

**KWAME NKRUMAH UNIVERSITY OF SCIENCE AND TECHNOLOGY
COLLEGE OF AGRICULTURE AND NATURAL RESOURCES
FACULTY OF RENEWABLE NATURAL RESOURCES
DEPARTMENT OF WILDLIFE AND RANGE MANAGEMENT**

**APPLIED AND THEORETICAL PERSPECTIVES ON THE COMMUNITY
DYNAMICS OF FRUIT-FEEDING BUTTERFLIES**

By

KWAKU ADUSE-POKU BSc. NRM (Hons), MSc. Ecology & Evolution

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DECLARATION

I hereby declare that this submission is my own work towards the PhD and that, to the best of my knowledge, it contains no material previously published by another person nor material which has been accepted for the award of any other degree of the University, except where due acknowledgement has been made in the text.

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Student's Name & ID Signature Date

Certified by:

.....
Supervisor's Name Signature Date

Certified by:

.....
Head of Dept. Name Signature Date

ABSTRACT

In this thesis, fruit-feeding butterflies (nymphalids) are used as a 'study system' for two broad aims: First, to develop an efficient and reliable rapid biodiversity assessment (RBA) protocol for monitoring Ghanaian forests (applied perspective) and second, to empirically evaluate neutral theory in mobile organisms (theoretical perspective). To achieve these two broad study aims, four individual studies, each with specific research questions and objectives were proposed for detailed investigation. The studies were conducted mainly in two protected forests in Ghana; Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB) between August 2006 and November 2007 using transects and fruit-baited butterfly traps. The first study examined two potential biases (due to temporal variation and vertical stratification) associated with RBA in Ghanaian forests. Both individual numbers and species richness were on average three to four times higher in the understorey than in canopy traps with strikingly different species composition (only 10% overlap in species between the two communities). Considerable temporal variation was observed in species richness and individual abundance at both the canopy and understorey levels. The study justified the importance of taking into account the effects of temporal and vertical stratification when using fruit-feeding butterflies as the model system for RBAs in Ghanaian forests. The second study evaluated the efficiencies of two different bait- and trap-types. It also assessed how the age of bait influences RBA results. The new trap type (with reduced entry/exit) performed at least three times better than the conventional vanSomeren-Rydon trap, in terms of the number of individuals and species trapped per trap-day. Using the same scale of measure, the novel bait type (banana bait mixed with palmwine) was found to be more productive and hence, more efficient compared to the old bait which consisted of only mashed banana fruit. The study revealed that age of bait does affect both the number and kind of butterflies trapped. the results of the study

suggest that, to make RBA more efficient, butterfly sampling need not exceed two days (if palmwine is mixed with mashed banana and allowed to ferment for 24 hours) or three days (when only mashed banana fermented for 24 hours is used as bait) on the same location. The third study sought to identify which fruit-feeding butterfly species-groups could be effectively used to monitor habitat changes in Ghanaian forests. The study identified the genera *Euriphene*, *Bebearia*, *Aterica*, *Gnophodes*, *Melanitis* and *Euphaedra* as potential indicator taxa of good conditioned forest habitats. The small bodied-sized *Bicyclus* (mostly of the *dorothea* species-groups) were identified as effective indicator taxa of disturbed habitats. Both relative abundances and diversities of these potential identified indicator taxa could be used as metric for evaluating habitat quality or human-induced disturbance. Overall, the first three studies of the thesis indicated high prospects in the use of fruit-feeding butterflies as a model system for monitoring forests in Ghana. Based exclusively on the findings of the first three studies of this thesis, two kinds of RBA frameworks were proposed for monitoring forests in Ghana: i) 'species and taxonomic surrogacy' and ii) 'All species' approach. The choice of either approach largely depends on the availability of butterfly taxonomists and the intent of the mission. The fourth study (the theoretical perspective of the thesis) evaluated the relative contribution of neutral processes in shaping the butterfly assemblages, using both direct (confronting the neutral model to species abundance data) and indirect approaches (testing the predictions of neutral theory against independent data). The results indicated that nymphalid assemblages are structured largely by species' (habitat) preference. However, neutral theory's contribution to explaining the observed fruit-feeding butterfly assemblages in three forests in Africa lies largely in identifying dispersal limitation, as a key process regulating fruit-feeding butterfly community structure patterns.

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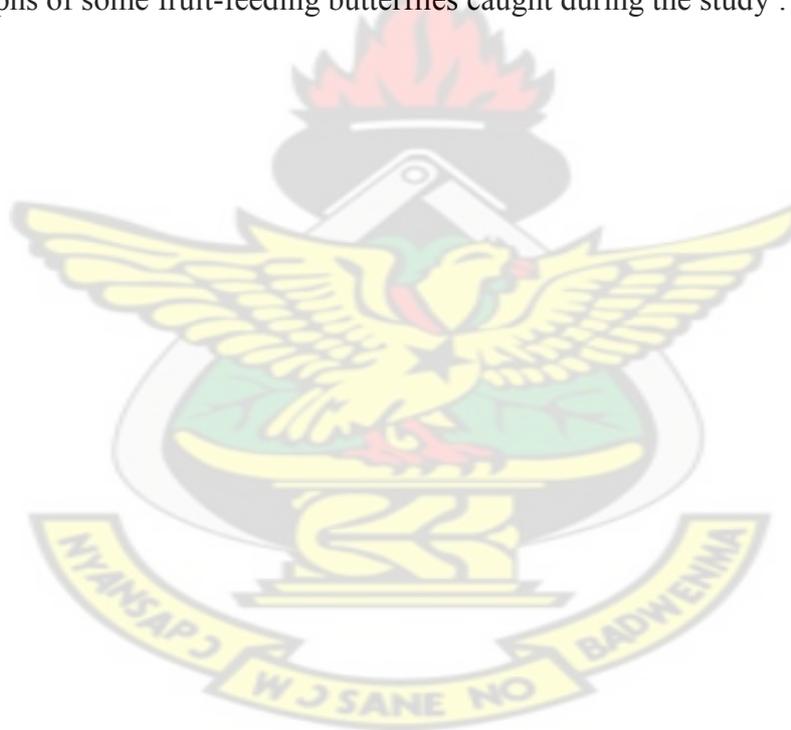
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CHAPTER ONE

1.0 INTRODUCTION

1.1 Background of the Thesis

The focus of butterfly research is currently taking a paradigm shift. The interest and popularity of the research is largely drifting away from orthodox practice of describing species and their habitats and/or habits (e.g. Ehrlich 1958; Van Someren 1963; Ehrlich & Ehrlich 1967; Smiles 1982), to a more pragmatic approach of using butterfly groups as 'study systems' for answering practical ecological problems or questions (e.g. Hanski 1994; Brakefield *et al.* 1996; Lawton *et al.* 1998; Koch *et al.* 2000; Keller & Waller 2002; McLaughlin *et al.* 2002; Parmesan & Yohe 2003; Dennis *et al.* 2004; Thomas 2005; Willis *et al.* 2009; Speed & Ruxton 2010).

Butterflies have so far been great in this new research direction for many reasons. Butterflies are arguably the best known, studied and loved group of invertebrates (New *et al.* 1995; Larsen 2005b; Bonebrake *et al.* 2010). They have been a source of inspiration for many historians and amateur collectors. As a result, valuable ecological information such as habitat preference, habits, host plants and geographical distribution are readily available for most species and species-groups. The proliferation of phylogenetics following the advancement of molecular markers in the last couple of decades has also made available key evolutionary information such as phylogeny (relatedness of species and species-groups), historical biogeography and times of divergences of most butterfly species and species-groups (Pena & Wahlberg 2008; Aduse-Poku *et al.* 2009; Kodandaramaiah & Wahlberg 2009; Wahlberg *et al.* 2009).

Using these arsenal of information, butterflies have been used as 'study systems' in answering some of the most intriguing questions in evolutionary development (e.g. Brakefield *et al.* 1996; Saenko *et al.* 2008), mimicry (e.g. Müller 1879; Koch *et al.* 2000; Speed & Ruxton 2010), biogeography (e.g. Aduse-Poku *et al.* 2009; Kodandaramaiah & Wahlberg 2009; Garcia-Barros & Benito 2010), inbreeding (e.g. Keller & Waller 2002; Joron & Brakefield 2003), predation (e.g. Gotthard 2000), metapopulation (e.g. Hanski 1994; Wahlberg *et al.* 1996; Ricketts 2001), climate change (e.g. McLaughlin *et al.* 2002; Parmesan & Yohe 2003; Algar *et al.* 2009; Willis *et al.* 2009), sexual selection (e.g. Boggs 1990; Gage *et al.* 2002), speciation (e.g. Arnqvist *et al.* 2000; Chamberlain *et al.* 2009; Dapporto 2010), habitat distributions models (e.g. Gutierrez *et al.* 2005; Rabasa *et al.* 2005), ecological niche theory (e.g. Yamamoto *et al.* 2007; Elias *et al.* 2008), conservation biology (e.g. Kremen 1994; Lawton *et al.* 1998; Hamer *et al.* 2003; Cleary 2004; Thomas 2005; Algar *et al.* 2009) and a host of other areas of ecological and evolutionary research.

1.2 Scope of the Thesis

In this thesis, fruit-feeding butterflies (nymphalids) are used as a 'study system' or 'study organisms' for two broad aims:

1. to develop efficient and reliable rapid biodiversity assessment (RBA) protocol for monitoring Ghanaian forests
2. to empirically evaluate neutral theory in mobile organisms

1.2.1 Development of an Efficient and Reliable Rapid Biodiversity Assessment (RBA) Protocol for Monitoring Ghanaian Forests

Forests in West Africa are rapidly disappearing and are among the most critically imperiled in the world (Myers *et al.* 2000; FAO 2006). About 90% of original West African forest has been destroyed during the past century (Leach & Fairland 2000; IUCN 2006). The remaining 10% (or less) is not without significant threat of depletion and fragmentation. For instance, within the past 15 years (1990-2005), Ghana has lost 1.9 million hectares or 26% of her forests cover (IUCN 2006). The current deforestation rate in Ghana is estimated at around 3% per annum (IUCN 2006).

The quest to either halt the process of biodiversity decline, or significantly reduce its rate of depletion has attracted immense global attention. Deforestation is seen today as one of the major global challenges facing humankind (Nowicki *et al.* 2008). In order to guide conservationists and policy-makers in deciding on appropriate conservation measures which are necessary for countering the drastic forest loss in Ghana, suitable biodiversity assessment programs are needed (Balmford *et al.* 2005b; Dobson 2005; Green *et al.* 2005). In the poor economic situation of West Africa, governmental organisations in the sub-region cannot afford large-scale biodiversity surveys. In addition, national monetary commitments to biodiversity conservation are woefully inadequate to keep pace with the region's fast forest alteration. Meanwhile, there is an urgent need to devise rapid, cost-effective and easily implementable sampling protocols that are accurately representative of the functional and taxonomic structure of the local biodiversity assemblage (United Nations 2002; Balmford *et al.* 2005a; Balmford *et al.* 2005b; Green *et al.* 2005). Given the present poor regional economic situation, the rapid deforestation rate and the limited availability of trained

staff, a rapid biodiversity assessment (RBA) programme seems ideal for monitoring West African biodiversity because such quick surveys involve less effort and costs compared to large-scale surveys (Beattie & Oliver 1995; Oliver & Beattie 1997; Balmford *et al.* 2005b).

However, the choice of inappropriate or insufficient sampling strategies in a RBA may nullify the value of the mission because such spot sampling may only sample temporally abundant taxa (Braithwaite 1991; Larsen 2005a; Aduse-Poku & Doku-Marfo 2007). An obvious consequence of a rapid, short-duration sampling approach is the omission of peak activity periods for some species. A species may appear rare in samples when it is, in fact, more abundant in the community at an earlier or later date. Although RBA approaches have been subjected to criticism (Brower 1995; Goldstein 1997; Trueman & Cranston 1997), RBA possesses an undeniable appeal to conservationists, forest resource managers and governments in Africa and many other developing countries because they provide a cost- and time-efficient means of assessing the impacts of environmental disturbances on an ecosystem. Given the continued destruction, disturbance and fragmentation of forests in the sub-region, and the associated extinction of species, it is useful to develop RBA approaches that provide reliable quantifiable information on the composition and quality of the ecosystems under study.

For any RBA approach to be sustainable and easily implementable, its framework should aim at using locally available materials in its design and operations. Most imperatively, such programs should be able to evaluate, monitor and predict human-induced changes on both the physical and biological composition of the ecosystems being studied. Since it is virtually impossible to inventory, monitor, and manage all aspects of a local or regional biota, specific taxa are usually

selected as 'indicator' or 'focal' species based on their ability to respond to changing environmental conditions and also reflect the diversity or health of an ecosystem (Howard *et al.* 1998; Noss 1999).

Butterflies, especially those of the fruit-feeding guild (also called nymphalids) have been used in biodiversity monitoring programmes with considerable success in Asia (Dumbrell & Hill 2005; Fermon *et al.* 2005; Benedick *et al.* 2006), in the Neotropics (Beccaloni & Gaston 1995; Barlow *et al.* 2007b) and in Africa (Kremen 1994; Fermon *et al.* 2000; Oduro & Aduse-Poku 2005; Bossart *et al.* 2006; Bossart & Opuni-Frimpong 2009). Several ecological characteristics of fruit-feeding butterflies make them potentially useful tools for monitoring both small and large-scale biodiversity trends (Kremen 1994; Larsen 2005b).

Like all other butterfly groups, nymphalids have short life cycle which makes them highly sensitive to changes in their habitats (Thomas & Clarke 2004). The fairly known alpha taxonomy of fruit-feeding butterflies also makes them a practical choice for monitoring biodiversity at both species and higher-taxa (community) levels. Again, owing to the splendid aesthetic beauty and charisma of most butterflies, both professional and amateur nature collectors were (and still are) fond of them. As a result, there is relatively more readily available information on the life history and ecology of most butterflies compared to other insect groups (Larsen 2005b; Thomas 2005). Like all butterflies, nymphalids are distributed over a broad range of habitats, making it possible to detect different impacts on varying ecosystems. Lastly and most importantly, fruit-feeding butterflies are speciose, easy to find and they can be sampled in standardized way using a bait trapping technique (DeVries 1987, 1988; Hughes *et al.* 1998). The standardization presents a more convenient way of tracking movements of individuals (Hughes *et al.* 1998; Fermon *et al.* 2003) and

monitoring changes in species abundance over time and space (DeVries *et al.* 1997; Devries & Walla 2001; Oduro & Aduse-Poku 2005; Bossart *et al.* 2006; Hamer *et al.* 2006; Molleman *et al.* 2006; Bossart & Opuni-Frimpong 2009).

There are approximately 1,100 West African butterfly species of which ~940 are present in Ghana (Larsen 2005b). These are mostly (82%) forest-dwelling species, and about a fifth of these forest-dwelling butterflies are fruit-feeders (Larsen 2005b; 2006; Larsen *et al.* 2009). Fruit-feeding butterflies belong to the family Nymphalidae and in Africa mainly include the subfamilies Charaxinae, Satyrinae, Limenitidinae and Nymphalinae (others belong to Biblidinae, Heliconiinae and Apaturinae). These subfamilies are speciose with high levels of diversity and endemism in West Africa (Larsen 2005b). Most of these species feed exclusively on fruits as adults, hence their common or informal name "fruit-feeders" or "fruit-feeding butterflies". They are therefore easy to measure and monitor using bait trapping technique.

The principal objective of this (applied) study was to develop efficient rapid biodiversity monitoring framework in Ghana using fruit-feeding butterflies as the focal or surrogate taxa. To help achieve this broad study objective, the following under-listed three individual studies, each with specific research questions were postulated for detailed investigation.

1. Effects of vertical stratification and temporal variation on fruit-feeding butterfly diversity estimates in West-African tropical forests.
2. Development of an efficient rapid butterfly biodiversity monitoring framework in Ghana: on the use of bait- and trap-type for sampling butterflies.
3. Assessing the use of fruit-feeding butterflies as indicators of habitat change in West African forests.

Findings of the three individual studies were in the end collated and synthesized to propose efficient sampling strategies for quick butterfly biodiversity surveys in forest ecosystems in Ghana (and West Africa).

1.2.1 Empirical Evaluation of Neutral Theory in Mobile Organisms

As recounted by Gaston and Chown (2005), the last two decades have seen two highly significant broad theoretical developments that address the core principles of ecology. The first of these has been the theory of metabolic scaling developed by James. H. Brown and his colleagues (West *et al.* 1997, 1999; Brown 2001), which sought to explore the relationship between body size and metabolic rate. The second significant broad theoretical development in ecology has been the neutral theory of biodiversity and biogeography by Hubbell (1997; 2001).

Hubbell's neutral theory or hypothesis builds on the foundations of the classical theory of island biogeography to explain patterns of species richness, abundance and distribution. Hubbell's hypothesis assumes that the differences between members of an ecological community of trophically similar species are 'neutral' or irrelevant to their success (Hubbell 1997; 2001). That is, individuals exhibit no traits associated with their species identity that have any influence over their reproductive success, longevity, movements or likelihood of speciation (Hubbell 2001; Gaston & Chown 2005). This assumption clearly challenges the classical adaptive, niche-based view of ecological community structure that stresses on functional differences between species (e.g. in colonization or competitive ability) as a key process shaping species-abundance distributions.

Like all novel and controversial theories, neutral theory is not spared of sharp criticisms and rebuttals (Chave 2004; Poulin 2004; Leibold & McPeck 2006;

Ricklefs 2006). Critics question the reality of its assumptions; such as patently ignoring species-specific traits like habitat preferences, physiological tolerances, dispersal abilities, etc. However, models of the theory have been demonstrated to fit empirical data rather well (Hubbell 2001; Condit *et al.* 2002; Olszewski & Erwin 2004; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* 2009) and in some cases better than all other relative species abundance models (Volkov *et al.* 2003).

Neutral theory is currently being accepted by many as a quantitative null model for ecological community structure (Alonso *et al.* 2006; Hubbell 2006; Leibold & McPeck 2006; Zillio & Condit 2007; Ellwood *et al.* 2009, but see McGill *et al.* 2006). Proponents (e.g. Alonso *et al.* 2006) argue the theory is a first approximation to reality (hence, a useful quantitative model), and that there is more to the theory than 'neutrality'. Subsequently, various authors have sought to explore the various aspects of the theory such as the sampling formulae (e.g. Chave & Leigh 2002; Etienne 2005; Munoz *et al.* 2007; Etienne 2009b, a) and the philosophy (e.g. McGill 2003; Gaston & Chown 2005; Gotelli & McGill 2006; Leibold & McPeck 2006; McGill *et al.* 2006; Morlon *et al.* 2009), with a few (e.g. Hubbell 2001; Condit *et al.* 2002; Olszewski & Erwin 2004; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* 2009) empirically evaluating the theory in study organisms or systems.

However, most of these empirical studies (e.g. Hubbell 2001; Condit *et al.* 2002; Olszewski & Erwin 2004; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* 2009) have been limited to resident organisms like trees and brachiopods, which largely depend on dispersal agents (e.g. winds, animals) for their establishments in an ecological system. This mode of establishment perhaps makes species-level traits such as habitat preference and tolerance less relevant, apparently satisfying the requirements of neutral theory. To fully appreciate the strengths and weaknesses of

neutral theory as a quantitative null model for ecological community structure, we must as well evaluate the model and its predictions in more mobile organisms.

In this part of the thesis, Hubbell's neutral theory of biodiversity was evaluated in a more mobile study organisms . Specifically, the plausibility of neutral theory in explaining the observed patterns of species richness, abundance and distribution of fruit-feeding butterfly communities in three protected forests in Africa was explored.

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1.3 Overview of the Thesis

The thesis is organized into seven chapters as follows:

Chapter 1 which includes this section provides an introduction to the thesis. It describes the background and the scope of thesis, and introduces the two broad aims or dimensions of the thesis - applied and theoretical perspectives on fruit-feeding butterflies' community dynamics. The chapter further outlines the four individual studies undertaken, and gives a brief overview of the seven chapters presented in this thesis.

Chapter 2 reviews previous scholarly works relevant to the thesis topic. The chapter highlights and appraises important past studies that use butterflies as the 'studyorganisms' to answer key research questions in ecology, conservation biology and evolution. The chapter proceeds to define and discuss key ecological concepts like indicator species concept, rapid biodiversity assessment (RBA) and neutral theory used in the thesis. Chapter 2 finally concludes with a short review of butterfly diversity in the world in and in Ghana, and the state of forests in Ghana.

