The value of forest matrix habitats for conservation: Butterfly distribution on a land-use gradient from mature forest to small-scale agriculture in Mabira Forest Reserve, Uganda

Therese Kronstad

Master of Science in Biology
Biodiversity, evolution and ecology

Department of Biology
Faculty of Mathematics and Natural Sciences
University of Bergen

March 2009

Front page:

*Neptis nicomedes***,** Mabira Forest Reserve, Uganda, April 2009**,** Photo: Therese Kronstad

Acknowledgements

I would first like to thank the Matrix project for the opportunity to study the effect of habitat change in tropical forest. I have learned and experienced very much.

Thereafter I would like to thank my main supervisor Richard Telford for his assistance with my thesis, for guidance, for helping me with statistics and for good advises. Also thanks to Vigdis Vandvik and Cathy Jenks for all their good help in the end of my writing.

Great thanks to Perpetra Akite who I joined in the field. She thought me much about butterflies and identifications. We spent many field days together and she toughened me up when it came to facing the tropical forest. I'm also very thankful for all her help with gathering information in Uganda and for good advises while I was writing my thesis.

I would also like to thank Jenny Reiniö for all the nice times and support in Uganda. She also helped me a great deal with my writing when the end of my master was getting near.

I would like to give my thanks to all the great Ugandans supporting me in and after field work. Most of all I am grateful for my devoted field assistant, bodaboda driver and friend Adam and to the loving Fazira who took so good care of us when staying at the Eco-tourism centre in Mabira forest. Also thanks to all the other lovely people in the villages around and within Mabira, who let me work in their gardens and supported my work.

Finally I would like to thank my boyfriend, good friends, my parents and brother who always took so good care of me and understood when I had to work. I'm also grateful for the support and help form Kristin Kaasa, Vivian Felde and the other co-students at the "office".

Abstract

Frugivorous butterfly composition was quantitatively sampled by the use of baited traps on a land-use gradient, to evaluate the conservation value of habitats with different degrees of modification. Matrix habitats surrounding the forest can be of conservation value by serving as an alternative habitat, a corridor for dispersal between forest fragments and as a buffer zone. Studies investigating the conservation value of forest matrix habitats have contradictory views. Some stress the importance of conserving the remaining primary forests while others argue the importance of including human-modified habitats in management plans. Habitats from mature and secondary forest, cardamom plantation, coffee and small-scale mixed gardens were sampled within Mabira forest and its surroundings, Uganda. In this study, there is a focus on the similarity of composition and the value of abundance in describing persistence and distribution of forest species as well as restricted-range species. The cardamom plantation has a high conservation value, with a butterfly composition highly similar to the forest, and a high percentage of forest species which indicates a persistence of the species present. The coffee garden and mixed small-scale garden show a lower similarity to forest habitats and a lower percentage of forest species. In these sites the abundance of forest species is low and the sites are less interesting for conservation. These results are reflected by canopy openness being the best predictor of butterfly distribution in this study. The modified habitats show low value in conserving rare and endemic species. Species richness and diversity showed an opposite pattern, with coffee and mixed garden habitats having the highest species richness. The species assemblage was, however, influenced by widespread and open habitat species. This demonstrates the importance of including the species identity in similar gradient studies.

Key words: land use gradient, conservation, butterfly, Mabira Forest Reserve, forest species

Table of Contents

1. Introduction

Global deforestation is happening at an alarming rate, with an estimated net loss of about 13 million hectares per year between 1990-2005 (FAO, 2005). Countries with the highest deforestation rates are found in the tropics. Habitat loss, over-exploitation and fragmentation are among the most important causes of biodiversity loss in the tropics (MEA, 2005). Most of the deforestation comprises conversion of forests to human-modified habitats like agro-ecosystems (MEA, 2005; FAO, 2005).

Previously, focus has often been on conserving biodiversity within the undisturbed forests and forest fragments, ignoring the surrounding human-modified habitats and their possible value in conserving forest biodiversity. The importance of the surrounding forest matrix habitats, as forest buffer, corridor for dispersal and an alternative habitat for forest biodiversity have lately been recognized (Kupfer *et al.*, 2006). Recent studies have focused on the conservation value of human-modified habitats around tropical forests (e.g.; Bobo, 2006; Lawton *et al.*, 1998; Barlow *et al.*, 2007b).

Studies evaluating the human-modified matrix habitat of tropical forests have contradictory views on the importance of including such habitats in management plans. Some studies stress the significance of human-modified habitats (Bhagwat *et al.*, 2008; Hamer, 2003; Chazdon *et al.*, 2009) while others focus on conserving the undisturbed forests and forest patches (Vu, 2009; Posa and Sodhi, 2006; Barlow *et al.*, 2007b). This can be described as a choice between wildlife-friendly farming and land sparing in terms of intensive often monocultural agriculture, as is discussed by Green *et al.* (2005). This study points out trade-offs in both situations, stressing the importance of gaining information on the reaction of species populations to increased crop yields to understand further how forest biodiversity will react to agricultural intensification.

A meta-analysis by Bhagwat *et al.* (2008) combined results from 36 studies in the tropics that compared species richness and similarity in composition of different taxa between primary forest and various types of agroforestry, in which native tree cover was preserved over agricultural crops. Bhagwat *et al.* (2008) found that, on average, the species richness in the agroforestry was 60% that of the forests, while the similarity in composition of herbs was 25% and for mammals was 65%. They argue that agroforestry can be valuable for biodiversity conservation of tropical forest. The majority of human-modification gradient studies compare similar indices as Bhagwat *et al.* (2008) to nearby forest habitats. High species richness is, however, not a very good

indicator of conservation value since the species found could be an assemblage of widespread generalists or an influx of species from the surrounding matrix and of less conservational concern (Bobo, 2006; Rice and Greenberg, 2000). Similarity in composition is more informative but there has been a lack of focus on species identity and ecological knowledge (Fermon *et al.*, 2005; Perfecto *et al.*, 2003). This may lead to overemphasizing the conservation value of the habitat if the species in common are widespread generalists. Most studies also use presence-absence data when comparing habitats. This is a potential problem as it may lead to failure to notice that where there is a persistence of forest species or species of restricted range, the species might just be a few individuals or singletons wandering in or getting lost in the matrix of the forest and not viable populations persisting in the habitat. According to Chazdon *et al.* (2009), further investigation on the conservation value of human-modified landscapes should be done in order to identify and promote proper management strategies.

Different taxa have been used in the studies of disturbance gradients from forest to farmland, including butterflies (Hamer, 2003), birds (Posa and Sodhi, 2006), and other insects (Jones *et al.*, 2003), plants (Mohan *et al.*, 2007) or, in some cases, a combination of different taxa focusing on the complementarities of the groups (Perfecto *et al.*, 2003).

Butterflies (Rhopalocera) of the Lepidoptera order is a well-known insect group and the individuals are relatively easy to sample and identify (Larsen, 1996; Larsen, 2005; DeVries, 1997). They are sensitive to habitat and microclimatic change, which makes them a good indicator group for monitoring and disturbance studies (Molleman *et al.*, 2006). Fruit feeding butterflies gives a quantifiable sampling when using baited traps. The importance of butterflies in capturing temporal and vertical stratification in biodiversity studies in the tropics is acknowledged (DeVries, 1997; Molleman *et al.*, 2006; Tangah *et al.*, 2004). Surveying butterflies only in the dry season, which is more practical in the field, and not capturing biodiversity responses to seasonal change, can give a different picture of the butterfly distribution, and often exaggerates the value of secondary forest and agricultural areas for conservation (Barlow et al., 2007b).

Uganda is described as "exceptionally important in terms of biodiversity", lying between the savannas in the east and the tropical forest in the west, and has a very high biodiversity compared to its size, 241,038 km^2 (CIA world fact book, USAID, 2007). Between 1990 and 2005, about 26% of the tropical broad-leaved forest cover was lost in Uganda (FAO, 2006). Charcoal production, illegal timber production, agricultural land expansion and forest clearing for sugar

cane and oil palm plantations are among the most important causes of degradation of Uganda's moist broad-leaved forest. The pressure on the forest is likely to continue (FOSA, 2001), as Uganda's population is still increasing rapidly, at a rate of 3.31% according to the Government of Uganda (Government of Uganda, 2005). Uganda is therefore a country in critical need of an efficient forest conservation and management practice.

This study aims to assess the relative value of human-modified habitats in maintaining forest biodiversity. The focus will be to test the ideas of Bhagwat *et al.* (2008) about the potential value of agroforestry.

With this objective, the abundance, species richness, diversity and composition of frugivorous butterflies are estimated along a land-use gradient from mature and secondary forest, to cardamom and coffee plantations, as well as mixed small-scale gardens.

While most short-term biodiversity surveys consider species richness and diversity (Scales and Marsden, 2008), I expect similarity in composition and percent forest species to be more informative in evaluating the modified habitat for conservation. Butterfly ecotypes used here are based on Davenport (1993) who used literature and field observations and included forest and non-forest types, while a regional biodiversity survey done in Uganda (Davenport *et al.*, 1996), included restricted-range taxa. The butterfly species information of specialisation and rarity is interesting, and will be used to investigate if the modified habitats contain butterflies of tropical forest conservational concern. The distribution of forest specialists and restricted range species will thereby be investigated.

In addition, the explanatory value of different environmental variables of the distribution of the butterflies such as forest structure and microclimate will be tested.

In evaluating the conservation value of the modified habitats, a weight will be put on the presence of forest species and restricted-range species and similarity in community composition, with and without abundance.

This study builds on the growing knowledge of the conservation value of altered habitats surrounding tropical forests. The study generates information which can be used to promote good management practice of the forest reserve. Additional information of butterfly presence and distribution in Mabira Forest Reserve and its surroundings can be used subsequently for management and future studies.

2. Materials and Methods

2.1 Study area

The study site is the 306km^2 Mabira Forest Reserve and its surroundings. The forest is situated in the Mukono district, Uganda. Mabira is geographically located between 0°24 and 0°35 N and between 32°52 and 33°07 E (Davenport *et al.*, 1996). The mean annual precipitation in this area is 725-1474mm (FAO, 2006). The maximum monthly temperature is 27°C and the minimum temperature 22°C, with a daily variation of about 10-13°C in Mukono and slightly lower in Mabira forest (MFMP, 2008). Mabira forest is primarily composed of medium-elevation (1070-1340m) moist semi-deciduous forest, and is the largest remaining forest fragment in the Lake Victoria area in Uganda (Davenport *et al.*, 1996).

According to the Mabira Forest Management Plan (MFMP, 2008), the forest has been influenced by humans for a long time. The forest was gazetted in 1932 but still heavily encroached, especially during the 1970s and early 1980s. Between 1988 and 1989 encroachers were evicted and a rehabilitation process started (Baranga, 2007). In 1994/1997 the forest was divided into a Conservation Zone consisting of a Strict Nature Reserve, surrounded by a Recreational/Buffer Zone and a low-impact Production Zone (MFMP, 2008). There are several enclaves inside the forest containing villages with small-scale agriculture and some larger plantations of tea, eucalyptus or coffee. The forest surroundings are composed of the same mosaic but have in addition larger plantations of sugar cane.

The Biodiversity report (Davenport *et al.*, 1996) recorded 199 butterfly species in the forest, which is about 16% of the 1248 butterfly species recorded in Uganda (Howard, 2000). Mabira was also ranked high (within the top 11-25% of 64 forests) in terms of butterfly species diversity and conservation value in the biodiversity survey. In all, the number of butterfly species previously recorded in Mabira stands at 218 species (MFMP, 2008; Davenport *et al.*, 1996).

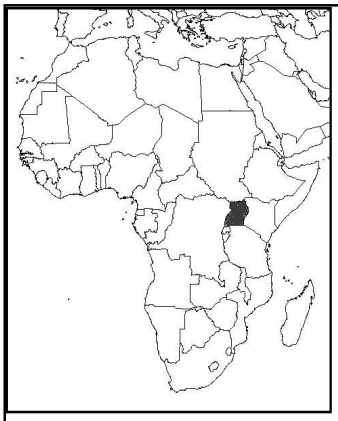


Figure 2.1 *Location of Uganda in Africa*

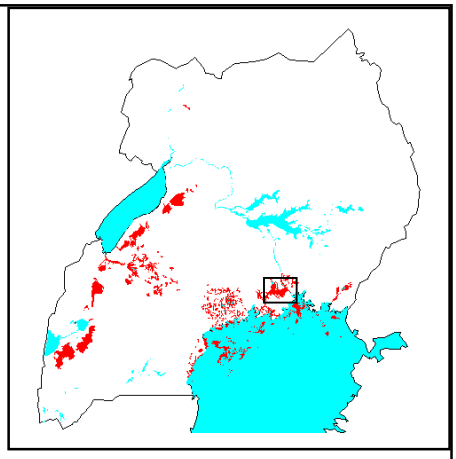


Figure 2.2 *Mabira Forest Reserve location in Uganda on a map including the distribution of mid-altitude evergreen and semi-evergreen broadleaf forest in Uganda (Sayer et al., 1992)*

