.	18.11.
Sampling day 1	01.10.	11.10.	21.10.	01.11.	10.11.	19.11.
Sampling day 2	02.10.	12.10.	22.10.	02.11.	11.11.	20.11.
Sampling day 3	03.10.	13.10.	23.10.	03.11.	12.11.	21.11.
Sampling day 4	04.10.	14.10.	24.10.	04.11.	13.11.	22.11.
Sampling day 5	05.10.	15.10.	25.10.	N/A	N/A	N/A
Sampling day 6	06.10.	16.10.	26.10.	N/A	N/A	N/A
Sampling day 7	N/A	N/A	27.10.	N/A	N/A	N/A

2.5 Sampling methods

2.5.1 Butterfly data

All butterflies were collected by using baited traps based on Austin and Riley (1995). These are tubular nets of black mosquito netting with a plastic base plate attached to the lower rim by strings (Figure 2.2c). All traps were 1.0 – 1.1 m in height to reduce risk of escape ones the butterflies had entered the trap (Austin & Riley 1995; Hughes et al. 1998). The diameters of the nets were 35 cm in the top and 25 cm in the bottom (the bottom was narrowed in to fit the diameter of the plastic base plate). The distance from the lower ring of the net and the base plate was 4 – 6 cm on all traps. Bait was placed in a small plastic cup duct taped to the center of the base plate (Figure 2.2c). The traps were hung with the base plates 0.5 – 1.0 m above the ground (Figure 2.2a). Each plot was equipped with one trap.

Traps were mainly baited with two spoons of bananas which had fermented for 2 – 4 days in a plastic container, and two spoons of fresh babanana (Austin & Riley 1995). However, due to initial low capture rates, raw papaya and fermented bamboo juice with an alcohol content of approximately 17 % or less were also used in an attempt to stimulate trap visits. These baits were difficult to obtain at a regular basis and were only used irregularly. In traps where the bait had become too watery or desiccated, the bait tray was replenished with new bait on the day of sampling.

On sampling days, traps were emptied and the butterflies identified in the field using a self-composed field guide specifically targeting nymphalid butterflies in the ANR/East Usambara area. The field guide is based on photos and descriptions from Kielland (1990), Larsen (1991) and various web-pages (Appendix I). Butterflies which were readily identified in the field were immediately released after being marked with a felt-tipped pen and given a unique number by using the 1-2-4-7- system (Ehrlich & Davidson 1960; Watt et al. 1977) (Figure 2.2b). Individuals that couldn't be reliably identified in the field were killed, pinned and brought to Belgium for identification at the Royal Belgian Institute of Natural Sciences. Two of these species turned out to not be nymphalids but members of *Acraeidae* and *Satyridae*. However, due to low capture results in general, I chose to include these species as well, as part of the fruit-feeding guild.

Additional information for each species was collected post field work. Wing ratio for each species was measured by using photos of sampled butterflies in the image processing software ImageJ version 1.47. Wing size was estimated based on scaled photos of sampled

butterflies and information about wing span on various web pages, in Kielland (1990) and in Larsen (1991). Larval food spectrum was retrieved from Kielland (1990). Two ecotypes were defined (F; only known from heavy forest habitats, f; known from heavy forest and open habitats). Differences in literature and findings of the present study warranted two ecotype-categories. Ecotype* was defined based on Kielland (1990) and Frontier Tanzania (2001), and Ecotype** was based on results from the present study.

Figure 2.2 a) trap positioning in the field, b) mark-recapture marking (red dots on wings) and c) close-up of base-plate with cup.

2.5.2 Environmental data

In each plot four environmental variables were recorded. GPS-coordinates and altitude were recorded using a handheld Garmin GPSMAP® 62s. Canopy openness (Jennings et al. 1999) was measured by visual estimation. I separated the canopy openness into five categories; < 10 %, 10 – 30 %, 30 – 50 %, 50 – 80 % and 80 – 100 %. All traps were hung in branches from trees. Therefore, the canopy openness directly above the traps occasionally differed greatly from the average openness of the plot area. Measurements of both scales have been included. Stand basal area (SBA) was measured by doing an angle count sampling with a standard bottle-opener dendrometer. I used the basal area factor 4. In addition, a brief overview of the dominant plant species was recorded. The environmental data for all plots are summarized in table 3.1. The mean values (+/- SD) of elevation, canopy openness and SBA for the habitats was calculated and are presented in table 3.2. When calculating the means for the categorical variables "Canopy openness above trap" and "Canopy openness plot average", the median values of percent canopy openness for each plot were applied.

Rain was recorded and calculated for each sampling round by separating it into three categories representing an increasing degree of rain from no rain (0) to low levels of rain (1) and high levels of rain (2). Rain during the night was not included.

2.6 Data analysis

All statistical analyses were performed in RStudio version 0.98.501 – © 2009-2013 RStudio, Inc. The significance level was $\alpha = 0.05$, unless otherwise stated. All abundance data was adjusted to standardize for varying trap days. The number of individuals per plot was adjusted according to both trap days per sampling round and sampling rounds per cycle. For sampling rounds with either reduced or increased number of sampling days, the count was divided by the number of sampling days and multiplied by two. To standardize the sampling effort to six days per cycle, all catch numbers for each of the last three cycles (which only contained two sampling rounds, i.e. four sampling days) were divided by four and multiplied by six. Abundance data from the meadow habitat was not adjusted for only including one plot and five cycles.

2.6.1 Species richness, abundance and distribution

Abundance data per habitat was analyzed with Pearson's Chi Squared to see if the difference between observed and expected values was larger than what could be attributed to chance, and thus investigate if the species had a random distribution across habitats and if the habitats had a random distribution of species.

The abundance data was not normally distributed. Therefore, to test if there was any significant difference in abundance between habitats, the non-parametric Kruskal Wallis rank sum test was applied. When significant, a multiple comparison for Kruskal Wallis test with Bonferroni correction was performed to test which habitats were significantly different from each other. To investigate the completeness of sampling, species accumulation curves were drawn for the species catch for all habitats combined and also for each habitat individually.

2.6.2 Zero-inflated Poisson regression

The count data for abundance had an excess of zeroes but no overdispersion in the non-zeroes. Therefore, a Zero-inflated Poisson regression (ZIP) was chosen to analyze the data. ZIP is a mixture model suited for count data, and differentiates the true zeroes and the false zeroes in the model (Zuur et al. 2009). It assumes a Poisson distribution for the count data (all counts and true zeroes) and a binomial distribution for the binary part of the data (false zeroes vs all other types of data; both counts and true zeroes). According to Zuur et al. 2009, the probability of measuring zero butterflies is given by the probability that we "measure a false zero plus the probability that we do not measure a false zero multiplied with the probability that we measure a true zero. The probability of measuring a non-zero is given by the probability that we do not measure a false zero multiplied with the probability of the count". For further details on the method, see Zuur et al. 2009.

Count (adjusted numbers of sampled individuals) was set as response variable. I had three main explanatory variables; Habitat, Species and Sampling round. Habitat had three sub variables; Canopy openness above trap, Plot average canopy openness and SBA (Table 3.1). All canopy openness intervals were altered to the median value to reduce the number of degrees of freedom. All three sub variables for Habitat were strongly collinear (67% - 84 % correlation, not shown). As such, they were never included in the same model together, but tested separately. Species had four sub variables; Ecotype, Larval food spectrum, Wing size and Wing ratio (Table 3.6), all also tested separately due to the laborious work of manual modelling. Sampling round only contained one sub variable; Rain. The rain values included in the modelling was an average of the three categories (0, 1 and 2) for the day of

sampling and the two previous days. ZIP is not able to calculate response variables with decimal numbers. Thus, all adjusted catch numbers were rounded off to integers.

No automatic model selection function for ZIP was found. Therefore, extensive work was put into systematically substituting the main variables with the sub variables manually. I used Akaike information criterion (AIC) to find the model with most support. The model with the lowest AIC score is the most supported model (Akaike 1974).

　　　Step 1: I first started with a main model containing combinations only of the three main variables Habitat, Species and Sampling round. Systematic testing was done by fixating the Count model (Poisson) with Habitat and inserting main variables in the Zero-inflated model (binomial) starting with one and increasing to three in both additive and interactive combinations. The procedure was repeated with Species and Sampling Round fixated in the Count model.

　　　Step 2: Then I fixated the Zero-inflated model with the most supported combination found in the previous step. Again, all combinations of the three main variables were inserted in the Count model.

　　　Step 3: Using the most supported model from the step 2, main variables were substituted with sub variables in the same systematic fashion as step 1 and 2.

2.6.3 Effects of environmental variables on butterfly distribution

The relationship between abundance and the four environmental variables; canopy openness directly above trap, canopy openness plot average, stand basal area and rain was investigated by applying the Pearson moment-product correlation coefficient (r) if the data was normally distributed and the Spearman's rank correlation coefficient (r_s) if not normally distributed. All canopy openness intervals were altered to the median value. Rain values were calculated as an average of the categorical values from the day of sampling and the three previous days, representing the whole sampling round.

2.6.4 Effects of species traits on butterfly distribution

The relationship between the species' morphological and ecological traits (larval food spectrum, wing size, length-to-width wing ratio, and two two variants of ecotype) and habitat distribution was investigated by comparing traits commonly related to dispersal abilities (polyphagy, large wing size, high wing ratio and known presence in open as well as closed forest habitats (ecotype f)) with the number of habitats the species was sampled in

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3. Results

3.1 Environmental data

Environmental data for all plots is summarized in table 3.1. Plot elevations range from 727 – 1048 meters above sea level. The largest elevation differences between plots within the same habitat are found in riverine forest and agroforest with 255 m and 176 m, respectively. Primary forest, moderately and heavily disturbed secondary forest have a maximum within-habitat elevation difference of <100 m (Table 3.1). For several plots there are some differences in canopy openness directly above the trap and the plot average, particularly for agroforest and riverine plots. There are also some differences of both canopy openness scales between plots representing the same habitat (Table 3.1).

Table 3.1 Summary of all environmental variables recorded for each plot including plots from cycle 1, before the traps were moved (P2O, P3O, M2O, M3O and H1O) (SBA = Stand basal area).

Plot	GPS-coordinates		Elevation	% canopy openness		SBA
	S	E	(m.a.s.l)	Above trap	Plot average	(m2/ha)
A1	05°06.293'	038 37.561'	952	30 - 50	50 - 80	6
A2	05°05.979'	038 38.332'	776	50 - 80	80 - 100	4
A3	05°07.777'	038 37.343'	867	30 - 50	50-80	4
R1	05°09.432'	038 36.211'	965	10 - 30	30 - 50	10
R2	05°05.683'	038 37.073'	982	50 - 80	80 - 100	12
R3	05°05.430'	038 38.544'	727	10 - 30	50 - 80	8
Me	05°05.723'	038 37.870'	976	30 - 50	50-80	14
P1	05°05.593'	038 38.009'	955	<10	<10	32
P2O	05°05.451'	038 37.760'	1001	< 10	10 - 30	24
P2	05°05.500'	038 37.772'	975	10 - 30	10 - 30	26
P3O	05°05.265'	038 37.699'	1022	10 - 30	10 - 30	60
P3	05°05.312'	038 37.703'	991	<10	30-50	32
M1	05°09.354'	038°36.018'	1038	<10	<10	52
M2O	05°09.694'	038 35.928'	1046	<10	10 - 30	32
M2	05°09.648'	038 35.958'	1047	10 - 30	30 - 50	36
M3O	05°10.050'	038 35.719'	1028	<10	<10	54
M3	05°10.112'	038 35.773'	1015	10-30	30-50	32
H1O	05°05.694'	038 37.217'	970	<10	10 - 30	40
H1	05°05.680'	038 37.219'	1005	10 - 30	10 - 30	40
H2	05°05.896'	038 37.177'	1030	<10	<10	54
H3	05°05.953'	038 37.719'	953	<10	<10	68

The stand basal area (SBA) may seem higher in the meadow plot (Me) than in agroforest plots (A1 – A3). However, this is due to the meadow plot having more surrounding forest than the agroforest plots. The area surrounding the trap was in fact less obstructed because of the presence of crop plants in the agroforest plots which is not visible in the SBA measurement. The mean values (+/- SD) of elevation, both scales of canopy openness and SBA for the habitats are summarized in table 3.2. Both scales of canopy openness increase from closed forest to open habitats while SBA decreases.

Table 3.2 Mean (+/- SD) values for environmental data for all six habitats. Percentage of canopy openness is based on the median plot values. MEADOW only consists of one plot and standard deviation is not available (NA). (SBA = Stand basal area).

Habitat	Elevation	% canopy openness		SBA
	(m.a.s.l)	Above traps	Plot averages	(m2/ha)
AGRO	865 +/- 88	48 +/- 14	73 +/- 14	4.7 +/- 1.1
RIVER	891 +/- 143	35 +/- 26	65 +/- 25	10.0 +/- 2.0
MEADOW	976 NA	40 NA	65 NA	14.0 NA
PRIMARY	989 +/- 25	14 +/- 6	22 +/- 11	34.8 +/- 14.5
MODERATE	1035 +/- 13	14 +/- 6	24 +/- 15	41.2 +/- 10.9
HEAVY	990 +/- 35	13 +/- 5	15 +/- 5	50.5 +/- 13.4

3.2 Species richness, abundance and distribution

The total observed butterfly catch was 116 individuals, excluding 10 recaptures and 79 specimens of *Satyridae* which were not included in the subsequent analyses. The total species richness was 19. Eighty-one individuals were identified to 16 species or subspecies. The remaining 35 individuals were not possible to identify to species level; one individual was identified as morphospecies and named to genus; one group of three similar individuals were identified to the same genus and one group of 31 individuals identified to the same genus (Table 3.3) and Appendix II). The adjusted number of individuals is 138.5.

The habitat with the highest abundance is agroforest with 58.5 % of the total catch (Table 3.3). Meadow and riverine forest have similar catch results to each other with 15 % and 14.1 % of the total catch, respectively. Agroforest, meadow and riverine forest also have the highest species richness, with 73.7 %, 52.6 % and 31.6 % of the total possibility of 19 species, respectively. All three closed forest sites had a very low percentage of the total catch. The lowest percentage was found in heavily disturbed secondary forest (3.3 %), followed by primary forest (4.2 %) and moderately disturbed secondary forest (5.1 %) (Table 3.3).