Chapter 3 assesses two potential sources of bias associated with Rapid Biodiversity Assessment (RBA) protocols in a West African rainforest ecosystem: temporal variation and vertical stratification. The chapter presents results of two butterfly biodiversity studies that used fruit-baited traps, hung at both the forest canopy and understorey and, operated during seven sampling periods throughout the year, including dry and wet seasons.

Chapter 4 evaluates the efficiency of two types of traps and baits used for sampling fruit-feeding butterfly diversity in West African forests. The chapter also investigates how the age of bait affects the type of species or species-group trapped, and RBA results in general.

Chapter 5 assesses the usefulness of fruit-feeding butterflies as bio-indicators of habitat change. The study seeks to identify potentially effective taxa that could be used as surrogates for monitoring forests in Ghana and West Africa.

Chapter 6 reports the results of a novel study designed to test whether the Hubbell's neutral theory of biodiversity fits the pattern of abundance, richness and diversity of fruit-feeding butterfly communities sampled from three forest fragments in Africa. The study represents the first attempt to empirically evaluate neutral theory in mobile organisms' assemblages using both direct (confronting neutral model to real species abundance data) and indirect approaches (testing the predictions of neutral theory against independent species-specific datasets and our knowledge of the system).

Chapter 7 concludes the thesis by generally discussing and summarizing the major findings of the four individual studies. Also in this chapter, the findings of the first three studies are collated and synthesized to propose two RBA frameworks for monitoring forests ecosystems in Ghana and West Africa.

CHAPTER TWO

2. LITERATURE REVIEW

2.1 Butterflies as model systems for ecological and applied biodiversity conservation and management research

Butterflies are by far the best known and most studied larger group of organisms apart from plants and vertebrates. They are speciose, but not overwhelmingly large (~20,000 in the world; ~4,000 in Afrotropics and ~940 species in Ghana) and they do not break down into “micro-species” with very small ranges (Larsen 2006). They are represented by a diverse yet relatively small and manageable number of species (at least when compared to moths) exhibiting a wide spectrum of ecological characteristics (Larsen 2005b). Butterflies have a fairly known and stable taxonomy with the natural history of most species and species-groups often relatively well studied and understood (Ackery *et al.* 1995; Larsen 2005b; Williams 2008). Information such as habitat preference, habits, host plants, geographical distribution, endemism and/or rarity of most species is readily available for use in biodiversity data synthesis and interpretation (Larsen 1991; Ackery *et al.* 1995; Larsen 2005b; 2006). This is in contrast with other insect groups, where it is only possible to work with morphospecies owing to the huge taxonomic impediment (Samways 1993).

New *et al.* (1995) and Bonebrake *et al.* (2010) present an insightful overview of how butterflies have helped shaped (applied) ecological research and/or biodiversity management and conservation in general. Whilst New *et al.* (1995) mainly discuss the conservation and management aspects of the species, Bonebrake *et al.* (2010) extend the discussion beyond the use of butterflies as bioindicators.

New *et al.* (1995) argue that by using butterflies as targets in biodiversity conservation, many co-existing and co-dependent organisms, like their food plants and natural enemies, may also be conserved. They (New *et al.* 1995) recount how public interest in butterflies has grown enormously within the last decades. A recent proliferation of artificial viewing spaces, such as butterfly houses, zoos, and gardens (Emmel & Boender 1991), exemplifies this interest, as does the increase in butterfly watching (as opposed to collecting) as a hobby (Pyle 1992). The aesthetic beauty and charismatic nature of many butterflies have the ability to invoke people's passion and interest, both of which are useful in butterfly conservation. Butterflies have even become a political force in some countries, with major building projects have been rejected and proposed motorways relocated simply to protect scarce butterfly populations (New *et al.* 1995).

Several authors (e.g. Kremen 1994; Simonson *et al.* 2001; Larsen 2005b; Larsen 2006; Aduse-Poku & Doku-Marfo 2007) have enumerated several reasons why butterflies can act as potential useful indicators for biodiversity conservation. Notably among these reasons are the high diversity, ubiquitous, stable taxonomy and ease of capture of most butterfly species (Kremen 1994; Fermon *et al.* 2000; Larsen 2005a; Molleman *et al.* 2006; Aduse-Poku & Doku-Marfo 2007). Other important reasons are the short (typically annual) life cycles of butterflies, and their greater sensitivity to changes in their habitats than other groups (Thomas 1994; Thomas *et al.* 2004). Butterflies are more likely to reflect changes occurring at a fine scale because they breed usually in small habitat patches (van Swaay *et al.* 2006). They have high sensitivity to changes in microclimate heterogeneity (Pollard & Yates 1993; Parmesan 1996) and a high correlation with spatial, structural, and taxonomic diversity of vascular plants (Spitzer *et al.* 1997; Panzer & Schwartz 1998; Simonson

et al. 2001), habitat complexity (Molina & Palma 1996), landscape structure (Wood & Samways 1992), topographic and moisture gradients (Kremen 1992). It is worth mentioning that butterflies are also not representative of all lifestyles and habitat types. For example, very few butterflies have predacious or parasitic larvae, there are no aquatic species and very few feed on decaying wood (Thomas *et al.* 1994).

2.1.1 Biodiversity indicator species concept

McGeoch (1998) in his influential paper, defines a biodiversity indicator as "a group of taxa (e.g. genus, tribe, family or order, or a selected group of species from a range of higher taxa), or functional group, whose diversity reflects some measure of the diversity (e.g. character richness, species richness, level of endemism) of other higher taxa in a habitat or set of habitats". The use of species or groups of species to reflect the condition of the environment or a component of biodiversity is not a new concept. Hall & Grinnell (1919) were among the first to use the indicator concept by associating plant and animal species to particular 'life zones' (i.e. large geographic areas with similar structural and compositional characteristics).

Since then, the concept has evolved substantially and is now widely applied in situations ranging from the verification of the compliance of industries to specific anti-pollution laws (Ellis & Macdonald 1998) to the assessment of habitat quality (Canterbury *et al.* 2000; Lindenmayer *et al.* 2000). Additionally, the use of indicators has frequently been incorporated into policies and regulations in order to monitor the ecological integrity of watersheds, lakes, semi-natural pastures rangelands, and forests (Carignan & Villard 2002). However, it is only in the recent past that rigorous methodologies have been developed and adopted for the identification of bioindicators (McGeoch 1998), and significant progress in the theoretical and

methodological development of bioindicators has recently been made (Noss 1990; Hilty & Merenlender 2000).

Although seemingly a useful concept, the use of indicator species in biodiversity conservation is not spared of criticisms. Carignan and Villard (2002) present the two popular arguments against the use of indicator species in ecological and conservation research. The first popular argument against the use of indicator species is inspired by the classical niche apportionment theory (Tilman 1999; Chesson 2000). Since no two species occupy the same niche, some authors (e.g. Rapport 1990) argue that no single species should be expected to act as an indicator for an entire ecosystem. However, as Carignan and Villard (2002) explain, this argument does not necessarily invalidate the indicator species concept. Rather, it means several species, representing different niche requirements and sensitivity to varying degrees of disturbances should be monitored in order to identify the causes of change more precisely and limit errors of interpretation.

The other common argument against the use of indicator species is that many factors which are unrelated to degradation of ecological integrity may affect the population status of an indicator species and, thus, complicate the detection and interpretation of population trends of indicator taxa. Carignan and Villard (2002) argue again that this view, like the previous one, does not discredit the use of indicator species but rather calls for caution in the interpretation of changes in their demographic parameters and distribution. Consequently, if management recommendations are to be issued based on changes in the status of indicator species, it is crucial to have an adequate knowledge of potential causal factors unrelated to the degradation of ecological integrity. Despite these few cautionary calls and remarks, the worth of using the indicator species concept in biodiversity conservation and management is

widely appreciated in literature (Kremen *et al.* 1993; Kremen *et al.* 1994; McGeoch *et al.* 2002). Indicator species possess an undeniable appeal for conservationists, land managers, and governments as they provide a cost- and time-efficient means to assess the impacts of environmental disturbances on an ecosystem (Kremen 1992; Kremen *et al.* 1994; McGeoch 1998; Ward & Larivière 2004).

2.1.2 Selection of indicator species

Since it is practically impossible for conservationists, land and forest managers to measure everything of potential interest within an ecosystem, the choice of what to measure is critical. This step is among the most difficult and controversial in developing a monitoring program (Noss *et al.* 1997). Consequently, various researchers (e.g. Noss 1990; Tschardtke *et al.* 1998) have proposed a number of criteria for selecting indicator species. Common to these proposals are, indicator taxa should be 1) sensitivity to habitat or stress change, 2) responsive to biodiversity patterns of other taxa, 3) well known taxonomy, 4) cost-effective to measure and easy to monitor by even non-specialists, 5) have a well studied life history or ecological information, 6) distributed over a broad range of habitats.

Based largely on the above and other criteria, various indicator taxa have been suggested or used. Previously used or suggested indicator organisms include plants (Schulze *et al.* 2004), *Drosophila* (da Mata *et al.* 2008), beetles (Dufrêne & Legendre 1997), termites (Jones & Eggleton 2000), ants (Andersen 1995), butterflies (Kremen 1992, 1994; Daily & Ehrlich 1995; Barlow *et al.* 2007b), amphibians (Adams 1999), birds (Waltert 2000; Schulze *et al.* 2004). Each of the above studies presents persuasive arguments on the suitability of each taxon as a potential indicator. For example, Dufrêne and Legendre (1997) recount that many studies show that

invertebrates in general are appropriate indicators of ecosystem integrity. Their presence is generally more strongly associated with environmental factors than with biological factors such as competition, predation and parasitism.

2.1.3 Biodiversity monitoring

The term 'monitoring' is often used in close association with indicator species. The usage of the term in biodiversity conservation and research has often been in a very broad context, resulting in varying explanations and interpretations of the term. Consequently, a clearer definition of the term is necessary to facilitate the design or development of regional and local monitoring programmes. Hellawell (1991) in trying to make the term more definitive, defines monitoring as "intermittent (regular or irregular) surveillance carried out in order to ascertain the extent of compliance with a predetermined standard or the degree of deviation from an expected norm". With respect to bioindication, McGeoch (1998) defines monitoring as "the repeated application of bioindicator taxa to provide information on the environmental conditions, or effects thereof, to which they were initially identified as suitably sensitive and for which baseline standards, thresholds or relationships have already been determined."

Hinds (1984) makes a further but useful distinction between what he terms 'biological' and 'ecological' monitoring. In his assertion, 'biological' monitoring uses taxa as 'surrogate filters to be analysed to indicate environmental quality', whereas 'ecological' monitoring is the 'purposeful and repeated examination of the state or condition of specifically defined biotic groups in relation to external stress'. The objectives of monitoring programmes are to evaluate the changes over time in

habitat structure, function and composition in response to natural factors, human activity or management practices (McGeoch 1998).

2.1.4 The rise and value of Rapid Biodiversity Assessment (RBA)

Rapid Biodiversity Assessment (RBA) approaches arose mainly to help conservationists and land managers overcome the many logistical constraints associated with large-scale invertebrate surveys (Ward & Lariviere 2004; Green *et al.* 2005). The two main objectives of RBA are to; 1) reduce the effort and cost of sampling, and 2) summarise complex ecological details so they can be understood by non-specialists (New 1998). Although RBA approaches have been subjected to criticism (Brower 1995; Goldstein 1997; Trueman & Cranston 1997), there is a need for invertebrate survey methodologies that can evaluate large numbers of species, increase ecological understanding, and can be undertaken at a reasonable financial cost (Kremen *et al.* 1993; Sparrow *et al.* 1994; Oliver & Beattie 1996).

The main arguments against RBA after its introduction by Oliver and Beattie (Oliver & Beattie 1993) had been its concept of 'taxonomic minimalism' (Brower 1995; Goldstein 1997). Taxonomic minimalism as described by Oliver and Beattie (1993, 1996), as well as Beattie and Oliver (1994; 1995) is the use of (morpho)species counts by non-specialists or parataxonomists as a shortcut to the assessment of conservation priority. The duo are of the notion that, “the identification of morphospecies involves exactly the same methods as alpha taxonomy” and argue for the operational superiority of local assessments of morphospecies or recognizable taxonomic units (RTUs) on grounds that they require only the data to hand and are more or less independent of existing Latin binomials, their associated hierarchies and phylogenetic trees (Beattie & Oliver 1994). In a

rather sharp rebuttal to this notion, Goldstein (1997) stresses a position shared by other researchers (like Brower 1995; Campbell 1995) that systematics provides a fundamental framework, outside which biological information cannot be interpreted.

The currently RBA arguments have moved from critiques and rebuttal seen on the early years of introduction to consensus building. Both proponents and opponents of the concept now recognize the need and value of RBA, especially in the developing countries where resources for biodiversity monitoring and evaluation are scarce or non-existent. Subsequently, there have been several forms and approaches of RBA, all in an attempt to improve its precision and efficiency. In their review of RBAs in Australia, Ward and Larivière (2004) outline four general categories of RBA approaches being used around the world: (1) sampling surrogacy, (2) species surrogacy, (3) taxonomic surrogacy, and (4) taxon-focusing.

The sampling surrogacy approach entails restricted sampling in place of intensive sampling. It usually includes shorter sampling duration, a reduced number of sampling methods employed, the use of less-intensive sampling methods than usual, as well as sub-sampling existing material (Ward & Larivière 2004). Statistical extrapolation methods like those provided by Colwell and Coddington (1994) are usually used to estimate species richness of surveys that employed the reduced sampling approach. Although proven successful under certain circumstances (e.g. Hammond 1994), Ward and Larivière (2004) caution that care must be taken to minimize the reduction in data quality as well as sampling effort. Surveys should have sufficient replication for statistical analyses.

The species surrogacy approach however, uses taxonomic levels higher than species such as genera, tribes, subfamilies, families, order, etc. This is the original approach proposed by Oliver and Beattie (1993). This approach has received

substantial attention in RBA and is being used extensively in both terrestrial and aquatic environments (Andersen 1995; Jones & Eggleton 2000; Obrist & Duelli 2010). The advantage of using higher taxonomic levels in surveys is that costs and effort could be substantially reduced as the time-consuming task of identifying specimens to species level becomes unnecessary. However, genus richness (as a measure of species richness) for example, is only reliable under limited circumstances and as Andersen (1995) has shown, the measure can be confounded by habitat, biogeography and sampling effort. In addition, higher taxonomic levels often contain species with a variety of feeding types and trophic levels and as a result individual species' responses can be masked by analysis at higher levels. This 'cancelling-out effect' has been observed for ground-dwelling invertebrates at the family level (Neville & Black 1997).

The third general approach described by Ward & Larivière (2004) is taxonomic surrogacy. Taxonomic surrogacy is similar to species surrogacy in approach except that the former uses what is now known as recognisable taxonomic units (RTUs) also known as morphospecies (MSP) or operational taxonomic units (OTUs). RTUs act as a surrogate for species-level identification (Beattie & Oliver 1994). This approach has received recent attention in RBA and has been particularly controversial as opponents argue against the reduction of taxonomic 'accuracy' in specimen identification (Brower 1995; Goldstein 1997). However, the use of 'parataxonomists' (non-specialist taxonomists) to sort mass samples of invertebrates into RTUs before specialist identification could increase cost effectiveness (Janzen 1991). Again, several interrelated problems arise with the RTU level approach. First, it is impracticable to maintain a consistent and unambiguous identification across sites and ideally across different ecological

surveys (Ward & Larivière 2004). Second, use of RTUs introduces a concern about data interpretation without knowledge of species assemblages. For example, Greenslade and Majer (1993) examined *Collembola* from forests and rehabilitated mines in Western Australia and found out that although both habitats contained similar numbers of species, the forest habitat largely contained native species, while cosmopolitan species predominated in the mined areas. Such differences can be overlooked without species level identification. As a result Ward and Larivière (2004) advise that RTUs should only be used as a stepping stone before formal species-level identification.

The last of the RBA approaches described by Ward and Larivière (2004) is taxon-focusing. This includes a range of approaches that aim to identify a species, or a group of species, that act as a surrogate for a wider range of taxa (Ward & Larivière 2004). These approaches are based on the assumption that the selection, and protection, of a restricted number of 'focal taxa' will also help the protection of other taxa (McGeoch 1998). The use of focal taxa (such as keystone species, umbrella species and indicators) has received considerable attention (Simberloff 1998; Fleishman *et al.* 2001; Caro 2003; Roberge & Angelstam 2004). Unfortunately, there are few guidelines for the selection of specific focal or indicator taxa, although a number of authors (e.g. Kremen *et al.* 1993; McGeoch 1998; Hilty & Merenlender 2000; Carignan & Villard 2002) have suggested objective and standardized scientific criteria.

2.2 Butterflies as model systems for evolutionary and theoretical research

Butterflies (and moths) are among the earliest examples and most important organisms for the understanding of evolution and ecology. The great discoveries in mimicry by Bates (1862) and Müller (1879) in the 19th century were all possible with the use of *Heliconius* (passion vine butterflies) as the model systems. Bates (1862) hypothesised that mimicry evolved to confuse predators. Edible butterflies, for instance, copied the wing patterns of toxic species so that predators would avoid eating them. Bates (1862) also described what looked like evolution in action: he observed that a continuum in species with different wing patterns were found together in the same locality, through to related species with different wing patterns. Now, modern science with the combination of population genetic, developmental and behavioural approaches has taken this to another level. Using flapping models of *Heliconius* butterflies with different patterns, the researchers (e.g. Mullen 2006; Jiggins *et al.* 2008; Chamberlain *et al.* 2009; Salazar *et al.* 2010) have shown that the butterflies, just like most other organisms, chose to mate with individuals that looked the same as themselves. Over time, different patterns are likely to split into new species. In addition, hybrids between populations with different patterns have intermediate patterns that are not recognised by predators as harmful and therefore suffer disproportionately from attacks, reinforcing the split into new species (Jiggins *et al.* 2008; Salazar *et al.* 2010).

Using *Bicyclus anyanana*, an African nymphalid butterfly, as a model system, a lot of formerly enigmatic issues are now making sense in the field of developmental biology. *Bicyclus anyanana* has become popular as a model organism for the study of developmental plasticity, developmental genetics and molecular genetics of wing pattern formation (Koch *et al.* 2000; Brakefield *et al.* 2003; Saccheri *et al.* 2006;

Saenko *et al.* 2008). It is likely to be the first insect group to have its whole genome sequenced after *Drosophila melanogaster*. The wing patterns of *B. anynana* butterflies provide an ideal opportunity to analyze different modes of phenotypic variation at different levels of biological organization (Koch *et al.* 2000; Saccheri *et al.* 2006). Scientists now have a better understanding of polyandry (a condition where there is an earlier adult emergence of males than females; Zijlstra *et al.* 2002), phenotypic plasticity (Brakefield *et al.* 1996; Brakefield *et al.* 2003) and the significance of dry and wet season forms of butterflies and other insect groups (Brakefield & Larsen 1984).

Looking into the future, the studies of *B. anynana* wing patterns (e.g. Koch *et al.* 2000; Brakefield *et al.* 2003; Saenko *et al.* 2008) now provide the opportunity to address other key issues in evolutionary-developmental biology, including 1) the evolution of morphological innovations and the co-opting of existing developmental pathways to produce new phenotypes; 2) modularity in development and how the developmental integration of traits might constrain their evolutionary change; 3) phenotypic plasticity and how the environment can influence development and 4) the functional integration and concerted evolution of different phenotypes, such as butterfly wing patterns and butterfly color vision.

In the field of modeling and theoretical development, butterflies have been used as model systems. Two recent works, Willis *et al.* (2009) and Algar *et al.* (2009) used butterflies as case systems in modeling both the current and potential future climate change impacts on biodiversity. Willis *et al.* (2009) used three British butterfly species in their dynamic distribution modeling approach and observed that each species' distribution prior to expansion was critical in determining the exact spatial pattern of the current distribution. Willis *et al.* (2009) also show that realistic

representation of dispersal is of key importance for modeling future range shifts. Algar *et al.* (2009) however, use global change as a pseudo-experiment, testing whether spatial relationships linking climate to butterfly species richness are able to predict how richness changed during the climate changes observed in the 20th century. Surprisingly, this approach proves at least as effective as species distribution models, suggesting both a new way to predict biodiversity responses to global change and that spatial macro-ecological relationships can truly be causative. These studies (Algar *et al.* 2009; Willis *et al.* 2009) produce a strong consensus that accurate predictions of future shifts in species diversity will demand more sophistication than simple projections of species' climatic niche space.