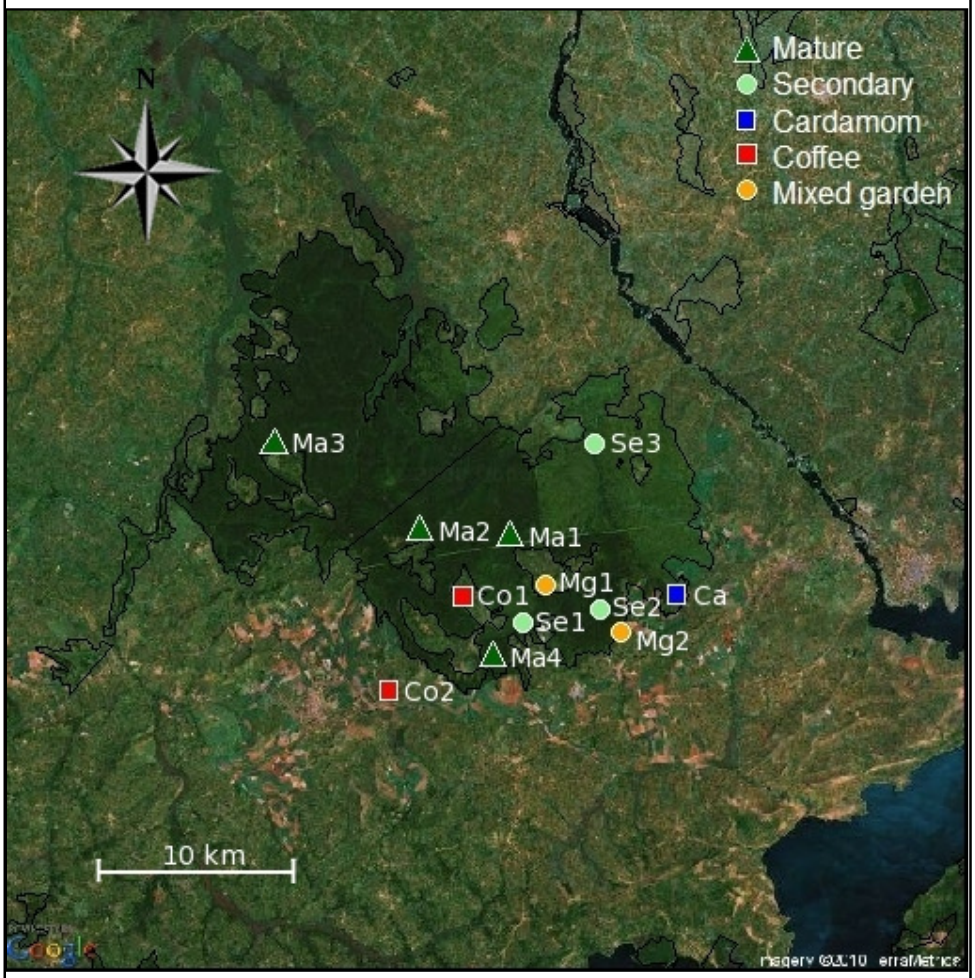


Figure 2.3 *Mabira Forest Reserve, showing sites sampled. Map is extracted from Google maps with R package RgoogleMaps (Markus Loecher and Sense Networks, 2009)*

2.2 Study sites and period

2.2.1 Sites

The study sampled 12 sites in Mabira Forest Reserve and its periphery: four sites in mature forest, three sites in secondary forest, and five sites on agricultural land (Fig 2.3). Two of the agricultural sites were situated within enclaves in the forest and two close to the forest boundary. The sites were chosen on the basis of the vegetative distribution of the forest using remote sensing (Google earth), the forest reserve maps available (Howard, 1991) and information from local people. Sites were selected to cover a large expanse of forest to avoid pseudoreplication where sites are similar because of their proximity, but also took into consideration the logistics of reaching sites. It was the intention to sample at least two replicates of the different habitat types, but it was difficult to find similar disturbed sites big enough to sample. In addition, there was limited information about any other sites similar to the cardamom plantation, which is an agroforestry scheme needing a high shade cover.

Mature sites

The mature forest is classified as sub-climax forest, which has been influenced by human activities for a long time. It is mainly dominated by tree species such as *Celtis, Albizia, Antiaris*, and *Chrysopyllum*. The understorey species include mainly *Funtumia, Trilepisium*, and *Diospyros* (MFMP, 2008).

Secondary sites

Unregulated exploitation and encroachment in the past has led to some compartments with a regenerating forest, lacking large old trees that characterize mature forest. The secondary forest is composed of similar species as the mature sites but with fewer large and old trees. The invasive paper mulberry (*Brussonetia papyriferra*) was present to some degree in all the secondary sites sampled. The secondary sites are located in the compartments which were last heavily degraded about 3-10 years ago (MFMP, 2008).

Cardamom

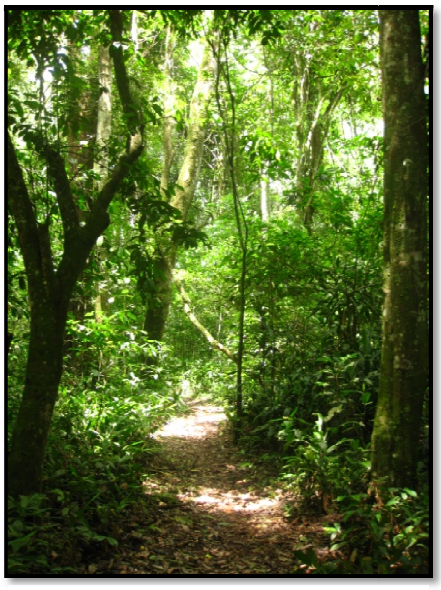
The cardamom plantation covers about 40 acres on the east boundary of the Mabira forest. The plantation has been cultivated for the last 50 years (information; manager Luigi). The forest canopy was characteristic of agroforestry, relatively intact with native forest trees while the understorey was cleared and planted with Cardamom (*Elettaria cardamomum*).

Coffee gardens

Two different types of coffee gardens were sampled. Site Co1 is situated within the Ssese enclave and quite close to old secondary forest. This coffee estate is approximately 220 acres but is elongated with a lot of edge which was avoided. There is a network of loose surface roads within the plantation which had to be included in the transect, although avoided as much as possible to minimize their possible influence on the butterfly catch. The Arabica coffee was planted with banana. The shade or remnant trees were a mix of forest trees (e.g.; *Maesopsis, Albisia* sp., and *Ficus natalensis*). Site Co2 was further from the forest boundary than the other site (ca. 2km). The coffee plantation was intermixed with banana and a monoculture shade canopy of Fig trees (*Ficus* sp.).

Mixed small-scale gardens

The mixed small-scale gardens were both in a mosaic of crop squares, each close to a household. The most common crop plants were cassava, coffee, beans, sweet potatoes, maize and yam. Shade trees included *Ficus natalensis*, *Mangifera indica*, and avocado trees (*Persea americana*) and the forest invasive, paper mulberry. Site Mg1 was located within the Bwola enclave and was the most open site in the study. Site Mg2 was located south-east of the forest boundary in Buvunja village and included more coffee plants than the former.



A

B

C

D

E

Figure 2.4 *Photographs of the typical habitats in the study*
***A)** = Mature forest, **B)** = Cardamom plantation, **C)** = Coffee 1, **D)** = Mixed garden 1, **E)** = Coffee 2*

Photos; Therese Kronstad.2009.

Table 2.1 *Details of survey sites in Mabira and the surrounding habitats. Elevation was recorded from GPS. Zonation and compartments from map (Howard, 1991)*

Habitat	Site	Highest elevation (m.a.s.l)	Forest compartment	Zonation
Mature 1	Ma1	1193	192	Production (low impact)
Mature 2	Ma2	1267	204	Strict Nature reserve
Mature 3	Ma3	1135	216	Production (low impact)
Mature 4	Ma4	1316	189	Recreation/buffer zone
Secondary 1	Se1	1199	190	Recreation-Buffer zone
Secondary 2	Se2	1210	177	Production (low impact)
Secondary 3	Se1	1137	181	Production (Encroachment)
Cardamom	Ca	1207	172	Production (Encroachment)
Coffee 1	Co1	1217		Enclave
Coffee 2	Co2	1237		Periphery
Mixed garden 1	Mg1	1208		Enclave
Mixed garden 2	Mg2	1229		Periphery

Table 2.2 *Butterfly sampling period in Mabira forest and the surrounding habitats. (TK=Therese Kronstad, PA=Perpetra Akite)*

Site	Sampling period		Entomologist		Transect checks	
	1	2	1	2	1st	2nd
Secondary 1	18.02-20.02	01.05-03.05	TK/PA	PA	6	6
Cardamom	22.02-24.02	01.05-03.05	TK/PA	TK	5	6
Mature 1	05.03-07.03	05.05-07.05	TK/PA	PA	6	6
Garden 1	09.03-11.03	16.05-18.05	TK/PA	TK	6	5
Secondary 2	20.03-22.03	20.05-22.05	TK	PA	6	5
Mature 2	24.03-26.03	16.05-18.05	TK/PA	PA	6	6
Coffee 1	28.03-30.03	20.05-22.05	TK/PA	TK	6	6
Secondary 3	05.04-07.04	24.05-26.05	TK/PA	PA	6	4
Mature 3	09.04-11.04	30.05-01.06	TK/PA	PA	5	6
Garden 2	19.04-21.04	24.05-26.05	TK/PA	TK	6	5
Mature 4	23.04-25.04	03.06-05.06	TK/PA	PA	6	6
Coffee 2	05.05-07.05	28.05-30.05	TK	TK	6	6

2.2.2 Sampling period

This study was carried out between 17th of January and 4th of June 2009. We conducted 3 trap-night surveys at each of the 12 sites during each field season[1] (Fig 2.2). This was meant to coincide with the dry season and the wet season, but weather was very unpredictable. Expected local weather from the Mabira Forest Management Plan (MFMP) and local forecasts (The New Vision, Ugandan Newspaper: weather data comes from the department of meteorology) were used as a basis for the field schedules.

2.3 Sampling methods

2.3.1 Butterfly data

Butterfly sampling was done using standard baited traps (DeVires *et al.* 1997). Baited traps are used to capture frugivorous butterflies that are mainly from the subfamilies Nymphalinae, Charaxinae, Satyrinae and Acraeinae (Pinheiro and Ortiz, 1992) and are frequently used in butterfly studies in tropical forests (Barlow *et al.*, 2007b; Bobo, 2006; Dolia, 2008; Mas and Dietsch, 2003). Data from baited traps are quantifiable and remove bias from entomologists experience when identifying butterflies in flight.

In order to determine the vertical variation in butterfly species distribution, canopy traps were set in addition to understorey traps as described by DeVires (1997), Fermon *et al.* (2005) and Molleman *et al.* (2006).

At each site, butterflies were sampled along a 500m transect directed away from the edge within the chosen habitat. Because of the difficulties of finding agricultural areas of large size and to avoid an edge effect, we started the transect 50m or more from the boundary of the habitat type (Rogo, 2001; Uehara-Prado *et al.*, 2007). Ten trapping stations were established at 50m intervals on alternate sides of the central line, each fitted with one understorey and one canopy trap. Standard bait traps (35cm diameter with 125cm tubular net) were used. The understorey traps were hung between 0.5 and 1m from the ground (Fig 2.5) while the canopy traps in the forest sites were hung between 10-15m. In the agricultural sites the canopy traps were hung as high as possible depending on availability of canopy trees. We baited the traps with banana fermented for 1-2 days, depending on how ripe they initially were. The bait was put on a plastic plate and placed in the centre of the trap table. In cases where the bait became sundried, eaten by other

[1] There were a few exceptions because of bad weather and time limitations

animals or lost, it was refilled during each trap check. The traps were installed in the afternoon around 15:00 (Dolia, 2008), and checked twice each day, in the morning at 9-10:00 and in the afternoon at 15-16:00, for 3 days. Trap checking was done only when the weather conditions were good (warm and dry), and not when it was raining or immediately after rain and specimens were wet.

Figure 2.5 *Understory trap, Coffee garden 1. Photo: Therese Kronstad (2009)*

One or more specimens of each species were collected as voucher specimens, otherwise butterflies were identified and released in the field. The abundance and sex was recorded in the field. The trapped specimens were identified to species level or at least to genus[2], with the use of the available standard field guides that included Kielland (1990), Larsen (1991) and Larsen (2005). Specimens that were difficult to identify were preserved in glassine envelopes for further taxonomic clarification using reference collections at the Zoology Museum in Makerere University. The species from a group of black Charaxes, which are commonly difficult to identify (Larsen, 2005), were classified into morpho-species on the basis of the underside colour, blue and green spots on the forewing and to some extent size. The analysis was limited to fruit-feeding butterflies from the Nymphalidae family. A parallel study which includes sweep netting looks at additional butterfly families with butterflies of different feeding guilds in the sites.

2.3.2 Environmental data

GPS co-ordinates of location and altitude were recorded for every trapping station (Garmin etrex Handheld GPS). A canopy picture was taken with a digital camera (Nikon D60) with a Fisheye lens (Opteka HD² 0.20X Professional Super AF Fisheye Lens for Nikon) at a height of 75 cm with the top facing south. The basal area of trees >10cm diameter at breast height was measured by the use of a prism (with a basal area factor of 10 m^2/ha) from a standing point within a radius of 2m from the mark of the trapping station. This gives a measure of the basal area of the trees within one hectare of forest from the standing point and was used to determine the forest structure at the site (Montgomery and Chazdon, 2001). A plot of 10m x 10m at each

[2] With 3 exceptions ; sp a, sp b, sp c

trapping station was established to determine the percent cover of understorey shrubs and herbs (2-3m height), the percent bare ground, and average top and low canopy height. Temperature and humidity were recorded with HOBO loggers, HOBO Pro v2, ext temp/RH (HOBOwarePro, 2002-2008), simultaneously at all ten trap stations in the first season and at the 1st, 5th and 10th trap stations in the second season. The loggers were placed between 0.2 and 1m above ground, protected from sunshine and rain, and set to take measures every 10 minutes during the sampling periods[3].

2.4 Statistical analysis

The statistical program R 2.10.0 (R Development Core Team, 2009) was used in all analysis. Canopy openness (%) values are extracted by processing canopy pictures in CAN_EYE-5 program (INRA-CSE, 2004).

2.4.1 Data manipulation

Pooled butterfly data from both sampling periods per site were used in all analyses. The environmental variables were averaged between the ten trap stations per site, while the microclimatic data was averaged as mean temperature of 6 sampling days (7:00-16:00), as well as averaged between sampling periods.

Non-parametric statistical tests were used, because it is difficult to tell if the small data sets come from a Gaussian distribution and because of their robustness (Motulsky, 1995). Kruskal-Wallis tests based on ranks were used to look for significant relationships between parameters and habitat type, with a pairwise Wilcox rank sum test with Bonferroni correlation if significant, to check which habitat significantly differed (Zar, 1984). When the habitat type is used as a parameter, the cardamom site was excluded because of its single value, which would give lower statistical power to the data. To compare understorey and canopy species and abundance a pairwise Wilcox test was used (Zar, 1984).

[3] These measurements are used in a study including sweep netting at specific times

2.4.2 Species richness and diversity

Species accumulation curves were drawn for each site to examine the completeness of the sampling (Colwell and Coddington, 1994). Rarefied species richness was estimated using the lowest abundance measured in any site, to see how many species there would be in the sites if this number of specimens were sampled (Hulbert, 1971). The non-parametric Chao1 estimation method for abundance data of homogeneous samples was used to estimate the "true" richness of each site (Koh, 2008; Colwell and Coddington, 1994; Magurran, 2004).

Simpson-index D, a probability measure of two randomly chosen individuals being from the same species, was used to calculate the diversity of each site (shown as 1-D, so that increased values signify increased diversity). This is a common and robust diversity index frequently used with community data (Magurran, 2004). The relationship between abundance, the different measures of species richness and diversity and the habitat types were tested.