The Kruskal Wallis rank sum test was significant (Kruskal-Wallis X^2 = 69.7432, df = 5, p-value = 1.159^{-13}), indicating that at least one habitat significantly differed from another. The multiple comparisons test revealed a significant difference in abundance between agroforest and all four forest habitats (riverine forest, primary forest, moderately and heavily disturbed secondary forest), as well as between meadow and all four forest habitats. There was no significant difference between agroforest and meadow, and no significant difference between any of the four forest habitats.

Of the species, four constitute > 10% of the total catch each (*Sallya* spp., *Melanitis leda africanus*, *Charaxes pollux mirabilis* and *Euxanthe tiberius tiberius* with 26.7 %, 14.1 % 13.5 % and 10.6 %, respectively). All other species constitute < 5 % of the total catch each, except *Charaxes acuminatus usambarensis* which constitute 7.2 % (Table 3.3).

Table 3.3 Adjusted numbers of individuals per species and subspecies per habitat, including total sums and the percentage of the total catch, and total number of species present in each habitat, including the percentage compared to the total species catch. Species and habitats with the highest percentages of total catch and total species catch are marked in black bold. Total numbers of individuals and species are marked in red bold.

Species	AGRO	RIVER	MEADOW	PRIMARY	MODERATE	HEAVY	No. of individuals per species	% of total catch
Acraea sp.	0	0	1.5	0	0	0	1.5	1.1
Aphysoneura pigmentaria pigmentaria	0	0	1.5	0	0	0	1.5	1.1
Byblia anvatara acheloia	1	0	0	0	0	0	1	0.7
Charaxes acuminatus usambarensis	4.5	5.5	0	0	0	0	10	7.2
Charaxes candiope candiope	0	1	1	0	0	0	2	1.4
Charaxes cithaeron kennethi	0	3	0	0	0	0	3	2.2
Charaxes macclounii	2.5	0	1.5	0	0	0	4	2.9
Charaxes pleione oriens	1.5	0	0	0	0	0	1.5	1.1
Charaxes pollux mirabilis	8	3	6.2	0	0	1.5	18.7	**13.5**
Charaxes violetta melloni	1.5	0	0	0	0	0	1.5	1.1
Eurytela dryope angulata	6.5	0	0	0	0	0	6.5	4.7
Euxanthe tiberius tiberius	1	1.5	0	3.2	6	3	14.7	**10.6**
Hypolimnas conf. anthedon wahlbergii	0	0	3	0	0	0	3	2.2
Junonia natalica	1	0	0	0	0	0	1	0.7
Junonia terea elgiva	1	0	1	0	0	0	2	1.4
Melanitis leda africanus	7.5	5.5	2.5	2.7	1	0	19.7	**14.1**
Neptidopsis opihone velleda	6.5	0	1	0	0	0	7.5	4.4
Neptis spp.	3	0	0	0	0	0	3	2.2
Sallya spp.	35.5	0	1.5	0	0	0	37	**26.7**
No. of individuals per habitat	81	19.5	20.7	5.8	7	4.5	**138.5**	
% of total catch	**58.5**	14.1	15.0	4.2	5.0	3.3		
Species richness per habitat	14	6	10	2	2	2	**19**	
% of total species richness	73.7	31.6	52.6	10.5	10.5	10.5		

The present study revealed six species which were not recorded in the Amani Nature Reserve Biodiversity Survey (Frontier Tanzania 2001) (Table 3.4).

Table 3.4 List of species and subspecies found in this study but not found in Amani Nature Reserve Biodiversity Survey (Frontier Tanzania 2001), including the habitat they were found in.

Species	Habitat
Aphysoneura pigmentaria pigmentaria	MEADOW
Byblia anvatara acheloia	AGRO
Charaxes pleione oriens	AGRO
Charaxes macclounii	AGRO, MEADOW
Junonia natalica	AGRO
Hypolimnas conf. *anthedon wahlbergi**	MEADOW

* *H. anthedon wahlbergi* is a highly variable species which may resemble *H. deceptor* Trimen 1873 with which it also shares much of its ecology. The three individuals captured were identified to *H. anthedon wahlbergi* in the field but there is a possibility that they were in fact *H. deceptor* in which case it was also found in the Biodiversity Survey (Frontier Tanzania 2001).

The X^2-value from the overall Chi Squared test was high (199.28) with a p-value <0.001 (Table 3.5). This indicates that overall the habitats had a significantly non-random distribution of species and the species had a significantly non-random distribution across habitats. However, when looking at the individual habitats and species, several did not have this significantly non-random distribution (Table 3.5).

Only five of 19 species had a significantly non-random distribution; *C. acuminatus usambarensis*, *C. cithaeron kennethi*, *E. tiberius tiberius*, *H.* conf. *anthedon wahlbergi* and *Sallya* spp. (p <0.05). In general, most species have a relatively small difference between observed and expected data. Pronounced overrepresentations are found in agroforest for *Sallya* spp., and in moderately disturbed secondary forest for *E. tiberius tiberius*. *E. tiberius tiberius* and *Sallya* spp. are noticeably underrepresented in agroforest and riverine forest, respectively. All three species found in the closed forest habitats (primary forest, moderately and heavily disturbed secondary forest) were also found in open habitats. The remaining 16 species were only found in open habitats. Four of the six habitats showed a significantly non-random distribution of species, including all three open habitats; agroforest, riverine forest, meadow and one closed forest habitat; moderately disturbed secondary forest. The other two closed forest habitats, primary forest and heavily disturbed secondary forest had a random distribution of species.

Table 3.5 Contingency table for Pearson's Chi Squared test: observed (O), expected (E) and Chi Squared values (X^2), degrees of freedom (df) and p-values (p). Grey cells represent O > E. Green cells represent O < E when O is > 0.00. Cells with bold numbers represent zero observations, but high expected values (1.0 – 5.21). All other cells have zero observations and low expected values (0.03 – 0.99). P-values <0.05 are in bold. The X^2 value for the overall test was 199, p-value <0.001.

Species	AGRO O	AGRO E	RIVER O	RIVER E	MEADOW O	MEADOW E	PRIMARY O	PRIMARY E	MODERATE O	MODERATE E	HEAVY O	HEAVY E	X^2	df	p
Acraea sp.	0.00	0.88	0.00	0.21	1.50	0.22	0.00	0.06	0.00	0.08	0.00	0.05	8.552	5	0.128
Aphysoneura pigmentaria pigmentaria	0.00	0.88	0.00	0.21	1.50	0.22	0.00	0.06	0.00	0.08	0.00	0.05	8.552	5	0.128
Byblia anvatara acheloia	1.00	0.58	0.00	0.14	0.00	0.15	**0.00**	**4.00**	0.00	0.05	0.00	0.03	0.710	5	0.982
Charaxes acuminatus usambarensis	4.50	5.85	5.50	1.41	**0.00**	**1.49**	0.00	0.42	0.00	0.51	0.00	0.32	14.948	5	**0.012**
Charaxes candiope candiope	**0.00**	**1.17**	1.00	0.28	1.00	0.30	**0.00**	**0.08**	0.00	0.10	0.00	0.06	4.902	5	0.428
Charaxes cithaeron kennethi	**0.00**	**1.75**	3.00	0.42	0.00	0.45	0.00	0.13	0.00	0.15	0.00	0.10	18.308	5	**0.003**
Charaxes macclounii	2.50	2.34	0.00	0.56	1.50	0.60	0.00	0.17	0.00	0.20	0.00	0.13	2.441	5	0.785
Charaxes pleione oriens	1.50	0.88	0.00	0.21	0.00	0.22	0.00	0.06	0.00	0.08	0.00	0.05	1.065	5	0.957
Charaxes pollux mirabilis	8.00	10.92	3.00	2.63	6.17	2.79	0.00	0.79	0.00	0.94	1.50	0.61	7.983	5	0.157
Charaxes violetta melloni	1.50	0.88	0.00	0.21	0.00	0.22	0.00	0.06	0.00	0.08	0.00	0.05	1.065	5	0.957
Eurytela dryope angulata	6.50	3.80	0.00	0.92	0.00	0.97	0.00	0.27	0.00	0.33	0.00	0.21	4.614	5	0.465
Euxanthe tiberius tiberius	1.00	8.58	1.50	2.07	**0.00**	**2.19**	3.17	0.62	6.00	0.74	3.00	0.48	70.224	5	**<0.001**
Hypolimnas anthedon wahlbergi	**0.00**	**1.75**	0.00	0.42	3.00	0.45	0.00	0.13	0.00	0.15	0.00	0.10	17.105	5	**0.004**
Junonia natalica	1.00	0.58	0.00	0.14	0.00	0.15	0.00	0.04	0.00	0.05	0.00	0.03	0.710	5	0.982
Junonia terea elgiva	1.00	1.17	0.00	0.28	1.00	0.30	0.00	0.08	0.00	0.10	0.00	0.06	2.206	5	0.820
Melanitis leda africanus	7.50	11.21	5.50	2.70	2.50	2.86	2.67	0.81	1.00	0.97	0.00	0.62	9.088	5	0.106
Neptidopsis opihone velleda	6.50	4.39	**0.00**	**1.06**	1.00	1.12	0.00	0.32	0.00	0.38	0.00	0.24	3.026	5	0.696
Neptis spp.	3.00	1.75	0.00	0.42	0.00	0.45	0.00	0.13	0.00	0.15	0.00	0.10	2.129	5	0.831
Sallya spp.	35.5	21.64	**0.00**	**5.21**	1.50	5.52	**0.00**	**1.56**	0.00	1.87	**0.00**	**1.20**	21.648	5	**<0.001**
X^2	29.652		42.568		47.153		19.211		42.597		18.096				
df	18		18		18		18		18		18				
p	0.041		<0.001		<0.001		0.379		0.001		0.449				

3.3 Species traits

Of the 19 species sampled, two species had one wide range trait (grey cells, Table 3.6), seven species had two or three wide range traits, two species had four wide range traits and one species had five wide range traits (Table 3.6). Of the three species with four or five wide range traits, only one (*M. leda africanus*) was found in five habitats. The remaining two species, *H. anthedon wahlbergi* and *C. candiope candiope*, were only found in one and two habitats, respectively. All other species (with 1 − 3 wide range traits) were also found in a number of habitats varying from one to five (Table 3.6). *Acraea* sp., *Neptis* spp. and *Sallya* spp. could not be identified to species level and all have two unknown (u.) characteristics (larval food plant spectrum and Ecotype *). Only one sampled subspecies is endemic to the Usambara Mountains; *A. pigmentaria pigmentaria* (Kielland 1990) and no sampled species or subspecies have been red listed by the International Union for Conservation of Nature (IUCN 2013).

Table 3.6 All measured morphological and ecological species traits: Larval (food plant) spectrum (monophagy (M), polyphagy (P)), wing size (relative size small (S), medium (M), large (L)), wing ratio, ecotype (Ecotype *) based on Kielland (1990) and Frontier Tanzania (2001) (only known from heavy forest habitats (F), known from heavy forest and open habitats (f)) and ecotype (Ecotype **) based on findings from the present study ("F" and "f" following the previously mentioned definitions). An additional category (u.) is given for those groups which could not be identified to species. Grey cells indicate possible dispersal traits; polyphagy, large wing size, wing ratio > 1.5 and ecotype "f". Also included: the number of habitats each species was present in, with n > 3 marked in bold.

Species	Wing ratio	Relative wing size	Larval spectrum	Ecotype *	Ecotype **	n habitats present
Acraea sp.	1.7	S	u.	u.	f	1
A. pigmentaria pigmentaria	1.6	S	M	F	f	1
B. anvatara acheloia	1.5	S	M	f	f	1
C. acuminatus usambarensis	1.4	L	P	F	f	2
C. candiope candiope	1.6	L	M	f	f	2
C. cithaeron kennethi	1.2	L	P	F	f	1
C. macclounii	1.4	L	M	f	f	2
C. pleione oriens	1.3	S	M	f	f	1
C. pollux mirabilis	1.3	L	P	F	f	**4**
C. violetta melloni	1.2	L	P	F	f	1
E. dryope angulata	1.5	S	M	f	f	1
E. tiberius tiberius	1.4	L	M	F	f	**5**
H. anthedon wahlbergi	1.8	L	P	f	f	1
J. natalica	1.3	M	M	f	f	1
J. terea elgiva	1.4	M	M	f	f	2
M. leda africanus	1.6	L	M	f	f	**5**
N. opihone velleda	1.2	S	M	f	f	2
Neptis spp.	1.5	S	u.	u.	f	1
Sallya spp.	1.5	S	u.	u.	f	2

3.4 Zero-inflated Poisson regression

The Zero-inflated Poisson regression revealed one model with most support (AIC = 931.293) in which the response variable Count (i.e. abundance) was the most influenced by the additive effect of the variables Habitat, Species and Rain in both parts of the model. The significant coefficients for the most supported model are presented in table 3.7. For the Zero-inflated model, which calculates the probability of false zeroes, the five habitats agroforest, riverine forest, primary forest, moderately and heavily disturbed secondary forest had a significant effect (i.e. only meadow does not). *C. acuminatus usambarensis*, *C.candiope candiope*, *C.pollux mirabilis*, *E.tiberius tiberius*, *M.leda africanus* are the only species with a significant effect, while *Sallya* spp. is near significant (p = 0.09).

Table 3.7 Summary of significant coefficients in Count model and Zero-inflated model for the most supported Zero-inflated Poisson Regression model (AIC = 931.2903). Coefficients significant at α 0.1 are marked in grey.

Count model (Poisson)		Zero-inflated model (binomial)	
Coefficient	p-value	Coefficient	p-value
HEAVILY	<0.01	AGRO	<0.01
MODERATE	<0.01	HEAVILY	<0.01
PRIMARY	<0.01	MODERATE	<0.01
RIVER	0.02	PRIMARY	<0.01
		RIVER	<0.01
C. candiope candiope	<0.05	*C. acuminatus usambarensis*	<0.05
E. tiberius tiberius	<0.05	*C. candiope candiope*	<0.05
Neptis spp.	0.09	*C. pollux mirabilis*	<0.01
		E. tiberius tiberius	<0.01
		M. leda africanus	<0.01
		Sallya spp.	0.09
Rain	<0.01	Rain	0.01

For the Count model, only four of six habitats had a significant effect; riverine forest, primary forest, and moderately and heavily disturbed secondary forest (i.e. agroforest and meadow does not). Only two species; *C. candiope candiope* and *E. tiberius tiberius* had a significant effect, while *Neptis* spp. had a near significant effect (p = 0.09). Rain was highly significant in both models.