In his over 550 times cited paper (as of June 2010), Hanski (1994) used three exceptionally well-studied butterfly metapopulations from South Finland and England to formulate what he calls 'a practical model of metapopulation dynamics'. Hanski's (1994) model predicts well the observed minimum patch size for occupancy and the numbers of extinctions and colonizations per year (turnover rate). Hanski's (1994) results suggest that local populations of the three butterflies in patches of 1 ha, which may support almost 1,000 adult butterflies, with an expected lifetime of 20-100 years. After Hanski (1994), various researchers (e.g. Wahlberg *et al.* 1996; 2002; Baguette & Schtickzelle 2006) have also used butterflies in similar population dynamics studies and arrived at outstanding results with significant outcomes.

In a rather unexpected fashion, Horvath *et al.* (2002) used an imaging polarimetry technique model, a quantitative model for determining photon absorptions to investigate the sensitivity of *Papilio* photoreceptors. They found a rather weak polarization sensitivity of *Papilio* photoreceptors and concluded that

the *Papilio* photoreceptors hardly influences colour perception under natural conditions (Horvath et al. 2002). Butterflies continue to be used as model systems in other specific studies like biogeography (Aduse-Poku *et al.* 2009; Kodandaramaiah & Wahlberg 2009; Garcia-Barros & Benito 2010), inbreeding (Keller & Waller 2002; Joron & Brakefield 2003), predation (Gotthard 2000), sexual selection (Boggs 1990; Gage *et al.* 2002), speciation (Arnqvist *et al.* 2000; Chamberlain *et al.* 2009; Dapporto 2010) and a host of others.

2.2.1 The neutral theory of biodiversity

Although the neutral theory of biodiversity (here sometimes referred to as 'neutral theory') is not entirely a new concept, it was a monograph titled "The unified neutral theory of biodiversity and biogeography" by Stephen Hubbell in 2001 that invigorated the theory. Before Hubbell (2001), Caswell (1976, 1983), Watterson (1974) and Leigh *et al.* (1993) had earlier attempted constructing neutral theory of forest dynamics and diversity following the assumptions of the neutral theory of population genetics (Kimura 1983). Kimura's neutral theory of molecular evolution ascribes random mutations and genetic drift as the main agents of evolutionary change. Translating these population genetics ideas into community ecology, the earlier proponents (Watterson 1974; Caswell 1976; Leigh *et al.* 1993) invoke neutral ecological drift (stochastic processes of death and birth) as the main factor controlling the assembly of ecological communities in their neutral models.

However, these earlier models of neutral theory did not receive much attention like Hubbell's did with his monograph. Hubbell's (2001) model differs from the previous models in its assumption. In addition to neutral ecological drift, Hubbell (2001) identifies random dispersal as one of the main factors controlling the

assembly of ecological communities. Hubbell's theory again assumes that the differences between members of an ecological community of trophically similar species are "neutral," or irrelevant to their success (Hubbell 2001). Various neutral models have been developed after Hubbell (2001). What is however common with all different neutral theory models is the assumptions of 'neutrality' or 'ecological equivalence' of species. There are two fundamental assumptions shaping the way in which the neutral theory works. The first fundamental assumption is the 'neutrality' of species. Neutrality is defined as per capita ecological equivalence among all individuals of every species at a given trophic level. "Per capita equivalence" means that all species are held to behave (i.e., reproduce and die) in the same way as one another and individuals of a particular species reproduce, die and behave in the same way (Hubbell 2001). In simple terms, the first assumption of neutral theory posits that all individuals belonging to all species are equivalent with regards to the probabilities of birth, death, dispersal and speciation. Thus, individuals exhibit no traits associated with their species identity, that have any influence over their reproductive success, longevity, movements or likelihood of speciation (Gaston & Chown 2005). The second fundamental assumption of the theory is what has come to be called zero-sum dynamics, where neutral theory assumes that the community is saturated with individuals, such that if one dies its place is taken by another, and individuals are thus engaged in a zero-sum game (Hubbell 2001). This assumption is being relaxed in later models of the neutral theory (e.g. Etienne *et al.* 2007a; Haegeman & Etienne 2008; Etienne 2009b).

Like all new theories, neutral theory is not spared of criticisms. The main criticisms of neutral theory centers on its neutrality assumption (Gaston & Chown 2005; Adler *et al.* 2007). The neutrality assumption of neutral models suggests that

species-level traits such as physiological tolerances, habitat preferences, energy usages, growth patterns, reproductive strategies, dispersal abilities and body sizes are all irrelevant when neutral theory is invoked as the putative explanation for an observed biodiversity. As Gaston & Chown (2005) lament, it is difficult to comprehend that this may be so. Gaston & Chown (2005) argue that if indeed individuals in an ecosystem exhibit no traits associated with their species identity, as neutral theory posits, then trophically similar species will be rather unspecialised, since they can potentially exploit the resources freed by the death of an individual of any other species in the community. On the contrary, many studies (e.g. Tilman 1994; Chesson 2000; Laird & Schamp 2006) have demonstrated how coexisting species partition their resources in order to coexist. Clearly, neutral theory contravenes the niche-assembly view, which proposes that coexisting species should have different niches and that the abundance and diversity of species are determined by interspecific competition and the diversity of resources (Tilman 1999; Chesson 2000).

However, recent studies have shown that neutral theory can explain the biodiversity of several plant (Condit *et al.* 2002; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* 2009) and brachiopod (Olszewski & Erwin 2004) communities. In some cases, the neutral models have fitted empirical data better than all other relative species abundance models (Volkov *et al.* 2003) but see (McGill 2003). Proponents argue that neutral theory is an ideal theory (Alonso *et al.* 2006). To further substantiate this, Alonso *et al.* (2006) draw a parallelism between neutral theory and kinetic theory of gases. They recount that neutral communities do not exist, neither do ideal gases. They opine that, similar to the kinetic theory of ideal gases in physics, neutral theory is a basic theory that provides the essential ingredients

to further explore theories that involve more complex assumptions (Alonso *et al.* 2006). Leibold and McPeck (2006) are of the view that the predictions of neutral theory can be used as null hypotheses in tests of more complex processes to explain patterns in community structure, much as Hardy-Weinberg expectations of genotype frequencies are used as the null expectation to evaluate the operation of evolutionary forces in population genetics. This view is now held by many ecologists, including even some critics of the theory. As a result, neutral theory is gradually gaining status as a quantitative null model for explaining ecological community structure (Alonso *et al.* 2006; Hubbell 2006; Leibold & McPeck 2006; Zillio & Condit 2007; Ellwood *et al.* 2009, but see McGill *et al.* 2006).

Alonso *et al.* (2006) summarizes the merits of neutral theory from three perspectives. The first is from a philosophical standpoint. They (Alonso *et al.* 2006) argue that science should aim at finding the most parsimonious set of processes that can satisfactorily explain observed phenomena. Neutral theory assumes very little about community dynamics and hence offers a simple representation of ecological community structure. Neutral theory in its simplest, spatially-implicit, form models population dynamics at two community levels: a local community and a metacommunity (Alonso & McKane 2004; Etienne 2005). The local community consists of co-occurring assemblages of trophically similar species that (potentially) compete for the same or similar resources in a localized area. The metacommunity is the larger (regional) pool of species from which species are assembled at random in the local community (Hubbell 2001).

The second usefulness of neutral theory is the practical merit it brings to the field of community ecology. As have been shown elsewhere (Olszewski & Erwin 2004; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* 2009) neutral theory

models fit pretty well empirical data and in some cases have outperformed other diversity indices. Neutral theory therefore provides a method (usually sampling formulae) to assess species diversity in a potentially better way than do previous diversity indices (Alonso *et al.* 2006). The third and perhaps the most significant of the neutral theory's merits is the colourful intellectual discourse it brings to community ecology. Neutral theory has fostered rich debate among ecologists (e.g. Chave 2004; Gaston & Chown 2005; Gewin 2006; Adler *et al.* 2007; Clark *et al.* 2007; Gardner & Engelhardt 2008) about community structure over the past few years, and has led to more rigorous, and much needed, tests of niche mechanisms and explanations of biodiversity. Ironically, neutral theory has reinvigorated niche theory as it challenges niche-based approaches with a simple combination of neutrality, stochasticity, sampling and dispersal. Neutral theory has inspired and will continue to inspire further developments in community ecology.

Although Hubbell (2001) claimed that neutral theory provides a “unified theory of biodiversity and biogeography”, some authors including McGill *et al.* (2006) believe that it is unlikely a single theory in ecology applies at all spatial, temporal and taxonomic scales. Some authors (e.g. Chave 2004; Gaston & Chown 2005) have suggested that perhaps, neutral theory of biodiversity is primarily concerned with non-migratory species-rich communities (like tropical forests, coral reefs, brachiopods) with so many rare species, such that the role of stochasticity at the individual scale becomes unavoidable. But proponents of the neutral theory (e.g. Bell 2001; Volkov *et al.* 2003; Etienne & Olf 2005; Alonso *et al.* 2006; Hubbell 2006) however believe the models of the neutral theory can explain the biodiversity of mobile organisms as well, although the theory remains to be tested in more mobile organisms.

2.3 Taxonomic breadth of Butterflies (Lepidoptera: Papilionoidea and Hesperioidea)

Insects including butterflies constitute a predominant fraction of biodiversity. They comprise more than half of all known species (Groombridge 1992) and are essential components of all terrestrial and freshwater aquatic ecosystems except those of the Polar regions (Brown 1991). In tropical forests, invertebrates make up over 90% of the animal biomass (Wilson 1987; Samways 1993). It is estimated that of the 10 million species on earth about 8 million are insects (Maes 2007). However, only about 7-10% of insects are scientifically described (Samways 1993). As of 1990, about 150,000 species of Lepidoptera have been described, with the world's total number of extant lepidopteran species estimated at 255,000 (Heppner 1991). Butterflies constitute about 9-12% of all lepidopteran species (Shields 1989).

There are between 18,000 and 20,000 known species of butterflies worldwide (Larsen 2005b). This figure represents about 1.5% of all known and described living organisms. Butterflies are roughly twice as diverse as birds (9,000 spp., Wilson 1992) and ants (11,000 spp., Hölldobler & Wilson 1990). Butterflies like most other organisms have higher abundance and diversity in the tropics. Larsen (2005b) gives informed estimates of the number of butterfly species in each of the major biogeographical regions (Table 2.3). The Afrotropical region is second to the Neotropics in terms of butterfly richness with an estimated 4,000 species. Nearly half of all butterflies are estimated to be in the new world tropics (7,500 spp., in Heppner 1991; Robbins & Opler 1996; Lamas 1997; and 8,000 spp., in Larsen 2005b & Table 2.1).

The extant butterfly taxa in Africa have a strong affinity with those in other biogeographical regions at the higher taxonomic level. For instance, all the six main families of butterflies in Africa occur in all other regions. Furthermore, as many as

92% and 84% of all identifiable butterfly subfamilies and tribes respectively in Africa occur as well in one or more other regions. However, at the species level, there are high levels of endemism in Africa. Only 47 (~1%) of the nearly 4,000 African species are also found in one or more other biogeographic regions (Larsen 2005b).

Table 2.1 The approximate number of butterfly species of the major biogeographical region of origin

Biogeographical region	Species total	Percent of world
TOTAL	18,600	100%
Neotropical	8,000	43%
Afrotropical	4,000	21%
Oriental	2,900	16%
Palearctic	2,000	11%
Papuan/Australian	1,000	5%
Nearctic	700	4%

Source: Larsen 2005b: Page 21

The Afrotropical butterfly fauna are more closely related to the Oriental than to the Neotropics (Larsen, 2005b), despite the latter been connected to Africa for most periods of the Cenozoic until about 100 million years ago (MYA), when Gondwanaland fragmented (Rabinowitz *et al.* 1983). Asia and Africa however, had been separated by the Tethys seas until their collision in the Miocene (19-12 MYA; Willis & McElwain 2002). The land connection between Africa and Asia in the Miocene is believed to have facilitated intense biotic exchanges between the two continents through the Arabian Peninsula (Kappelman *et al.* 2003). Two recent butterfly

phylogenetic studies on *Charaxes* Ochseneimer, 1816 and *Junonia* Hubner, 1819 (Kodandaramaiah & Wahlberg 2007; Aduse-Poku *et al.* 2009) provided strong evidence for an African origin of some extant Asian lineages. It is very likely that many of the extant African and Oriental lineages followed the Africa-Asia or Asia-Africa dispersal routes via the forested corridor within the Arabian Peninsula in the Miocene.

On the African continent, places with the greatest number of butterflies are in rainforests between eastern Nigeria and Central Africa (Larsen 2005b). Larsen (2005b) reports that the richest single locality in Africa with more than 1,000 species is the Oban Hills/Korup National Park, which jointly straddles the Nigeria-Cameroun border. There are approximately 1,100 West African butterfly species of which ~940 are present in Ghana (Torben B. Larsen, *pers comm.*). This is almost a quarter of the 4,000 butterfly species known to occur in the Afrotropical Region.

The wet evergreen and the moist evergreen forests of West Africa represent important repositories of butterfly biodiversity in Ghana. About 83% of butterflies in Ghana are resident in these forests and hence are classified as forest-dwelling species (Larsen 1994). The forest butterflies in Ghana however, often require somewhat different ecological conditions. Some forest butterflies are found only in the wettest forest types, while others are found only in the rather special upland forests. Yet others occur only in the drier semi-deciduous forests where they begin to approach the savannah habitats. Some actually prefer secondary growth near forest in prime condition. No single forest can be expected to house all of Ghana's forest butterflies (Larsen 2006).

About 13 % of Ghana's butterflies are savannah (open-habitat) species (Larsen 1994). The butterfly composition of the savannah habitats seems to be more

stable than in the forest habitats, though there is a strong contrast between the Guinea and the Sudan Savannahs (Larsen 2006). In Ghana, the Sudan Savannah elements do not seem to have a natural home and are scattered in an unpredictable manner across the extreme north of the country along the Burkina Faso frontier (Larsen 2006).

About 4% of the total butterfly species recorded in Ghana are however either ubiquitous (found everywhere) or found in special habitats (Larsen 1994).

About a fifth of Ghana's butterflies are fruit-feeders (Larsen 2005b). Fruit-feeding butterflies belong to the Nymphalidae family and in Africa mainly include the subfamilies Charaxinae, Satyrinae, Limenitidinae, Nymphalinae, Biblidinae, Heliconiinae and Apaturinae). These subfamilies are speciose with high levels of diversity and endemism in West Africa (Larsen 2005b). About 129 (or 13% of) species known from Africa are endemic to the subregion (Larsen 2001; 2006). More than 24 of these subregional endemics are strictly endemic to Ghana and in some cases, to the adjoining forests of western Côte d'Ivoire (Larsen 1994).

2.4 State and fate of forests in Ghana

Ghana is ecologically divided into a high-forest zone in the south, accounting for about a third of the land area (8 million hectares), a savanna zone (14.7 million hectares) mostly in the north, and a transition zone (1.1 million hectares) between the north and the south (ITTO 2006). Estimates of the total forested area in Ghana range between 2.72 million hectares and 6.34 million hectares (FAO 2005), the former estimate excludes the non-Permanent Forest Estates (PFEs). In total, there are 266 PFEs in Ghana (Hawthorne & Abu-Juam 1995; ITTO 2006), 204 forest reserves in the high-forest zone covering an area of 1.62 million hectares

and 62 forest reserves in the savanna zone covering 600,000 hectares (ITTO 2006). The forests in the high-forest zone of Ghana, according to the International Timber Trade Organization's (ITTO) most recent country report (ITTO 2006) are functionally classified as: timber production, 762,400 hectares (47%); permanent protection, 352,500 hectares (22%); rehabilitation, 122,000 hectares (7%); conversion, 127,000 hectares (8%); and not inventoried, 270,000 hectares (16%). Most of Ghana's forests in the high-forest zone are closed canopy (Hall & Swaine 1976). There are forest plantations (non-PFEs) distributed all across the country with the majority occurring in the high-forest zone in southern Ghana. The estimated area of planted forest in 2003 was about 97,000 hectares (ITTO 2006). The dominant species in these forest plantation estates is *Tectona grandis* (Teak). Ghana began planting *Tectona grandis* (Teak) in the Volta region in 1975. Between 2000 and 2004, more than 50,000 hectares of new planted forest had been established, 60% of which were teak plantations (ITTO 2006).

It is widely believed that the beginning of the twentieth century saw an approximately one-third of Ghana's 238,500 km² land area covered by natural tropical forest (Wagner & Cobbinah 1993). Since then, the tropical forests in Ghana have faced continual pressures of destruction. Across all the countries of the West African sub-region, the major proximate cause of deforestation is claimed to be conversion of land for agriculture, with logging playing a major role in some areas (Leach & Fairland 2000). According to Fair (1992) Ghana's rainforests have been reduced from 8.2 million hectares to 2 million hectares since 1900. Leach & Fairland (2000) recount that forests in West Africa have generally experienced marked deforestation during the twentieth century, only accelerated in the last few decades (Leach & Fairland 2000). For instance, in a space of 15 years (1990 – 2005), Ghana has lost 1.9

million hectares or 26% of her forest cover (IUCN 2006). The rate of forest loss in Ghana remains the highest in the West African sub-region (Sayer *et al.* 1992; FAO 1993; Tables 2.2 and 2.3).

Table 2.2 Forest cover in West African countries estimated at 1985 as percentage of the 'original' forest cover

Country	'Original' forest cover (in thousand hectares)	Forest area in 1985 (in thousand hectares)	Percent of forest area in 1985
Benin	1,680	42.4	2.5
Ghana	14,500	1,584.2	10.9
Guinea	18,580	765.5	4.1
Ivory Coast	22,940	2,746.4	12.0
Liberia	9,600	4,123.8	43.0
Sierra Leone	7,170	506.4	7.1
Togo	1,800	136.0	7.6

Source: Sayer *et al.* (1992): Page 74

Table 2.3 Forest cover change between 1980 and 1990 in West African countries

Country	Forest areas in 1990 (tropical rainforest and moist deciduous forest) (in thousand hectares)	Forest loss /year 1981-1990 (in thousand hectares)	Percent of total forest lost /year
Benin	1,183	56.7	1.4
Ghana	9,171	134.0	1.5
Guinea	6,565	86.6	1.2
Ivory Coast	10,831	119.4	1.1
Liberia	4,634	25.4	0.5
Sierra Leone	1,889	12.3	0.7
Togo	1,318	21.8	1.6

Source: FAO (1993): Annex 1, Tables 7a and 8a

Presently only about 13% of the original forest cover in West Africa remains (Poorter *et al.* 2004). The remaining 13% forest cover is not without significant

threat of depletion and fragmentation. The current deforestation rate in Ghana is estimated at around 3% per annum (IUCN 2006).

KNUST



CHAPTER THREE

Effects of vertical stratification and temporal variation on fruit-feeding butterfly diversity estimates in West-African tropical forests

Abstract

Because tropical forests face serious threats and are usually situated in developing countries, cheap and easy Rapid Biodiversity Assessment (RBA) seems an ideal strategy for documenting changes in habitat quality and setting conservation priorities. Fruit-feeding butterflies are often used as focal taxa to document biodiversity trends in tropical forests. However, the choice of inappropriate sampling strategies may nullify its value. More extensive data sets that sample multiple months and seasons, and incorporate the vertical dimension are needed as a baseline for designing reliable sampling regimes. Such studies have been so far lacking for fruit-feeding butterflies in West Africa. Here, butterfly trapping studies were undertaken in the two protected forests in Ghana, using both understory and canopy traps, and sampling seven periods covering dry and wet seasons. Both relative species abundance and species richness were on average three to four times higher in the understory than in the canopy traps with strikingly different species composition (only 10% overlap in species between the two communities). The number of individuals and species recorded in a month varied extensively. This study underlined the importance of taking into account temporal variation and vertical stratification when designing RBAs of fruit-feeding butterflies in West African forests. The study recommends the use of both understory and canopy traps, and the inclusion of both 'wet' and 'dry' seasons into RBA sampling regimes.