2.4.3 Ecotype distribution

Ecotype information (Table 3.8) of each species was obtained from Davenport (1996). Forest ("F") and lowland forest ("FL") were combined and called forest species ("F"), because Mabira is a lowland forest. For the specimens not identified to species level, an extra unknown category was made ("u."). To visualize the distribution of forest species along the human-modification gradient, different approaches were used. First, a mosaic plot was made of ecotype allocation on relative abundance and relative species richness per site. It was tested if the percentage of forest species and forest species abundance per site was significantly correlated with the habitat types. Second, a species abundance curve of mean abundance was made of each site to visually distinguish the evenness difference between the habitats. Third, a species abundance curve was made for all the ecotype taxa, with a focus on forest species.

2.4.4 Ordination analysis

Multivariate statistics were used to analyse the community structure. The butterfly data were standardized to relative abundance and square-root transformed per site, which reduces the influence of dominant species and the difference in site abundance which had a large spread (Gotelli and Colwell, 2001). Detrended Correspondence Analysis (DCA) was performed to determine the length of the first axis which can indicate if the species have a linear or unimodal response to the underlying gradient. A unimodal relationship is assumed as the length of the first axis is 3.3 SD. Correspondence analysis (CA), an eigenvector model based on Chi-square

distances and related to a unimodal response model was used to decrease the dimensions of the data for visualization of the distances between sites. CA is sensitive to rare species hence species occurring only once in the data were removed, leaving 89 species in the dataset (Legendre and Gallagher, 2001). The Jaccard similarity index, frequently used in community studies, was used to supplement the results from the ordination (Legendre and Legendre, 1998). This index was also used by Bhagwat *et al.* (2008) when they calculated the compositional similarity between agroforestry and adjacent forest habitat. The Jaccard index is based on presence–absence data (Chao *et al.*, 2005) and can be used to compare similarity between species lists where 0 means no species in common and 1 indicates an identical composition. The Horn-Morisita similarity index was used on square-rooted relative abundance data. This diversity index is commonly used in community studies (Fermon *et al.*, 2005; Lewis, 2001). It is a version of the Morisita similarity index which can handle any abundance data where it takes into account the relative abundance of the species and has been shown to be insensitive to variations in species richness and diversity among samples (Wolda, 1981). A Principal Component Analysis (PCA) was performed to describe the different sites and to determine the relationship between the environmental variables, which were first standardized to unit variance (centres the variables and brings their means to zero and their variance to one) to make a correlation biplot (Lepš and Šmilauer, 2003). Constrained ordination was preformed with Constrained Correspondence Analysis (CCA) including the explanatory environmental variables (canopy openness, tree basal area, understorey cover, bare ground, canopy top height, canopy low height, temperature, humidity). It was anticipated that there would be much inter-correlation between the environmental variables, so forward selection and the application of conditioned variables were used to find the most important variables explaining the compositional variation.

3. Results

3.1 Environmental variables describing the sites

Details of the environmental data collected are summarized in Table 3.1. The percent canopy openness varies from 21% in a mature site (Ma1) to 50% in a coffee garden site (Co2). The gradient of openness is clear. Although the mixed small-scale garden sites have a higher decline in observed canopy trees, the canopy pictures were to some degree affected by shade from a large quantity of banana palm leaves. Elevation ranges from a mean value of 1112m (Ma3) to 1260m (Ma4). Canopy top height and tree basal area show a general decrease towards the more open sites. Percent of understorey cover, ranging from about 50 to 10% cover, is highest in the secondary sites and lowest in coffee and mixed garden sites. The amount of bare ground is, not surprisingly, large in coffee and mixed garden sites and considerably lower in the forest sites. The mean temperature, as a result of the structural changes, decreases towards the open sites while humidity shows the opposite response.

Figure 3.1 *Hemispherical photo used to estimate percent canopy openness. Example from Coffee garden 2*

Table 3.1 *Environmental variables of the sites.*

Habitat	Canopy openness (%)	Elevation (m.a.s.l)	Canopy top height (m)	Canopy low height (m)	Tree basal area (m^2/ha)	Understorey cover (%)	Bare ground (%)	Temperature (c°)	Humidity (%RH)
Mature 1	21	1181 ± 9.8	25 ± 5.3	11 ± 2.6	108 ± 3.4	37 ± 10.3	7 ± 2.4	21.84± 1.17	93.88± 2.07
Mature 2	22	1260 ± 4.5	20 ± 4.1	11 ± 2.4	104 ± 3.0	17 ± 16.0	6 ± 1.6	21.70± 0.87	93.50± 4.24
Mature 3	23	1112 ± 13.5	27 ± 4.2	13 ± 2.4	101 ± 3.3	44 ± 21.3	7 ± 6.3	21.27± 0.58	99.09± 4.04
Mature 4	22	1260 ± 40.6	25 ± 4.1	11 ± 2.1	107 ± 2.9	30 ± 19.4	12 ± 10.2	22.07± 1.49	92.75± 7.93
Secondary 1	23	1180 ± 12.0	19 ± 2.6	12 ± 3.5	64 ± 2.0	50 ± 20.1	17 ± 16.3	21.46± 0.97	96.16± 5.07
Secondary 2	23	1202 ± 5.9	20 ± 3.3	9 ± 0.6	89 ± 1.8	43 ± 14.5	10 ± 9.3	22.57± 1.32	90.82± 7.59
Secondary 3	22	1126 ± 5.2	19 ± 3.7	11 ± 2.1	91 ± 2.5	44 ± 16.6	9 ± 6.4	21.03± 1.89	98.22± 7.72
Cardamom	30	1179 ± 12.4	24 ± 3.2	14 ± 3.2	93 ± 2.0	18 ± 9.1	15 ± 16.3	22.16± 0.72	90.54± 0.81
Coffee 1	42	1210 ± 5.7	15 ± 8.8	12 ± 3.7	20 ± 1.1	11 ± 6.2	42 ± 20.0	24.30± 0.50	79.61± 0.65
Coffee 2	50	1229 ± 4.7	11 ± 8.1	11 ± 2.1	41 ± 2.2	11 ± 5.2	42 ± 32.0	24.25± 1.63	81.46± 6.78
Mixed garden 1	47	1201 ± 4.0	3 ± 6.3	7 ± 4.1	11 ± 1.0	22 ± 21.8	46 ± 37.4	25.44± 1.23	73.02± 5.58
Mixed garden 2	45	1218 ± 8.0	5 ± 6.9	8 ± 1.8	27 ± 1.4	14 ± 9.7	34 ± 26.9	23.64± 2.02	83.90± 10.36

3.1.1 Principal component analysis with environmental variables

The PCA (Fig. 3.2) illustrates the vegetative structure and micro-climate at the different sites. Coffee and mixed garden sites show a more open canopy and more bare ground than the forest sites. The cardamom site is similar to mature forest sites. The mature habitat shows some variation, where site Mg3 is distinguished from the other sites by having higher understorey cover and a lower elevation. The secondary sites have more understorey cover, lower canopy height and less tree basal area than the mature sites.

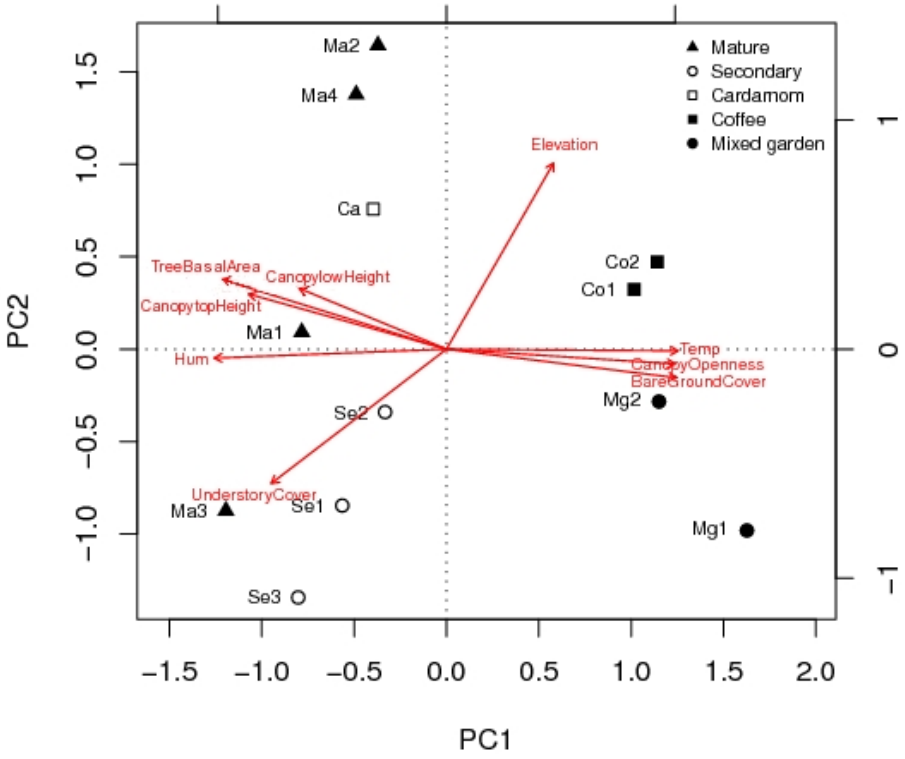


Figure 3.2 *PCA with standardized environmental variables to equalize variance*

3.2 Characterizing the butterfly fauna

The sites were checked 137 times in total[4] during the field period (Tab 2.2), during which 4582 specimens from 125 species[5] were recorded at the 12 study sites. Species and individuals belonged to the following subfamilies; Satyrinae (26 species; 2991 individuals), Nymphalinae (52; 852), Charaxinae (34; 681), Apaturinae (1; 24), Acraeinae (7; 13), Libytheinae (1; 9) and Riodininae (1; 3)[6]. The species list, including occurrence in the sites and ecotype, is found in Appendix I.

3.2.1 Restricted range-species and new species in Mabira

In this study we recorded 79 species out of 128 Nymphalidae species, from the biodiversity report, which was sampled by both sweep netting and trapping with a different bait mixture (Davenport *et al.*, 1996). We recorded 22 additional Nymphalidae, but only seven species (Appendix IV) were not recorded in other butterfly studies known from Mabira (Akite, 2006; Bwanika, 1995). Compared to the number of species found per subfamily in the biodiversity survey, the only Nymphalidae subfamilies under sampled here are Danainae and Acraeinae (Davenport *et al.*, 1996). Many of the species form these subfamilies are feeding on nectar and must be sampled with sweep netting.

In the biodiversity surveys of Davenport *et al.* (1996), 27 restricted-range species (16 Nymphalidae), two sub endemic species and six species unique to Mabira forest were found. This present study recorded nine restricted-range species, of which two species have not been recorded in Mabira by past surveys (Tab. 3.2). The newly recoded restricted-range species were not recorded in the forest and thereby not expected to be found by past forest surveys ("f.": *P boisduvali*; "O": *B. ena*). In addition nine sub-endemic species were registered in this study, mainly in the forest sites (Tab 3.3).

[4] 7 checks in total were not included because of weather and time limitations
[5] 102 Positively identified, 11 genera and 12 morpho species
[6] *Abisara neavei*, the only butterfly excluded because it is not from the Nymphalidae family, 3 specimens found in Se3 because it was amazingly abundant at this site.

Table 3.2 *Restricted-range species found in Mabira and surroundings. Restricted range species are species found in 5 or less forest reserves out of the 64 sampled under the biodiversity survey (Davenport et al., 1996). * Species not recorded in Davenports survey in 1993-1995 (Davenport et al., 1996), Bwanika MCs thesis (Bwanika, 1995) or other known surveys (Akite, 2006).*

Species	Abundance	Ecotype	Present at site
Apaturopsis cleochares	24	F	Ca, Co1, Ma2-4, Mg1-2, Se1-3
Euphaedra rex	16	F	Ma2-4, Se1-2
Palla usseri	4	F	Ma3, Se2
Charaxes porthos	1	F	Ma2
Charaxes pythodoris	1	f.	Se2
Acraea semivitrea	1	F	Co1
Charaxes zelica	1	F	Co1
*Bicyclus ena**	1	O	Mg1
*Pseudacraea boisduvali**	1	f.	Mg2

Table 3.3 *Sub-endemic species found in Mabira and surroundings. The sub endemic regions are; 3: "Somalia-Masai" region of north-eastern Africa (Eritrea, Ethiopia, Somalia, Sudan, Kenya, Tanzania and Uganda), 4: Central forest block (from Nigeria to W. Uganda, W. Tanzania, W. Zambia and Angola), 5: West Africa (from the Mahoney gap to Senegal).*

Species	Abundance	Ecotype	Sub endemic to Region :	Present at site
Elymnias bammakoo	1	F	4,5	Ma1
Mesoxantha ethosea	1	F	3,4,5	Ma4
Bicyclus mesogena	9	F	3,4,5	Ma2-4, Se3
Euphaedra preussi	104	F	4	Ma1-4, Se1-3
Hypolimnas monteironis	3	F	3,4	Ma2, Ma4, Se2
Hypolimnas salmacis	8	F	3,4,5	Ma2-3, Se3
Acraea lycoa	1	F	3,4,5	Se3
Hypolimnas dinarca	5	F	4,5	Se3
Neptis metella	23	f.	3,4,5	Ma3, Se1, Se2, Mg1

Table 3.4 *The 10 most abundant species registered in the Mabira area in this study*

Species	Abundance	Ecotype
Bicyclus uniformis	649	U
Bicyclus mollitia	619	F
Bicyclus smithi	446	F
Bicyclus golo	240	F
Henotesia peitho	228	W
Charaxes cynthia	177	F
Cymothoe herminia	148	F
Sallya garega	108	M
Euphaedra preussi	104	F
Bicyclus sophrosyne	104	f.

Figure 3.3 *Elymnopsis bammakoo, Mabira Forest Reserve, Uganda, April 2009. A sub-endemic species registered in Mabira. Photo: Perpetra Akite.*

3.2.2 Sampling completeness

The rarefaction curve (Fig.3.4) shows that many of the sites were under-sampled, and none reached an asymptote. The steep slopes of especially the secondary and mixed small-scale gardens indicate that a lot more species are expected to be found here. The slope was decreasing but not reaching asymptote in the cardamom site and all the mature sites including one of the coffee garden sites (Co2) as well as one secondary site (Se2), though additional species are expected to be found here as well.

The percent sampling completeness (Tab.3.7) from the Chao1 estimated species pool indicates that only 39% of the true species richness at Mg 1 was sampled, while 53% was sampled from Se3 site. The other sites all sampled >60% of their estimated species pool according to Chao1. This concurs with the rarefaction curve in indicating an incomplete sampling.