3.5 Correlations between abundance and environmental variables

Abundance had a significant positive relationship (p-values < 0.05) with both scales of canopy openness; 99% correlation with canopy openness directly above the trap (Fig 3.1a) and 93 % correlation with plot average canopy openness (Fig 3.1b). There was a barely significant negative relationship (Pearson, r = -0.76, p = 0.049) between abundance and rain (Fig 3.1c) and a near significant negative relationship (Spearman's, r_s = -0.48, p = 0.07) with SBA (Fig 3.1d).
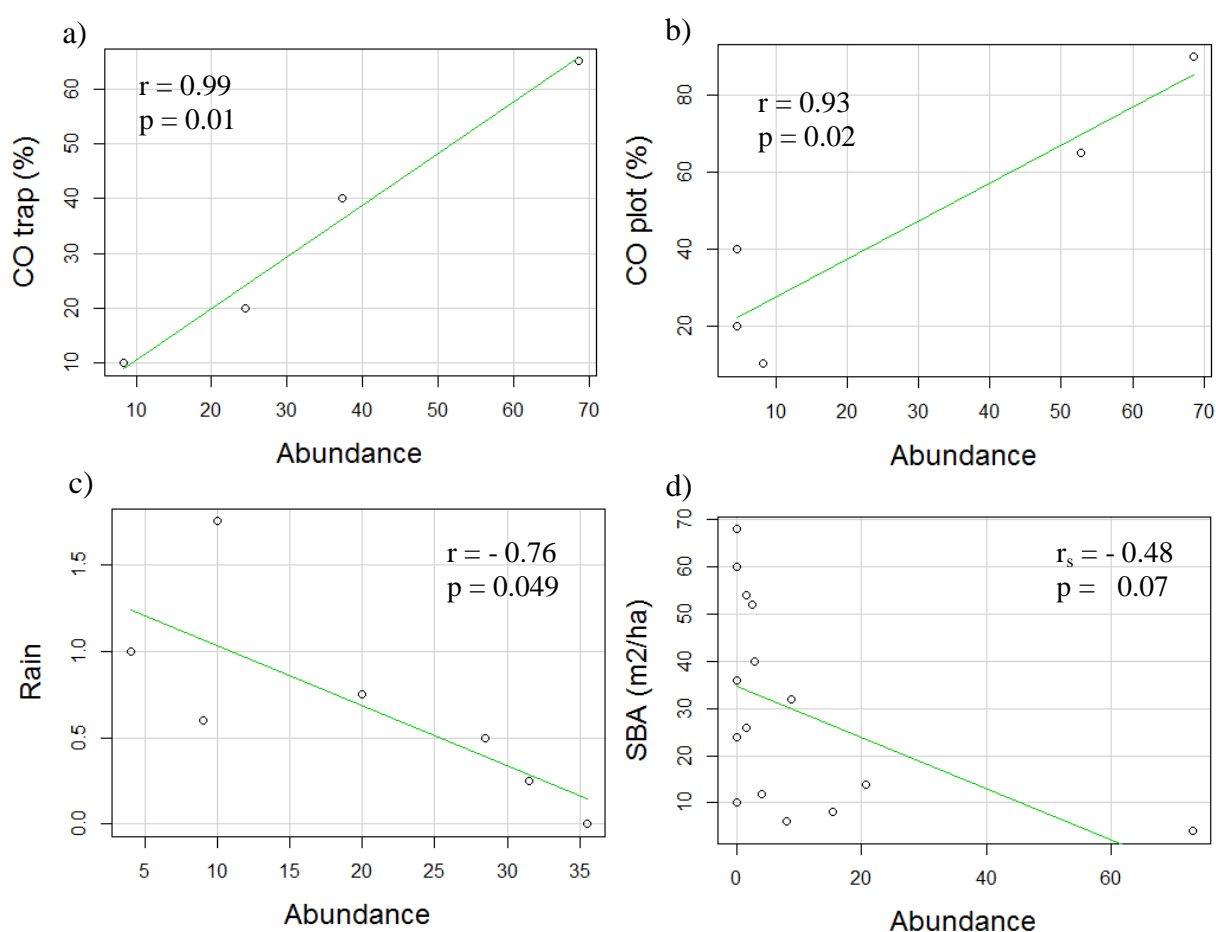
Fig 3.1 a) Pearson product-moment correlation coefficient (r) and corresponding p-values (p)and regression lines (green lines) for abundance and a) canopy openness above trap (CO trap), b) plot average canopy openness (CO plot) and c) rain (average value of sampling day and the three previous days) and d) Spearman's rank correlation coefficient (r_s) for abundance and stand basal area (SBA), also with corresponding p-value (p) and regression line (green line).

3.6 Mark-recapture analysis

10 individuals of 7 species were recaptured during the study (Table 3.8). Of these individuals, nine were captured twice and one was captured five times. No recaptures were made in a different plot or habitat than the one in which the individual was first recorded.

Table 3.8 Individuals recaptured during the study, including their individual ID number (ID#), plot and sampling rounds of first captures and all subsequent recaptures.

| Species	ID #	Plot	1st capture	1st recapture	2nd recapture	3rd recapture	4th recapture
C. acuminatus usambarensis	#6	R3	4.2	4.4	-	-	-
C. pollux pollux	#7	R3	4.2	4.4	-	-	-
E. dryope angulata	#3	A2	2.4	2.6	-	-	-
E. dryope angulata	#5	A2	3.6	4.2	-	-	-
E. tiberius tiberius	#4	M1	4.1	4.3	-	-	-
E. tiberius tiberius	#6	P2	4.2	4.4	-	-	-
M. leda africanus	#8	A3	3.1	3.3	-	-	-
N. ophione velleda	#4	A2	2.4	2.6	-	-	-
N. ophione velleda	#6	Me	2.4	2.6	3.2	3.4	3.7
Sallya spp.	#3	A2	1.4	1.6	-	-	-

3.7 Sampling completeness

The total number of trap days was 470 (all trap days for all traps combined). Each trap had 30 trap days except R2, R3 and Meadow with 28, 24 and 25 days, respectively. This was due to two incidents of stolen traps and two incidents of flooding which made the traps inaccessible. Also, P1, P2, P3 and Meadow had one additional trap day in cycle 3 due to transport issues on the scheduled sampling day, resulting in 31 trap days for these traps. All habitats had 45 samplings (sampling rounds) except riverine forest and meadow with 41 and 12 samplings, respectively.
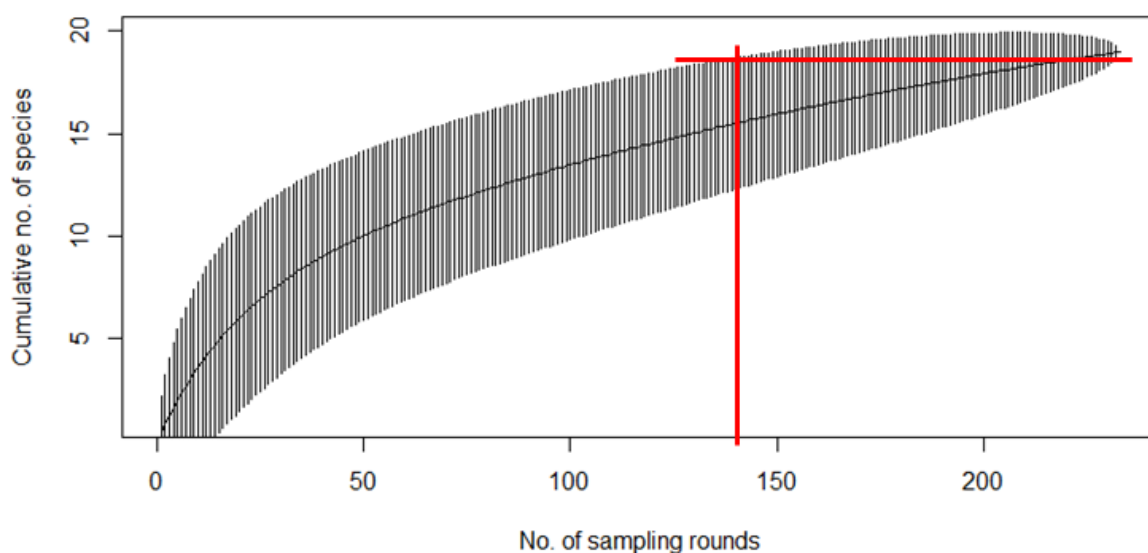
Fig. 3.1 Sample-based species accumulation curve for all habitats combined; 243 sampling rounds and 19 species in total. Bars are 95 % confidence intervals. Red lines indicate point of no further significant increase in species accumulation with increased sampling effort.

The species accumulation curve for all 243 sampling rounds for all 16 plots combined (Fig. 3.1) shows that with increasing sampling effort the curve becomes less steep but is still not near an asymptote. As such, the sampling effort does not represent the full species inventory in the area sampled, although after ca 140 sampling rounds there is no more significant increase in species accumulation with increased sampling effort.
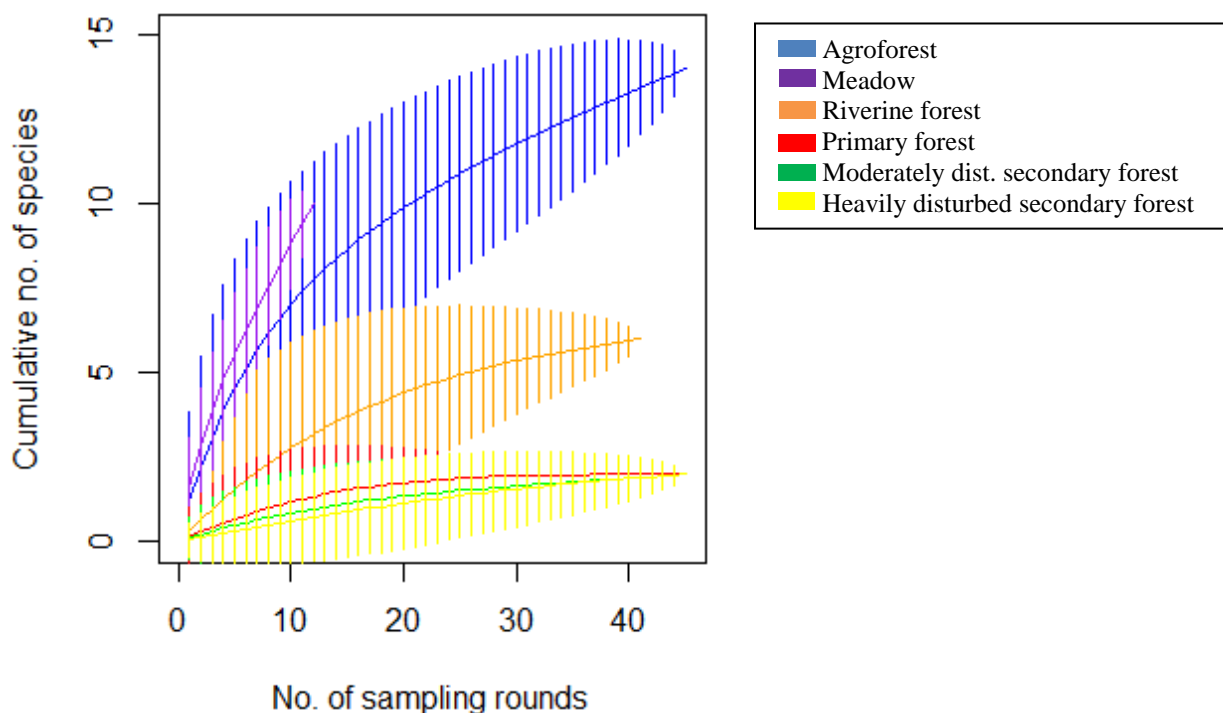
Fig. 3.2 Sample-based species accumulation curves for each habitat. Blue = agroforest (45 sampling rounds, 14 species), Orange = riverine forest (41, sampling rounds, 6 species), Purple = meadow (12 sampling rounds, 10 species), Red = primary forest (45 sampling rounds, 2 species), Green = moderately disturbed secondary forest (45 sampling rounds, 2 species), Yellow = heavily disturbed secondary forest (45 sampling rounds, 2 species). Bars are 95 % confidence intervals.
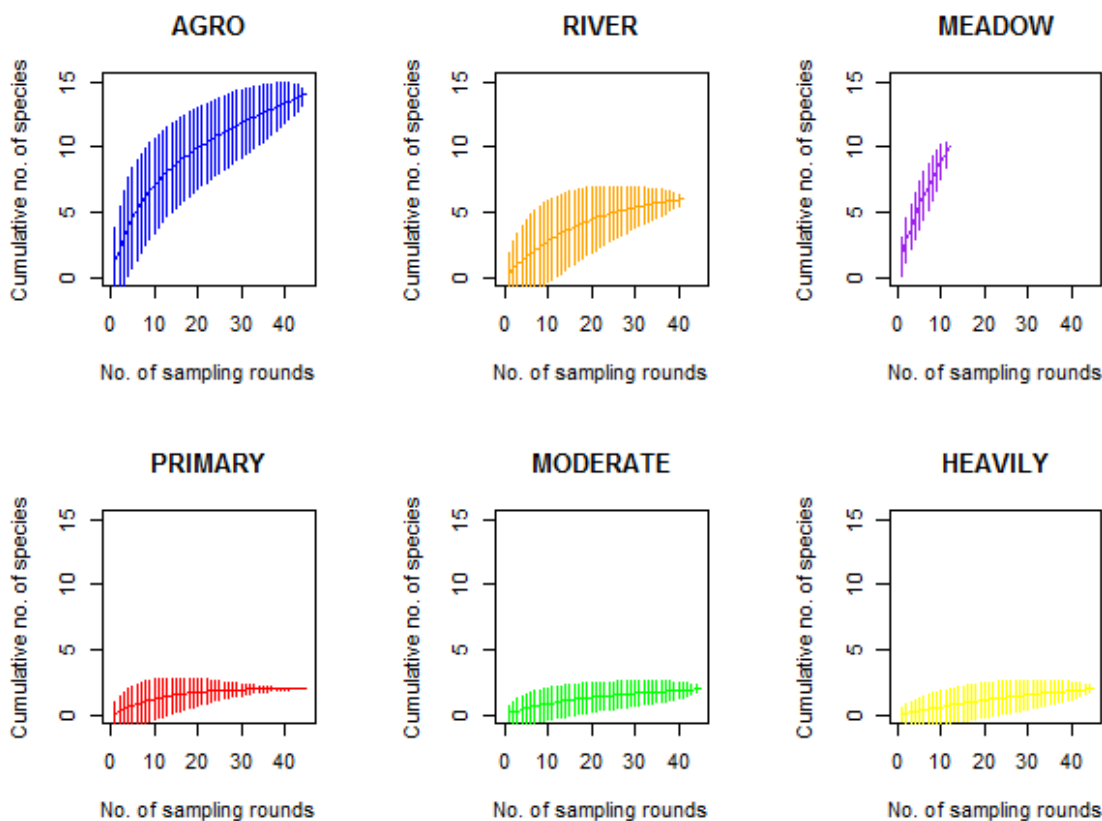
Fig. 3.3 Sample-based species accumulation curves for all habitats individually. Bars are 95% confidence intervals.