3.1 INTRODUCTION

Natural habitats in the tropics are globally threatened, and this is expected to cause massive loss of species. Both to document changes in species composition and abundance, and to focus conservation efforts, reliable biodiversity assessment is needed. With limited funds and expertise available, important choices have to be made regarding the type of organisms investigated and the spatial and temporal design of sampling (Trueman & Cranston 1997; Balmford *et al.* 2005b; Green *et al.* 2005). In tropical forests, trapping of fruit-feeding butterflies is often one of the methods of choice. The use of butterflies presents advantages such as; (i) relative ease of identification to species level and a fairly stable taxonomy, (ii) their presence in all terrestrial habitats, (iii) high sensitivity to microclimate heterogeneity and disturbance. In the case of fruit-feeding butterflies, their amenability to standardized repetitive sampling protocols using bait trapping presents a further advantage (New 1997). Moreover, butterflies (Lepidoptera) have been used in most parts of the world in biodiversity assessment programs (e.g. Kremen 1994; Hamer *et al.* 2003; Hill & Hamer 2004; Aduse-Poku & Doku-Marfo 2007; Barlow *et al.* 2007b; Akite 2008), thus providing a global context.

However, few studies have documented the temporal, spatial, and vertical patterns of fruit-feeding butterfly diversity extensively enough to allow an estimation of the value of small-scale biodiversity assessments. These extensive studies all show that the temporal variation in butterfly species richness and abundance is high (DeVries 1988; DeVries & Walla 2001; Hamer *et al.* 2005; Molleman *et al.* 2006). Moreover, the temporal pattern often differs strongly among years. The degree of vertical stratification appears to differ among continents with about half of the species in the Neotropics being canopy specialists (DeVries 1988; DeVries & Walla

2001) while elsewhere, fewer canopy specialists are found (Fermon *et al.* 2003; Fermon *et al.* 2005; Molleman *et al.* 2006). The degree of vertical stratification tends to be reduced when forests are disturbed so that butterflies typical for the canopy are then trapped at ground level (DeVries 1988; DeVries & Walla 2001; Fermon *et al.* 2005). This is important to note because it means that when there is no effect of disturbance, understory trapping would suggest higher species richness in disturbed forests, while in fact canopy species are missed in the undisturbed forests.

Forests in West Africa are among the most imperiled in the world (FAO 1999, 2005), and information on the status of biodiversity in the region is critically needed. About 90% of original West African forest has been destroyed within the last 100 years (Leach & Fairland 2000). Most notably, Nigeria leads globally with deforestation of more than 50% of primary forest between 2000 and 2005 alone (FAO 2005). The deforestation rate in Ghana is estimated at around 3% per annum (IUCN 2006). Other threats such as disturbance, fragmentation, defaunation, pollution and climate change are less readily quantified but will cause important changes in community structure and loss of species. Given these threats, the poor economic situation, and the limited availability of trained staff, a cheap and easy Rapid Biodiversity Assessment (RBA) program is desired for monitoring West African biodiversity (Oliver & Beattie 1997).

West African forests have a sufficiently diverse butterfly fauna to warrant their use as biodiversity indicators. There are approximately 1,100 butterfly species in West Africa of which about 940 are present in Ghana (Larsen 2005b). These are mostly (82%) forest-dwelling species, and about a fifth of these forest-dwelling butterflies are fruit-feeders, to varying degrees (Larsen 2006). Fruit-feeding butterflies belong to

the Nymphalidae family and in Africa mainly include the subfamilies Charaxinae, Satyrinae, Limentidinae and Nymphalinae.

The aim of this study was to quantify two potential sources of bias associated with RBA in a West African rainforest ecosystem: temporal variation and vertical stratification. Two butterfly trapping studies in Bia Biosphere Reserve and Bobiri Forest Reserve, both in Ghana were performed with two transects in a disturbed forest and two transects in a primary forest. Traps were hung both at the understory and canopy, and operated during seven sampling periods throughout the year, including 'dry' and 'wet' seasons.

3.2 MATERIALS AND METHODS

3.2.1 Description of Study Areas

The studies were conducted mainly in two protected forests in Ghana; Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB) between August 2006 and November 2007. BIA is located in the transitional zone between the moist semi-deciduous and evergreen forests, it forms part of the vulnerable upper Guinean rainforest (a strip of tropical moist forest stretching from Sierra Leone to Ghana), listed as one of the world's 25 biodiversity hotspots (Myers *et al.* 2000). It lies in the South Western part of Ghana (06°20" - 06°39"N, 02°58" - 03°13"W) and shares a border with Côte d'Ivoire to the west (Figure 3.1). The reserve is situated in the wet semi-equatorial climatic zone, and has two main climatic seasons; the 'wet'- and 'dry' seasons. The 'wet' season is made up of a major and minor season which are between mid-March to late July and September to early November, respectively. The main 'dry' season is between late December and mid-March. There is also a brief

'dry' period in August between the major and minor 'wet' seasons. It has an annual mean precipitation of about 1,500 mm with temperatures ranging between 20.5°C and 34°C within the year.

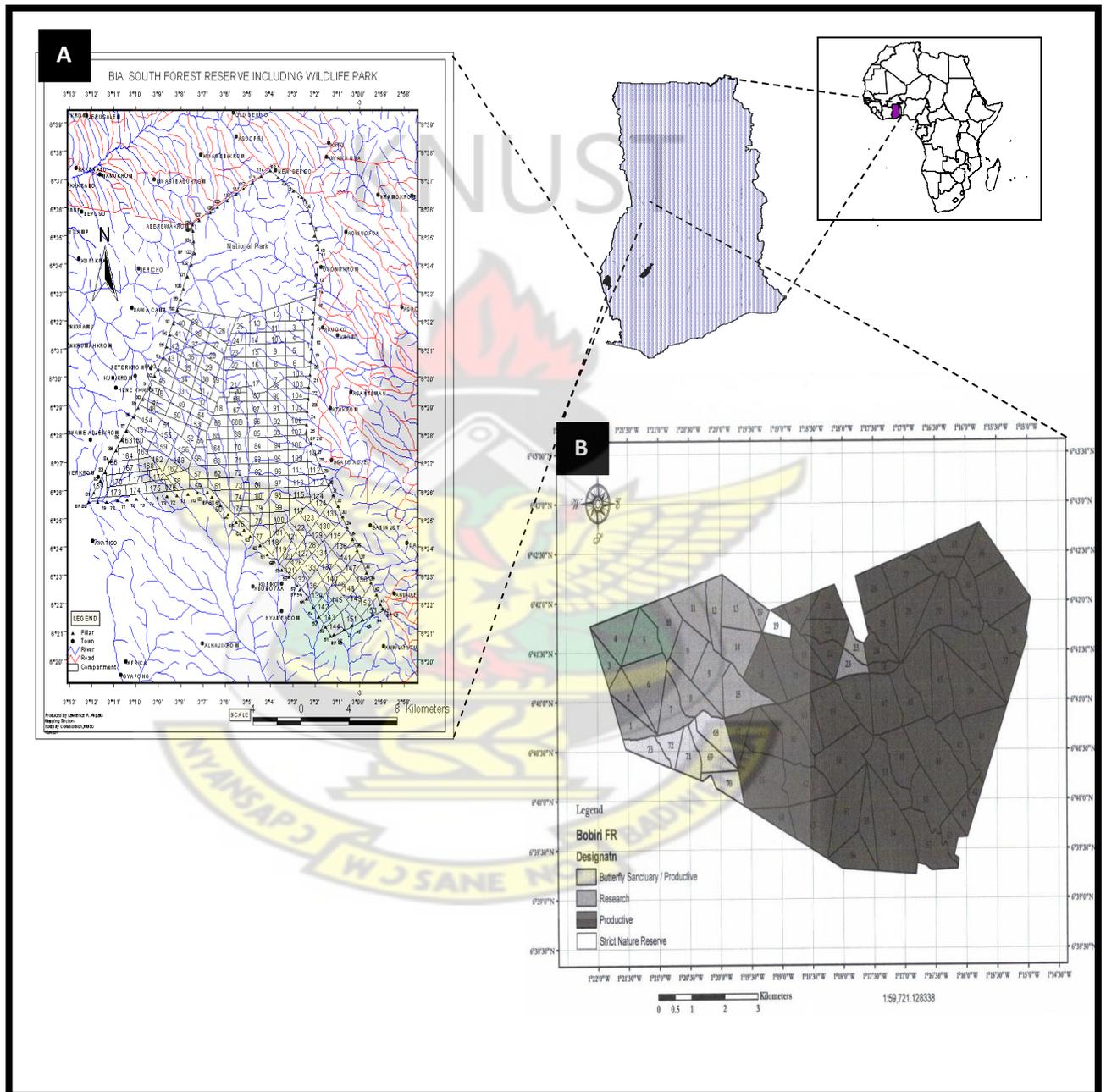


Figure 3.1 Map of study areas showing the two sections or forest blocks in a) Bia Biosphere reserve (BIA) and b) Bobiri Forest Reserve.

BIA is a home for many endemic and rare butterfly species including *Abantis tanobia* and *Liptena seyboui* (Larsen 2001). It holds a viable population of forest elephants *Loxodonta africana*, the highly threatened Bongo, *Tragelaphus eurycerus* and small populations of vulnerable (and nearly extinct) primates like Olive Colobus (*Procolobus verus*) and Miss Waldron's Red Colobus (*P. badius waldroni*) monkeys. It is believed to be the only forest fragment providing a haven for the small endangered chimpanzee (*Pan troglodytes*) population in Ghana. Characteristic of this park is the unique floristic composition of the rainforest and abundance of valuable timber species. There are diverse flora with characteristic herbaceous moist evergreen and semi-deciduous trees. The topography is generally undulating with elevations between 170 and 240 meters above sea level.

The reserve covers a total area of 305.62 km² and it is made up of a National Park in the northern part and a Resource Reserve in the south. The Resource Reserve has noticeable evidence of past logging activities (Hawthorne & Abu-Juam 1995). The vegetation in the National Park however, is generally primary rainforest in good condition with relatively low human impact. The trees in the national park are believed to be among the tallest in West Africa with the highest emergent ones being about 65 meters tall (Martin, 1982). Subsequently, based on the history of logging activities in the reserve, BIA could be categorized into two forest types; 1) primary forest, located within the National Park and 2) secondary forest within the Bia Resource Reserve.

The second study area was Bobiri Forest Reserve (BOB). BOB, also referred in some quarters as Bobiri Butterfly Sanctuary is located in the middle belt of Ghana and about 200km away from BNP (Figures 3.1 and 3.2). BOB lies within the

tropical moist semi-deciduous forest zone (Hall and Swaine, 1981) with a grid reference of latitude 6°25' N and longitude 2°40' W. The reserve covers an area of 54.5 km². It has an average annual rainfall of ~1400mm and is characterized by a long dry season during December and March. Temperatures range between 20.5°C and 34°C over the year. Its mild and major wet seasons are from mid March to June and from late July to November, respectively. The reserve records an average annual rainfall of between 1,200 and 1,750 mm. Unlike BIA, Bobiri Forest Reserve is managed mainly for its timber production and is depleted of mega wildlife fauna like elephants, bongo, antelopes, and monkeys. However, butterflies, and other insects are still abundant in the reserve.

Like BIA, the reserve could also be categorized into two forest blocks, primary (relatively undisturbed) and secondary (disturbed), based on the past logging regimes (Figure 3.1b). The primary forest constitutes portions of the forest adopted by the Forestry Research Institute of Ghana (FORIG) for research purposes several decades ago. These (FORIG experimental plots) compartments are a relatively undisturbed section of the reserve, characterized by tall trees with thick trunks and sparse understory vegetation. The secondary forest however comprises the production compartments which still carry out the orthodox timber production, and features few large trees and a dense understory. The selected compartments for establishing the experimental plots were last logged at least 30 years ago.

3.2.2 Butterfly sampling

The study was conducted between August 2006 and June 2007 in BIA and from December 2006 to November 2007 in BOB. At each study area, butterflies were sampled using four transects; two in each of the two forest types. The distances

between transects were at least a kilometer. Seven (in BIA) and six (BOB) trap stations, spaced 100m apart were demarcated on each transect.



Figure 3.2a Canopy trap mounted between 20-30m with ropes running over emergent trees. The trap is indicated by the white arrow.



Figure 3.2b The author setting out fruit baited trap, made out of IKEA children's toys storage bag.

At each trap station, two traps (one at the forest understorey and the other at the canopy) were installed for quantitative butterfly biodiversity sampling (i.e. in total 56 and 48 stations in BIA and BOB respectively). The forest understorey traps were set between 0.1m and 0.2m above the forest floor (see Figure 3.2a). Canopy traps were suspended between 20m and 30m above the ground with thin ropes running over tree branches forming a pulley system, such that traps could be serviced directly when ropes are lowered (see Figure 3.2b).

Fruit-feeding butterflies were trapped using baited traps, made out of children's toys storage bag ("Manifangst" brand, IKEA, Figure 3.2). The trap

consisted of cylinders of light-viridian coloured nylon netting sewn onto a frame of four plastic hoops, closed and covered by a transparent plastic sheet at the top, and a velcro-fastened slit on the side for removing trapped insects. The basic difference between the modified trap and the standard VanSomeren-Rydon traps used in most similar studies (e.g. DeVries 1987; Hughes *et al.* 1998; Fermon *et al.* 2000; Fermon *et al.* 2005; Oduro & Aduse-Poku 2005; Bossart *et al.* 2006; Molleman *et al.* 2006) is the amount of space provided for butterflies entering the trap. The modified traps have only one slit opening of about 20-25cm at one side, as opposed to an opening around the whole circumference of the cylinder's base in the old trap design.

Small bait-holding plastic plates were velcro-fastened at the bottom of the traps to prevent baits from being toppled over by wind. Otherwise, all baits were refreshed every two days, using the original stock of bait prepared on the first day. A sticky gum, 'Tangle-foot' was applied to the nylon ropes close to traps to prevent ants and other butterfly predators from attacking trapped specimens. The effectiveness of these traps was evaluated in a different experimental set up (see Chapter four of this thesis).

The actual sampling period lasted for seven sampling weeks between August 2006 and June 2007 in BIA, and 11 sampling weeks between December 2006 and November 2007 in BOB. A sampling week consisted of six consecutive days within every month. Butterfly sampling period was designed such that it covered all the climatic seasons within the year. Forty-eight hours prior to setting out the traps, bait of mashed overripe banana mixed with palm wine was prepared and allowed to ferment to increase its attracting potency.

After setting up traps at each trap station, they were inspected daily between 10.00 and 15.00 GMT hours and re-baited when bait was loosened. This process was

repeated for six consecutive days at each trap station during each sampling week except for August in BIA, where data collection could not be done on the sixth day (10th August 2006). Some trap stations could not be used at certain times of the sampling period because their canopy traps were either removed after heavy rainstorm or pushed off by falling tree branches. In total, the quantitative sampling protocol described generated a total of 1,974 and 1,896 trap-days in BIA and BOB respectively. One trap-day is equivalent to one trap sample per day (24 hours after setting out trap). Bait eaten by rodents and traps heavily infested with ants were replaced or refreshed on the day of detection.

3.2.3 Specimen handling and identification

Trapped specimens were transported to the field station in glassine envelopes for identification and analysis. Good quality specimens were retained as DNA samples for other studies (e.g. Aduse-Poku et al. 2009) or as voucher specimens for a planned butterfly curation project at the newly created KNUST museum. Specimen identification was mostly done in the field using available taxonomy treatises (e.g. D'Abrera 1997; Larsen 2005b). Specimens were identified to species-level and grouped into respective taxonomic units (putative species-groups, genus, subfamily, family) following the proposed higher-level classification for Nymphalidae by Wahlberg *et al.* (2003). Charaxinae specimens were identified using Henning (1989) and grouped following proposed phylogeny by Aduse-Poku *et al.* (2009). Satyrinae specimens were identified using Larsen (2005) and grouped following proposed phylogeny by Monteiro and Pierce (2001) and Kodandaramaiah and Wahlberg (2009). Limenitidinae specimens were identified using Hecq (1999, 2000, 2002).

Endemicity, habitat associations (preference for certain forest types), geographic distributions and rarity status of trapped species were adopted from Larsen (2006).

3.2.4 Climatic data

Two HOBO Pro Data Loggers (see Figure 3.3) each were installed at BOB and KIB, one in each forest type, to record ambient temperature and Relative Humidity (RH). Before installing these devices, the protocol and instrumentations were pre-tested in July 2006 and seemed to be working correctly. The HOBO Loggers were programmed to take temperature and RH readings at hourly intervals throughout the study period. Unfortunately, the entire data could not be retrieved because of miscommunication between the gadget and its software at the end of the project. Nevertheless, mean monthly climatic readings for BIA were obtained from the regularly updated climatic database hosted by the European Commission for Protected Areas in Africa (<http://www-tem.jrc.it/pa/>).



Figure 3.3 HOBO data logger being installed on a transect at Bia Biosphere Reserve. The photo of the device is inserted in the top right corner of the plate.

3.2.5 Data Analysis

The terminologies used in the data analysis are defined as follows; *Community* is used here to mean, "a collection of species occurring at a specified place and time" (Magurran 2004). The term *assemblage* however refers to "phylogenetically related members of a community" (Magurran 2004). The *guild* denotes "groups of species that exploit the same resources" (Magurran 2004). *Community composition* refers to "relative abundance of species and guild assemblages" (Putz et al. 2000).

Species richness is defined here as "the number of species of a taxonomic group that can be found in a habitat in a given time-span. *Species diversity* as used here is "the relationship of species richness to the relative abundance or evenness of the individual species present in a habitat". In other words, it is *species richness* and relative species abundance in space and time (Hubbell 2001). *Evenness* however, is "a measure of how equitably individual species are represented in a population".

The outlined study design generated a rich data set consisting of butterfly biodiversity data, species presence-absence data and relative individual abundance over seven and 11-months periods in BIA and BOB respectively. This permitted rigorous assessment of the key concepts of the study in both spatial and temporal dimensions (Magurran 2004). A critical probability (p -)value of 0.05 or less was considered significant for all statistical tests carried out, unless otherwise stated.

The EstimateS package (Colwell 2009) was used to compute all the biodiversity functions, estimators and indices. The mean of six commonly used abundance-based richness estimators (ACE, CHAO2, JACK1, JACK2, MMEAN & BOOTSTRAP) was used to estimate the number of species of fruit feeding butterflies at the canopy, understory and in the reserve. This was more useful since each of these estimators has its own assumptions, which the data rarely met. Using a combination

of these took advantage of the strengths of each and presented more reliable estimates of the community structures. The first four are nonparametric methods of estimating species richness.

Details of the philosophy and computation of these estimators can be found in Magurran (2004) and Krebs (1999). The Michaelis-Menten function (MMMean) estimates species richness by asymptotic functional extrapolation (Colwell & Coddington 1994). Bootstrap richness estimator (BOOTSTRAP) is a parametric method of estimating species richness. A BOOTSTRAP estimator performs better if the assemblages contain too many rare species (Poulin 1999). Bootstrapping is therefore less likely to overestimate true richness, independently of how frequent rare species occur in the community. The estimated richness of each of the six estimators is computed and presented, separately for each vertical strata (canopy and understorey) community in BOB and BIA.

To further provide more information about butterfly community composition and structure in the different strata in the different study areas, the three most widely used indexes of species diversity (Fisher's alpha, Shannon and Simpson) that combine information on richness and relative abundance in different ways (Magurran 2004) were computed for each dataset. Fisher's alpha is a parameter of the log series model fitted to the species abundance data. Shannon and Simpson are however computed as below;

$$H' = -\sum_{i=1}^s p_i \ln p_i \quad \text{and} \quad D = \sum_{i=1}^s p_i^2 \quad (\text{Magurran 2004})$$

Where H' = Shannon index;

D = Simpson index and

S = Number of observed species

the quantity p_i = the proportion of individuals in the i th species.

The Morisita-Horn index was used to quantify the similarity between the two communities. This estimator is among the most robust estimators to sample size and quantifies differences in terms of both the identities and abundances of species (Magurran 2004). It quantifies species turnover in terms of both the identities and abundances of species. The index value ranges from 0 (when no species is shared between the compared communities, **a** and **b**) to 1 (when the compared communities comprise the same species in identical proportions). The Morisita-Horn index (C_{mH}) is calculated as below (Magurran 2004);

$$C_{mH} = \frac{2 \sum_{i=1}^s (n_{ai} \times n_{bi})}{(d_a + d_b) \times (N_a \times N_b)} \quad \text{where} \quad d_b = \frac{\sum_{i=1}^s n_{bi}^2}{N_b^2}, \quad d_a = \frac{\sum_{i=1}^s n_{ai}^2}{N_a^2}$$

and

s = total number of species at both sites

N_a = the total number of individuals of all species collected at site a

N_b = the total number of individuals of all species collected at site b

n_{ai} = the number of individuals of the i th species collected at site a

n_{bi} = the number of individuals of the i th species collected at site b

and, in the denominator, there are two terms summed that are defined as:

An interactive computer program for null model analysis in community ecology, EcoSim (Gotelli & Entsminger 2009) was used to test for community patterns by rarefaction. The rarefaction technique was used to standardize and compare species richness computed from samples of different sizes. Rarefaction allowed for the calculation of the species richness for a given number of sampled individuals and also constructs rarefaction curves. These rarefaction curves are plots of the number

of species as a function of the number of individuals sampled. EcoSim performs Monte Carlo randomizations to create "pseudo-communities", and then statistically compares the patterns in these randomized communities with those in the real data matrix.