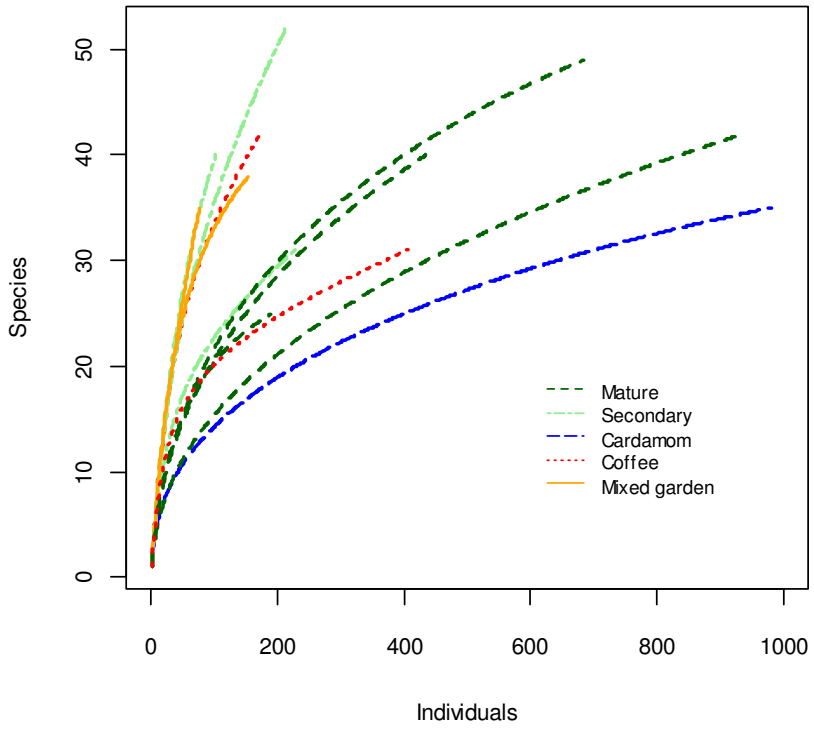


Figure 3.4 *Rarefaction curve for butterfly data pooled by sites sampled (12). Shows expected number of species in a randomly repeated resample from each sites species pool (Gotelli and Colwell, 2001).*

3.2.3 Species richness and diversity

Given that the slopes of the accumulation curve and that the total abundance differed (Tab 3.7) in spite of the standardized sampling method, the species richness was extrapolated as well as rarefied with a 76 individual maximum. The mean observed species richness (Tab 3.6) is highest in the secondary forest (mean 41±10.54), lower in mature forest (39±10.10), followed by the coffee garden and mixed garden with similar richness (36.5±7.78, 36.5±2.2), while the cardamom is least species rich (35, no s.d. when single site). Rarefied and Chao1 estimated richness indicate the highest richness to be the mixed garden habitat (32.4±3.62, 68.0±31.36). There is no significant relationship between observed, rarefied or Chao estimated species richness and habitat type [Kruskal-Wallis; Obs: χ^2=0.67, df = 3, p=0.88; Rare: χ^2=7. 59, df = 3, p=0.055; Chao: χ^2=0.1667, df = 3, p=0.98]. High relative species richness is found in human modified habitat compared to richness found in forest sites (Tab. 3.5). Abundance varied from 76 (Mg1) to 981 (Ca) individuals per site, but there is no significant relationship between the abundance and the habitat types [Kruskal-Wallis; χ^2=5.93, df = 3, p=0.12].

Table 3.5 *Mean species richness of the modified habitats relative to the forest sites as percentage. Values over 100 indicate higher richness in the modified habitat.*

Forest sites	Richness	Secondary	Cardamom	Coffee	Mixed Garden
Mature	***Observed***	112%	96%	100%	100%
	Rarefied	169%	76%	143%	192%
	Chao1 estimated	136%	91%	117%	139.2%
Secondary	***Observed***	NA	89.2%	93.0%	93.0%
	Rarefied	NA	46.60%	88.9%	119.0%
	Chao1 estimated	NA	74.3%	95%	110.0%

Table 3.6 *Mean measure of abundance and observed, rarefied and Chao estimated species richness including standard deviation*.

	Mature		Secondary		Cardamom		Coffee		Mixed garden	
	Mean	s.d	Mean	s.d	Mean	s.d	Mean	s.d	Mean	s.d
Abundance	561.8	±321.6	181	±68.8	981	NA	289	±165.5	115	±55.2
Observed richness	39	±10.10	41	±10.54	35	NA	36.5	±7.78	36.5	±2.12
Rarefied (n=76)	17.3	±2.48	28.7	±7.32	12.8	NA	24.1	±7.91	32.4	±3.62
Chao1 estimated	54.6	±16.93	66.2	±28.01	44.4	NA	57.0	±10.84	68.0	±31.36

The Simpson diversity index (Tab 3.7) shows high diversity in the disturbed sites and secondary sites except in the cardamom plantation, and the mature forest sites show a lower diversity value. The Simpson diversity index shows no significant correlation with habitat types [Kruskal-Wallis; χ^2=7.303, df=3, p=0.08], and although Figure 3.5 might indicate a difference, it is difficult to find significant results with only a few observations per sample.

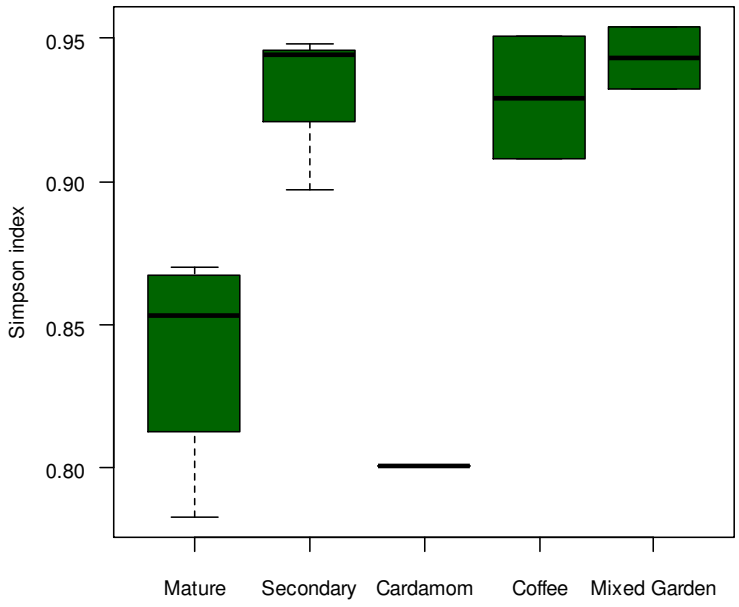


Figure 3.5 Simpson index (1-D) per habitat

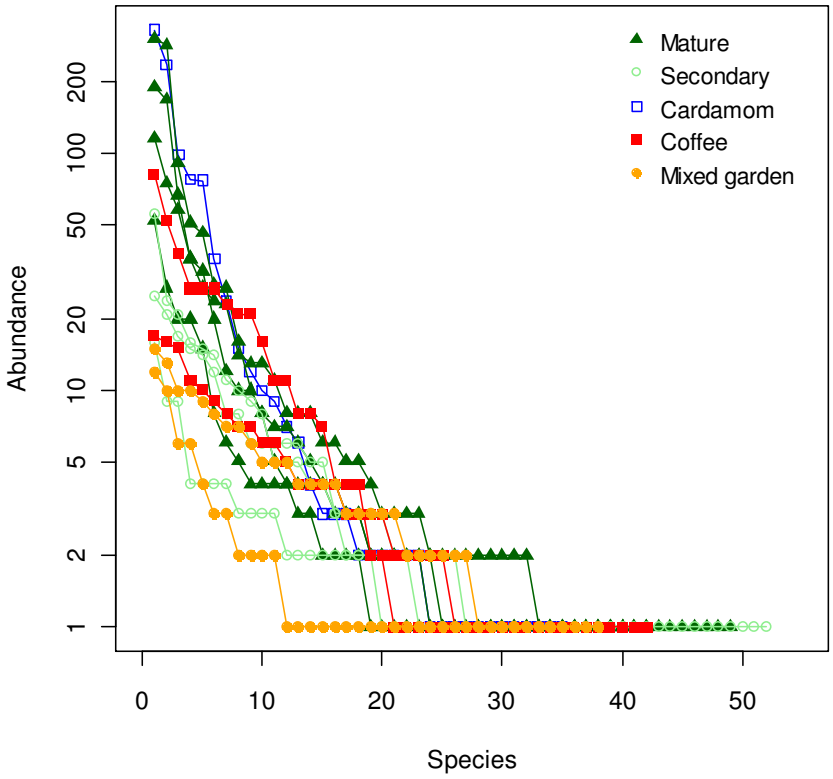


Figure 3.6 *Species abundance curve per site including all the species found of the different taxa on a log scaled y-axis. Colour and point coded to habitat type.*

The species abundance curve in Figure 3.6 has a steep curve for the cardamom site indicating high dominance of relatively few species. The slope is then very similar to many of the mature sites especially Ma2 though with lower rarity. The species present in the coffee garden seem to be more abundant than species in the mixed garden site, especially in Co2. The slopes of Co1 and Mg2 are similar and show most evenness of the disturbed sites.

Figure 3.7 gives an image of the species abundance relationship while showing the site curves for each ecotype. The figure shows highest evenness and rarity in the mature and secondary habitats for the forest species. It also illustrates the high dominance and lack of rarity of forest species in the cardamom plantation. The coffee and mixed small-scale gardens show higher evenness of widespread and migrating species and a steep curve of forest species, although the species present show less abundance then the cardamom site. With forest taxa (Fig. 3.7), coffee site Co2 show an abrupt change dominated by few abundant species.

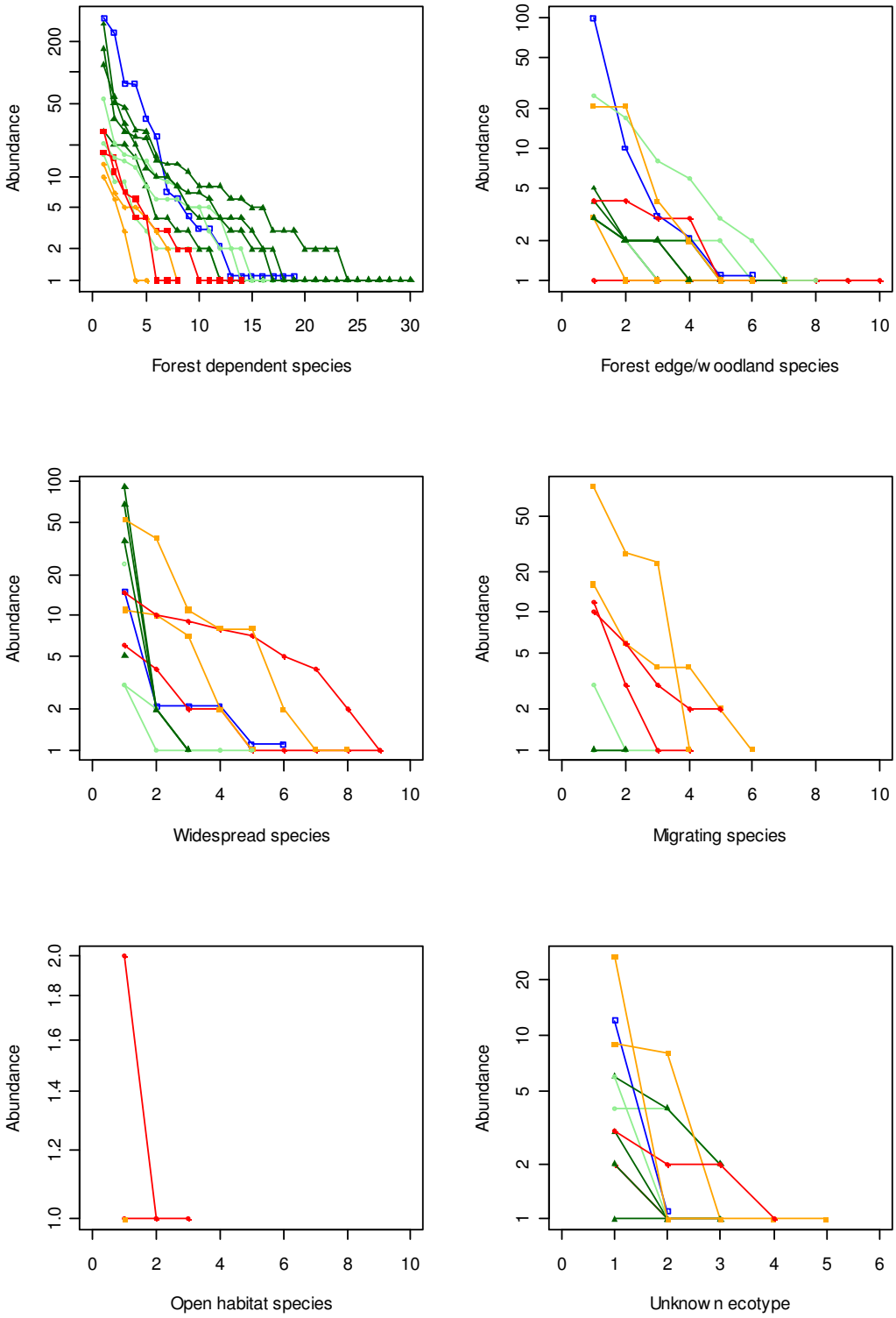


Figure 3.7 *Species abundance curves per site on a log scaled y-axis. One plot for each different ecotype showing the dominance and rarity of the ecotype earmarked species. Unknown habitat preference includes "U" and "u." Note different length of x-axis. Modified for clarity by jittering the cardamom plantation with +0.1 species. Legend as in Figure 3.4.*

Table 3.7 *Butterfly abundance, total species richness, rarefied- and extrapolated species richness per site. Percent completed sampling (Species richness recorded/Species richness extrapolated), and Simpson diversity index.*

Habitat	Code	Abundance	Species richness	Rarified Species richness (n=76)	Extrapolated Species richness Chao1	SE Chao1	Percent completed sampling (Chao1)	Diversity Simpson (1-D)
Mature 1	Ma1	190	25	18.3	29.2	± 6.08	0.86	0.870
Mature 2	Ma2	937	42	13.6	63.9	± 17.62	0.66	0.783
Mature 3	Ma3	685	49	19.0	62.6	± 10.26	0.78	0.843
Mature 4	Ma4	435	40	18.1	62.7	± 19.81	0.64	0.864
Secondary 1	Se1	102	40	34.6	52.8	± 9.09	0.76	0.944
Secondary 2	Se2	228	31	20.5	47.5	± 20.20	0.65	0.897
Secondary 3	Se3	213	52	30.9	98.4	± 32.76	0.53	0.948
Cardamom	Ca	981	35	12.8	44.4	± 9.17	0.79	0.801
Coffee 1	Co1	172	42	29.7	64.7	± 19.81	0.65	0.950
Coffee 2	Co2	406	31	18.6	49.3	± 28.65	0.63	0.908
Mixed garden 1	Mg1	76	35	35.0	90.2	± 47.24	0.39	0.932
Mixed garden 2	Mg2	154	38	29.9	45.9	± 8.00	0.83	0.954

3.2.4 Ecotype distribution

The mosaic graph (Fig. 3.8) shows a clear decline in forest specialists towards the more intensively managed sites where they are replaced by the presence of migratory (M), widespread (W) and open habitat (O) species. There is a significant relationship between the percent forest species and habitat type [Kruskal-Wallis; χ^2=8.69, df=3, p=0.03]. When performing a non-parametric Kruskal-Wallis Rank Sum Test the sample size becomes too low and no significant differences are found. A parametric TukeyHSD multiple comparison test was then performed to indicate which habitats differed in addition to the visual difference in Fig 3.11. A significant difference between the percentage of forest species was then found between mature forests and coffee gardens [TukeyHSD, $p<0.05$] and with mixed garden habitats [TukeyHSD, $p<0.001$]. The secondary forest habitats are also significantly different from the coffee [TukeyHSD, $p<0.05$] and the mixed garden habitats [TukeyHSD, $p<0.01$].