Fig. 3.3 displays species accumulation curves for all six habitats individually. The curve for agroforest show a decreasing steepness but the curve is still not flattening out completely/reaching an asymptote. Riverine forest has a less steep curve from the beginning and flattens out although not reaching a full asymptote. As such, both agroforest and riverine forest are slightly under-sampled, according to these calculations. On the other hand, meadow has a very steep curve indicating that the accumulated number of species is not nearly representing the habitat. All three closed forest habitats (primary forest, moderately and heavily disturbed secondary forest) have curves which flatten out almost completely/all reach an asymptote, indicating that they are adequately sampled.

There is no significant difference in species accumulation between meadow and agroforest. There is a significant difference between the remaining four habitats (river and all closed-forest habitats) after ca 10 and 20 sampling rounds for meadow and agroforest, respectively. After ca 27 sampling rounds, river also differ significantly from the closed forest habitats (Fig. 3.2).

4. Discussion

The rapid degradation and loss of the world's forests has caused a pressing concern for the future perseverance of the associated biodiversity. The main threats to natural forest are logging and land conversion (Contreras-Hermosilla 2000). The majority of the world's biodiversity is found in the tropics (Dirzo & Raven 2003), as are also the highest rates of deforestation and land conversion in addition to the highest population growth rates in the world (Cincotta et al. 2000) and a vast number of people living below the poverty line (Fisher & Christopher 2007). Several conservation techniques have been applied in attempts to remedy these past and current biodiversity losses, with mixed results. One such approach is to protect areas of natural forest from all human activities, including subsistence activities by local inhabitants, e.g. collection of fire wood, hunting and agroforestry. The actual effects of these activities are subject to great dichotomy, and the assigned conservation values of anthropogenic habitats such as secondary forest and agroforest are equally contentious (Barlow et al. 2007). The present study, although small-scale, revealed a trend supporting the view that agroforest could be a valuable conservation asset in the difficult trade-off situation between conservation of biodiversity and the sustainability of rural livelihoods.

4.1 Species richness and sampling completeness

The species accumulation curve for the total study indicates that although there is no more significant increase in species accumulation after ca 140 sampling rounds, the total sampling effort of 243 sampling rounds does not represent the full species inventory of fruit-feeding butterflies in the area sampled (Figure 3.1). According to Kielland (1990) there are at least 116 nymphalid species known to inhabit the ANR/East Usambara area. Frontier Tanzania (2001) sampled individuals from 112 butterfly species of 9 families, including 46 *Nymphalidae*, 6 *Satyridae* and 14 *Acraeidae* within Amani Nature Reserve. Their effort yielded a substantially higher species richness than the present study. The variation between the results could be due to pronounced local differences in butterfly assemblages and dissimilarities in sampling methods (e.g. sweep netting in addition to fruit traps). Regardless, it draws into question the validity of the reduced steepness of the species accumulation curve in Fig 3.1.

None of the species accumulation curves for the three open habitats reach an asymptote, indicating that the total sampling from each of the habitats does not represent the full species inventory of fruit-feeding butterflies. The meadow habitat in particular is severely under-sampled (Figure 3.3). The curves for each habitat indicate that there is no significant difference in accumulated species richness between agroforest and meadow. After ca 20 sampling rounds the accumulated species richness is significantly higher in both these habitats than all other habitats (Figure 3.2). The accumulated species richness also becomes significantly higher in riverine forest than the three closed-forest habitats (primary forest, moderately and heavily disturbed secondary forest) after ca 25 sampling rounds. The species accumulation curves for the three closed forest habitats quickly flatten out and as such indicate almost complete sampling. However, with only two species sampled in each of the closed forest habitats, solid estimates are difficult to calculate. None of the three closed forest habitats differ significantly from each other (Figure 3.2). Again, the solidity of the estimates is questionable due to the very low number of sampled species.

In spite of several shortcomings of the method applied in the present study (see section 4.7 and 4.8), the trends for the accumulated species richness is relatively clear; separating the open habitats (agroforest, meadow and riverine forest) from the closed forest habitats (primary forest, moderately and heavily disturbed secondary forest) and also the meadow and agroforest from riverine forest in terms of higher accumulated species richness. This is also visible in Table 3.1 where the additive contribution of all open habitats constitutes all 19 species whereas the additive contribution of the closed-forest habitats only constitutes three species.

4.2 Species distribution and the effect of species traits

The overall distribution of species across habitats was not random, based on the high X^2-value for the overall Chi Squared test (Table 3.5). For the individual species, however, only five of the 19 sampled species had a significantly non-random distribution across habitats. This could be a result of low capture rates (i.e. observed abundance) which the Chi Square test uses to calculate if the difference to the expected abundance is larger than what can be attributed to chance. When looking at habitats, all except primary forest and heavily disturbed secondary forest had a significantly non-random distribution (Table 3.5). These are both closed forest habitats with very low catch numbers (n = 5.8 and 4.5, respectively). These low capture rates give a small difference between observed and expected values and may not represent the

actual species distribution which could have become apparent with larger samples. This is also reflected in the species accumulation curves (Fig 3.3), which are near asymptotic but with only two species, it is probably difficult to calculate solid estimates. The significance in moderately disturbed secondary forest is most likely due to the overrepresentation of *E. tiberius tiberius.*

Interestingly, all sampled species had at least one individual sampled in one of the two open habitats agroforest and meadow. This includes six species which have been characterized as strict forest species by Kielland (1990) and Frontier Tanzania (2001) (Table 3.6). This emphasizes the difficulties with creating categories based on one or a few studies. However, the individuals in question may simply be vagrants, moving into open habitats due to the extraordinary resources produced by human alterations, while still being dependent on closed forest as a main habitat (Ghazoul 2002; Khan et al. 2011). Both the agroforest plots and the meadow plot were relatively close to forests. Of the 19 species sampled in the present study, six were not recorded in the Frontier Tanzania Biodiversity Survey (Table. 3.4). All of these were sampled in either an agroforest plot of in the meadow plot. It is possible that the Biodiversity Survey did not sample in these types of habitat, but restricted their sampling mainly to forested areas although this is not specified in the paper and further information from the authors of the Biodiversity Survey was not possible to obtain.

Dispersal abilities in insects are a highly complex suit of functionally connected traits, such as "hormone titers, development time and growth rate, distribution of energy stores, flight propensity and age-specific reproduction" (Roff & Fairbairn 2007). In addition, certain morphological traits of the adult insect have been linked to dispersal abilities or speed as speed is often used as a proxy for dispersal ability (Fairbairn & Roff 1990; Palmer & Dingle 1989). In butterflies, a positive correlation with speed has been shown for wing span, thorax mass, thorax width and body mass and body length (Dudley 1990; Hill et al. 2001). Thorax mass is in effect flight muscle mass (Srygley & Chai 1990). A negative correlation has been found with relative abdomen mass which is generally associated with reproductive organs (Srygley & Chai 1990). However, several other studies have found opposite relationships or no correlation at all (Hanski et al. 2002; Lewis & Thomas 2001), suggesting that the use of morphological traits as indicators of dispersal should be used with caution. For instance, flight morphology could also be related to predator avoidance tactics. Srygley & Chai (1990) found a positive correlation between palatability and thoracic mass. They argue that palatable

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species allocate more mass to the thorax, i.e. flight muscles, to sustain a fast anti-predatory flight pattern, while toxic species are not as dependent on this allocation.

With an increasing fragmentation of the landscape, understanding how species and populations respond to this is essential to develop successful conservation strategies. Research has in the recent years turned to investigate how habitat fragmentation and edge-mediated processes affect dispersal rates and behavior (Hill et al. 1999). This is partly obtained by studies of morphological and ecological traits related to dispersal (Skórka et al. 2013). The surrounding matrix is generally heterogeneous and as such can propose a differing degree of permeability for even closely related species, making the effective isolation of a habitat patch species dependent (Ricketts 2001). In the past decades, scientific focus has been directed towards traits which are related to meta-population recolonization of empty habitat patches following local extinction (Thomas et al. 1998).

In the present study, only rough measurements of relative wing size and wing length-to-width ratio was possible to obtain in addition to the known number of plant families the larvae feed on and the types of habitat they were previously known from (Kielland 1990) (Table 3.6). Of the 19 species sampled, two species had one wide range trait, seven species had two and three wide range traits, two species had four wide range traits and one species had five wide range traits. Of the three species with four or five wide range traits, only one (*M. leda africanus*) was found in five habitats. The remaining two species, *H.* conf. *anthedon wahlbergi* and *C. candiope candiope*, were only found in one and two habitats, respectively. All other species (with 1 – 3 wide range traits) were also found in a number of habitats varying from one to five. Therefore, the number of wide range traits possessed by a species did not relate well with the number of habitats it was present. When looking at individual traits, only one possible trend in regards to small wing size was revealed.

4.2.1 Morphological traits

In terms of wing size, nine species were characterized as large and two species as medium-sized. The nine large species included eight members of subfamily *Charaxinae* and *M. leda africanus* (*Satyridae*). Although thoracic measurements were not possible to obtain, the *Charaxinae* are known to have a powerful build (Kielland 1990; Larsen 1991). However, only two Charaxinae (*C.pollux mirabilis* and *E. tiberius tiberius*) were found in four or five habitats, while the remaining were only present in one or two habitats. Males of the genus *Charaxes* are known to be very territorial and aggressive (Larsen 1991). As such, individuals may not roam far, but others could be pushed further away and as such increse distribution for

the species as a whole. Interestingly, *C. pollux* is usually less territorial than other charaxids (Larsen 1991), while still having the widest habitat distribution in this study. The two medium-sized species (genus *Junonia*) are also known as strong fliers, but were also only present in one or two habitats. In summary, species with a medium or large wing size had both narrow and wide habitat distributions. On the other hand, all eight species with a small wing size were found only in one or two habitats (either agroforest or meadow, i.e. open habitats). For the wing length-to-width ratio, of the five species with a high ratio, three were found in one habitat, one was found in two habitats and only one in five habitats. The same lack of correlation was also seen in species with low ratio, ranging from one to five habitats.

Hill et al. (2001) found that butterflies in gaps were larger than in shade habitats and also had lower recapture rates, both of which were interpreted as signs of high dispersal ability. On the other hand, a migration study on the Glanville fritillary butterflies by Hanski et al. (2002) found no correlation between either body size or wing size and migration rates, arguing that they should not be used as proxy measurements for mobility. They suggest that even sedentary species depend on strong flight morphology to successfully forage for food, mate and reproduce. This supports the findings of Lewis and Thomas (2001) that *Pieris brassicae* communities after over 100 generations of captivity did not have any reduction in relative thorax size, a measure frequently used for migration analyses. However, in the same study wing size did decrease. They argue that this is a possible result of the reduced need for long distance flight and an increased need for maneuverability due to the constrained habitat in small cages. However, they found it hard to conclusively say what drove the adaptations. All relationships with body size is difficult to entangle as the trait also correlates to a wide range of other life-history traits (Benedick et al. 2006).

4.2.2 Ecological traits

According to the niche-breadth-theory, species with a greater degree of generalization are more likely to also have a wider geographical distribution (Brown 1984). Although the theory has been criticized for lack of evidence, recent studies of butterflies in both tropical and temperate regions have revealed strong positive relationships between geographical range and host plant range (Benedick et al. 2006; Charrette et al. 2006; Quinn et al. 1997). A link has also been placed between the extent of distribution within the native range and the ability to colonize foreign areas (Charrette et al. 2006). The butterfly larvae are chiefly herbivorous (Hamer et al. 2006), displaying either monophagy (here defined as feeding on only one family of plants) or polyphagy (here defined as feeding on several families of plants). The presence

of larval host plants has been linked to butterfly diversity (Koh & Sodhi 2004). In the present study, larval feeding habits did not seem to affect the number of habitats a species was present (Table 3.6). Species with monophagous larvae were present in up to five habitats. Of the five polyphagous species, four were only found in one or two habitats. The fifth polyphagous species, *C. pollux mirabilis*, was present in four habitats.

Neither the Pearson's Chi Squared-test nor the assessment of species traits and habitat distribution provided any evidence for specializations in any of the sampled species (Table 3.5 and 3.6). Of the 10 species found in only one habitat, all were found in very low numbers as well as having low expected values. The six species found in two habitats also had relatively low numbers except for *Sallya* spp. with 35.5 (adjusted) individuals (Table 3.5). However, the *Sallya* group contains individuals from at least five species and as such, the abundance per actual species may not be particularly high. Interestingly, for all 16 species found in one or two habitats, the habitats in question were solely open ones (agroforest, riverine forest and meadow).

Of the aforementioned 16 species, only *C. acuminatus usambarensis, C. cithaeron kennethi, H.* conf. *anthedon wahlbergi* and *Sallya* spp. had significantly non-random distributions across habitats (p= 0.01, <0.01, <0.001, <0.01, respectively). However, *C. cithaeron kennethi* and *H.* conf. *anthedon wahlbergi* had particularly low observed and expected numbers, providing poor basis for statistical power. *C. acuminatus usambarensis* did show a moderate overrepresentation in the riverine forest. In spite of being characterized as a forest species (F) by Kielland (1990) and Frontier Tanzania (2001), it was not present in any of the closed-forest habitats in the present study. Contradictory, in addition to riverine forest it was also found in agroforest (Table 3.3). *C. acuminatus usambarensis* is a large butterfly with polyphagous larvae. Adults have a powerful fligth and their preferred food sources are tree sap and fermenting fruit. These traits could partly explain their unusual distribution found in this study. The group of *Sallya* spp. also had a significantly non-random distribution across habitats (p<0.001). It was markedly overrepresented in agroforest with 35.5 observed individuals versus 21.64 expected. In addition, it was moderately underrepresented in riverine forest and medaow in which zero and 1.5 individuals were sampled, respectivly. Again, this is a group of several species and as such cannot be directly compared to the other species. However, all *Sallya* species known to be present in the region prefer forest habitats, but are also greatly attracted to fermenting fruit (Kielland 1990) which could explain their presence in open habitats, but not their absence from all forest habitats.