Patterns of species dominance or evenness were compared between habitats using species rank–abundance plots. Rank-abundance curves represent both species richness and evenness, which are important measures of biodiversity. It overcomes the shortcomings of the biodiversity index, which cannot display the relative role different variables played in its computation. Species evenness is derived from the slope of the line that fits the graph; a steep gradient indicates low evenness as the high ranking species have much higher abundances than the low ranking species. A shallow gradient indicates high evenness as the abundances of different species are similar.

The statistical package R (R Development Core Team 2009) was used for the data analyses. Individual abundance per sampling period was calculated as the mean number of individuals per trap per day to correct for the slight temporal variation in trap numbers. The Wilcoxon rank-sum statistic (Mann–Whitney) was used to test the null hypothesis that the two (canopy and understorey) samples are drawn from a single population. Wilcoxon rank-sum statistic is one of the best-known non-parametric significance tests for equal sample sizes. Rank-based tests are argued to be more powerful than parametric tests for very (positively) skewed (heavy tailed) distribution dataset like those obtained in the study. Rank-based tests are relatively efficient in dealing with outliers than most parametric tests (Quinn & Keough 2002).

A generalized linear mixed-model (GLMM, Bolker et al. 2009) with Poisson link function was used for evaluating the variations of butterfly biodiversity in time (seasons) and in space (vertical stratification and forest types) because of the inherent log-linear distribution of count data. In this particular case the mixed-effects model was particularly useful because the assumption of independence of error was violated. Measurements were taken at the same paired sites in different seasons creating a temporal pseudoreplication (repeated measurements). The mixed-model took care of the non-independence of errors by modeling the covariance structure introduced by the many groupings (e.g. transect and trap stations) inherent in the present study data (Crawley 2007). To test for differences between the individual abundances of species captured at canopy and understorey levels, a two-tailed χ^2 - chi-square test was performed .

3.2.6 Minimization of Experimental Error

In any community study, there exists an incalculable and viable error term associated with estimating the relative abundance of each species (Kremen 1994). For these studies, different species might have differently been attracted by the bait or might have possibly escaped from the trap. While these or similar sources of error cannot be eliminated in estimating relative abundance of multi-species assemblages, they were minimized in this study by standardized sampling across the trap stations. To avoid committing either type I (rejecting the null hypothesis when it is indeed true) or type II error (accept the null hypothesis when it is false) error, a level of significance of $p < 0.05$ was adopted for all statistical analyses in the study.

3.3 RESULTS

3.3.1 Species composition in Bia Biosphere Reserve and Bobiri Forest Reserve

In BIA, a total of 1,974 trapdays between August 2006 and June 2007 yielded 2,764 individuals of 140 (observed) fruit-feeding butterfly species from 28 trap stations (Appendix 1). All but three specimens were positively identified to species-level. Butterflies captured came from seven subfamilies and 27 genera, all belonging to the fruit-feeding guild – Nymphalidae (Table 3.1). As many as 45 of the species captured were recorded for the first time in BIA (refer to Appendix 1 for the list of Reserve first-time-record species).

In BOB, a total of 4,783 butterfly individuals belonging to 110 (observed) species, 28 genera and eight subfamilies were recorded during the entire study period (1,896 trap days, December 2006 – November 2007). The 110 species excludes four additional species (*Bebearia maledicta*, *Bicyclus maesseni*, *Euphaedra perseis*, *Euriphene ampedusa*) which were recorded only during the reconnaissance survey in August 2006. All but two species (*Zophopetes cerymica* and *Gamia shelleyi*) were from the Nymphalidae family of butterflies. All specimens (except for one, *Cymothoe* sp) were positively identified to species. Five fruit-feeding butterfly species (*Bicyclus maesseni*, *B. auricruda*, *Euriphene atossa*, *Bebearia lucayensis* and *Euphaedra splendens*) were recorded for the first time in the reserve.

In both BOB and BIA, the pooled samples were dominated by members of the Satyrinae and Limenitidinae subfamilies (Table 3.1). The two subfamilies alone constituted about 90% and 80% of the total individuals caught in BOB and BIA respectively.

Table 3.1 Summary of the fruit-feeding butterfly subfamilies and genera recorded in Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB). The numbers in the parentheses are the relative percentages of individuals from the genus. The dominant genera are in **bold** type.

Subfamily	Genus	Number of individuals		Number of species	
		BIA	BOB	BIA	BOB
Apaturinae	<i>Apaturopsis</i>	13 (0.5)	51 (1.1)	1	1
Biblidinae	<i>Eurytela</i>	2 (0.1)	7 (0.1)	2	2
	<i>Sevenia</i>	2 (0.1)	--	2	--
	<i>Neptidopsis</i>	1 (0.0)	1 (0.0)	1	1
	<i>Byblia</i>	--	1 (0.0)	--	1
Charaxinae	<i>Charaxes</i>	482 (17)	406 (8.5)	28	25
	<i>Palla</i>	35 (1.3)	31 (0.6)	4	4
	<i>Euxanthe</i>	1 (0.0)	3 (0.1)	1	1
Satyrinae	<i>Bicyclus</i>	939 (33)	2,647 (55)	22	17
	<i>Gnophodes</i>	140 (5.1)	442 (9.2)	2	2
	<i>Melanitis</i>	54 (2.0)	190 (4.0)	1	2
	<i>Hallelesis</i>	21 (0.8)	--	1	--
	<i>Elymniopsis</i>	6 (0.1)	24 (0.5)	1	1
Libytheinae	<i>Libythea</i>	3 (0.1)	14 (0.3)	1	1
Limenitidinae	<i>Euphaedra</i>	383 (14)	336 (7.0)	26	13
	<i>Euriphene</i>	259 (9.4)	160 (3.3)	7	8
	<i>Bebearia</i>	257 (9.3)	266 (5.6)	18	13
	<i>Euryphura</i>	46 (1.7)	33 (0.7)	1	1
	<i>Cymothoe</i>	43 (1.6)	77 (1.6)	6	6
	<i>Aterica</i>	42 (1.5)	51 (1.1)	1	1
	<i>Pseudacraea</i>	11 (0.4)	12 (0.3)	2	2
	<i>Harma</i>	6 (0.2)	15 (0.3)	1	1
	<i>Catuna</i>	5 (0.2)	2 (0.0)	3	1
	<i>Neptis</i>	2 (0.1)	--	2	--
	<i>Pseudathyma</i>	2 (0.1)	1 (0.0)	2	1
	<i>Pseudoneptis</i>	--	1 (0.0)	--	1
Nymphalinae	<i>Salamis</i>	4 (0.2)	--	1	--
	<i>Hypolimnas</i>	3 (0.1)	3 (0.1)	2	1
	<i>Antanartia</i>	2 (0.1)	1 (0.0)	1	1
	<i>Kallimoides</i>	--	5 (0.1)	--	1
	<i>Junonia</i>	--	1 (0.0)	--	1
Heliconiinae	<i>Lachnoptera</i>	--	1 (0.0)	--	1

In BIA, the Limenitidinae subfamily was represented by 69 species from 11 genera and constituted 41% (1,160) of all individuals caught. Satyrinae, consisting of 38 species from four genera, made up another 38% (1,056) of the total sampled individuals in BOB. The remaining 21% of the sampled (pooled) individuals were predominantly composed of ~95% (518) Charaxinae subfamily members. Similar trends of dominance were also observed in BOB with trapped species and individuals mainly came from three Nymphalidae subfamilies; Limenitidinae, Satyrinae and Charaxinae. Again, Limenitidinae was the most dominant subfamily, contributing nearly half of the total species and 20% of the 4,783 individuals trapped. The Satyrinae on the other hand made up 19 (20%) of the total species but were dominant (75%; 3,303) among the total butterfly individuals captured during the entire study period in BOB. The Charaxinae subfamily made up 10% and 27% of the total sampled individuals and (observed) species respectively. The remaining trapped specimens were from the Nymphalinae, Biblidinae, Apaturinae and Libytheinae subfamilies (Table 3.1).

Individual species abundances ranged from 1,403 in BOB and 154 in BIA (all for *Bicyclus funebris*) to a single individual (for 18 and 28 species in BOB and BIA respectively). Within subfamilies, samples were dominated by just one or two abundant genera, which in turn were dominated by a few common species. For instance, in BIA, 81% of the 1,160 Satyrinae individuals belong to the genus *Bicyclus*, which were dominated by four species (*B. funebris*, *B. sandace*, *B. abnormis* and *B. zinebi*). These four species together constituted ~60% (533) of the total trapped *Bicyclus* individuals, equivalent to 45% of the total Satyrinae individuals trapped and ~20% of all individuals captured in BIA (Table 3.1). Similarly, there was higher abundance of *Charaxes* (93%) within Charaxinae,

and *Euphaedra* (36%), *Euriphene* (25%) and *Bebearia* (24%) within the Limenitidinae subfamilies (Table 3.1). The five most abundant *Charaxes* species (*C. cynthia*, *C. etheocles*, *C. lucretius*, *C. protoclea* and *C. tiridates*) made up 62% of the 28 *Charaxes* species trapped (Appendix 1).

The situation was no different in BOB, where *Charaxes* alone constituted 406 (92%) of the total 440 Charaxinae individuals caught in BOB during the entire study period. Of the total 954 Limenitidinae individuals trapped, *Euriphene*, *Bebearia* and *Euphaedra* made up 17%, 27% and 35% respectively. Approximately 80% (2,647) of the total Satyrinae individuals caught were *Bicyclus*. *Bicyclus* alone made up more than half (55%) of the total number of individuals caught in BOB (Table 3.1). A closer examination of relative species abundance revealed that the genus is further dominated by only a few species in the reserve. For instance, more than half (53%) of the total 2,647 *Bicyclus* individuals trapped in BOB were of one species, *Bicyclus funebris* (Appendix 1). Nearly 70% of the remaining 47% (1,244) *Bicyclus* individuals were of three species; *B. vulgaris* (193), *B. abnormis* (226), and *B. sandace* (443).

The sample-based, non-randomized (traditional) species accumulation curve generated, using data pooled from all trap stations in BIA (Figure 3.4a) and BOB (Figure 3.4b) did not reach an asymptote, suggesting that further sampling effort could have yielded additional species. Similar non-asymptote curves were obtained when the data was partitioned into understorey and canopy strata communities and analyzed separately (Figure 3.4). The mean estimated number of fruit-feeding butterflies in BIA and BOB using six commonly-used richness estimators (ACE, CHAO1, JACK1, JACK2, MMEAN and BOOTSTRAP) were 162 ± 11 (mean \pm SD) and 126 ± 8 respectively. The computed alpha diversities of fruit-feeding butterflies in

the reserves were 20.3 (SD=3.2 for BOB) and 31.1 (SD=4.1 for BIA). The estimated richness and diversity values of the various biodiversity indices for the different datasets are presented in Table 3.2.

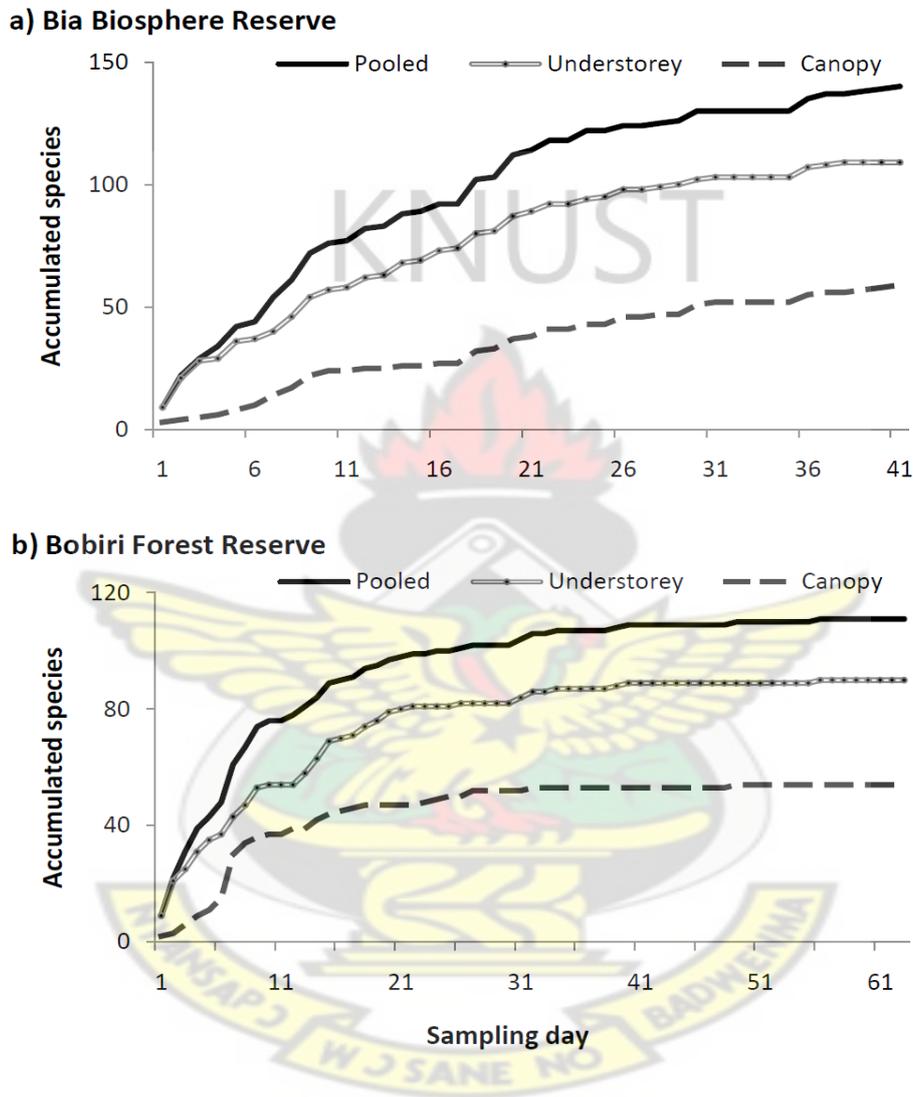


Figure 3.4 Sample-based species accumulation curves for the different vertical strata communities and a combined data set (Pooled) in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve

Table 3.2 Comparison of estimated species richness and diversity (mean values with standard deviations in parentheses) of the understorey and canopy strata, and both strata combined, for Bia and Bobiri forest reserves

Study area Dataset	Trap ^a days	Indiv	Sobs	Estimate species richness						Computes species diversity		
				ACE	Chao2	Jack1	Jack2	Bootstrap	MM	Alpha	Shannon	Simpson
Bia Biosphere Reserve												
Canopy	987	577	59	81.4 (1.45)	74.45 (9.2)	78.51 (4.4)	87.3 (1.8)	67.86 (0.7)	66.22	16.5 (1.3)	3.28 (0.01)	18.5 (0.1)
Understorey	987	2,187	109	120 (1.55)	119.4 (6.4)	127.5 (4.4)	132 (3.2)	118.5 (0.8)	116.1	24.1 (1.2)	3.83 (0.01)	31.3 (0.2)
Canopy + Understorey	1,974	2,764	140	162 (2.01)	159.8 (9.7)	168.3 (5.6)	178 (3.6)	153.7 (0.9)	147.3	31.1 (1.3)	4.11 (0.01)	41.9 (0.4)
Bobiri Forest Reserve												
Canopy	948	631	54	70.5 (1.73)	65.48 (7.9)	68.76 (4.1)	75.7 (2.1)	60.75 (0.7)	60.43	14.1 (1.1)	3.35 (0.01)	21.5 (0.3)
Understorey	948	4,152	90	98.9 (1.09)	96.95 (4.7)	105.8 (4.7)	106 (2.4)	98.30 (0.6)	93.55	16.2 (0.7)	2.87 (0.02)	7.18 (0.2)
Canopy + Understorey	1,896	4,783	110	126 (1.72)	123.5 (7.4)	130.7 (4.6)	137 (0.9)	120.6 (0.9)	115.5	20.3 (0.8)	3.18 (0.02)	9.08 (0.3)

^aTrap day is calculated as the number of sampling days multiplied by the number of trap used

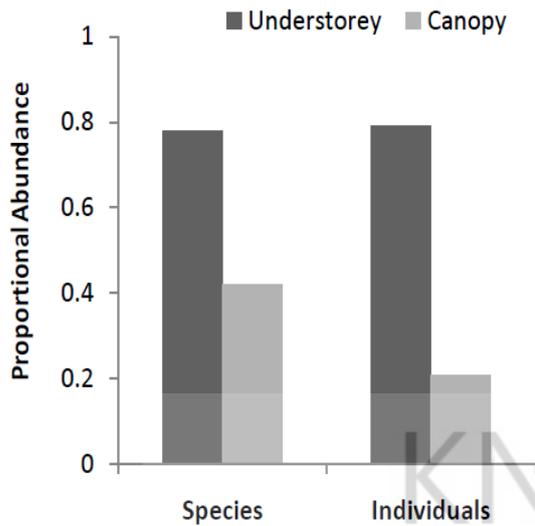
The figures in parentheses are the standard deviations of each of the corresponding biodiversity indexes. Indiv = number of individuals, Sobs = number of observed species, ACE = Abundance-based coverage estimator, Chao 2 = Chao 2 richness estimator, Jack 1 = Jackknife first order richness estimator, Jack 2 = Jackknife second order richness estimator, MM = Michaelis-Menten richness estimators, Alpha = Fisher's alpha diversity

3.3.2 Vertical stratification pattern of fruit-feeding Butterflies in Bia Biosphere Reserve and Bobiri Forest Reserve

Both individual numbers and species richness were higher in the understory than in the canopy traps (Figures 3.5 and 3.6). Using pooled data from all microhabitat types (canopy and understory, in disturbed and 'undisturbed' forest blocks) in BIA, I found the mean individual abundance per trapday to be nearly five times higher in the understory (2.21 ± 0.04 , mean \pm SD) than in the canopy (0.58 ± 0.09 ; Wilcoxon rank sum test, $W = 731995.5$, $p < 0.001$). In BOB, I observed an even larger differential between the two vertical strata communities; there were at least seven times as many individuals per trap at the understory (4.35 ± 0.24 , mean \pm SD) than there were at the canopy traps (0.60 ± 0.04 ; Wilcoxon rank sum test, $W = 652550.5$, $p < 0.001$).