The relative numbers of non-dependent forest species are distributed quite evenly across the sites, with the highest occurrence in Mg1 and Se1. There were just a few migratory species found in forested sites and most were found in the coffee plantations and the mixed gardens. The open habitat species were only found in the coffee plantations and in the mixed small-scale gardens. Widespread species are present in all the sites but are more species rich in the most open sites.

The abundance of forest species is highest in the cardamom site (Ca) but dominated by only a few species. The sample size was larger in the forest sites than in the cardamom site, but the relative abundance shows they are dominated by forest species. The open agricultural sites were highly dominated by widespread (W) and migratory (M) species and had a low occurrence of forest species. There is no significant relationship between forest species abundance and habitat type [Kruskal-Wallis, χ^2=7, df=3, p=0.07]. However in the mature forest sites there was a considerable quantity of specimens without an ecotype ("U"). This is because the most abundant species in the data (*Bicyclus uniformis*) is not fitted with an ecotype from the description of Davenport *et al.* (1993). If there was an ecotype for this species it would produce a more dramatic decline in forest species abundance towards disturbed areas. Female individuals of the *Bicyclus* genus were difficult to identify to species level when lacking the distinctive pencil hairs, thus contributing to the high amount of unknown ecotypes, in addition to the individuals only identified to genus and morpho-species ("u.").

Table 3.8 *Ecotype definition (Davenport, 1993)*

F	Forest-dependent species
FL	Lowland closed forest species
f.	Forest edge/woodland species
M	Migratory species
O	Open habitat species
W	Widespread species
U	Unknown habitat preference
u.	Unidentified to species level

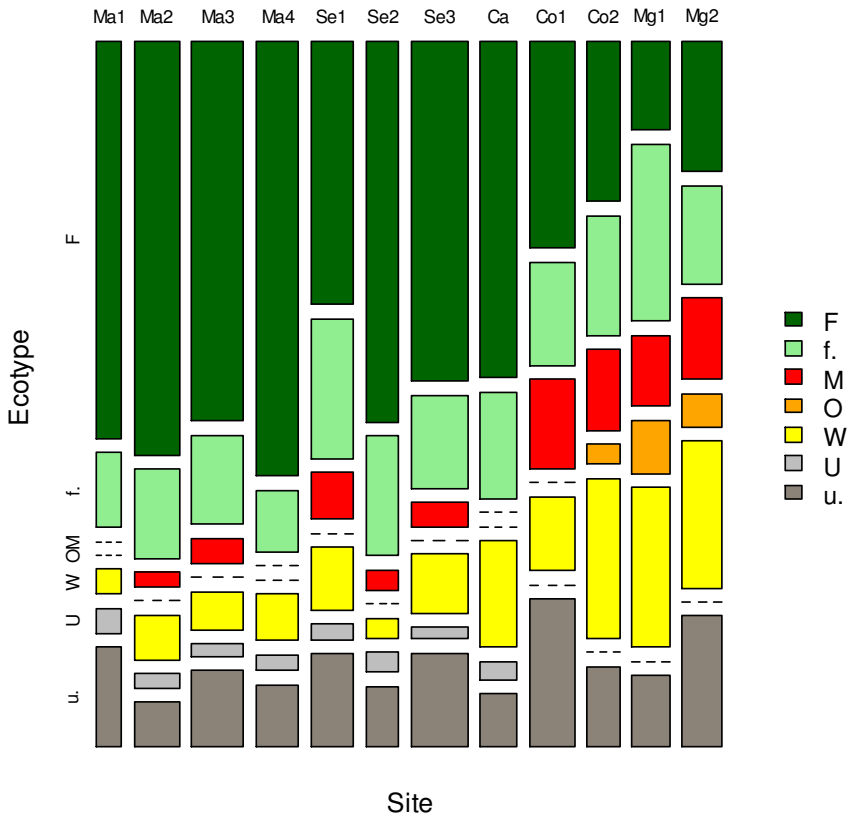


Figure 3.8 *Ecotype distributions of species. Ecotype (Tab 3.4) shows relative no. of species, while site width shows observed species richness present at that site. Mature (Ma1-4), Secondary (Se1-3), Cardamom (Ca), Coffee (Co1-2), Mixed garden (Mg1-2).*

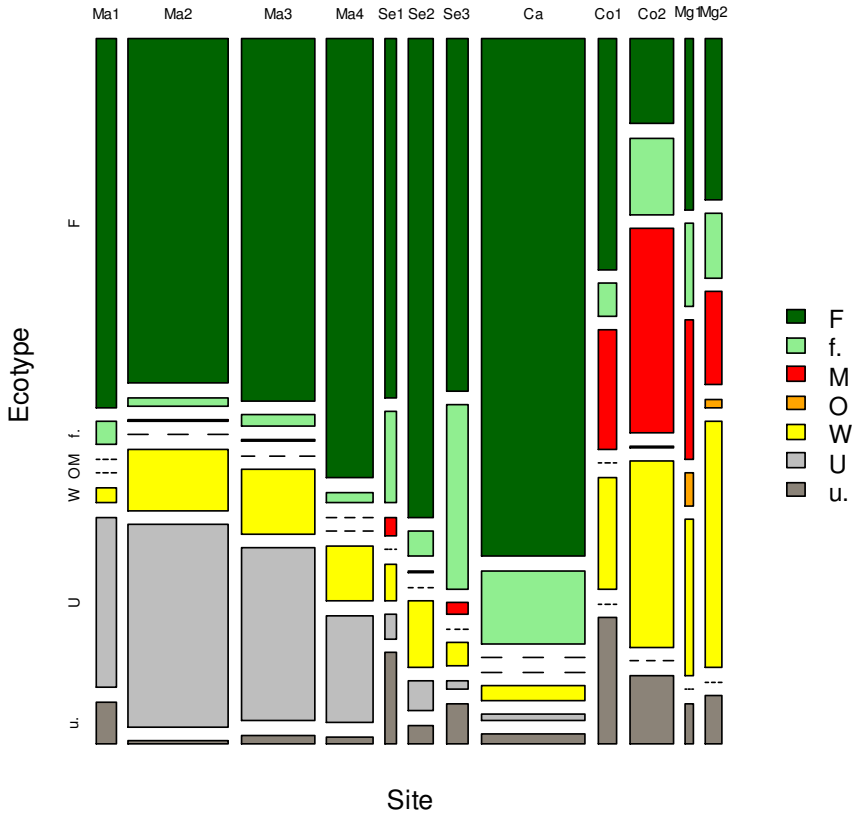


Figure 3.9 *Ecotype distribution of abundance. Ecotype (Tab 3.4) shows relative abundance, and width shows butterfly abundance at each site. Mature (Ma1-4), Secondary (Se1-3), Cardamom (Ca), Coffee (Co1-2), Mixed garden (Mg1-2).*

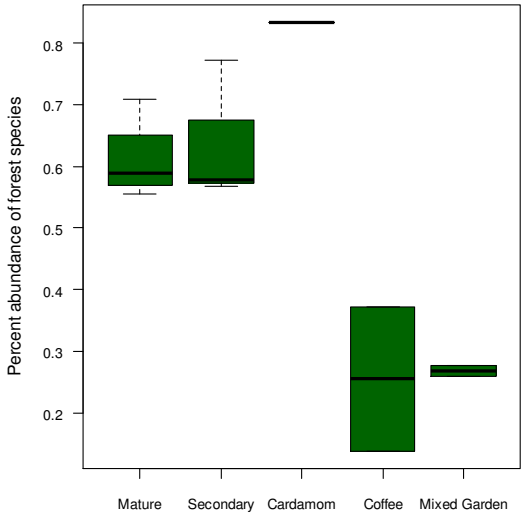


Figure 3.10 *Percent abundance of forest species per habitat*

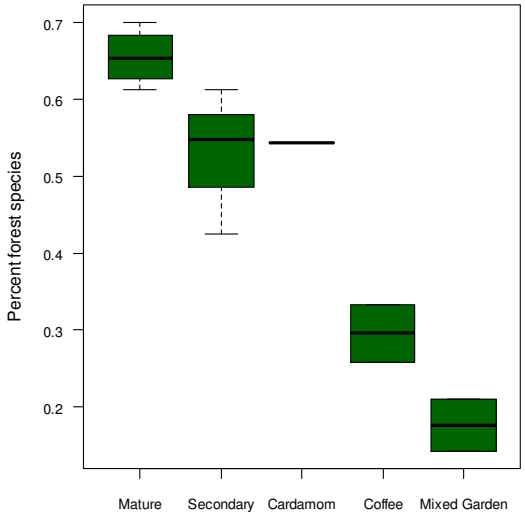


Figure 3.11 *Percent forest species per habitat*

3.2.5 Similarity in species composition

There is a clear grouping of the forest sites and the most open agricultural sites in the CA ordination plots (Figs. 3.12 and 3.13). The first axis (Fig. 3.12), significantly explaining 34.5% of the total inertia, seems to reflect a canopy openness and habitat modification gradient. The cardamom site (Ca) is an outsider on the second axis in the CA ordination with abundance (Fig. 3.13), but when the abundance value is removed and only the composition is used, it becomes more similar to a mature or a secondary site (Ma3, Se1). This is because of the high abundance and clear dominance in the cardamom site of relatively few species such as *Bicyclus smithi* (333 individuals), *Bicyclus golo* (238) and *Bicyclus sophrosyne* (99). Site Se2, which is the oldest secondary forest site, seems to be more similar to the mature sites than the other secondary sites with and without abundance (composition; 37-45% similar to mature, with abundance; 64-75%). The mixed garden sites and the coffee sites are grouped together in both ordinations, though being more dissimilar in CA with composition.

Table 3.9 *Pairwise Jaccard similarity indices of species composition (presence–absence data), showing mean values of similarity index ± s.d.*

	Similarity				
	Mature	**Secondary**	**Cardamom**	**Coffee**	**Mixed Garden**
Mature	0.43 ± 0.050				
Secondary	0.39 ± 0.048	0.35 ± 0.067			
Cardamom	0.40 ± 0.027	0.37 ± 0.068	NA		
Coffee	0.15 ± 0.049	0.18 ± 0.052	0.23 ± 0.014	0.40 ± NA	
Mixed Garden	0.13 ± 0.046	0.18 ± 0.058	0.25 ± 0.006	0.44 ± 0.075	0.46 ± NA

Table 3.10 *Pairwise Horn-Morisita similarity indices of square-rooted relative abundance data, showing mean values of similarity ± s.d*

	Similarity				
	Mature	**Secondary**	**Cardamom**	**Coffee**	**Mixed Garden**
Mature	0.86 ± 0.051				
Secondary	0.56 ± 0.142	0.52 ± 0.133			
Cardamom	0.28 ± 0.054	0.38 ± 0.050	NA		
Coffee	0.12 ± 0.054	0.22 ± 0.077	0.13 ± 0.009	0.63 ± NA	
Mixed Garden	0.11 ± 0.029	0.24 ± 0.070	0.15 ± 0.001	0.63 ± 0.055	0.70 ± NA

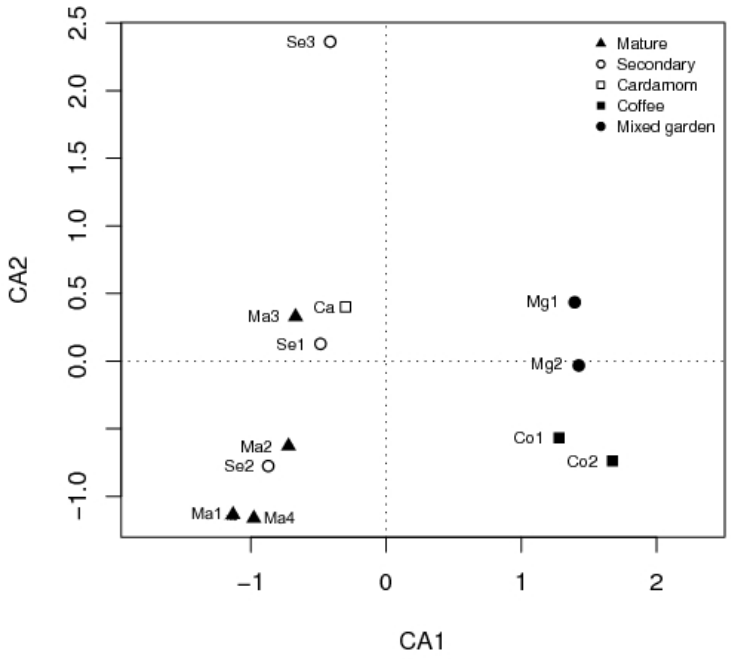


Figure 3.12 *Correspondence analysis ordination with presence/absence data*

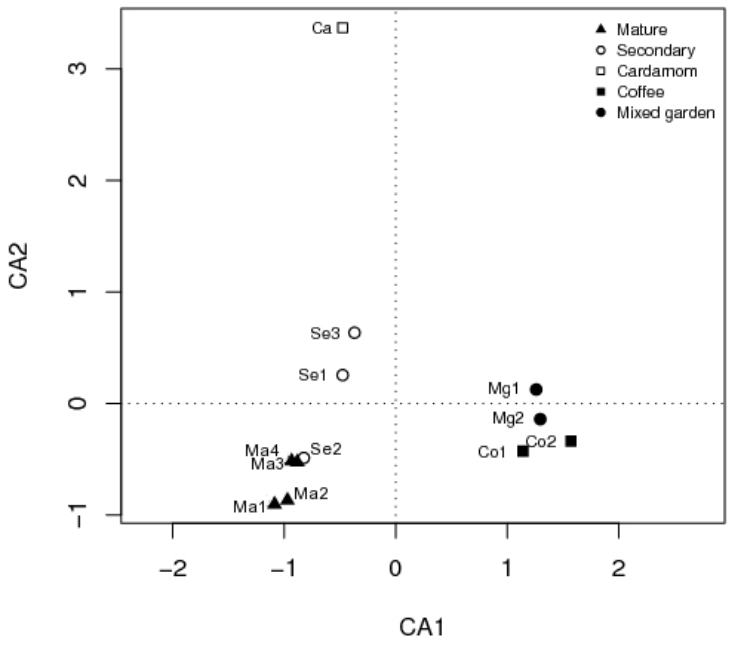


Figure 3.13 *Correspondence analysis ordination with square- rooted relative abundance data without singletons*

The secondary site, Se3, which is similar to the other secondary sites in ordination with abundance, becomes a strong outlier on the second ordination axis using only species composition. This site is situated further north-east from the other sites at a greater distance from mature forest, and shows a less similar species assemblage compared to the other forest sites. The pairwise similarities between habitats also reflect the same information as the ordination. The similarity measures are significantly different between two or more habitat types within the Jaccard similarity of composition [Anosim; R=0.667, p=0.003, perm=4999] and Horn-Morisita similarity of square relative abundance [Anosim; R=0.865, $p=2e^{-4}$, perm=4999] (Clarke, 1993).