Interestingly, the only other of these 16 species with any pronounced differences between observed and expected values was *Byblia anvatara acheloia*. The species had an expected value of 4 compared to the observed zero individuals in primary forest. The species was only sampled in one habitat, agroforest, where the single sampled individual (observed value = 1.0) was very close to the expected value (0.58). *Byblia anvatara acheloia* is one of the most common butterflies in Africa. It is found in a wide range of habitats, from open savannahs, gardens, forest roads and glades to denser woodland forests (Kielland 1990) . It's ditribution was not significantly non-random across habitats (p = 0.98) but it is likely that the small sample size confounds the statistical calculations. They are also greatly attracted to fermenting fruit and frequently enter banana traps (Kielland 1990), but in the present study the species was only represented by one individual.

All three species found in closed-forest habitats were the species with the widest habitat distributions (*C. pollux mirabilis, E. tiberius tiberius* and *M. leda africanus* present in 4, 5 and 5 habitats, respectively). Of these, only *E. tiberius tiberius* had a significantly non-random distribution (p<0.001), while both others had near-significance (p = 0.16 and 0.11 for *C. pollux mirabilis* and *M. leda africanus*, respectively). Of these, only *E. tiberius tiberius* had a noticeable overrepresentation with six individuals sampled in moderately disturbed secondary forest where the expected value was 0.74 (Table 3.5). It was also slightly overrepresented in the other two closed-forest habitats (primary forest and heavily disturbed forest). Additionally, it was markedly underrepresented in agroforest and slightly underrepresented in the other two open habitats (meadow and riverine forest). As such, it seems to be able to utilize both habitat types but prefer the closed forests. It was also observed flying in all three closed-forest habitats on multiple occasions, but never in the open habitats. These findings are in congruence with the species' previously identified preference for understorey in dense lowland forests (Kielland 1990). The larvae of *E. tiberius tiberius* are monophagous to *Sapindaceae* species (the soapberry family) which may partially constrain their distribution to forested areas. However, it is also a large butterfly capable of a powerful flight and greatly attracted to fermenting fruit (Kielland 1990) which could explain its presence in the less preferred open habitats.

Even the crepuscular, shade-loving *M. leda africanus* was found in five habitats, including all three open habitats (agroforest, meadow and riverine forest). It is mostly known from woodlands and forest margins (Kielland 1990). However, like most satyrids they feed on monocotyledons e.g. grasses (*Poaceae*) (Larsen 1991) which were abundant in the open plots. The highest observed numbers were in agroforest and riverine forest, with 7.5 and 5.5

individuals, respectively. It was moderately underrepresented in agroforest and moderately overrepresented in riverine forest. All other habitats had a relatively small difference between observed and expected values (Table 3.5). *C. pollux mirabilis* is a large species with a polyphagous larvea and is known from both deep forest an open habitats. As such, it's habitat distribution in the present study represent it's ecology quite well.

Some species may be adapted to the conditions of naturally occurring secondary forest, such as after tree falls and fires and will naturally be widespread (Hill et al. 1999). When they quickly inhabit human induced secondary forest, they may be percieved as generalists, but are in reality specialists on a type of habitat which is offered increasingly by anthropogenic disturbance, making the species even more widespread (Thomas 1991). Also savannah species have been found in equally high numbers in their savannah habitat as disturbed forest, but were limited in intact forest (Sundufu & Dumbuya 2008). On the other hand, deforestation has a particularly adverse effect on endemic and restricted-range species (Thomas 1991). By losing these, but gaining the species adapted to secondary forest there may not be a noticeable decrease in diversity or species richness. This is why diversity, particularly local (alpha) but also regional (beta) is not necessarily a good measure; the composition of rare and endemic species is still unaccounted for (Thomas 1991).

Both the present study and the Biodiversity Survey by Frontier Tanzania (2001) only revealed one endemic butterfly species each. This may indicate a relatively low number of (known) endemic butterflies in the area. Therefore, it is difficult to discuss this subject based on my findings. However, the *Acraea* sp., *Neptis* spp. and *Sallya* spp. were not identified to species level, but of the 11 *Neptis* spp. and 5 *Sallya* spp. possibly inhabiting ANR and described in Kielland (1990), none are mentioned as endemic. None of the sampled subspecies are categorized by the IUCN Red list (IUCN 2013) because they have not been assessed yet. When investigating only the species, not subspecies, a few have been assessed but given status as Least Concern (IUCN 2013). The *Acraea* sp., *Neptis* spp. and *Sallya* spp. could not be checked since they were not identified to species level. However, of species within these genera known to be present in Amani Nature Reserve (Kielland 1990) only a few have been assessed and of those, all are classified as Least Concern (IUCN 2013).

4.3 Abundance and the effect of environmental variables

In spite of a robust sampling design the study resulted in a relatively low number of sampled individuals (n = 138.5). Similarly to the accumulated species richness, the total butterfly abundance was also significantly higher in both agroforest and meadow compared to all other habitats, with 58.5 % and 15 % of the total sampled abundance, respectively. Although riverine forest contained a close 14.1 % of the abundance, the multiple comparisons test categorized it as significantly different from meadow. None of the four forest habitats (riverine forest, primary forest, moderately and heavily disturbed secondary forest) differed significantly from each other in terms of butterfly abundance.

According to the most supported Zero-inflated Poisson regression model, abundance (Count) was affected the most by the main variables Habitat, Species and Rain, in both parts (Poisson and binomial). The sub variable Rain was more supported than Sampling round, which in effect is an expression for time. Rain was highly significant in both the count model and the binomial model ($p < 0.01$ and $p = 0.1$, respectively). The Pearson's correlation test revealed that the relationship was negative, with a 76 % correlation (p-value = 0.04933). Previous research have revealed opposing trends for species diversity and abundance in relation to seasonal changes depending on geographical locations (DeVries et al. 1997; Molleman et al. 2006) and also between primary forest and secondary forest within the same geographical area (Hamer et al. 2005). The present study was performed on a small temporal scale, and a longer sampling period of a full year could have provided more solid results (Molleman et al. 2006). However, the rain pattern during field work was also slightly confounding; with periods of heavy rain in the end of the dry season, and long dry periods in the wet season.

Ideally, the coefficients of the model output should be used to e.g. make predictions plots. However, the main variables Habitat and Species are too course to move further with in this respect but also provide little explanatory value to the observed abundances as they stand. Although including the sub variables for Habitat in the models only increased the AIC values, it was still of interest to examine their relationships with abundance. By performing correlation tests between abundance and the environmental sub variables for Habitat, the relationships between them became clearer (Fig 3.1). Canopy openness directly above the trap had a 99 % positive correlation with abundance (p-value = <0.01), closely followed by canopy openness for the plot in general, with a 93 % positive correlation (p-value = <0.05). This is in congruence with earlier findings which have also linked canopy openness as main

predictor for butterfly diversity and composition, with a positive relationship (Hill et al. 2001; Koh & Sodhi 2004). Alterations in light availability following habitat modification can impact butterflies directly by causing changes in microclimatic conditions which in turn can affect adult and larval development (Hill et al. 2001). Additionally, an indirect effect can come from altered quality in food resources (Hill et al. 2001). Stand basal area (SBA) is closely related to canopy openness as fewer m^2/ha of stand basal area indicates fewer or smaller trees, i.e. reduced canopy. However, unlike the extremely strong correlation with canopy openness, SBA only had a 48 % correlation with abundance (Fig 3.1d). The relationship was negative, as expected, with decreasing abundance following an increase in SBA. However, the relationship was only near significant (Spearman's, r_s = -0.48, p = 0.07). Again, the small sample size gives weak statistical power to the calculations, and a larger sample size could have provided a more nuanced pattern. None of the sub variables for Species gave a more parsimonious AIC-value. They were only assessed through a qualitative analysis (see section 4.2.1).

Riverine forest had a higher abundance than the three closed forest habitats, as well as higher observed species richness. Few studies have investigated butterfly diversity in riverine forest, but Vu & Vu (2011) found that riverine forests had a high abundance but medium richness and diversity compared to primary forest and bamboo habitats. They propose that riverine forest is a less layered habitat, and as such support fewer species but have features such as shrubs and flowering plants which attract many individuals of those species present. Results from the present study contradicts these findings with much lower species richness and abundance in the primary forest than the riverine forest, although a small sample size does not provide solid estimates. Interestingly, of the three agroforest plots A2 stood out as containing the majority of individuals and the highest species richness. The environmental factors measured at each plot varied to a certain degree (Table 3.1). A2 was even more open than the other two plots, containing only a few crop trees. Although crop plants such as banana (*Musa* genus), were present, a large part of the area was more dominated by small flowering plants than either of the other plots. As with the explanation by Vu & Vu (2011) for abundance in riverine forest, these flowering plants may explain the high abundance in A2, but not the high species richness.

The Akaike Information Criterion (AIC) is a method for finding the model with the best trade-off between goodness of fit and model complexity. As such, it does not measure the correctness of the model but gives a value of this trade-off relative to other models containing different variables and combinations (Akaike 1974). Since none of the measured

environmental variables or species traits decreased the AIC-value of the models, there must be other variables defining Habitat and Species which are more explanatory. Possible species traits affecting abundance could be territoriality (Pinheiro 1990), and level of attraction to baited traps (Hill et al. 2001). Differences in species abundances have also been linked to their individual habitat preferences (Hill et al. 2001). Although closely related to canopy openness, microclimatic conditions such as humidity and temperature can also have independent effects on butterfly distribution (Hill et al. 2001). Ideally, these species and environmental variables should have been measured. Also more detailed information on the structural and vegetative quality of the habitat would have been preferable, as well as an investigation into the presence of larval and adult food resources. Particularly for agroforest plots and the meadow plot, the quality of and distance to the surrounding forests could have been of relevance. These variables were not investigated as it was difficult to obtain solid information and due to a constrained time frame and limited resources. However, it should receive attention in future research.

4.4 Mark-recapture analysis

All sampled individuals were marked with an individual number to record recapture rates. This could be used to calculate species population sizes and longevity. However, only 10 individuals of seven species were recaptured during this study (Table 8). Of these, only one was recaptured more than once; with four recaptures. These numbers were considered too low to run any analyses on, both for individual species and as a whole (Ricketts 2001). However, interpreting the data qualitatively, there could be several reasons for the low recapture rates. Either the populations are very large or, more likely; there may be a high turn-over rate of individuals, especially for species with large thoraces which have been linked to higher mobility i.e. dispersal rates (Hill et al. 2001). Alternatively, with low capture rates in general, it is likely to assume the recapture rates will be even lower. Further research with a larger sample size is required to obtain more accurate predictions.

4.5 Possible explanations for low capture rates

Some of the species observed in the forests were (according to my in-flight identification) the same species as sampled in traps in other habitats (e.g. *H.* conf. *anthedon wahlbergi*, although accurate identification of this species is difficult in the field). Also, individuals of species already recorded in a forest plot, were seen either in the surrounding or even close to the trap

(*C. pollux mirabilis* and *E. tiberius tiberius*). These could be either the same individuals as previously trapped or new individuals. Either way, it shows that even though an individual is close to a trap and is known to enter it; they do not always do so, thus affecting the abundance recorded and possibly the recapture rates. One particularly abundant observed species was the unmistakable *Catuna sikorana*, seen several times fluttering around the traps, particularly in the closed forest plots. *C. sikorana* is known by Kielland (1990) to enter banana traps. Also *Euphaedra neophron* was observed but never trapped. This is another species highly attracted to fermenting fruit (Kielland 1990). The endemic *Hypolimnas antevorta* Distant, 1879 was also observed in the river habitat on multiple occasions, although it may have been the same individual. When investigating the effect of fruit fall on the capture success of adult butterflies, neither Hamer et al. (2005) nor Barlow et al. (2007) found any significance. However, the results might have been influenced by butterfly behavior and variations in trap efficiency (Barlow et al. 2007). Based on these findings, it is possible that natural fruit fall made the traps of the present study less attractive.

Interestingly, when experimenting with baited traps, Sourakov & Emmel (1995) did not capture a single individual in fruit-baited traps, but attracted high numbers to traps with rotten fish and shrimp. Similarly to the present study, their captured species included individuals mainly from the family *Nymphalidae*. However, they do not provide any possible explanation to their findings. An alternative explanation to the low capture rates in the present study is that the species in question may have particularly high escape rates (Hughes et al. 1998). In addition to the observed species possible to identify in flight, several other unidentified species were present, which may or may not have been part of the fruit-feeding guild. A more successful sampling of these species could have altered the species richness and abundance results.

4.6 Implications for conservation in and around ANR

The general disagreement on effects of human-induced disturbances on flora and fauna is pronounced, with results varying with e.g. study group, geographical location, spatial and temporal scale and biodiversity indices utilized. This can be directly linked to the current situation in and around Amani Nature Reserve. In 2002 the Derema Reserve was gazetteded as a wildlife corridor between the northeastern part of ANR and other forested areas north of it. The Derema Reserve, also called Derema corridor, has a long history of human settlement and agriculture, particularly cardamom farming. After the establishment of the corridor,

farmers lost all or most of their land and the forest is now a mix of primary forest and revegetated secondary forest (Miller 2013). The dichotomy in research findings of faunal response to human induced landscape modifications and their possible conservation value is greatly reflected by the empirical studies on birds executed by Dr. Bill Newmark and Dr. Norman Cordeiro in th East Usambara Mountains. Their separate research on birds have led them to opposing conclusions about the state of the populations, and consequently, the value and necessity of the Derama corridor as wildlife dispersal facilitator (Miller 2013). In light of the differing results, caution is warranted when implementing management schemes involving local farmers and stakeholders, as the ultimate success of the protection depends on their cooperation and upholding of the restrictions (Miller 2013).

The present study, although small-scale, revealed a trend supporting the view that agroforest could be a valuable conservation asset in the continuously difficult trade-off situation between conservation of biodiversity and the sustainability of rural livelihoods. No clear trends were found for primary forest versus moderately and heavily disturbed secondary forest. The current body of research on the subject matter is greatly biased towards certain taxonomic groups and geographical locations (Irwin et al. 2010), resulting in a high degree of extrapolation (Colwell & Coddington 1994). Consequently, there is a growing call for descriptive, replicated large-scale and long-term studies which thoroughly investigate the relationships between all levels of biodiversity and the full gradient of habitat disturbances (Chazdon et al. 2009; Irwin et al. 2010; Norris et al. 2010).