Similarly, using the number of trapped species as the metric, the mean trapday richness was about four times higher in the understory in BIA (1.90 ± 0.06 , mean \pm SD) compared to the canopy's 0.52 ± 0.03 (Wilcoxon rank sum test, $W = 731995.5$, $p < 0.001$). In BOB, the mean richness per trap per-day was at least three times higher at the understory (2.3 ± 0.09 , mean \pm SD) than at the canopy (0.7 ± 0.07) (0.7 ± 0.07 ; Wilcoxon rank sum test, $W = 639295$, $p < 0.001$). The pattern of differences between both mean abundance and richness per trapday in the two strata was consistent for each forest type, suggesting little influence of forest types on vertical stratification of fruit-feeding butterflies (GLMM, $p > 0.05$, for both BOB and BIA). In the same vein, the estimated species richness (using mean of six commonly used estimators) was higher in the understory (122 ± 6 and 100 ± 5 , mean \pm SD for BIA and BOB respectively) than in the canopy stratum community (78 ± 8 and 67 ± 6 for BIA and BOB respectively).

a) Bia Biosphere Reserve



b) Bobiri Forest Reserve

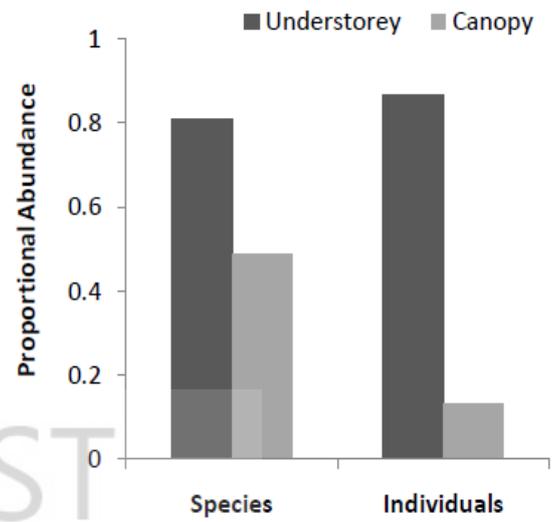
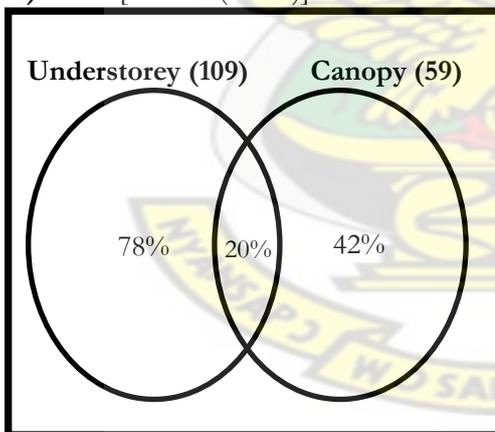


Figure 3.5 Proportions of individuals and species of fruit-feeding butterflies captured in banana baited traps installed at two different vertical strata or heights (understorey and canopy) in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve

a) BIA [N=140 (100%)]



b) BOB [N=110 (100%)]

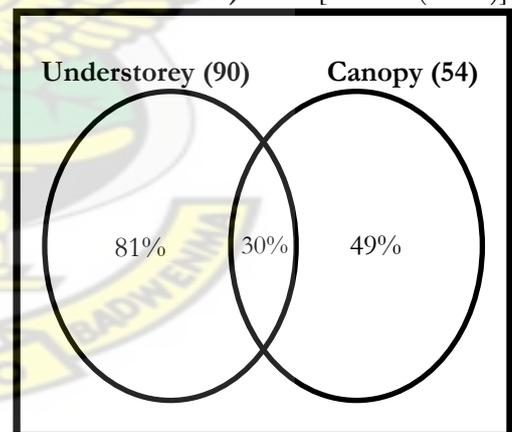
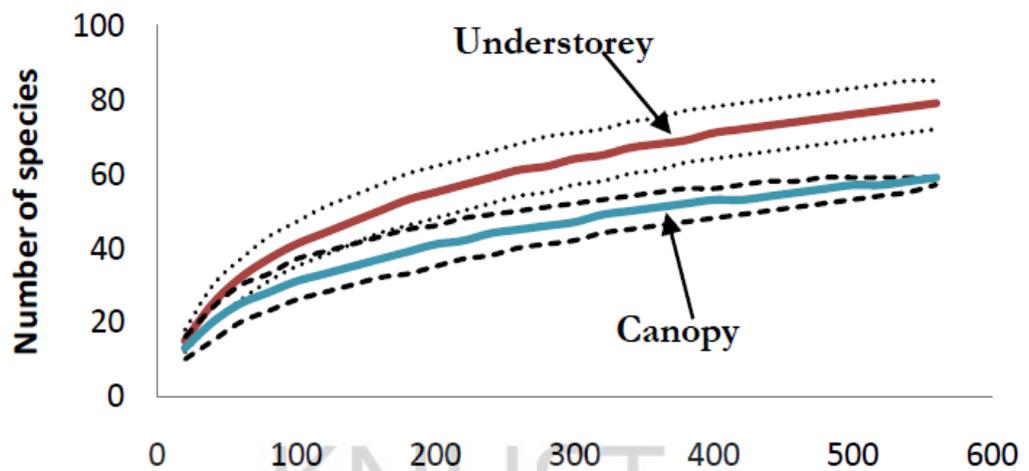


Figure 3.6 Percentage of species captured from the different strata communities in a) Bia Biosphere Reserve (BIA) and b) Bobiri Forest Reserve (BOB). The total number of species (140 for BIA and 110 for BOB) recorded are expressed as 100% for each reserve. The actual numbers of species caught at each strata community are indicated above the circle.

To allow for effective comparison of butterfly species richness between the understorey and canopy strata, a rarefaction technique was used to standardize stratum-level sample sizes. Drawing 560 and 631 individuals randomly from each stratum's community dataset in BIA and BOB respectively, rarefaction curves with 95% confidence limits were generated (Figure 3.7). The rarefied individual-based species accumulation curves suggested a significantly higher expected number of species in the BIA understorey than in its canopy (Figure 3.7a). In BOB, the difference between the two strata was not significant, although the understorey had marginally higher species richness than the canopy (56 versus 54; Figure 3.7b).

The composition of species in the canopy and understorey communities in both BOB and BIA was strikingly different at all taxonomic levels: subfamily, genus and species (Figure 3.8, Appendix 1). The canopy-understorey similarity index generated using the Morisita-Horn index indicated a low (11% in BIA and 20% in BOB) species overlap between the two strata. In both study areas, the understorey fruit-feeding butterfly community was composed almost entirely of members of the Limenitidinae and Satyrinae subfamilies. *Bicyclus* contributed the largest proportion of the total understorey individuals in both BIA and BOB (Appendix 1). Individuals of this genus alone made up 43% (918) and 62% (2,571) of the total butterflies caught at the understorey in BIA and BOB respectively. *Euphaedra*, *Euriphene* and *Bebearia* contributed 30%, 20% and 20% respectively of the remaining 57% (1,269) understorey individuals in BIA. In BOB, the remaining 38% (1,580) understorey individuals were made of 26% (409) *Gnophodes*, 21% (336) *Euphaedra* and 17% (266) *Bebearia*.

a) Bia Biosphere Reserve



b) Bobiri Forest Reserve

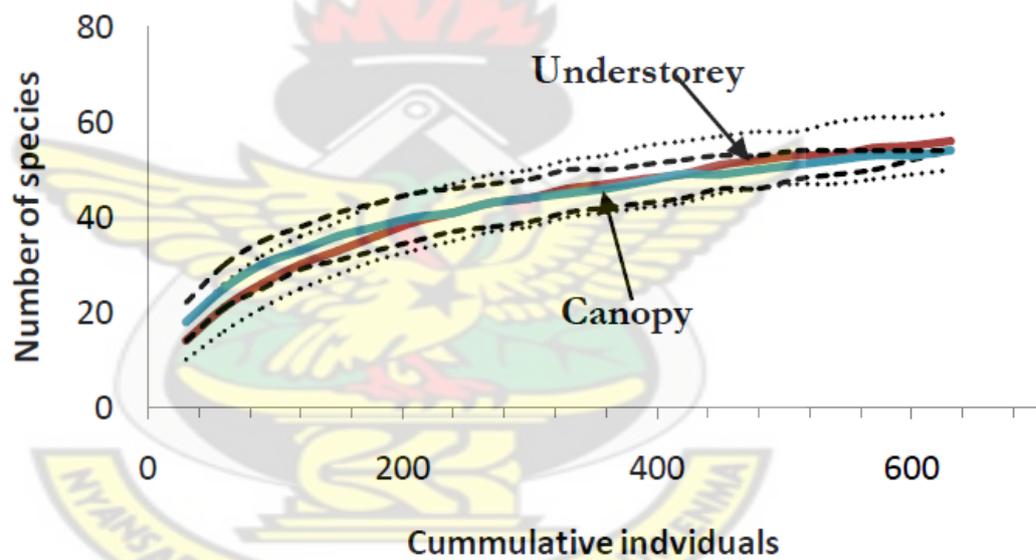


Figure 3.7 Individual-based rarefaction curves comparing fruit-feeding butterfly species richness at the understorey and canopy levels in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve. The dashed lines fitted to each thick line show the 95% confidence intervals.

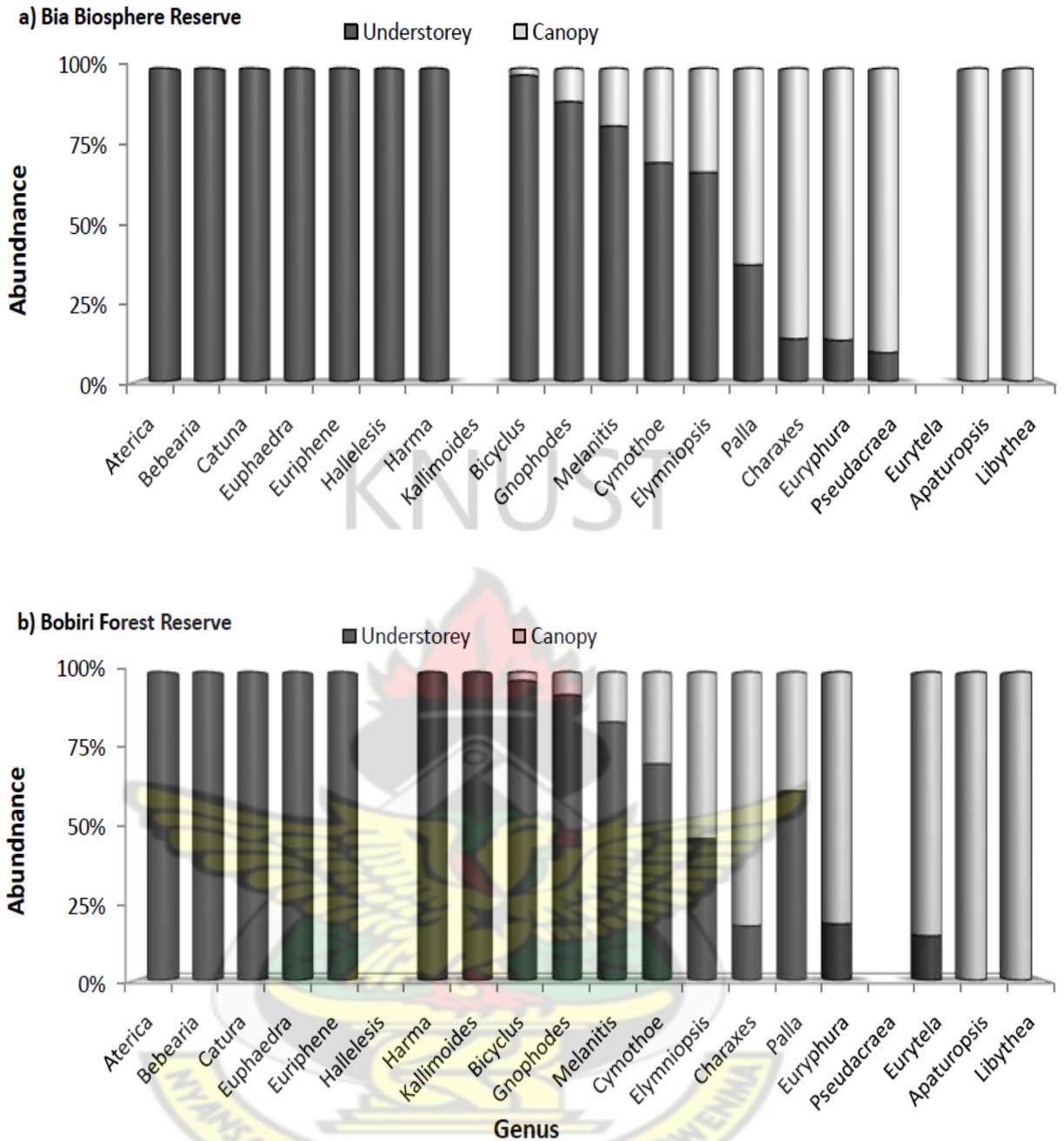


Figure 3.8 Percentage of the 20 most abundant genera at different trap heights (canopy and understorey) in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve. A gap on the genus axis means that no member of the genus was captured at that particular local community.

Euphaedra contributed the most to the overall understorey species richness in BIA with 26 observed species. *Bicyclus* followed with 22, only seven of which were also recorded at the canopy. In BOB, *Bicyclus* contributed 17 of the 90 understorey species, with *Euphaedra* and *Bebearia* contributing 13 each to the total understorey species pool. None of the individuals (941 in BIA; 762 in BOB) and species (53 in BIA; 34 in BOB) of *Bebearia*, *Euphaedra*, and *Euriphene* were captured at the canopy (Figure 3.8). Apart from these 53 and 34 apparently dedicated understorey specialists in BIA and BOB respectively, species of genera like *Aterica*, *Catuna*, *Hallelesis*, *Harma* and *Kallimoides* were also only captured at the forest understorey. Performing a two-tailed χ^2 (chi-square) test on each species using the number of individuals of the species caught at canopy and understorey levels, it came to light that, 52 and 42 fruit-feeding butterflies in BIA and BOB respectively could be categorized as truly 'understorey species' (Table 3.3). Refer to Appendix 1 for the list of 'understorey species'. As many as 39 and 25 other species were caught only at the understorey in BIA and BOB respectively, but their individual abundances were not enough to allow for an evaluation of their vertical strata affiliations.

In contrast, the canopy stratum was largely preferred by species of the Charaxinae (*Charaxes* and *Palla*) subfamily and genera *Euryphura*, *Apaturopsis* and *Libythea* (Figure 3.8). Nearly 90% (440 of 518) and 80% (349 of 440) of the total Charaxinae individuals sampled were from the canopy in BIA and BOB respectively. Species of these genera dominated the canopy in terms of both number of species (richness) and individual abundance. In BIA, the genus *Charaxes* constituted 72% of the total 577 individuals captured at the canopy and contributed 28 of the total 59 canopy species richness in BIA. *Euryphura* and *Palla* made up 25% and 14% of the remaining 92 canopy individuals. In BOB, *Charaxes* made up 53% of the total 631 canopy individuals and contributed 23 of the total 54 canopy species. Other genera

with strong affiliation to the forest canopy were *Apatuopsis*, *Libythea* and *Pseudacraea* (Figure 3.8). The χ^2 -test did indicate that 15 and 13 species in BIA and BOB respectively were true 'canopy specialists' (Table 3.3). Refer to Appendix 1 for the list of 'canopy species'. Some species (24 in BIA and 25 in BOB) were as well caught only at the canopy but their individual abundances were not enough to evaluate their vertical strata affiliations.

Even among the species captured at both trap heights (shared species, 28 in all in BIA, and 34 in BOB), similar polarization was visible. Almost invariably, the shared *Bicyclus* species contributed more to the total of understorey individuals than expected by chance alone (see Appendix 1). We found a similar situation with shared *Charaxes* species' contribution to the sampled canopy individuals. *Charaxes fulvescens* was however an exception to this recurring observation, recording a significantly larger individual abundance at the understorey than at the canopy level ($\chi^2=0.43$; $df=1$; $p<0.05$). Only 7% and 15% of the species trapped in BIA and BOB respectively could be categorized as generalists (Table 3.3).

Table 3.3 Number of species trapped in Bia Biosphere Reserve and Bobiri Forest Reserve with categorization to stratum.

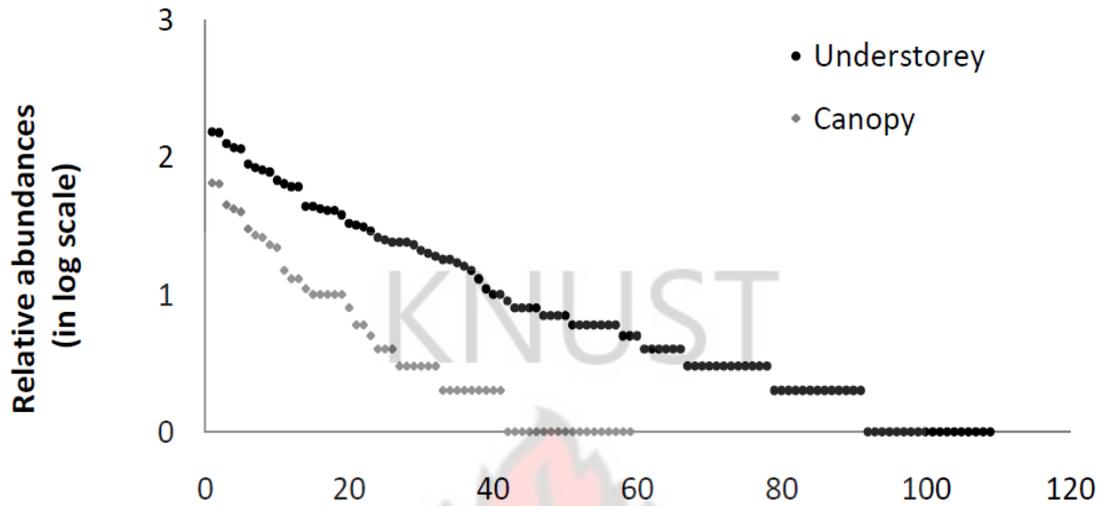
Study area	Total number of species captured	Number of species				Generalists
		Understorey specialists	Only in the understorey, but not significant	Canopy specialists	Only in the canopy, but not significant	
Bia Biosphere Reserve	140	52	39	15	24	10
Bobiri Forest Reserve	110	42	25	13	14	16

Regarding heterogeneity or evenness, the understorey butterfly community exhibited a more even species-abundance distribution (Figure 3.9a) with higher alpha diversity scores of 24.13 ± 1.15 than the canopy (16.46 ± 1.25) in BIA. Values of Shannon and Simpson diversity indices for the understorey strata community were higher than the canopy (Table 3.2). However, in BOB there were conflicts in the diversity indices; Fisher's alpha scored the understorey strata as the more diverse, with the Shannon and Simpson indices suggesting the canopy strata to be more diverse than the understorey (Table 3.2). Nevertheless, close examination of the Whittaker plots generated for the two strata communities in BOB (Figure 3.9b), revealed that their diversities do not significantly differ (Kolmogorov-Smirnov two-sample test; $D = 0.173$, $p = 0.10$).