3.2.6 Environmental variables explaining the species composition

From a CCA analysis with the environmental variables measured, canopy openness explained most of the variation (explaining 0.5984 of total 1.7978 inertia) in the butterfly composition with forward selection [ANOVA, p=0.005].

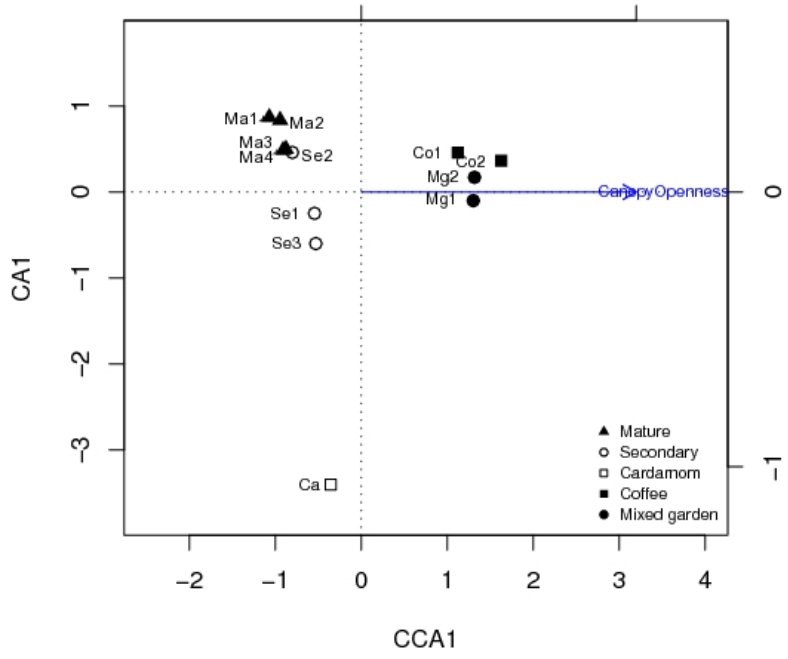


Figure 3.14 *Constrained correspondence analysis, showing significant variable.*

From the PCA with environmental variables (Fig. 3.2), canopy openness is highly positively correlated with bare ground and temperature and negatively correlated with tree basal area and humidity. When canopy cover is partialled out, no other explanatory variables explain any community variation significantly.

3.3 Vertical variation

Abundance was significantly greater in the understorey than the canopy [paired Wilcox test, p=0.00048]. There was no significant vertical stratification in rarefied species richness [paired Wilcox test, p=0.57].

The unique species found in the canopy are given in Appendix III, with 10 positively identified species, including four individuals identified to genus and one morpho-species. Few individuals were found of unique canopy species, however two restricted-range species were found amongst the unique canopy species (*C. porthos* and *P. boisduvali*, see Tab. 3.2). There was no significant relationship between percentage of observed canopy species found at each site and habitat type [Kruskal-Wallis, χ^2=6.37, df=3 p=0.09].

Table 3.11 *Species richness, abundance and number of unique species found in understorey and canopy*

	Understorey	Canopy
Species richness	109 (88%)	87 (70%)
Unique species	37 (30%)	15 (12%)
Abundance	3712 (81%)	867 (19%)

4. Discussion

Several metrics are used in different studies to measure the conservation value along a gradient of land-use habitats. Most studies include species richness and diversity, and recently most studies also investigate similarity in community composition, while some include abundance and sometimes distribution of forest dependent species. In this study, some of these measures disagreed over the ranking of the habitats. Rarefied species richness and Simpson diversity index gave a high ranking to the coffee and mixed small scale garden as well as the secondary forest in this study. These metrics ignores the high loss of forest species as well as rare and restricted-range species in the coffee and mixed small-scale garden. When looking at the distribution of forest species these land-use habitats have a significantly lower percentage of relative species richness to the mature and secondary forest. The similarity in community composition is also relatively low, especially compared to the mature forest. When looking at the cardamom plantation however, the rarefied species richness gave the lowest rank of value for conservation. On the other hand, the cardamom plantation had a high percentage of forest species and a very high percentage of similarity in community composition to the mature forest. When the similarity in composition included a value of abundance, it decreased as a reflection of its high dominance and low rarity value compared to the forest. The modified habitats showed a low value in conserving rare and restricted range species.

Compared to observed species richness, rarefied richness accounts for the possible differences in sampling efficiency, for instance, in terms of day condition, where all the sites have the same number of individuals (Gotelli and Colwell, 2001). Rarefied and Chao1 estimated richness show parallel ranking of the habitats with highest richness in mixed small-scale agriculture followed by secondary forest, mature and cardamom plantation. The percent species richness of the disturbed habitats, however, shows a very high richness compared to the mature and secondary forest in all the richness estimates. In the cardamom plantation there is a lower similarity in rarefied richness compared to the forest sites (46.6%-76.6%). This does not give a proper image of the conservation value compared to the coffee and mixed garden habitats. The two butterfly studies included in the meta-analysis of Bhagwat *et al.* (2008) have a richness similarity of 50% Schultze *et al.*, (2004) and 80% (secondary) - 103% (primary) (Bobo *et al.,* 2006). The mean species richness in agroforestry habitats of the 19 insect taxa compared to mature forest is 86% (44-250%). There is a large spread in these findings and low congruence, though the richness found in this study would be comparable.

Secondary forests are known to have high species diversity, as found in this study, as a result of being intermediately disturbed. Matrix habitats have more boundary habitats that show edge effect symptoms, and so contain species from several ecotypes. A diversity index was not used as a basis for conclusions by Bhagwat *et al.* (2008), but has been used in several other studies that investigate the value of human-modified habitats (Spitzer *et al.*, 1993, Vu and Yuan, 2003). The diversity index does not necessarily reflect the indicated conservation value of the disturbed habitats. When evaluating habitats for their conservation value, species richness and diversity indices have limited information with gradient studies. They are of more use when the goal is to conserve the most diverse area of similar habitats.

A review including 20 butterfly gradient studies in Asia by Koh (2007) pointed out that nine studies show an increased richness in disturbed areas, and seven studies report a contrary pattern. Scales and Marsden (2008) collated 52 small-scale agriculture studies on variety of taxa from plants to bats, comparing richness and abundance between agroforestry and primary forests. In this collation, 34 out of 43 comparable studies record an increase in richness or diversity in primary forest. The contradicting results could reflect local differences and complex biodiversity responses to habitat change, though Koh (2007) argues it can also be a result of methodological biases. Biases mentioned include that only eight of eleven studies in the review controlled for sampling effects, the difference in spatial scale (>1ha; >3 ha) gave different ranking of undisturbed areas and the lack of studies sampling the canopy.

Of all the studies reviewed by Scales and Marsden (2008), only 11 studies compare beta diversity between habitats with compositional similarity. There are difficulties comparing similarities recorded in the different studies because of the wide variety of similarity indices used (Scales and Marsden, 2008).

When looking at the similarity in composition in Mabira, the cardamom site has a similarity of 37-40% compared to the forest sites, which is comparable with the similarity within the forest sites. The agroforestry study using butterflies as indicator taxa referred to in Bhagwat *et al.* (2008) registered a 19-31% similarity (Bobo, 2006), while the mean similarity in composition registered for insect taxa is 49% (2-98% spread). All the studies vary between similarities of 25-65% compared to primary and secondary sites. The more open coffee plantations and mixed garden sites have a similarity to the forest sites of 15-18% and 13-18%, respectively. The similarity in

composition with and without abundance would seem to be good estimates for the value of conservation.

Using presence-absence data, the cardamom site seems to be relatively similar to the forest sites, whilst the similarity of the more open sites indicates a lower value for forest conservation. When including the abundance measure, the cardamom site shows less similarity to the forest sites (28-38%) because of the high dominance of a few species. The abundance value actually increases the similarity of the coffee and mixed small-scale gardens to the secondary forest, and slightly decreases their similarity to the mature forest. The intra-habitat similarity increases for each habitat when including abundance.

From the point of view of conservation of forest biodiversity and the value of the different matrix habitats, it is essential that these habitats support forest specialists, which are of greater conservational concern as they are threatened with local extinction when the forest habitats are degraded and removed. From the ecotype distribution there is a clear loss of forest species in the open matrix habitats where it is replaced with widespread, open habitat and migrating species, as expected. The cardamom site, which has a higher percentage of shade cover, is an exception and its relative forest-species richness is quite similar to the forest habitats, especially the secondary forest.

The capacity of habitats to support endemic and rare species is important for biodiversity conservation. The focus for conservation should be on forest species and degree of endemism. Only one restricted-range species was sampled in all the habitats (*A. cleochares*) and was relatively common in the Mabira area. Three other restricted-range forest-associated species found in the altered habitats were only found as single individuals. Of the sub-endemic species found in this study only one was found from a human-modified habitat (Mg1). These findings support the conclusion frequently found in similar gradient studies that modified habitats have a negative impact on rare and endemic species (Bobo, 2006; Vu, 2009; Wood and Gillman, 1998).

It is often difficult to select similar sites for gradient studies, and the PCA analysis of environmental variables shows that there is heterogeneity in structure especially within the mature habitat. Mature forests are complex and consist of forest gaps, small rivers and a general heterogeneous mix of microhabitats. The agricultural habitats were only represented by two habitats from the coffee and mixed small scale garden and a single habitat from cardamom

plantation. More sites per habitat would have given a stronger argument for the habitats conservation value.

Canopy openness was the only variable to significantly explain the distribution of butterfly species in this study. This variable is the strongest predictor in most studies that include the effects of environmental variables (Barlow *et al.*, 2007b; Hilt *et al.*, 2006). Dolia (2008) registered a negative effect of canopy cover on species richness and abundance, which could coincide with the highest species richness being found in the mixed garden in this study.

Comparing results from different gradient studies can be difficult because of the "gestalt" division of habitats. Mas and Dietsch (2003) introduced a management index, including a given value for several environmental variables and culminating with an index reflecting management intensity. They stress that the index can be used instead of the qualitative division of the sites and habitats, and that it could be used as a certification criterion for conservational benefit. Species richness of their measured taxa declined with increasing index value. Given that it is difficult to compare studies with variations within the structure of the habitat, this could be an interesting way for the easier implementation of proper management plans. The variables included ought to be highly evaluated and occasionally followed up by biodiversity studies. The reaction of biodiversity to modification can be very different depending on area and the taxa and species most threatened

While this study only considers frugivorous butterflies, other butterfly guilds like the nectarivorous butterflies might show a different response to habitat modification. Harvey *et al.* (2006) found that only the fruit-feeding butterfly guild showed significantly higher richness and abundance in forest fallows and secondary forests compared to more open habitats. The availability of fruit will be less in modified habitats if the fruit trees are removed, although in the modified habitats of mixed small-scale gardens the trees retained were often fruit trees. Barlow *et al.* (2007b) included amount of fruit fall as an explanatory variable in their analysis, but it did not show any relation to abundance or species richness. It would have been interesting to see if it had an effect on distribution of species composition.

Two possibly new species to Mabira Forest Reserve were recorded, while three new forest edge species were recorded from its surroundings. Of these, one new restricted-range forest edge

species was recorded in a mixed small scale garden in Buvunja on the south-east forest boundary (*P.boisduvali*).

Inspecting the vertical stratification, 12% of the species[7] was found only in canopy traps (Appendix III), whereas 30% of the species was found only in the understorey traps. A long-term temporal and vertical butterfly study by Molleman *et al.* (2006) characterized about 14% of the species as canopy species and 68% of the species as understorey specialists. Butterflies are designated as specialized canopy species when only captured in the canopy, but there is a high uncertainty for those with low abundance, especially those that are only registered once. The number of species restricted to the understorey would be highly affected by the trap height in the garden sites. It would be interesting to look at the difference in stratification between the sites, excluding the mixed gardens. Disturbance is found to disrupt the vertical stratification of butterflies, with canopy species coming to the ground in forest openings (DeVries, 1988). When the canopy and understorey data were rarefied separately, there was no significant difference in species richness. This could mean a relatively high richness in the canopy, also registered in other studies, or a highly similar species pool being sampled due to the trap height and exchange of species. Although Fermon *et al.* (2005) found a significant difference between an understorey assemblage and one at 15m, practical problems in hanging canopy traps has led to the sampling of species composition at a mid-storey level compared to canopy level in other studies (Molleman *et al.*, 2006).

[7] Including morpho-species and species identified to genus

Implications for conservation

The indicated value of cardamom plantation reflects that canopy openness was the main structural variable in this study. Butterflies are sensitive to changes in microclimate, which is an indirect effect of the removal of canopy cover. Since forest species of other taxa may also be dependent on canopy cover (Naidoo, 2004), this study encourages wildlife friendly farming in the surroundings and within forest enclaves. This would increase the persistence of forest species, creating a buffer zone, and aiding dispersal abilities over areas with agricultural habitats. Since some parts of Mabira Forest Reserve are relatively narrow, it is highly affected by edge effects (Ries and Sisk, 2008). When forest patches have a large circumference, the effective forest area exposed of minor influence from the surrounding disturbance decreases. The cardamom plantation sampled in this study is a very good example of agroforestry conserving forest biodiversity, even though it lacks rare species.