4.7 Practical limitations of the study and possible effects on the results

The design of the present study contains a series of caveats and shortcomings, due to the practical limitations of the field work. This may have had a grave effect on the resulting data for species richness and abundance. First of all, it was executed on a small spatial scale, with two accompanying repercussions. First, the selected plots representing the forest habitats are most likely pseudo replicates of the habitat in question. The forested areas within ANR are highly heterogenic in terms of e.g. vegetation composition and topography and as such cannot be fully represented by only one geographical location. Ideally, plots should have been chosen with a greater distance between them or be placed in separate forest areas of the same habitat type (Hill & Hamer 2004). Secondly, there may also have been a pseudo replication in terms of species community in plots in close proximity to each other. This was particularly the case for the heavily disturbed secondary forest plots and primary forest plots, of which some had

less than the preferred minimum distance of 200 m between them. I could not find any research specifically on the distance a butterfly can cover, but a minimum distance of 200 m is generally used as seen is studies such as (Ghazoul 2002) although flight distances have been recorded at least up to 515 m for individuals of *Phengaris nausithous* (Skórka et al. 2013). However, distinct butterfly assemblages have been found in traps 50 − 100 meters apart (Pinheiro & Ortiz 1992). Additionally, several plots were located in close proximity to human infrastructure or settlements. The heavily disturbed forest plots and riverine forest plots had the shortest distances to roads and open areas. Several species which are naturally occurring in open areas are well known to enter forests through small paths and openings (Kielland 1990) and could as such have influenced the sampled communities. The plots in meadow and agroforest were frequently utilized by villagers. The presence of local villagers near the trap could both scare away butterflies from the area and also increase escape rates of those trapped by causing a panicked flight movement inside the trap (Hughes et al. 1998).

The study was also undertaken on a small temporal scale. Long-term studies on Neotropical butterflies have shown low abundance and richness in the dry season, increasing into the rainy season (DeVries et al. 1997), while an opposite trend have been found in Bornean rain forests (Hamer et al. 2005) and in a study in Uganda, the temporal variation was pronounced but without clear trends in regards to season (Molleman et al. 2006). Opposing temporal trends have also been found in primary and disturbed forests (Hamer et al. 2005). Although it was attempted to sample from dry season into rainy season in the present study, 10 weeks is likely to be too short to correct for possible temporal variations in butterfly diversity (Khan et al. 2011). Molleman et al. (2006) suggest that a full year of sampling is advisable.

Another limitation of the method is the lack of canopy sampling. Several studies have revealed partly distinct butterfly communities in the canopy and understorey strata, suggesting that sampling only one stratum is insufficient (DeVries 1988; DeVries & Walla 2001). However, due to the practical problems of erecting canopy traps, these were not part of the present study. Sampling in the canopy strata could possibly have increased the number of species sampled; particularly in the forest habitats (meadow and agroforest technically didn't have a canopy stratum). Also, for the sampled understorey strata there was only one trap per plot. An intensification of trapping effort could have been achieved through an increased number of traps in transects at each plot or additional sweep netting. The meadow habitat was only represented by one plot (i.e. one trap) due to lack of similar habitat within appropriate distances, and sampling was only performed from cycle 2. As a result, the sampling effort for

the meadow habitat is constrained to only 12 sampling rounds in contrast to 45 for the other habitats (41 for riverine forest). This could explain why the species accumulation curve is much steeper for the meadow than for the other habitats.

The method of fruit-baited traps is in itself biased towards species of this particular fruit-feeding guild, and as such does not represent the full species richness of the area. This could affect the results for habitat influence on species richness and abundance as other guilds, for instance the nectar-feeding guild, have been shown to have different responses to variation in tree cover compared to the fruit-feeding guild (Harvey et al. 2006). Additionally, some species are more attracted to the bait than others, possibly skewing the representation of the individual species trapped (Hughes et al. 1998).

Finally, the butterfly identification in the field was done solely by the author, without supervision of a field lepidopterist. As such, there is a risk of some individuals being identified to the wrong species. This goes particularly for the three individuals of *Hypolimas* genus, which may have been *H. anthedon wahlbergi* or *H. deceptor*. Also several of the butterflies collected for identification at the Royal Belgian Institute of Natural Sciences were not possible to identify to species level due to mold damages and insects eating the dried specimens while under preparations.

4.8 Effects of data manipulation

There had to be made several adjustments to catch numbers, due to differing number of trap days in a sampling round and differing numbers of sampling rounds within cycles (see section 2.6). However, the sampling resulted in many instances of zero catch which are not possible to adjust for varying trap days. This caused a systematic error in the final data which could be influencing the correctness of my results. I was later informed of the offset function in R, which can add trap days into the model without increasing the degrees of freedom. This may have been a better way to process my data but time did not allow for it to be changed. Further manipulation of the catch data occurred because ZIP can only function with integers. Therefore all adjusted catch numbers were rounded off to the nearest integer.

The environmental variable "Rain" also required certain adjustments to fit the statistical methods. The assigned values of rain per day were based on daytime recordings only; rain during the night has not been accounted for. The rain calculations for ZIP were based on the average value of the day of sampling and the three preceding days. In cycle 3 primary forest plots and the meadow had an additional day in the last sampling round.

However, this day had no additional rain compared to the original sampling day and for the purposes of this analysis the rain value was set as the same as for the original day. For correlation between rain and abundance, the average rain value was calculated from the value of the sampling day and the preceding three days, representing the full sampling round, except sampling round 3.3 which included rain values for five days instead of four due to the extraordinary sampling day. It was not possible to perform a Principal Component Analysis (PCA) on the rain variable because all values were averages with standard deviations, which PCA cannot operate with. Had proper measurements of rain in milliliter been performed, it might have given a clearer picture of the relationship between species abundance and rain.

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APPENDIX I

Table A. Web pages utilized to retrieve photos and information for the field guide, with period of access.

Web page	Access months 2013
http://learnaboutbutterflies.com/Africa	May - July
http://projects.bebif.be/enbi/albertinerift/butterfly/	May - July
http://lepidoptera.pro	May - July
http://tolweb.org	May – July
http://nhm.ac.uk	May – July
http://butterflycorner.net	May - July

APPENDIX II

The following is a compilation of information on the butterfly species and subspecies sampled in this study. It is mainly based on Kielland (1990) and Larsen (Larsen 1991) but also includes the newly revised classification of the species in question. This is provided by http://nymphalidae.net (Wahlberg) administered by Niklas Wahlberg and Carlos Peña. The webpage aims to be a comprehensive and updated database for the *Nymphalidae* family, but is not yet fully complete.

The families are listed in an alphabetical order with their associated species and subspecies also in an alphabetical order. An additional sheet for tribe *Charaxini* is included.

Acraea sp.　Fabricius 1807

Literature	Family	Subfamily	Tribe
Kielland	*Acraeidae*	-	*Acraeini*
Larsen	*Nymphalidae*	*Acraeinae*	-
nymphalidae.net	*Nymphalidae*	*Heliconiinae*	*Acraeini*

Acraeidae is a family of approximately 200 species, mostly found on the African continent with some representatives in Asia South America (Kielland 1990). They are small to medium-sized, chiefly in shades of red to yellow and black or brown. Many species are polymorphic, especially the females. As such, they can be difficult to identify. Some groups are also highly similar, and previously thought to be the same species (Larsen 1991). Extensive study and revision was done by Pierre (1987) at the Paris Museum, who split the *Acraea* genus into two sub genera; *Actinote* Hüb and *Acraea* Fabricius and also included the genus *Bematistes* Hemming as a subgenus within *Acraea* (Kielland 1990; Larsen 1991). Kielland (1990) has kept these as separate genera while Larsen (1991) chiefly accepts Pierre's regrouping. Acraeids are also mimicked by species of several genera (e.g. *Pseudacraea* and *Mimacrae*) (Kielland 1990). All Acraeids contain toxic cyanide compounds which can be exuded with a fluid, making them distasteful to birds. These toxins are created from cyanogenic compounds acquired from their host plants. However, also the species which do not feed on plants containing the cyanogenic compounds are toxic and it is possible that they are synthesized metabolically (Larsen 1991). Their flight is often slow and buoyant but many are able to fly faster if needed (Kielland 1990). The eggs are mostly placed on leafs of the larval food plants of *Passifloraceae* or *Urticaceae*, but sometimes also of other plant families (Kielland 1990). Some species lay their eggs singly while others lay the eggs in clusters of up to at least 300. These are the biggest egg clusters found in any butterfly species. Smaller clusters are normally placed tidy on the leaf while larger clusters often are laid hap hazardously (Larsen 1991). The larvae have a cylindrical shape with no spines on the head but six rows of branched spines along the body, typical to the nymphalid tribe *Nymphalini*. The pupae are generally long, slender and smooth although some have dorsal or ventral spines (Kielland 1990; Larsen 1991). They are characteristically pearly white with black and brown markings (Larsen 1991). The *Acraea* are found in a vast array of habitats, ranging from rainforest to open clearings (Larsen 1991). Some are even found in the driest habitats any butterfly is able to survive in. However, the individual species are normally confined to the ecological conditions of only a few habitats. Few other families have evolved such high numbers of species with exceptional variation in habitat adaptation and behaviour. Some *Acraea* have sudden population explosions (Larsen 1991). There are 88 *Acraea* species in Tanzania (Kielland 1990).

Photos: Cecilie Notø 2013

Family *Nymphalidae* - The Brushfooted Butterflies

The *Nymphalidae* is a highly speciose family of butterflies, with over 6000 species described (Wahlberg). Over 1200 species are found in Africa, making it the second largest butterfly family, after the *Lycaenidae* (Larsen 1991). Over 220 of these are found in Tanzania (Kielland 1990). The species display a wide array of behavior, life history traits and ecological requirements (Larsen 1991). This, in addition to their large size, conspicuous morphology and ease of breeding, has made the *Nymphalidae* a subject to extensive study and research. Their large variation in color, patterns and wing shapes also make them highly attractive to collectors worldwide (Larsen 1991). Their classification is not fully understood yet and is being revised by several independent research groups. Particularly the taxonomic status of the families *Libytheidae*, *Satyridae*, *Acraediae* and *Danaidae*, have recently been suggested as sub families within *Nymphalidae* (Larsen 1991).

The main feature connecting all *Nymphalidae* is their reduced and modified forelegs. Thus they are easily recognizable as just having four walking legs instead of the normal six. The feature is the reason behind their vernacular name; Brushfooted butterflies. Males have the most reduced forelegs. The females of some species use the reduced forelegs to investigate the suitability of plant leaves as food, by scratching the surface but otherwise the function is largely unknown (Larsen 1991).

Byblia anvatara acheloia **Wallengren 1857**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Nymphalinae*	*Biblini*
Larsen	*Nymphalidae*	*Nymphalinae*	*Biblini*
nymphalidae.net	*Nymphalidae*	*Biblidinae*	*Biblidini*

The *Biblini* tribe contais 14 Afrotropical species with morphology and early stage features very unlike the other tribes of *Nymphalinae* (Larsen 1991). Particularly the eggs differ, with their extremely thin chitinous spines covering the body. The females deposit the eggs on the underside of the leaves of *Euphorbiaceae* plants, particularly *Dalechampia* spp., *Tragia* spp. and *Ricinus communis* (the castor oil plant). *Ricinus communis* is increasingly used as a crop plant and may provide an increasingly important food source for the butterflies (Larsen 1991). The larvae are similar to that of all the representatives of the *Nymphalinae* subfamily, with branching spines along the body; the two closest to the head being longer in a forward-pointing direction (Larsen 1991). In 1991, Larsen (1991) predicted that with further taxonomic researh, *Biblini* would be classified as a separate subfamily. This is now the case, as presented by nymphalidae.net (Wahlberg).

The *Byblia* genus contains only two species; *B. acheloia* and *B. ilithya* which are similar in morphology and ecology and sometimes fly together where their ranges overlap. Their habitats are open areas such as savannah and gardens but also woodland forest, forest roads and open glades where they fly low above the ground. They are present in altitudes ranging from sea level to high mountains. Of the two, *B. acheloia* is much more widespread and is one of the most common species in Africa. On the other hand, *B. ilithya* is also found in Arabia, India and Sri Lanka, while *B. acheloia* is strictly Afrotropical (Kielland 1990). Adults rarely visit flowers, but are attracted to sap from damaged plant stems and fermented fruit (Kielland 1990; Larsen 1991). They often enter banana traps (Kielland 1990).

Photos: Cecilie Notø 2013

Subfamily *Charaxinae*

The Charaxinae subfamily have evolved separately mainly in the Neotropics and the Afrotropical region. The Neotropical group is endemic and not closely related to the Afrotropical group. Members of Afrotropical *Charaxinae* are divided between three tribes; *Charaxini*, *Euxanthini* and *Pallini*, each only containing one genus (*Charaxes*, *Euxanthe* and *Palla*) (Larsen 1991). However, nymphalidae.net also includes *Polyura* in *Charaxini* (Wahlberg). The *Charaxinae* could be closely related to the *Satyridae*, reflected by the fact that some larvae feed on monocotyledons, a trait mainly reserved for satyrids. Some *Charaxinae* larvae also have a bifurcate tail, another feature also found in satyrids (Larsen 1991). *Charaxinae* are easily recognized by their medium to large size, powerful wings and beautiful colour patterns, but there are great differences in wing shape and behaviour between the tribes (Larsen 1991).

The *Charaxes* genus is mainly found in tropical Africa but a few species are present in Asia and Australasia. There are ca 180 Afrotropical species (Larsen 1991), of which ca 65 are represented in Tanzania (Kielland 1990). They are recognized by distinctly falcate (sickle-shaped) forewings and one or two tails on the hind wings, although there are exceptions without tails and sickle-shape (Larsen 1991). The species display a wide array of colour and pattern, with different systems of dimorphism, sexual dimorphism and even female polymorphism (Larsen 1991). Although the patterns normally are species specific, making them easy to identify, a complex of "black" *Charaxes* remain untangled (Kielland 1990; Larsen 1991). Many species are local and scarce (Larsen 1991).