3.3.3 Vertical distribution of species of conservation concern

Overall, 20 West African endemic fruit-feeding butterflies species were recorded in BIA; 14 (11 of them *Euphaedra*) were captured only at the understorey, three (*Cymothoe mabillei*, *Bicyclus abnormis* and *B. maesseni*) at both levels and two (*Charaxes plantroui* and *C. petersi*) exclusively from canopy traps (Table 3.4). Three of the West African endemics (*Euphaedra ignota*, *E. mariaechristinae*, and *E. minuta*) were restricted to Ghana. Except for two very rare species (*Euphaedra ignota* and *Charaxes petersi*), all the trapped endemics were generally common or very common in distribution across Ghana. In BOB, I caught eight West African endemics, one (*Euphaedra minuta*) a Ghanaian endemic. All endemics were caught at the understorey except three species (*Bicyclus abnormis*, *B. zinebi* and *Cymothoe mabillei*) whose individuals were trapped at the canopy as well (Table 3.4).

a) Bia Biosphere Reserve



b) Bobiri Forest Reserve

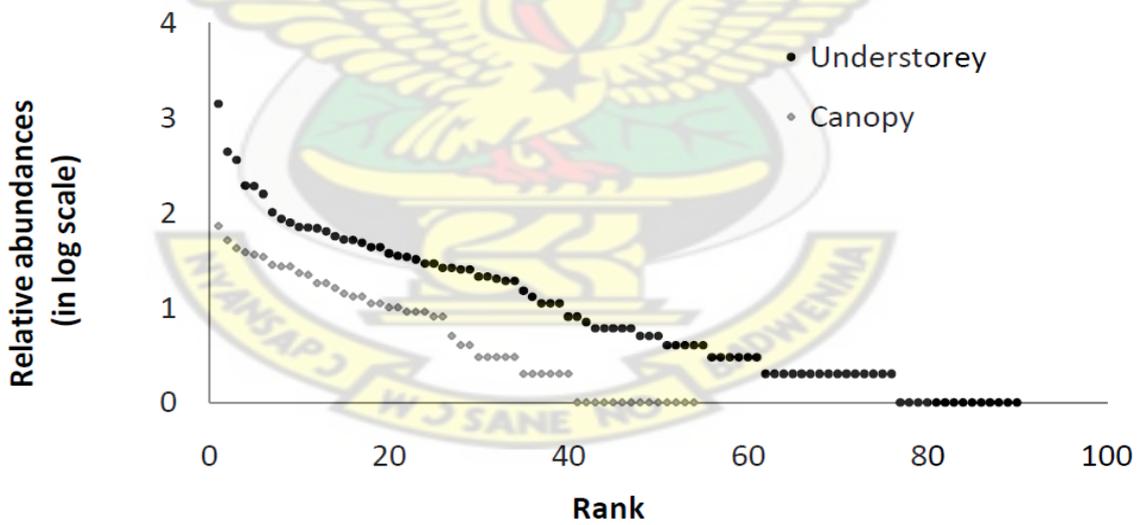


Figure 3.9 Rank-abundance distribution of fruit-feeding butterflies captured at the forest understory and canopy in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve

Table 3.4 List of species of conservation importance (rare and regional endemics) in Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB)

Subfamily Species	Endemicity ^a	Rarity ^b	Number of individuals			
			BIA		BOB	
			Understorey	Canopy	Understorey	Canopy
Apaturinae						
<i>Apatuopsis cleochares</i>		RA	--	13	--	51
Limenitidinae						
<i>Euphaedra mariachristinae</i>	en	NR	4	--	--	--
<i>Euphaedra modesta</i>	en	NR	4	--	--	--
<i>Euphaedra minuta</i>	en	RA	3	--	3	--
<i>Euphaedra cf tenebrosa</i>	en	VR	1	--	--	--
<i>Euphaedra ignota</i>	en	VR	3	--	--	--
<i>Bebearia arcadius</i>	ww	RA	7	--	--	--
<i>Euphaedra phaethusa</i>	ww	CO	61	--	48	--
<i>Cymothoe mabillei</i>	ww	CO	6	8	19	13
<i>Euphaedra crockeri</i>	ww	NR	41	--	--	--
<i>Euphaedra francina</i>	ww	NR	1	--	--	--
<i>Euphaedra gausape</i>	ww	NR	6	--	2	--
<i>Euphaedra perseis</i>	ww	NR	9	--	--	--
<i>Euphaedra zampa</i>	ww	NR	5	--	--	--
<i>Euriphene simplex</i>	ww	NR	33	--	37	--
<i>Bicyclus abnormis</i>	ww	CO	117	10	190	36
<i>Euphaedra eupalus</i>	ww	RA	2	--	11	--
<i>Bebearia barce</i>		RA	1	--	--	--
<i>Bebearia demetra</i>		RA	6	--	2	--
<i>Bebearia lucayensis</i>		RA	2	--	8	--
<i>Bicyclus auricruda</i>		RA	8	--	2	--
<i>Euphaedra splendens</i>		RA	2	--	1	--
<i>Euriphene incerta</i>		RA	3	--	1	--
<i>Neptis paula</i>		RA	--	1	--	--
<i>Neptis strigata</i>		RA	--	1	--	--
<i>Pseudathyma falcata</i>		RA	1	--	--	--
<i>Pseudathyma sibyllina</i>		RA	--	1	--	1
<i>Bebearia maledicta</i>		VR	1	--	--	--
<i>Cymothoe lurida</i>		VR	--	--	2	1
Satyrinae						
<i>Bicyclus zinebi</i>	ww	NR	115	--	8	2
<i>Hallelesis halyma</i>	ww	NR	21	--	--	--
<i>Bicyclus ephorus</i>		RA	8	--	--	--
<i>Bicyclus ignobilis</i>		RA	2	--	--	--
<i>Bicyclus nobilis</i>		RA	3	--	--	--
<i>Bicyclus uniformis</i>		RA	--	--	2	--
Charaxinae						
<i>Charaxes petersi</i>	ww	VR	--	3	--	--
<i>Charaxes plantroui</i>	ww	RA	--	1	--	--
<i>Charaxes hildabrandti</i>		RA	--	--	--	1
<i>Charaxes mycerina</i>		RA	--	1	--	2
<i>Charaxes porthos</i>		RA	--	2	--	--
<i>Charaxes zelica</i>		RA	--	3	--	1
<i>Charaxes eudoxus</i>		VR	--	1	--	--
<i>Charaxes bocqueti</i>		VR	--	5	--	2

^a **en** = endemic to the Ghana subregion; **ww** = endemic to Africa west of the Dahomey Gap

^b **CO** = common – species that are usually found on 75% of visits to most suitable localities; **NR** = not rare – met with frequently but often not common; **RA** = rare – species that are usually found on less than 10-20% of visits to most suitable localities; **VR** = very rare – species that are usually found on less than 5% of visits to most suitable localities. Adopted from Larsen (2006).

Based on the categorizations by Larsen (2006), 21 rare (usually found on less than 10-20% of visits to most suitable localities) and six very rare (usually found on less than 5% of visits to most suitable localities) species were caught in BIA. Sixteen and 11 of the rare and very rare species were recorded exclusively at the understorey and canopy respectively in BIA (Figure 3.10a). In BOB, I caught two (*Charaxes bocqueti* and *Cymothoe lurida*) very rare species; one (*Cymothoe lurida*) at the canopy and the other (*Cymothoe lurida*) at both the forest canopy and understorey. Eight and two rare species were recorded exclusively at the understorey and canopy respectively in BOB (Figure 3.10b).

The canopy-restricted rare- and very rare species were mainly *Charaxes* (seven out of 11 species, 64% in BIA, and four out of seven species, 58% in BOB). The understorey-restricted rare- and very rare species however, were largely *Bebearia* and *Euphaedra* (six out of nine species, 67% in BOB, and 10 out of 17 species, 59% in BIA). (Refer to Table 3.4 for the complete list of rare and very rare species at the different levels).

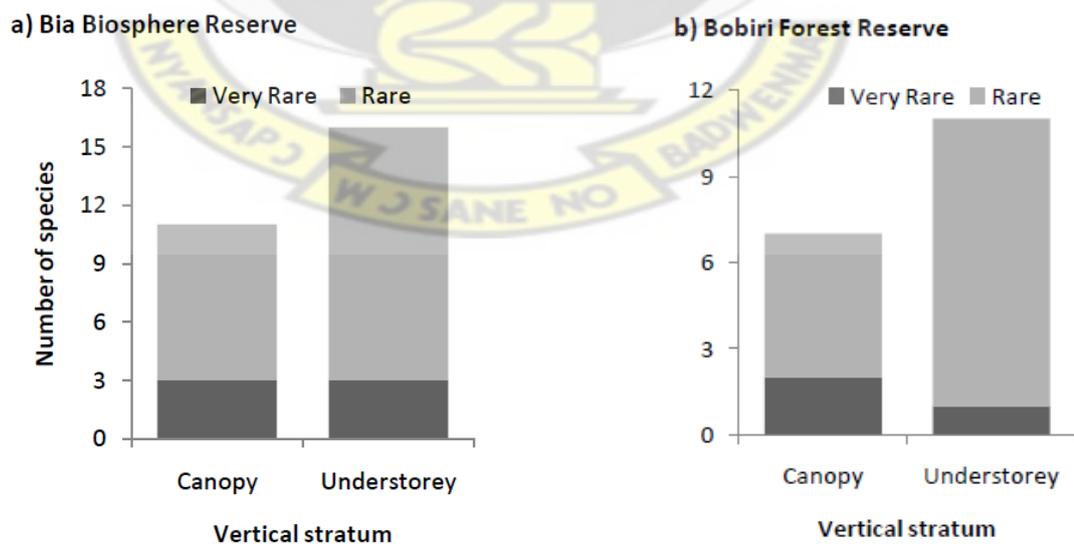


Figure 3.10 Spatial distributions of 'regionally rare species' by vertical strata in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve

3.3.4 Temporal variations in fruit-feeding butterfly diversity in Bia Biosphere Reserve and Bobiri Forest Reserve

Considerable temporal variation was observed in both species richness and number of individuals at both trap heights in both study areas. Using data pooled from all trap stations in BIA, species richness and number of trapped individuals showed regular increases and decreases through time, reaching their peaks in January and February (Figure 3.11a, b). The pronounced increases in January and abrupt crashes in March are remarkable in both graphs (Figure 3.11a, b). Using the similar dataset for BOB, I observed again a non-uniform pattern in the number of individuals trapped on a temporal scale (Figure 3.11c). The highest mean number of individual butterflies trapped in BIA were also in January and February, just as in BIA.

Table 3.5 and Figure 3.12 present the average estimated species richness and distribution of the fruit-feeding butterfly species in the different sampling months in BIA and BOB. In Tables 3.6 and 3.7, and Figures 3.13 and 3.14, I present separately for each strata community the estimated species richness in the different sampling months. In general, January was observed to be the most speciose month. The estimated species richness generally declines gradually after January till March, after which it rises briefly in April (and June) and then declines again (Table 3.5- 3.7 and Figures 3.12 - 3.14).

The period ('sampling week' or month) of sampling was found to influence both the mean number of individuals and species trapped significantly in both BIA and BOB (GLMM; $p < 0.001$ in both the understorey and canopy strata communities). Results from the Morisita-Horn similarity matrix in BIA indicated that the fruit-feeding butterfly composition in June, August and September were more similar in species and in abundance compared with other sampling months (Figure 3.15a).

Likewise January and November also recorded a high (averagely 70%) species overlap. The strongest dissimilarity scores in BIA were between fruit-feeding butterfly compositions in February and June (28%), and February and August (23%). In BOB, the largest fruit-feeding butterfly species overlaps were between the months January, February and December (averaging 88%) and June, July and August (averaging 80%). The lowest species overlaps were between January and August (3%), January and July (4%), January and September (5%), and February and August (7%, Figure 3.15b).

Although there were consistently significant higher mean individual abundances and richness in the understorey than the canopy throughout all sampling periods, the pattern of mean differences significantly changed between periods (GLMM; $p < 0.001$), suggesting that the peak activity periods for canopy nymphalid butterflies differed from their understorey colleagues. For instance, the greatest individual abundances per canopy trap in BIA were recorded in June and in March. In general, the difference in mean individual abundances and richness per trap between the canopy and understorey in BIA was about twice as large in January and February (mean difference = 2.77) compared to June, August, November, September (mean difference = 1.42).

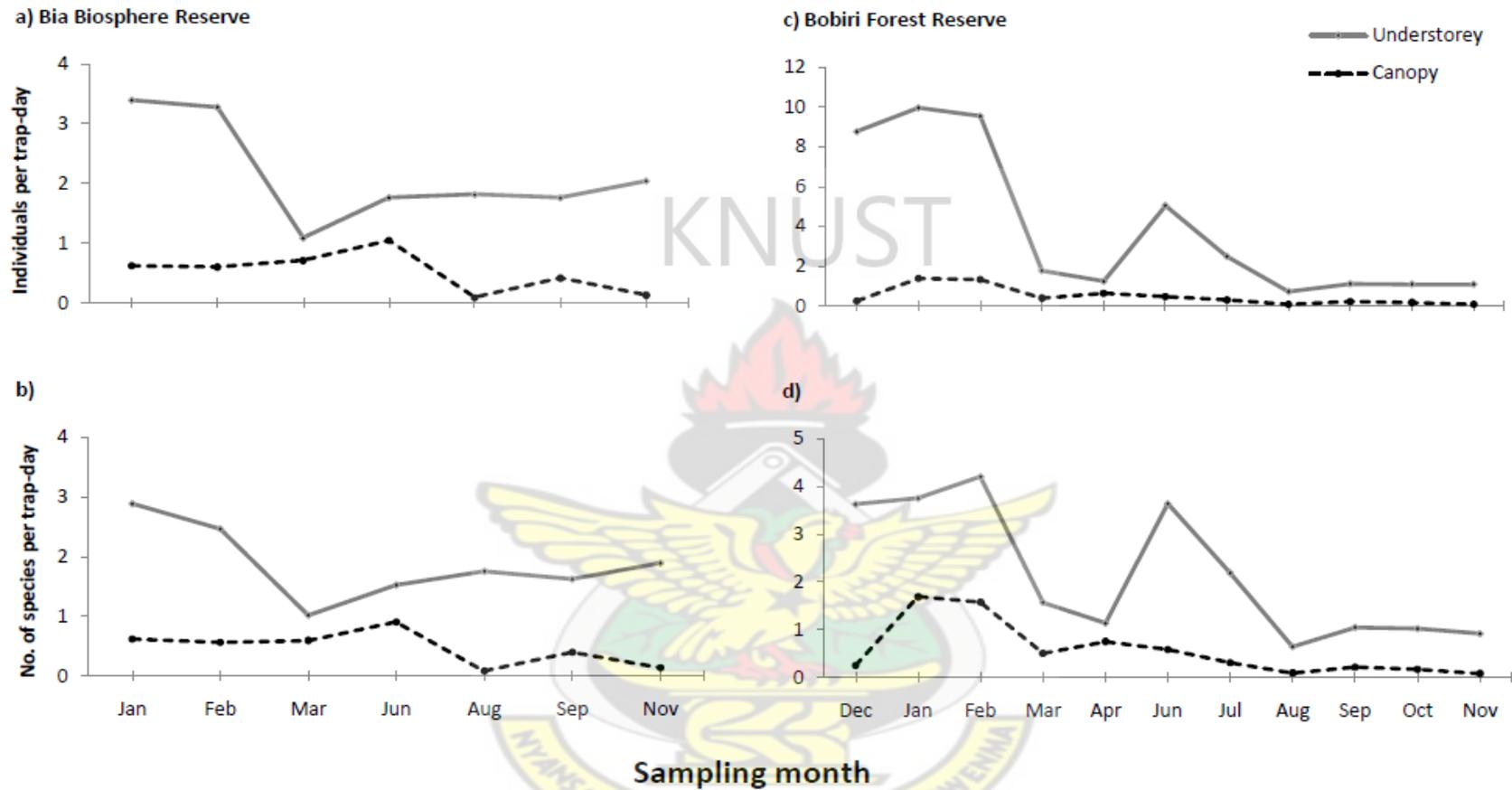


Figure 3.11 Temporal variation of fruit-feeding butterflies by vertical height (canopy and understory) in a,b) Bia Biosphere Reserve and c,d) Bobiri Forest Reserve. (a, c) and (b, d) are respectively the mean number of species and individuals trapped per trap per day for each sampling month. Each point on the graph is a mean of six sampling days.

Table 3.5 Estimated species richness (mean values with standard deviations in parentheses) for the different sampling months using combined data from the canopy and understorey strata in Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB).

Sampling Month	Trapdays ^a		Indiv		Sobs		Estimated species richness									
	BIA	BOB	BIA	BOB	BIA	BOB	BIA					BOB				
							ACE	Chao2	Jack1	Jack2	Bootstrap	ACE	Chao2	Jack1	Jack2	Bootstrap
Jan	204	336	1,721	676	76	100	127.9 (7.6)	120.6 (9.4)	129.2 (6.7)	140.2 (6.9)	113.9 (3.9)	86.8 (2.42)	86.0 (5.94)	94.0 (3.46)	98.8 (3.95)	85.0 (1.54)
Feb	144	336	932	653	69	81	105.9 (2.7)	103.6 (11)	105.2 (3.8)	117.0 (1.7)	92.1 (3.45)	79.6 (3.13)	74.3 (3.58)	83.3 (4.13)	85.1 (2.31)	76.5 (1.69)
Mar	204	336	287	298	52	60	77.3 (7.22)	79.2 (10.5)	80.0 (5.63)	90.1 (7.80)	69.1 (4.49)	65.6 (4.03)	62.2 (6.33)	67.8 (5.07)	73.6 (3.27)	59.6 (2.52)
Apr	204	--	203	--	52	--	--	--	--	--	--	60.0 (3.74)	84.9 (18.8)	72.0 (6.83)	84.8 (5.93)	60.8 (3.67)
Jun	104	336	292	472	52	73	90.5 (4.67)	89.7 (8.96)	93.8 (4.90)	103.0 (5.8)	82.8 (2.37)	74.7 (7.45)	74.5 (12.4)	70.8 (3.94)	80.3 (5.08)	60.5 (2.89)
Jul	132	--	183	--	42	--	--	--	--	--	--	57.8 (7.74)	50.7 (5.76)	56.2 (2.39)	61.1 (4.01)	48.8 (1.30)
Aug	132	150	53	143	24	42	52.5 (4.45)	72.8 (18.5)	59.6 (5.15)	70.5 (5.42)	49.7 (3.27)	76.2 (27.2)	52.3 (19.5)	38.2 (3.00)	47.9 (3.60)	30.0 (1.73)
Sep	144	240	95	261	31	68	104.4 (4.4)	99.0 (14.1)	97.2 (7.57)	112.5 (4.9)	81.1 (3.97)	37.3 (3.84)	36.0 (3.89)	41.8 (5.23)	44.1 (4.03)	36.5 (2.47)
Oct	144	--	91	--	33	--	--	--	--	--	--	50.3 (4.30)	44.3 (7.42)	47.2 (2.71)	53.7 (2.45)	39.5 (1.44)
Nov	132	240	77	261	26	60	74.3 (4.83)	77.7 (9.71)	80.0 (3.87)	89.6 (5.96)	69.2 (2.41)	36.2 (3.96)	33.2 (5.46)	36.8 (2.39)	41.2 (3.77)	31.1 (1.61)
Dec	188	--	846	--	48	--	--	--	--	--	--	67.1 (5.49)	62.3 (8.81)	63.8 (4.55)	71.7 (4.17)	55.3 (2.42)

^aTrapday is calculated as the number of operational traps multiplied by the number of sampling days within a 'sampling week' or month, Indiv=Number of individuals, Sobs= Observed species

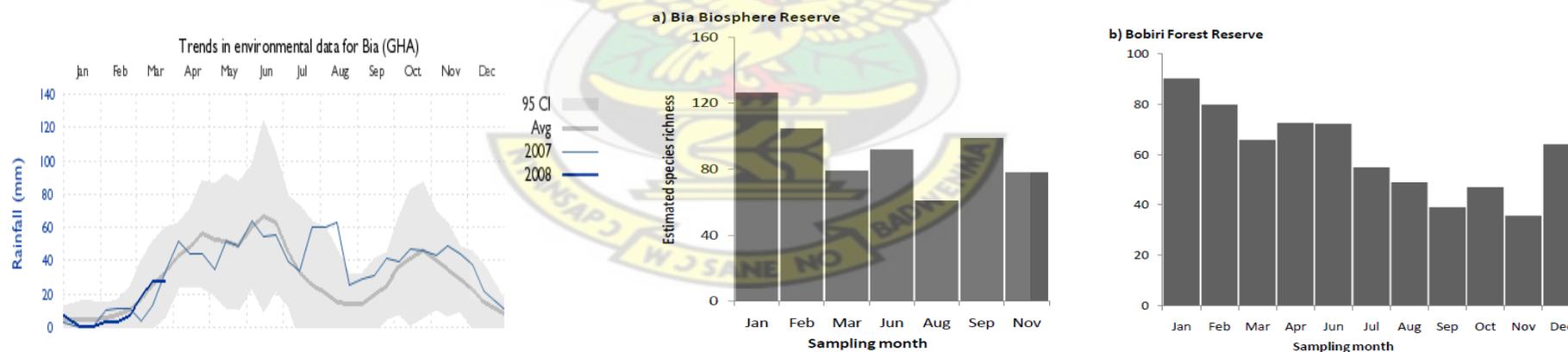


Figure 3.12 Comparison of estimated species richness (mean value of ACE, Chao2, Jack1, Jack2, and Bootstrap) for different sampling months using a combined data of the canopy and understorey in Bia Biosphere Reserve and b) Bobiri Forest Reserve. The rainfall pattern beside for comparison is the 2007 distribution (in gray solid line), which are the average rainfall readings for Bia during the sampling period

Table 3.6 Estimated species richness (mean values with standard deviations in parentheses) for the different sampling months using only data from the understorey stratum in Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB)