There is a wide support from reports in Uganda for increasing the level of shade on gardens and plantations for biodiversity conservation (Boffa *et al.*, 2005). However, only a number of crops can grow sufficiently well under increased shade cover. These crop types could be encouraged around and within the forest. There is still a question if one can obtain the same yield with a higher level of shade. A study by Steffan-Dewenter *et al.* (2007) investigated the trade-offs between income and biodiversity and ecosystem functioning, concluding that low-shade agroforestry is the best compromise for both parts.

.

5. Conclusions

This study agrees with Bhagwat *et al.* (2008) that some types of agroforestry can be valuable for conservation, though stressing the importance of investigating the similarity in composition and distribution of forest species in the land-use gradient. The indication of reduced endemics in disturbed and modified habitats is in agreement with previous studies. The study also supports the findings that canopy openness is the main predictor for fruit feeding butterfly biodiversity in a gradient from forest to different land-use types. More studies should have been done on the trade-offs between percentage of shade cover, biodiversity and crop yield.

6. References

Akite, P. (2006) Butterflies and Dragon flies. (eds R. Kityo & D. Pomeroy). *Biodiversity of key sections of the proposed new Bujagali to Kampala Transmission line with special reference to Mabira, Kifu and Namyoya Central forest reserves and the Lubigi swamp*. Makerere university, Kampala.

Baranga, D. (2007) Observations on resource use in Mabira Forest Reserve, Uganda. *African Journal of Ecology,* **45,** 2-6.

Barlow, J.O.S., Overal, W.L., Araujo, I.S., Gardner, T.A. & Peres, C.A. (2007b) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology* **44,** 1001-1012.

Bhagwat, S.A., Willis, K.J., Birks, H.J.B. & Whittaker, R.J. (2008) Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology & Evolution,* **23,** 261-267.

Bobo, K.S. (2006) From forest to farmland: butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. *Journal of Insect Conservation* **10,** 29-42.

Boffa, J.-M., Turyomurugyendo, L., Barnekow-Lilles, J.-P. & Kindt, R. (2005) Enhancing Farm Tree Diversity as a Means of ConservingLandscape-based Biodiversity. *Mountain Research and Development,* **25,** 212-217.

Bwanika, J. (1995) *Species diversity and distribution of butterflies in Mabira forest reserve*. MSc Thesis, Makerere University, Kampala.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters,* **8,** 148-159.

Chazdon, R.L., Harvey, C.A., Komar, O., Griffith, D.M., Ferguson, B.G., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Breugel, M.V. & Philpott, S., M (2009) Beyond Reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica,* **41,** 142-153.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18,** 117-43.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions: Biological Sciences,* **345,** 101-118.

Davenport, T., Howard, P.C. & Baltzer, M. (1996) Biodiversity Report; Mabira Forest Reserve. Forest Department, Kampala,Uganda.

Davenport, T.R.B. (1993) The Butterflies of Uganda - An Annotated Checklist. Uganda Forest Department,Kampala, Uganda.

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

DeVries, P.J. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society,* **62,** 343-364.

Dolia, J. (2008) Adult butterfly communities in coffee plantations around a protected area in the Western Ghats, India. *ANIMAL CONSERVATION,* **11,** 26-34.

FAO (2005) Global Forest Resources Assessment 2005, 15 Key findings.

FAO (2006) Special report; FAO/GIEWS review of Crop and Food Situation in Uganda. *FAO Global Information and early warning system on Food and Agriculture. World Food Programme* (ed S. Ahmed).

Fermon, H., Waltert, M., Vane-Wright, R.I. & Mühlenberg, M. (2005) Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodiversity and Conservation,* **14,** 333-350.

FOSA (2001) UGANDA. *Forestry outlook studies in Africa*, pp. 32.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters,* **4,** 379-391.

Government of Uganda (2005) Uganda National Census Report,2005. Uganda Bureau of Statistics, Entebbe.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005) Farming and the Fate of Wild Nature. *Science,* **307,** 550-555.

Hamer, K.C. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology,* **40,** 150-162.

Harvey, C.A., Medina, A., Sànchez, D.M., Vilchez, S., Hernàndez, B., Saenz, J.C., Maes, J.M., Casanoves, F. & Sinclair, F.L. (2006) Patterns of Animal Diversity in Different Forms of Tree Cover in Agricultural Landscapes. *Ecological Applications,* **16,** 1986-1999.

Hilt, N., Brehm, G. & Fiedler, K. (2006) Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes. *Journal of Tropical Ecology,* **22,** 155-166.

HOBOwarePro (2002-2008) Software for HOBO Data Loggers & Devices. Onset Computer Corporation.

Howard, P.C. (1991) Nature conservation in Uganda's tropical reserves. IUCN. Gland,Switzerland.

Howard, P.C. (2000) Protected area planning in the tropics: Uganda's national system of forest nature reserves. *Conservation Biology,* **14,** 858-875.

Hulbert, K.L. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology,* **52,** 577-586.

INRA-CSE (2004) Can_Eye-processing digital photographs for canopy structure characterization. Baret,F.

Jones, D.T., Susilo, F.X., Bignell, D.E., Hardiwinoto, S., Gillison, A.N. & Eggleton, P. (2003) Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *Journal of Applied Ecology,* **40,** 380-391.

Kielland, J. (1990) *Butterflies of Tanzania.* Hill House Melbourne.

Koh, L.P. (2007) Impacts of land use change on South-east Asian forest butterflies: a review. *Journal of Applied Ecology,* **44,** 703-713.

Koh, L.P. (2008) Can oil palm plantations be made more hospitable for forest butterflies and birds? *Journal of Applied Ecology* **45,** 1002-1009.

Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography,* **15,** 8-20.

Larsen, T.L. (1996) *Butterflies of Kenya and Their Natural History.* Oxford University Press.

Larsen, T.L. (2005) *Butterflies of West Africa.* Apollo books.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watt, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature,* **391,** 72-76.

Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologica,* **129,** 271-280.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology.* Elsevier.

Lepš, J. & Šmilauer, P. (2003) *Multivariate Analysis of Ecological Data using CANOCO.* Cambridge.

Lewis, O.T. (2001) Effect of experimental selective logging on tropical butterflies. *Conservation Biology,* **15,** 389-400.

Magurran, A.E. (2004) *Measuring Biological Diversity* Blackwell.

Markus Loecher and Sense Networks (2009) RgoogleMaps: Overlays on Google map tiles in R. R package version 1.1.6 http://CRAN.R-project.org/package=RgoogleMaps.

Mas, A.H. & Dietsch, T.V. (2003) An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. *Ecological Applications,* **13,** 1491-1501.

MEA (2005) Ecosystem and Human Well-being; Biodiversity Synthesis. *Millennium Ecosystem Assessment*. World Resources Institute, Washington, DC.

MFMP (2008) Mabira Forest Management Plan (Draft).

Mohan, S., Ramachandran Nair, P.K. & Long, A.J. (2007) An Assessment of Ecological Diversity in Homegardens: A Case Study from Kerla State,India. *Journal of Sustainable Agriculture,* **29,** 135-153.

Molleman, F., Kop, A., Brakefield, P.M., DeVries, P.J. & Zwaan, B.J. (2006) Vertical and temporal patterns of biodiversity of fruitfeeding butterflies in a tropical forest in Uganda. *Biodiversity and Conservation,* **15,** 107-121.

Montgomery, R.A. & Chazdon, R.L. (2001) Forest Structure, Canopy Architecture, and Light Transmittance in Tropical Wet Forests. *Ecology,* **82,** 2707-2718.

Motulsky, H. (1995) *Intuitive Biostatistics.* Oxford University Press.

Naidoo, R. (2004) Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Animal Conservation,* **7,** 93-105.

Perfecto, I., Mas, A., Dietsch, T. & Vandermeer, J. (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. *Biodiversity and Conservation,* **12,** 1239-1252.

Pinheiro, C.E.G. & Ortiz, J.V. (1992) Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography,* **19,** 505-511.

Posa, M.R.C. & Sodhi, N.S. (2006) Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines. *Biological Conservation,* **129,** 256-270.

R Development Core Team (2009) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing.

Rice, R.A. & Greenberg, R. (2000) Cacao Cultivation and the Conservation of Biological Diversity. *Ambio,* **29,** 167-173.

Ries, L. & Sisk, T. (2008) Butterfly edge effects are predicted by a simple model in a complex landscape. *Oecologia,* **156,** 75-86.

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

Sayer, J.A., Hartcourt, C. & Collins, N.M. (1992) The Conservation Atlas of Tropical Forests: Africa. New York.

Scales, B.R. & Marsden, S.J. (2008) Biodiversity in small-scale tropical agroforests: a review of species richness and abundance shifts and the factors influencing them. *Environmental Conservation,* **35,** 160-172.

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

Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M.M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S.R., Guhardja, E., Harteveld, M., Hertel, D., Höhn, P., Kappas, M., Köhler, S., Leuschner, C., Maertens, M., Marggraf, R., Migge-Kleian, S., Mogea, J., Pitopang, R., Schaefer, M., Schwarze, S., Sporn, S.G., Steingrebe, A., Tjitrosoedirdjo, S.S., Tjitrosoemito, S., Twele, A., Weber, R., Woltmann, L., Zeller, M. & Tscharntke, T. (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences,* **104,** 4973-4978.

Tangah, J., Hill, J.K., Hamer, K.C. & Dawood, M.M. (2004) Vertical distribution of fruite-feeding butterflies in Sabah, Borneo. *Sepilok Bulletin,* **1,** 17-27.

Uehara-Prado, M., Brown, J., Keith Spalding & Freitas, A.V.L. (2007) Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. *Global Ecology and Biogeography,* **16,** 43-54.

USAID (2007) Uganda Biodiversity and Tropical Forest Assessment. United States Agency international development.

Vu, L.V & Yuan, D. (2003) The differences of butterfly (Lepidoptera, Papilionoidea) communities in habitats with various degrees of disturbance and altitudes in tropical forests of Vietnam. *Biodiversity and Conservation,* **12,** 1099-1111.

Vu, L.V. (2009) Diversity and similarity of butterfly communities in five different habitat types at Tam Dao National Park, Vietnam. *Journal of Zoology,* **277,** 15-22.

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

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

Zar, J.H. (1984) *Biostatistical Analysis.* 2nd ed.Prentice Hall, New Jersey.

Appendix I

Table A *Species list of recordings from Mabira forest and surroundings in this study including ecotype and total and site abundance.*

Species	Ecotype	Total abundance	Ma1	Ma2	Ma3	Ma4	Se1	Se2	Se3	Ca	Co1	Co2	Mg1	Mg2
LYCANIDAE														
Riodininae														
Abisara neavei	F	3	0	0	0	0	0	0	3	0	0	0	0	0
NYMPHALIDE														
Satyrinae														
Bicyclus auricrudus	F	82	0	0	2	1	0	1	0	77	0	1	0	0
Bicyclus buea	F	81	0	0	0	1	2	0	0	78	0	0	0	0
Bicyclus campinus	f.	10	0	0	0	2	0	0	8	0	0	0	0	0
Bicyclus ena	O	1	0	0	0	0	0	0	0	0	0	0	1	0
Bicyclus funebris	F	33	0	1	1	1	0	2	1	24	0	0	3	0
Bicyclus golo	F	240	0	0	1	0	0	0	1	238	0	0	0	0
Bicyclus graueri	F	45	1	16	8	4	0	0	15	1	0	0	0	0
Bicyclus jefferyi	f.	26	0	0	0	0	1	0	0	0	0	21	1	3
Bicyclus mandanes	F	13	0	2	8	1	1	0	1	0	0	0	0	0
Bicyclus mesogena	F	9	0	3	2	3	0	0	1	0	0	0	0	0
Bicyclus mollitia	F	619	27	288	169	116	3	16	0	0	0	0	0	0
Bicyclus safitza	W	13	0	0	0	0	0	0	0	0	0	2	1	10
Bicyclus sambulos	F	46	4	8	5	10	2	8	3	6	0	0	0	0
Bicyclus sandace	F	23	1	0	0	1	2	0	14	1	0	1	0	3
Bicyclus sebetus	F	7	0	7	0	0	0	0	0	0	0	0	0	0
Bicyclus smithi	F	446	2	27	11	32	16	4	21	333	0	0	0	0
Bicyclus sophrosyne	f.	104	0	0	1	0	2	1	1	99	0	0	0	0
Bicyclus uniformis	U	649	52	304	191	75	4	11	3	9	0	0	0	0
Bicyclus vulgaris	W	89	0	0	0	0	3	0	2	15	2	52	6	9
Bicyclus.sp	u.	36	6	3	2	0	2	0	6	12	1	1	1	2
Elymnias bammakoo	F	1	1	0	0	0	0	0	0	0	0	0	0	0
Gnophodes betsimena	F	76	0	0	13	4	2	1	6	3	6	27	10	4
Gnophodes chelys	F	47	20	1	13	2	4	5	2	0	0	0	0	0
Gnophodes.sp	u.	2	0	0	0	0	0	0	1	1	0	0	0	0
Henotesia peitho	W	228	5	91	67	36	1	24	3	1	0	0	0	0
Melanitis leda	W	65	0	2	2	2	1	0	1	2	7	38	2	8
Charaxinae														
Charaxes anticlea	f.	6	0	5	0	0	0	0	0	0	0	0	0	1
Charaxes bipunctatus	F	71	4	10	3	10	2	9	2	1	15	4	6	5
Charaxes brutus	f.	29	0	1	0	1	0	1	0	0	1	21	0	4
Charaxes candiope	W	24	0	1	0	1	1	0	1	2	11	1	1	5
Charaxes castor	W	24	0	0	0	0	0	0	0	0	10	8	2	4
Charaxes cynthia	F	177	20	7	36	20	0	56	1	36	1	0	0	0