Their preferred habitat is forest, where they normally inhabit the canopy strata. However, many species are observed on forest roads and open areas in search of food. Some species have evolved to strict savannah species (Larsen 1991). Males are highly territorial. They have large strong bodies enabling them to achieve fast and powerful flight and they are known to chase away intruders, even birds (Kielland 1990).The costa of their wings are often serrated, at trait which may be used as a weapon during fights. However, the function is unknown and could also include aerodynamic benefits (Larsen 1991). Their diet varies. Most species are not particularly attracted to flowers but have an exceptionally strong preference for fermented fruit and will often aggregate in large groups on the same piece. Males also feed on rotten meat and excrements, particularly carnivore excrements (Larsen 1991).

The eggs are barrel shaped with some ridges and keels on the sides. Females normally deposit the eggs singly on a variety of host plants and many species have polyphagous larvae. The larvae are smooth and green with a characteristic double pair of horns on the head. The horns can reach a considerable size (Larsen 1991).

Charaxes acuminatus usambarensis van Someren 1963

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	*Charaxini*
Larsen	*Nymphalidae*	*Charaxinae*	*Charaxini*
nymphalidae.net	*Nymphalidae*	*Charaxinae*	*Charaxini*

C. acuminatus is mainly a montane butterfly found in eastern parts of Africa (Larsen 1991).
A result of this montane ecology is the separation of the species into 12 isolated subspecies
(Larsen 1991). *C. acuminatus usambarensis* is not endemic to the Usambara Mountains,
but is only found there and in the Pare Mountains. They are generally found in low-lying to montane
forests between 500 and 1800 meters altitude (Kielland 1990). Other subspecies mostly inhabit
higher altitudes (Larsen 1991). They mainly inhabit the understorey strata. Males are very territorial
and make frequent aggressive flight (Larsen 1991).

The preferred food sources of *C. acuminatus* are tree sap and fermenting fruit, but males are
also highly attracted to water (Larsen 1991). The larvae are polyphagous and feed on many
plants in the undergrowth, e.g. *Allophylus* spp. (*Sapindaceae*) and *Bersama* spp.(*Melianthaceae*)
(Kielland 1990).

Photos: Cecilie Notø 2013

VII

Charaxes candiope candiope **Godart 1823**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	*Charaxini*
Larsen	*Nymphalidae*	*Charaxinae*	*Charaxini*
nymphalidae.net	*Nymphalidae*	*Charaxinae*	*Charaxini*

C. candiope candiope is a wide ranging species covering most of tropical Africa (Larsen 1991).
It is extremely common and found in all suitable habitats in Tanzania (Kielland 1990).
It is known as a long distance disperser, which could explain the fact that throughout its geographical range in Africa the species display very little, if any, variation (Larsen 1991).

The preferred habitat is forest and riverine forest from sea level to ca 2600 m (Kielland 1990), but the species is also able to successfully inhabit dry and open areas such as gardens and agricultural areas (Larsen 1991).

There is only a slight sexual dimorphism in the tails, which are more strongly developed in females than in males (Larsen 1991). Its most notable feature is the green veins (Kielland 1990).

The larvae mainly feed on *Croton* spp. (*Euphorbiaceae*) but can also feed on some grasses (*Poaceae*) (Larsen 1991).

Photos: Cecilie Notø 2013

Charaxes cithaeron kennethi **Poulton 1926**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	*Charaxini*
Larsen	*Nymphalidae*	*Charaxinae*	*Charaxini*
nymphalidae.net	*Nymphalidae*	*Charaxinae*	*Charaxini*

The preferred habitat of *C. cithaeraon kennethi* is low-lying evergreen forest from sea-level to 800 but has been found in altitudes up to 1700 m (Kielland 1990). It is considered a coastal subspecies which occasionally strays inland to dense savannah and riverine forest (Larsen 1991). The species is found from South Africa to southern Kenya (Kielland 1990)

Fermented fruit is an attractive food source for both sexes, but males are also attracted to fermented meat and excrements (Larsen 1991).

The larvae are polyphagous and feed on plants from *Leguminosae*, *Ulmaceae*, *Linaceae*, *Sterculiaceae*, *Tiliaceae* and probably others (Kielland 1990; Larsen 1991).
.

Photos: Cecilie Notø 2013

Charaxes macclounii Butler 1895

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	*Charaxini*
Larsen	*Nymphalidae*	*Charaxinae*	*Charaxini*
nymphalidae.net	*Nymphalidae*	*Charaxinae*	*Charaxini*

C. macclounii is mainly found in the central and eastern parts of Africa (Kielland 1990). Their preferred habitat is savannah and open mountain forests containing bamboo (Kielland 1990; Larsen 1991). They are considered a coastal species (Larsen 1991) but range from sea-level to 2000 m as long as there is a suitable bamboo habitat (Kielland 1990). It closely resembles *C. lasti* which is dependent on dense evergreen forest. As such, they are rarely found together (Larsen 1991)

Adults feed on the substrates generally representative of *Charaxinae*, but the males are also attracted to water (Larsen 1991).

The larvae are monophagous and only feed on bamboo species such as *Oxytenanthera abyssinica* and *Arundinaria alpine* (Kielland 1990). While most pupae of *Charaxinae* are green, the pupae of *C. macclounii* are grey and white (Larsen 1991).

Photos: Cecilie Notø 2013 (from the top: male and female)

Charaxes pleione oriens **Plantrou 1989**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	*Charaxini*
Larsen	*Nymphalidae*	*Charaxinae*	*Charaxini*
nymphalidae.net	*Nymphalidae*	*Charaxinae*	*Charaxini*

C. pleione oriens mainly inhabit coastal areas in the West African and Central African forest block (Larsen 1991) in an altitude of ca 250 – 1600 m (Kielland 1990).
It is one of the smaller *Charaxes* and the flight is slower and weaker than in other *Charaxes*.
Males can be found sun basking (Larsen 1991).

Adults of both sexes feed on fermented fruit and tree sap but only males are attracted to rotting meat and excrements (Larsen 1991).
The larvae are monophagous and feed on *Acacia* spp. (*Leguminosae*) (Larsen 1991).

Photos: Cecilie Notø 2013

Charaxes pollux mirabilis **Trulin 1989**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	*Charaxini*
Larsen	*Nymphalidae*	*Charaxini*	*Charaxini*
nymphalidae.net	*Nymphalidae*	*Charaxini*	*Charaxini*

C. pollux is a species mainly inhabiting evergreen forests but can be found in riverine forest as well as open habitats (Larsen 1991), within an altitude range of 1200 – 2100 m (Kielland 1990). Its geographical range covers most of the forested areas of Africa (Larsen 1991).

The males are usually less aggressive than in the other large *Charaxes'* and are normally found perching high up in the canopy (Larsen 1991).

Males and females of the species are attracted to plant sap and males are also attracted to rotting meat and excrements (Larsen 1991).
The larvae are polyphagous and feed on plants of several families, including *Melianthaceae*, *Anacardiaceae*, *Sapindaceae* and *Euphorbiaceae* (Kielland 1990).

Photos: Cecilie Notø 2013

Charaxes violetta melloni **Fox 1963**

Literature	Family	Subfamily	Tribe
Kielland	Nymphalidae	Charaxinae	Charaxini
Larsen	*Nymphalidae*	Charaxini	Charaxini
nymphalidae.net	*Nymphalidae*	Charaxini	Charaxini

C. violetta is a coastal species with a geographical range from Mozambique
to Kenya (Larsen 1991). There are two subspecies in Tanzania (*maritimus*
and *melloni*) of which melloni is found in the Usambara Mountains (Kielland 1990).

Its morphology and habits are similar to that of *C. cithaeron* with which
It often flies although *C. violetta* is much less common (Larsen 1991).
The preferred habitats are coastal forests and evergreen thickets from
300 – 1700 m (Kielland 1990).

The larvae are polyphagous and feed on plants from *Sapindaceae* (*Blighia unijugata)*,
Deinbollia and *Caesalpinioideae* (*Afzelia quanzensis* and *Brachystegia spiciformis*)
(Kielland 1990).

Photos: Cecilie Notø 2013

Eurytela dryope angulata Aurivillus 1898

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Nymphalinae*	*Biblini*
Larsen	*Nymphalidae*	*Nymphalinae*	*Biblini*
nymphalidae.net	*Nymphalidae*	*Biblidinae*	*Biblidini*

The *Eurytela* genus is strictly African (Larsen 1991) but have a widespread distribution within their geographical range (Kielland 1990). Their preferred habitats are forests and heavy woodland in which they are quite common (Kielland 1990). However, *E. dryope* often visit forest edges, rivers, savannah sand other open areas (Larsen 1991).

Adults of both sexes are attracted to fermenting fruit and can be trapped in great numbers in banana traps (Kielland 1990). They are fragile butterflies and their wings can easily be damaged when handled or in a trapping net (Kielland 1990).

The larvae are monophagous and only feed on *Euphorbiaceae* plants (*Ricinus communis* and *Tragia benthamii*) (Kielland 1990) where they are well camouflaged in a position along the mid-rib of the leaf (Larsen 1991).

Photos: Cecilie Notø 2013

XIV

### *Euxanthe tiberius tiberius* Grose-Smith 1889

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Charaxinae*	-
Larsen	*Nymphalidae*	*Charaxinae*	*Euxanthini*
nymphalidae.net	*Nymphalidae*	*Charaxinae*	*Euxanthini*

The *Euxanthini* tribe only contains six species, all of which are limited to the African continent (Larsen 1991). Anatomically, the *Euxanthe* genus clearly belongs in the *Charaxinae* but the adult butterfly look very different from any other members of the subfamily. Their rounded forewings is not seen in any other African butterflies. All species are attracted to fermenting fruits as are many *Charaxinae*, but they do not come to rotting meat and excrement (Larsen 1991).

E. tiberius are only found in a few populations in Kenya and Tanzania (Larsen 1991). Their preferred habitat is dense lowland forest where they normally remain hidden in the understorey (Kielland 1990), a feature much more resembling the *Satyridae* than the *Charaxidae* (Larsen 1991). Their altitudinal range spans from near sea-level to ca 1350 m (Kielland 1990). They have bright red and white colouring and are possibly mimicking *Danainae* species or aposematic day flying moths (Larsen 1991). Members of the species can differ greatly in size. The size difference are possibly related to season (Larsen 1991).

Contrary to the adult *E. tiberius*, the larvae and pupae have features typical of the *Charaxinae* subfamily (Larsen 1991). The larvae are monophagous and feed on *Deinbollia* species (*Sapindaceae*) (Kielland 1990).

Photos: Cecilie Notø 2013 (top row: female, bottom row: male)
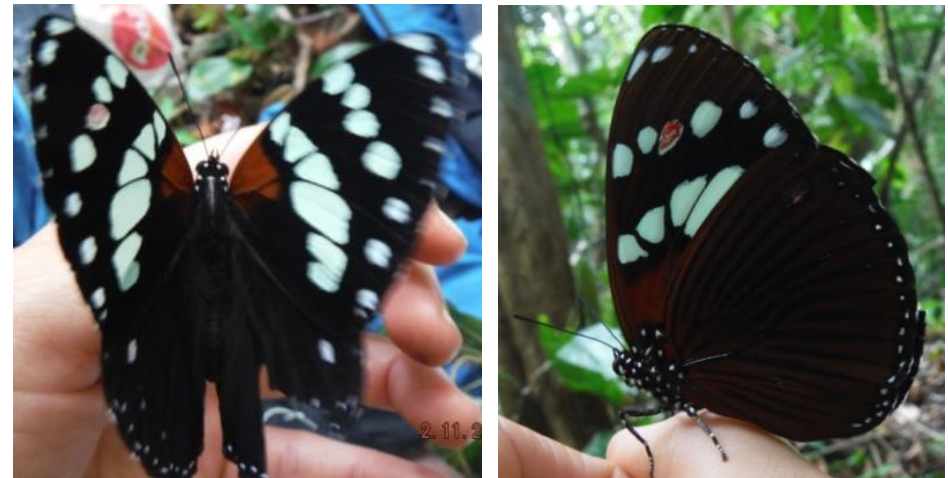
Hypolimnas **conf.** *anthedon wahlbergi* **Wallengren 1857**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Nymphalinae*	*Nymphalini*
Larsen	*Nymphalidae*	*Nymphalinae*	*Nymphalini*
nymphalidae.net	*Nymphalidae*	*Nymphalinae*	*Junoniini*

The *Nymphalini* tribe is widely distributed and found in all faunal regions.
There are 69 Afrotropical species, also with a wide distribution (Larsen 1991).
Larvae and pupae are generally quite similar throughout the whole tribe (Larsen 1991).
The *Hypolimnas* genus contains 12 African species but is also numerous in
Asia. Species of the two continents are not closely related (Larsen 1991).
Many species display great polymorphism and sexual dimorphism (Kielland 1990).
Eggs are generally deposited in small clusters, except for in *H. misippus* and
H. bolina which lay the eggs singly (Larsen 1991). Parental care is found in one
oriental species where female shelters the eggs with her body (Larsen 1991).

H. anthedon is a medium-size to large species which mimics several species,
particularly members of *Danainae* (Larsen 1991). Their preferred habitat is
forests and heavy woodland where they are very common (Kielland 1990).
They are found in almost all Afrotropical forest, also on Madagascar and
Sao Thomè (Larsen 1991), from sea-level to 1700 m (Kielland 1990).

Adults generally visit flowers and damp patches but attraction to excrement
and rotten meat is rare and limited to males of the larger species (Larsen
1991).The larvae of *H. anthedon* mainly feed on *Fleurya* species (*Urticaceae*)
and *Berkheya spekeana* (*Compositae*) (Kielland 1990) while other species are
highly polyphagous (Larsen 1991).

Photos: Cecilie Notø 2013

Junonia natalica Felder 1860

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Nymphalinae*	*Nymphalini*
Larsen	*Nymphalidae*	*Nymphalinae*	*Nymphalini*
nymphalidae.net	*Nymphalidae*	*Nymphalinae*	*Junoniini*

For tribe *Nymphalini*, see *Hypolimnas anthedon wahlbergi*.

The *Junonia* genus is widely distributed with representatives both in the New World and the Old World. In Africa, 16 species are described of which many are extremely widespread and common (Larsen 1991). They are found in a wide array of ecological conditions where some species are dependent on primary forest and others are strict dry-zone species (Larsen 1991). They are small but active and can be strong flyers (Larsen 1991). The members of this genus was previously placed in the *Precis* genus (Larsen 1991).

J. natalica are distributed through most of southern and eastern Africa (Larsen 1991). It is found in several habitats, such as woodland, savannah, riverine thickets and forest roads from sea-level to 2200 m (Kielland 1990). All adults visit flowers but many are also attracted to rotten meat. They display a slight seasonal dimorphism (Larsen 1991).

Females deposit a single egg on the larval food plants of *Acanthaceae*.
Both the larvae and pupae have forms typical of the *Nymphalini*
tribe (Larsen 1991).

Photos: Larsen 1991 (top) and Cecilie Notø 2013 (bottom).

XVII

Junonia terea elgiva Hewitson 1864

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Nymphalinae*	*Nymphalini*
Larsen	*Nymphalidae*	*Nymphalinae*	*Nymphalini*
nymphalidae.net	*Nymphalidae*	*Nymphalinae*	*Junoniini*

For tribe *Nymphalini*, see *Hypolimnas anthedon wahlbergi*.
For genus *Junonia*, see *Junonia natalica*.

Junonia terea elgiva is a widely distributed and common species
(Larsen 1991). It is generally found in forests and heavy woodland
from sea-level to 2200 m but has adapted exceptionally well to
forest disturbance (Kielland 1990).

The larvae are monophagous and only feed on *Ruellia patulata*
(*Acanthaceae*) (Kielland 1990).

609 i

Photos: Cecilie Notø 2013 (left) and Larsen 1991 (right).

Neptidopsis opihone velleda **Aurivillus 1898**

Literature	Family	Subfamily	Tribe
Kielland	*Nymphalidae*	*Nymphalinae*	*Biblini*
Larsen	*Nymphalidae*	*Nymphalinae*	*Biblini*
nymphalidae.net	*Nymphalidae*	*Biblidinae*	*Biblidini*

The *Neptidopsis* genus is strictly African and only contains two species;
 N. ophione and *N. fulgurata*. *N.fulgurata* is more of a coastal species
and is also found on Madagascar, but the two species often cohabit on
the African mainland (Larsen 1991).

The preferred habitat of *N. ophione* is forest and woodland where they
are common (Kielland 1990) but their range can occasionally extend to
riverine vegetation and dense savannah (Larsen 1991). Their distribution
is almost pan-African only excluding the southernmost parts (Larsen 1991)
and includes most areas of suitable forest habitat from sea-level to 2200
meters (Kielland 1990). They are fragile creatures and their wings can easily
be damaged when handling or in traps (Larsen 1991). Many of their habits
are shared by *Neptis* species which also have a similar flight pattern (Larsen 1991).

Adults of both sexes are attracted to fermented fruit but rarely visit
flowers (Larsen 1991). The larvae are monophagous and only feed
on *Tragia brevipes* (*Euphorbiaceae*) (Kielland 1990).

Photos: Cecilie Notø 2013

XIX
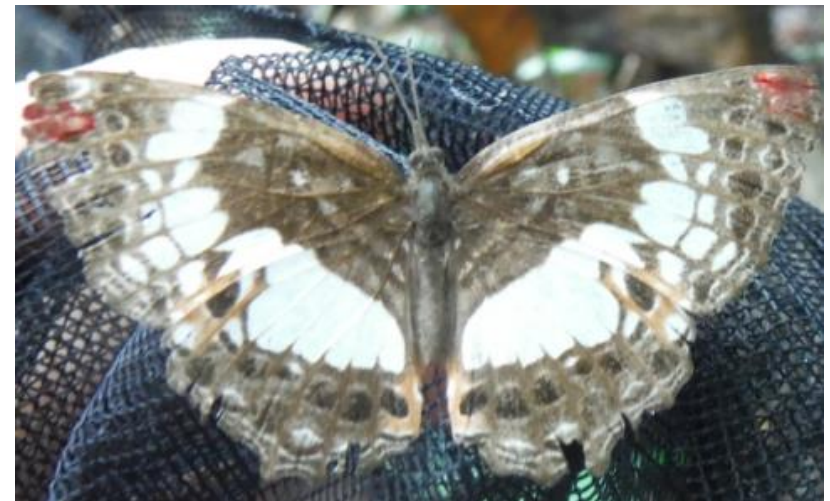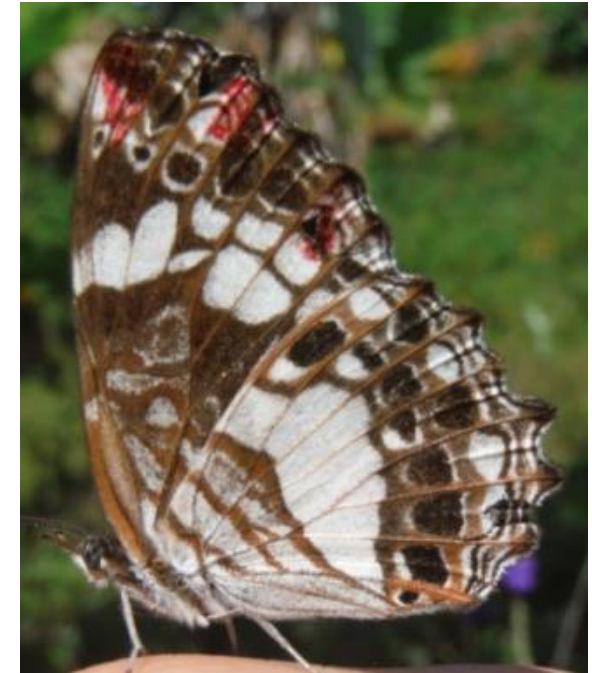
Neptis spp. Fabricius 1807

Literature	Family	Subfamily	Tribe
Kielland	_Nymphalidae_	_Nymphalinae_	_Limenitidini_
Larsen	_Nymphalidae_	_Nymphalinae_	_Neptini_
nymphalidae.net	_Nymphalidae_	_Limentidinae_	_Neptini_

Kielland (1990) includes the _Neptini_ tribe in the _Limenitidini_ tribe while Larsen (1991) separate the two due their differences in the early stages as well as adult size. Australasia support several genera, including _Neptis_, which is the only representative of the tribe in Africa. They have a wide distribution, extending into the Palearctic region and in a few cases also into Europe (Larsen 1991).

There are 62 African species (Larsen 1991). In Tanzania there are 26 species, of which 11 are possible to find in the East Usambara Mountains (Kielland 1990).

The _Neptis_ genus rich in species, most of which have an extremely similar white and black pattern and many can only be identified by their genitalia, particularly members of the _laeta_ group and the _melicerta – goochi_ complex (Kielland 1990). Their preferred habitat is generally forests and woodlands form sea-level to ca 2000 meters, although some species are limited to the upper half of this (Kielland 1990).

Females deposit a single egg on the larval food plant. In contrast to the adults, the larvae and pupae of _Neptis_ are found in a variety of dissimilar patterns (Larsen 1991). The larvae are often polyphagous and feed on plants from many families such as _Sapindaceae_, _Urticaceae_ and _Euphorbiaceae_ (Kielland 1990). The larvae of some species create a camouflaging shelter by biting of a piece of the leaf and fasten it with silk (Larsen 1991).

Photos: Cecilie Notø 2013

XX

Sallya spp. Hemming 1964 (_Sevenia_ spp. Kocak 1996)

Literature	Family	Subfamily	Tribe
Kielland	_Nymphalidae_	_Nymphalinae_	_Catagrammini_
Larsen	_Nymphalidae_	_Nymphalinae_	_Catagrammini (Eunicini)_
nymphalidae.net	_Nymphalidae_	_Biblidinae_	_Epicaliini_

The _Catagrammini_ tribe is only found in Africa and the Neotropics and is absent from the Oriental region. It is quite numerous in the Neotropics while only represented by a single genus, _Sallya_, in Africa. They are close relatives of the Neotropical genus _Eunica_ Hubner 1819 and some researchers have suggested that they are congeners. However, their geographical segregation warrants separate genera (Larsen 1991).

The genus contains 17 species, some restricted to Madagascar (Larsen 1991). Tanzania is inhabited by 11 species of which five are present in the East Usambara Mountains; _S. amulia, S. boisduvali, S. moranti, S. natalensis_ and _S. pseudotrimeni_ (Kielland 1990). Many _Sallya_ species are highly gregarious and can often be found in large groups settled in trees. Like their Neotropical relatives, several of the species migrate and often fly in enormous swarms (Larsen 1991).

Adults of both sexes are attracted to fermented fruit and plant sap, but rarely visit flowers (Larsen 1991). They are reportedly able to penetrate fruit skin (even apple) with their proboscis and can cause great crop damage (Larsen 1991). Their flight is quite untypical for the _Nymphalinae_ and is unpredictable, with much more vertical than horizontal movement (Larsen 1991). The females deposit a single egg on the larval food plant (Larsen 1991). Some species have monophagous larvae only feeding of _Euphorbiaceae_ species, while others are polyphagous and also include _Bignoniaceae_ and _Sterculiaceae_ species in their diet (Kielland 1990).

Photos: Cecilie Notø 2013

Family *Satyridae* (Kielland 1990), (subfamily *Satyrinae* (Larsen 1991))

Satyridae is a cosmopolitan family with species ranging from the Arctic region to tropical rainforests. However, their pattern of dull colors and eyespots on the underside of all four wings is largely uniform across their entire geographical range. This pattern is assumed to be the ancestral pattern of all butterflies (Larsen 1991).

Most species have a slow and weak flight and are normally found hovering low above the ground in the understorey of forest or in open grasslands (Larsen 1991). They are often shade-loving and many are crepuscular (Kielland 1990). The adults of some species can aestivate during the dry season and thus survive for many months. Polymorphism and seasonal variation is prominent in most species, particularly those restricted to habitats exposed to long dry periods (Kielland 1990). Adult butterflies are mostly attracted to rotting fruit and in some cases carrion and excrement, but few are known to ever visit flowers (Larsen 1991).

The eggs are generally smooth and rounded (Kielland 1990) and laid either singly or in twos and threes (Larsen 1991). The eggs are normally deposited on the blade of a grass or are dropped in a grassy area, as is the case for some non-African species. The larvae of all species feed on monocotyledons, mainly grasses and bamboo (*Poaceae*). They are able to consume most types of grass, possibly because few grasses contain any defensive compounds. As a result, none of the satyrids larvae are aposematic (Larsen 1991). Many species have a nocturnal feeding habit and remain hidden on the ground during the day.

In Africa, at least 298 species are present (Larsen 1991).

Aphysoneura pigmentaria pigmentaria **Karsch 1894**

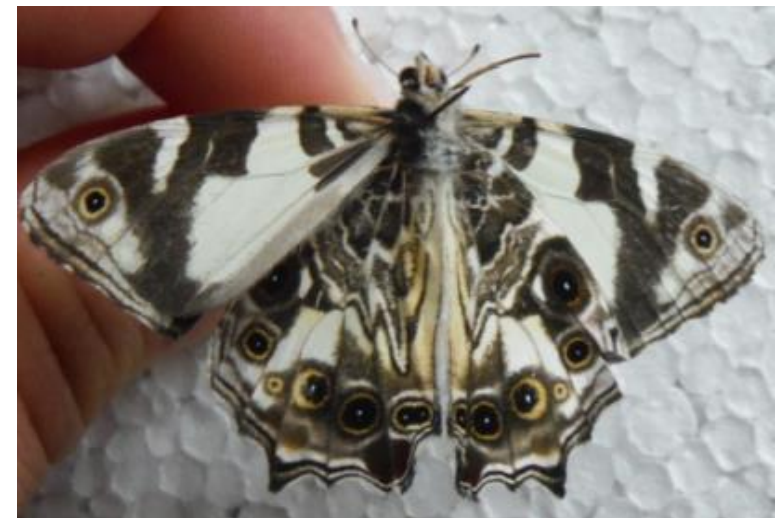| Literature	Family	Subfamily	Tribe
Kielland	*Satyridae*	*Elymniiae*	*Lethini*
Larsen	*Nymphalidae*	*Satyrinae*	*Lethini*
nymphalidae.net	*Nymphalidae*	*Satyrinae*	*Satyrini*

The *Lethini* tribe is nearly cosmopolitan and the highest number of species is found between the Palearctic and the Oriental regions, although in general there is only a limited number of species and genera present in any given area. In Africa, only five species are present (Larsen 1991).

The genus *Aphysoneura* is constituted by only two of these species and is only found in submontane and montane bamboo habitats in the East African mountain zones (Kielland 1990). They have both developed several distinct subspecies within short geographical distances (Kielland 1990; Larsen 1991).

The white and black coloring of *Aphysoneura pigmentaria* differs greatly from that of the other *Satyridae*'s dull shades of brown. Also, *A. pigmentaria* is sun-loving and is often found sun basking in open areas while most other satyrids are shade-loving or crepuscular. However, they share the satyrid feature of flight low above the ground (Larsen 1991). The species are often local but not necessarily rare. The subspecies *A. pigmentaria pigmentaria* is endemic to the Usambara Mountains and have two seasonal forms (Kielland 1990).

The larval food plants are bamboos of the *Poacaea* family. Adults are somewhat attracted to fermented fruit (Larsen 1991).

Photos: Cecilie Notø 2013

Melanitis leda africanus **Fruhstorfer 1908**

Literature	Family	Subfamily	Tribe
Kielland	*Satyridae*	*Biinae*	-
Larsen	*Satyridae*	*Satyrinae*	*Melanitini*
nymphalidae.net	*Nymphalidae*	*Satyrinae*	*Melanitini*

The *Melanitini* tribe is found in all tropical regions but contain only a few genera and species. In Africa, there are only two genera with three species each (Larsen 1991).

The *Melanitis* genus is Palaeotropical (Larsen 1991). Only three species are found in Africa while the oriental region contains slightly more species. The only species found in both places is *Melanitis leda*. Unlike Kielland (1990), Larsen (1991) does not accept the subspecies *fulvesence* and *africanus*, only the species *M. leda leda* (Linnè 1758).

M. leda is quite large relative to most other satyrids and they display seasonal dimorphism (Larsen 1991). They are mostly crepuscular, like the *Satyridae* (Kielland 1990) and spend the day hiding in the underbrush (Larsen 1991). The preferred habitat is woodland and forest margins from 0 – 2000 m (Kielland 1990).

Both adult sexes are very attracted to fermented fruit, but rarely visit flowers (Larsen 1991). The larvae are mostly monophagous and mainly feed on *Poaceae* plants (e.g. sugar cane (*Saccharum* species), rice (*Oryza* species) and several other grasses), but may possibly also feed on *Cyperaceae* (Larsen 1991).

Photos: Cecilie Notø 2013