Charaxes etesipe	f.	6	0	0	0	0	0	0	0	0	1	4	1	0
Charaxes eupale	F	12	0	0	0	0	0	0	0	0	1	11	0	0
Charaxes fulvescens	F	53	2	2	14	8	9	10	6	2	0	0	0	0
Charaxes lucretius	F	6	0	0	0	0	0	0	0	0	2	4	0	0
Charaxes numenes	f.	14	1	2	2	3	1	3	0	1	1	0	0	0
Charaxes paphianus	F	2	0	0	0	0	1	0	1	0	0	0	0	0
Charaxes pleione	f.	2	0	0	0	0	0	1	0	0	0	0	1	0
Charaxes pollux	f.	2	0	0	0	0	0	0	0	0	0	2	0	0
Charaxes porthos	F	1	0	1	0	0	0	0	0	0	0	0	0	0
Charaxes protoclea	f.	2	0	0	1	0	0	0	0	0	1	0	0	0
Charaxes pythodoris	f.	1	0	0	0	0	0	1	0	0	0	0	0	0
Charaxes tiridates	F	97	3	6	8	12	1	21	2	7	17	7	0	13
Charaxes varanes	W	30	0	0	0	0	0	0	0	0	0	11	4	15
Charaxes zelica	F	1	0	0	0	0	0	0	0	0	1	0	0	0
Charaxes zingha	F	2	1	0	0	1	0	0	0	0	0	0	0	0
Charaxes.sp	u.	22	1	1	4	1	3	4	0	2	5	0	0	1
Charaxes "black 1"	u.	2	0	0	0	0	0	0	0	0	1	1	0	0
Charaxes "black 1f"	u.	21	0	0	0	0	0	0	0	0	4	16	0	1
Charaxes "black 2"	u.	2	0	0	0	0	0	0	0	0	1	0	0	1
Charaxes "black 2f"	u.	5	0	0	0	0	0	0	1	0	2	0	1	1
Charaxes "black 3"	u.	39	0	0	0	0	0	0	0	0	9	27	1	2
Charaxes "black 3f"	u.	5	0	0	0	0	0	0	1	0	3	0	0	1
Charaxes "black 4"	u.	14	0	0	1	0	0	0	0	0	8	0	2	3
Charaxes "black 4f"	u.	1	0	0	0	0	0	0	0	0	1	0	0	0
Palla ussheri	F	4	0	0	3	0	0	1	0	0	0	0	0	0
Euxanthe crossleyi	F	3	0	1	0	1	0	0	0	1	0	0	0	0
Euxanthe eurinome	F	1	0	0	0	0	0	0	0	0	0	1	0	0
Euxanthe.sp	u.	2	0	0	0	2	0	0	0	0	0	0	0	0
Apaturinae														
Apaturopsis cleochares	F	24	0	3	2	4	1	5	1	3	2	0	1	2
Nymphalinae														
Antanartia delius	F	7	0	0	0	0	0	0	0	0	7	0	0	0
Ariadne albifascia	F	5	0	0	0	0	0	0	0	0	0	0	0	5
Ariadne enotrea	F	20	0	1	0	0	0	0	5	4	3	0	0	7
Aterica galene	F	1	0	0	1	0	0	0	0	0	0	0	0	0
Bebaeria.sp	u.	2	0	0	1	0	0	0	1	0	0	0	0	0
Bebearia cocalia	f.	5	0	0	2	0	2	0	0	0	1	0	0	0
Byblia anvatara	M	24	0	0	0	0	0	0	0	0	1	1	12	10
Byblia ilithya	O	3	0	0	0	0	0	0	0	0	0	0	2	1
Catuna crithea	F	2	0	1	1	0	0	0	0	0	0	0	0	0
Cymothoe caenis	F	2	0	2	0	0	0	0	0	0	0	0	0	0
Cymothoe herminia	F	148	3	51	27	58	2	0	6	1	0	0	0	0
Euphaedra eleus	F	6	0	0	6	0	0	0	0	0	0	0	0	0
Euphaedra medon	F	8	1	4	1	0	0	0	1	1	0	0	0	0

Euphaedra preussi	F	104	15	46	23	4	1	14	1	0	0	0	0	0
Euphaedra rex	F	16	0	1	5	4	1	5	0	0	0	0	0	0
Euphaedra uganda	F	1	0	0	0	0	0	1	0	0	0	0	0	0
Euphaedra.sp	u.	12	4	1	1	0	4	2	0	0	0	0	0	0
Euptera.sp	u.	2	0	0	1	0	0	0	1	0	0	0	0	0
Eurytela dryope	W	19	0	0	1	0	0	0	0	2	0	8	1	7
Eurytela hiarbas	f.	25	0	2	1	2	1	0	0	10	3	1	1	4
Harma theobene	F	98	8	28	24	5	9	15	8	0	1	0	0	0
Hypolimnas anthedon	F	6	0	1	0	0	0	0	0	0	4	0	1	0
Hypolimnas dinarcha	F	5	0	0	0	0	0	0	5	0	0	0	0	0
Hypolimnas monteironis	F	3	0	1	0	1	0	1	0	0	0	0	0	0
Hypolimnas salmacis	F	8	0	1	6	0	0	0	1	0	0	0	0	0
Junonia chorimene	O	3	0	0	0	0	0	0	0	0	0	1	1	1
Junonia stygia	f.	9	0	0	0	0	0	0	6	2	0	0	1	0
Junonia terea	W	3	0	0	0	0	0	0	0	1	1	0	1	0
Junonia westermanni	F	4	0	0	0	0	0	0	1	0	3	0	0	0
Lachnoptera anticlia	f.	4	4	0	0	0	0	0	0	0	0	0	0	0
Mesoxantha ethosea	F	1	0	0	0	1	0	0	0	0	0	0	0	0
Neptidopsis ophione	f.	10	0	0	0	0	0	0	1	3	1	1	1	3
Neptis conspicua	F	1	0	0	0	0	0	0	1	0	0	0	0	0
Neptis melicerta	F	16	0	0	2	1	0	1	12	0	0	0	0	0
Neptis metella	f.	23	0	0	3	0	2	0	17	0	0	0	1	0
Neptis nemetes	f.	8	0	0	0	0	2	2	3	0	0	0	1	0
Neptis nicomedes	f.	35	2	1	2	0	3	0	25	1	0	0	1	0
Neptis saclava	W	4	0	0	0	0	0	0	1	0	0	1	0	2
Neptis serena	W	1	0	0	0	0	0	0	0	0	0	0	0	1
Neptis.sp	u.	2	0	0	0	0	0	0	2	0	0	0	0	0
Phalanta eurytis	M	2	0	0	0	0	0	0	0	0	2	0	0	0
Precis octavia	W	1	0	0	0	0	0	0	0	0	0	0	1	0
Pseudacraea boisduvali	f.	1	0	0	0	0	0	0	0	0	0	0	0	1
Pseudacraea eurytus	F	2	0	1	0	1	0	0	0	0	0	0	0	0
Pseudacraea lucretia	f.	4	0	1	0	0	1	0	2	0	0	0	0	0
Pseudacraea.sp	u.	3	2	0	0	1	0	0	0	0	0	0	0	0
Salamis parhassus	f.	1	0	0	0	0	0	0	0	0	0	0	1	0
Sallya boisduvali	M	37	0	0	1	0	1	0	0	0	4	27	1	3
Sallya garega	M	108	0	1	0	0	0	0	0	0	16	82	3	6
Sallya occidentalium	M	36	0	0	0	0	1	0	3	0	6	23	1	2
Sallya.sp	M	1	0	0	0	0	1	0	0	0	0	0	0	0
Euryphura.sp	u.	1	0	0	0	0	0	0	1	0	0	0	0	0
Acraeinae														
Acraea aurivilli	F	1	0	0	1	0	0	0	0	0	0	0	0	0
Acraea jodutta	F	1	0	0	0	0	0	0	1	0	0	0	0	0
Acraea lycoa	F	1	0	0	0	0	0	0	1	0	0	0	0	0
Acraea penelope	F	5	0	0	3	0	0	0	0	1	0	0	0	1
Acraea semivitrea	F	1	0	0	0	0	0	0	0	0	1	0	0	0

Acraea servona	F	2	0	0	1	1	0	0	0	0	0	0	0	0
Acraea.sp	u.	2	0	0	0	0	1	1	0	0	0	0	0	0
Libytheinae														
Libythea labdaca	M	9	0	0	1	0	0	1	1	0	4	0	0	2
Unknown														
Species A	u.	4	0	0	0	0	4	0	0	0	0	0	0	0
Species B	u.	1	0	0	0	0	1	0	0	0	0	0	0	0
Species C	u.	1	0	0	0	1	0	0	0	0	0	0	0	0

Appendix II

Table B *The location shown in decimal degrees of all the trap stations per site, recorded with GPS in the field. (Four decimals give an accuracy of 11.1m which all recordings were within).*

Trap number	N	E	Trap number	N	E
1.1	0.4047	33.0316	**7.1**	0.4195	33.0019
1.2	0.4050	33.0315	**7.2**	0.4192	33.0023
1.3	0.4052	33.0316	**7.3**	0.4190	33.0028
1.4	0.4059	33.0315	**7.4**	0.4188	33.0031
1.5	0.4063	33.0318	**7.5**	0.4185	33.0035
1.6	0.4068	33.0317	**7.6**	0.4184	33.0040
1.7	0.4072	33.0317	**7.7**	0.4181	33.0043
1.8	0.4076	33.0317	**7.8**	0.4181	33.0049
1.9	0.4080	33.0317	**7.9**	0.4181	33.0053
1.10	0.4084	33.0316	**7.10**	0.4179	33.0058
2.1	0.4180	33.1040	**8.1**	0.4879	33.0628
2.2	0.4183	33.1035	**8.2**	0.4880	33.0633
2.3	0.4184	33.1029	**8.3**	0.4879	33.0638
2.4	0.4188	33.1024	**8.4**	0.4878	33.0643
2.5	0.4193	33.1021	**8.5**	0.4876	33.0647
2.6	0.4197	33.1016	**8.6**	0.4878	33.0652
2.7	0.4201	33.1012	**8.7**	0.4885	33.0654
2.8	0.4204	33.1006	**8.8**	0.4890	33.0654
2.9	0.4208	33.0998	**8.9**	0.4892	33.0649
2.10	0.4211	33.0992	**8.10**	0.4898	33.0648
3.1	0.4435	33.0253	**9.1**	0.4861	32.9169
3.2	0.4440	33.0254	**9.2**	0.4862	32.9169
3.3	0.4444	33.0254	**9.3**	0.4869	32.9165
3.4	0.4449	33.0254	**9.4**	0.4871	32.9170
3.5	0.4454	33.0253	**9.5**	0.4874	32.9173
3.6	0.4458	33.0254	**9.6**	0.4881	32.9174
3.7	0.4463	33.0254	**9.7**	0.4885	32.9174
3.8	0.4467	33.0252	**9.8**	0.4889	32.9177
3.9	0.4471	33.0253	**9.9**	0.4894	32.9175
3.10	0.4475	33.0251	**9.10**	0.4900	32.9176
4.1	0.4259	33.0407	**10.1**	0.4001	33.0760
4.2	0.4255	33.0409	**10.2**	0.4006	33.0759
4.3	0.4250	33.0411	**10.3**	0.4011	33.0760
4.4	0.4245	33.0414	**10.4**	0.4016	33.0761
4.5	0.4241	33.0416	**10.5**	0.4021	33.0761
4.6	0.4236	33.0419	**10.6**	0.4025	33.0759
4.7	0.4232	33.0422	**10.7**	0.4030	33.0762
4.8	0.4228	33.0426	**10.8**	0.4032	33.0767

4.9	0.4226	33.0431	**10.9**	0.4037	33.0770
4.10	0.4225	33.0437	**10.10**	0.4040	33.0774
5.1	0.4110	33.0665	**11.1**	0.3906	33.0156
5.2	0.4115	33.0665	**11.2**	0.3906	33.0160
5.3	0.4119	33.0666	**11.3**	0.3904	33.0165
5.4	0.4123	33.0666	**11.4**	0.3906	33.0171
5.5	0.4128	33.0666	**11.5**	0.3911	33.0173
5.6	0.4132	33.0666	**11.6**	0.3909	33.0179
5.7	0.4137	33.0666	**11.7**	0.3908	33.0184
5.8	0.4141	33.0666	**11.8**	0.3907	33.0189
5.9	0.4146	33.0666	**11.9**	0.3903	33.0196
5.10	0.4150	33.0666	**11.10**	0.3899	33.0198
6.1	0.4473	32.9854	**12.1**	0.3760	32.9709
6.2	0.4476	32.9851	**12.2**	0.3755	32.9707
6.3	0.4479	32.9848	**12.3**	0.3752	32.9705
6.4	0.4482	32.9845	**12.4**	0.3752	32.9700
6.5	0.4485	32.9842	**12.5**	0.3749	32.9698
6.6	0.4489	32.9839	**12.6**	0.3751	32.9694
6.7	0.4491	32.9836	**12.7**	0.3754	32.9677
6.8	0.4490	32.9831	**12.8**	0.3759	32.9690
6.9	0.4489	32.9827	**12.9**	0.3764	32.9689
6.10	0.4488	32.9823	**12.10**	0.3762	32.9694

Appendix III

Table C *Species only registered in the canopy during the study in Mabira forest.*Restricted-range species. **Species restricted to the canopy in a butterfly study in Kibale, Uganda, Molleman (2006).*

Species	Abundance	Ecotype	Present at sites;
Acraea lycoa	1	F	Se3
Charaxes paphianus	2	F	Se1,Se3
Charaxes porthos /**	1	F	Ma2
Charaxes zingha	2	F	Ma1,Ma4
Elymnias bammakoo	1	F	Ma1
Euxanthe eurinome	1	F	Co2
Mesoxantha ethosea	1	F	Ma4
Neptis conspicua	1	F	Se3
*Pseudacraea boisduvali**	1	f.	Mg2
Pseudacraea eurytus	2	F	Ma2,Ma4
Euptera.sp	2	u.	Ma3,Se3
Euryphura.sp	1	u.	Se3
Euxanthe.sp	2	u.	Ma4
Pseudacraea.sp	3	u.	Ma1,Ma4
Charaxes "black 1"	2	u.	Co1-2

Appendix IV

Table D *Species found in this study and not found under following known studies; Davenport's survey in 1993-1995(Davenport et al., 1996), Bwanika MCs thesis (Bwanika, 1995) and other surveys (Akite, 2006). The species found in the surrounding area is included, whereas some are forest edge species.*

Species	Abundance	Ecotype	Present at sites;
Found in forest sites (Ma+Se)			
Bicyclus buea	81	F	Ca,Se1,Ma4
Bicyclus campinus	10	f.	Se3,Ma4
Found in disturbed area			
Bicyclus ena	1	O	Mg1
Byblia ilithya	3	O	Mg1-2
Charaxes pollux	2	f.	Co2
Lachnoptera anticlia	4	f.	Ma1
Pseudacraea boisduvali	1	f.	Mg2