Sampling Month	Trapdays ^a		Indiv		Sobs		Estimated species richness									
	BIA	BOB	BIA	BOB	BIA	BOB	BIA					BOB				
							ACE	Chao2	Jack1	Jack2	Bootstrap	ACE	Chao2	Jack1	Jack2	Bootstrap
Jan	102	168	570	1472	75	54	95.0 (5.1)	88.2 (7.12)	95.8 (4.2)	102 (5.2)	85.1 (2.3)	59.6 (2.5)	60.4 (4.6)	66.9 (4.2)	69.8 (3.9)	60.5 (2.1)
Feb	72	168	551	800	66	56	89.7 (7.2)	82.7 (9.96)	86.8 (2.0)	96.0 (1.7)	75.7 (1.1)	91.9 (6.7)	76.5 (11)	74.8 (6.2)	83.9 (4.2)	64.6 (3.9)
Mar	102	168	178	225	49	43	68.4 (9.7)	70.4 (12.4)	67.3 (6.4)	77.7 (8.8)	57.2 (4.3)	54.1 (3.4)	52.1 (6.2)	56.3 (3.6)	61.7 (3.3)	49.3 (2.0)
Apr	102	0	--	48	--	23	--	--	--	--	--	69.5 (26)	48.0 (18)	36.3 (2.5)	45.4 (2.8)	28.6 (1.4)
Jun	52	168	296	262	53	42	74.8 (6.3)	74.1 (11.9)	72.2 (6.0)	82.7 (7.0)	61.6 (3.4)	58.1 (1.9)	60.3 (12)	56.3 (1.4)	63.8 (2.0)	48.4 (1.1)
Jul	66	0	--	164	--	35	--	--	--	--	--	45.9 (6.5)	40.9 (4.5)	45.8 (2.4)	49.2 (3.5)	40.3 (1.30)
Aug	66	75	136	48	36	23	41.0 (3.3)	52.0 (11.0)	48.8 (5.0)	56.2 (4.8)	41.8 (3.0)	69.5 (26)	48.0 (18)	36.3 (2.5)	45.4 (2.8)	28.6 (1.4)
Sep	72	120	211	80	49	25	72.9 (3.3)	68.2 (10.5)	69.0 (4.8)	79.1 (1.6)	58.1 (1.7)	29.2 (3.1)	28.8 (3.4)	33.3 (4.6)	35.2 (3.3)	29.2 (2.4)
Oct	72	0	--	79	--	31	--	--	--	--	--	45.1 (4.7)	41.0 (6.80)	44.3 (2.4)	50.2 (2.4)	37.2 (1.4)
Nov	66	120	245	72	52	23	64.2 (4.9)	71.4 (11.5)	69.5 (4.4)	79.2 (6.8)	59.9 (2.9)	30.2 (1.3)	26.8 (3.4)	31.3 (1.70)	33.2 (1.7)	27.1 (1.0)
Dec	94	0	--	823	--	37	--	--	--	--	--	44.1 (2.4)	42.7 (4.8)	46.2 (2.4)	49.8 (2.7)	41.4 (1.4)

^aTrapday is calculated as the number of operational traps multiplied by the number of sampling days within a 'sampling week' or month, Indiv=Number of individuals, Sobs= Observed species

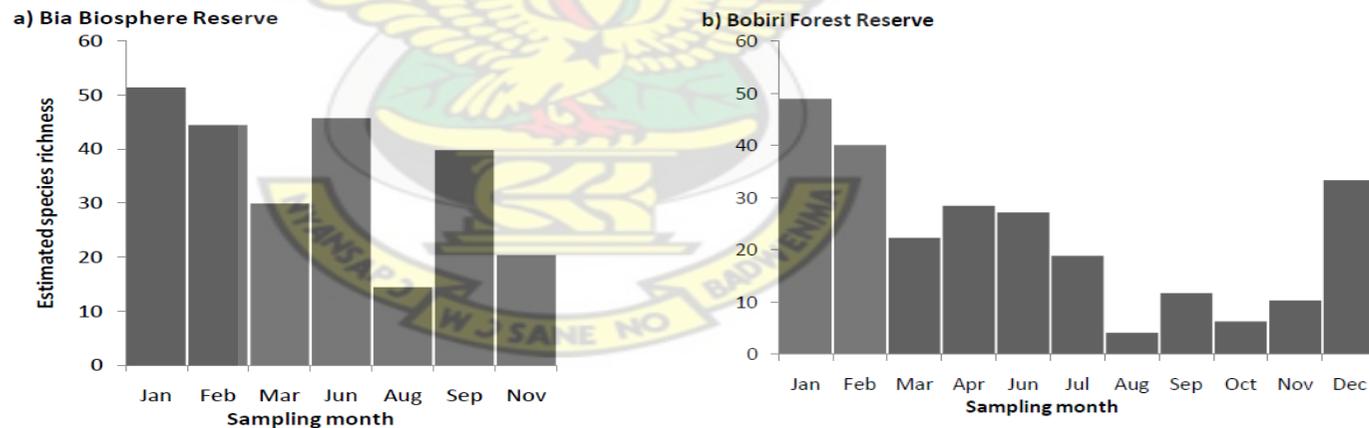


Figure 3.13 Comparison of estimated species richness (mean value of ACE, Chao2, Jack1, Jack2, and Bootstrap) for different sampling months using only data from understorey stratum in Bia Biosphere Reserve and b) Bobiri Forest Reserve

Table 3.7 Estimated species richness (mean values with standard deviations in parentheses) for the different sampling months using only data from the canopy stratum in Bia Biosphere Reserve (BIA) and Bobiri Forest Reserve (BOB)

Sampling Month	Trapdays ^a		Indiv		Sobs		Estimated species richness									
	BIA	BOB	BIA	BOB	BIA	BOB	BIA					BOB				
							ACE	Chao2	Jack1	Jack2	Bootstrap	ACE	Chao2	Jack1	Jack2	Bootstrap
Jan	102	168	570	234	75	37	56.1 (7.1)	50.9 (10.2)	50.0 (4.6)	58.3 (7.31)	41.7 (3.1)	47.5 (2.5)	50.0 (9.4)	49.0 (3.5)	56.0 (2.6)	42.4 (1.9)
Feb	72	168	551	132	66	32	41.2 (5.3)	50.0 (13.8)	43.3 (5.1)	51.9 (5.4)	35.8 (3.0)	39.7 (2.5)	37.3 (4.1)	41.8 (1.4)	44.9 (3.2)	36.8 (1.1)
Mar	102	168	178	63	49	17	30.8 (6.1)	28.0 (4.58)	30.5 (2.8)	33.8 (4.5)	26.5 (1.8)	24.3 (2.9)	19.9 (3.1)	22.8 (3.0)	24.8 (1.6)	19.8 (1.4)
Apr	102	0	--	76	--	22	--	--	--	--	--	26.1 (2.4)	28.0 (5.5)	29.5 (2.8)	33.4 (2.3)	25.4 (1.5)
Jun	52	168	296	30	53	15	44.9 (2.9)	49.5 (12.4)	44.5 (3.4)	52.4 (1.8)	37.4 (1.6)	43.2 (8.4)	23.3 (6.8)	23.3 (2.3)	27.4 (2.7)	18.7 (1.6)
Jul	66	0	--	20	--	10	--	--	--	--	--	27.3 (6.9)	18.8 (8.9)	15.8 (2.4)	20.0 (2.9)	12.4 (1.5)
Aug	66	75	136	6	36	3	21.0 (6.3)	18.0 (10.8)	10.8 (3.0)	14.4 (3.2)	8.0 (1.9)	4.0 (1.78)	3.8 (1.48)	4.3 (0.67)	5.0 (0.74)	3.6 (0.61)
Sep	72	120	211	15	49	8	45.8 (8.9)	40.7 (11.3)	37.3 (5.1)	45.3 (5.0)	29.8 (2.9)	11.7 (2.4)	10.7 (3.4)	12.0 (1.3)	14.1 (1.5)	9.8 (0.85)
Oct	72	0	--	12	--	5	--	--	--	--	--	7.0 (3.11)	5.3 (0.74)	6.5 (0.97)	6.8 (1.64)	5.8 (0.74)
Nov	66	120	245	5	52	5	29.5 (13)	18.8 (7.5)	17.7 (1.1)	21.9 (0.6)	13.9 (0.4)	15.0 (1.9)	11.7 (6.8)	8.3 (0.67)	10.0 (0.7)	6.5 (0.61)
Dec	94	0	--	23	--	15	--	--	--	--	--	57.0 (33)	33.3 (14)	25.0 (3.9)	31.9 (3.9)	19.2 (2.2)

^aTrapday is calculated as the number of operational traps multiplied by the number of sampling days within a 'sampling week' or month, Indiv=Number of individuals, Sobs= Observed species

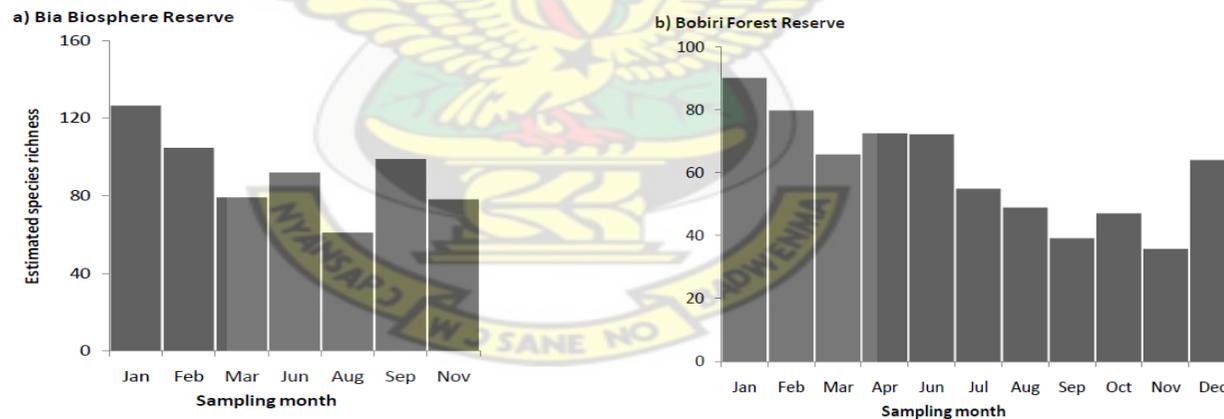
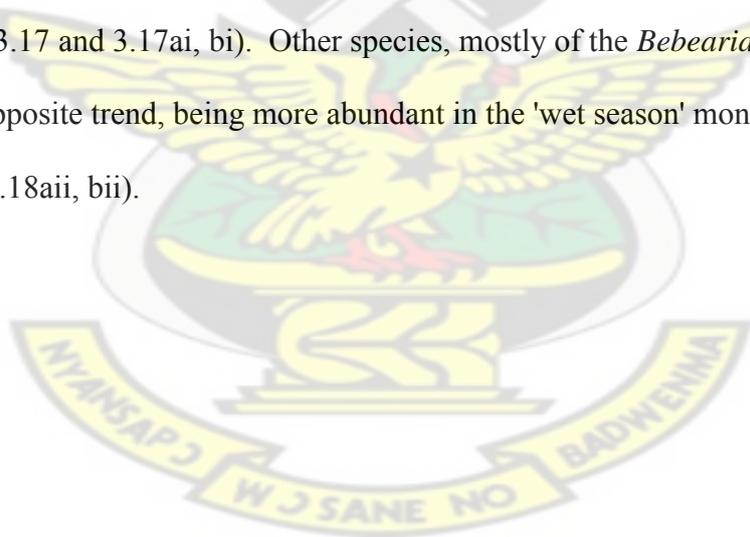


Figure 3.14 Comparison of estimated species richness (mean value of ACE, Chao2, Jack1, Jack2, and Bootstrap) for different sampling months using only data from understory stratum in Bia Biosphere Reserve and b) Bobiri Forest Reserve

After further partitioning and analyzing the data within subfamilies, I observed that different species-groups responded differently to the temporal variation within the year. Satyrinae were highest during the 'dry' months (December, January and February) in both BOB and BIA. In contrast, the mean individual abundance of Limenitidinae per trap-day, were highest in the 'wet' season months in both study areas (June and July; Figure 3.16).

Some species may also appear rare in samples when they are actually more abundant in the community at an earlier or later date. Satyrinae species like *Bicyclus funebris*, *B. sandace*, *B. vulgaris*, *Gnophodes betsimena*, and *Melanitis leda* appeared extremely abundant between December and February sampling months. Before and after these sampling months, these four species were relatively rare in the samples (Figure 3.17 and 3.17ai, bi). Other species, mostly of the *Bebearia* genus showed a rather opposite trend, being more abundant in the 'wet season' months (June and July, Figure 3.18aii, bii).



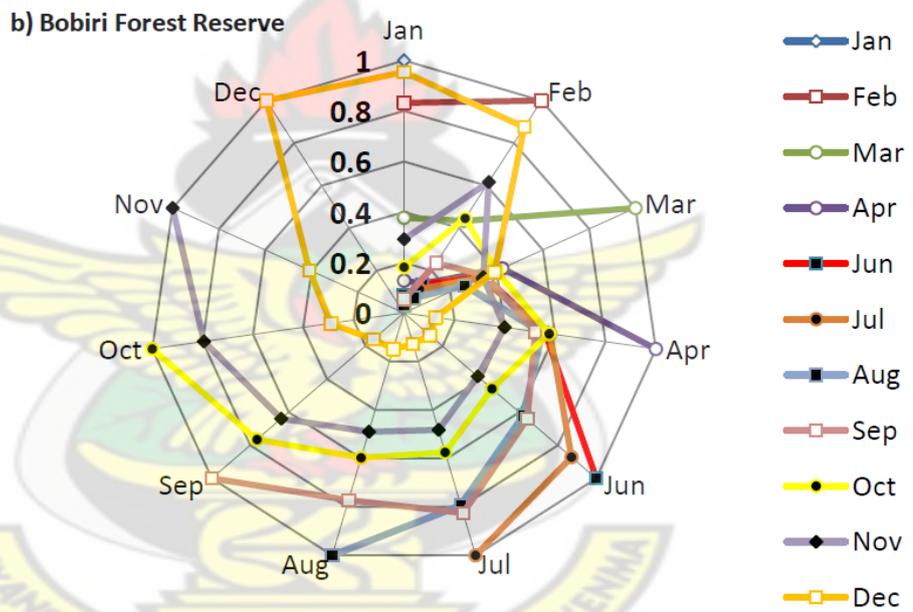
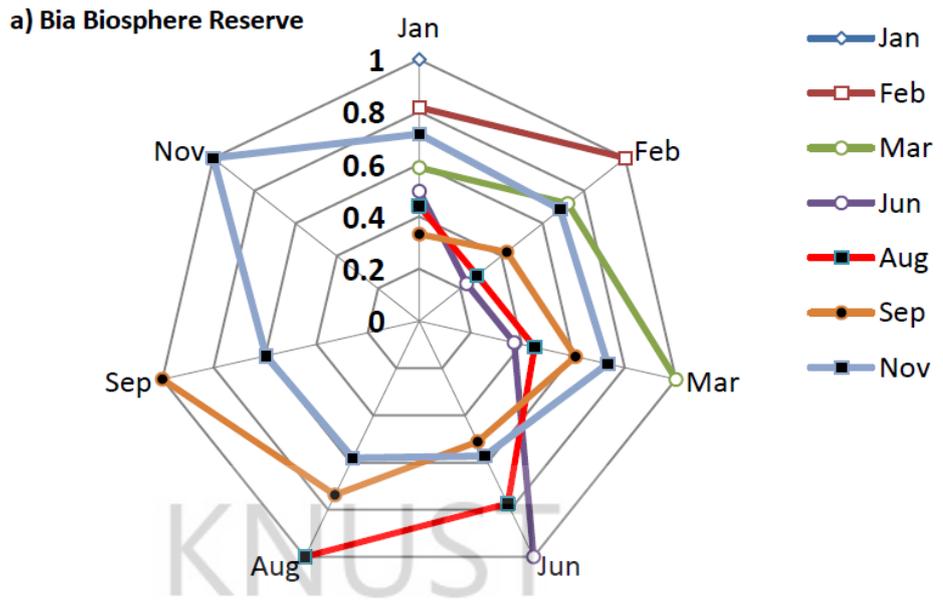
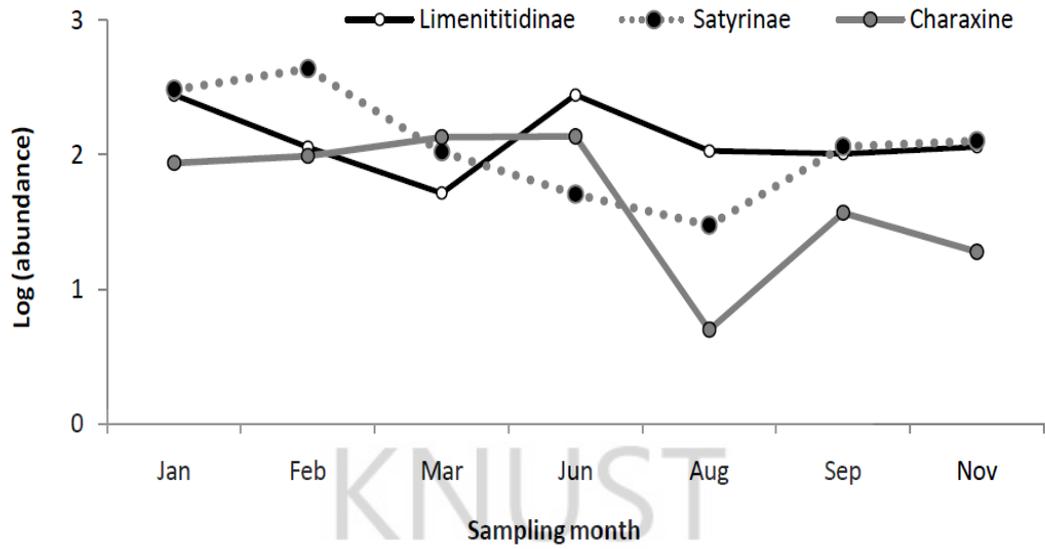


Figure 3.15 Radar plot of the biodiversity composition similarity between fruit-feeding butterflies trapped at different sampling months in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve. Similarity scores (Morisita-Horn) range from 0 (when no species is shared between the comparing sampling months) to 1 (when each of the comparing sampling month comprises the same species in identical proportions). For example, in BIA, November shares approximately 60% of species with June, August and September, just as there are about 90% overlap in species between December, January and February in BOB.

a) Bia Biosphere Reserve



b) Bobiri Forest Reserve

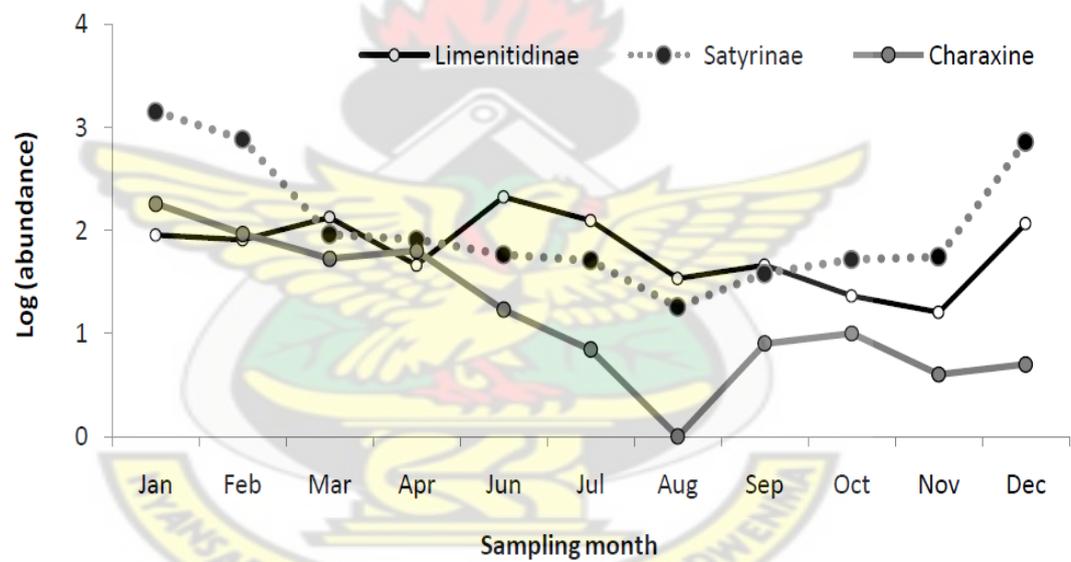
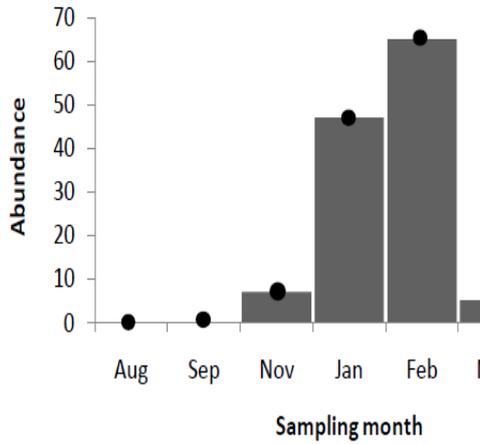


Figure 3.16 Temporal variations of the three largest fruit-feeding butterfly subfamilies (Limenitidinae, Satyrinae and Charaxinae) in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve

a) Bia Biosphere Reserve



b) Bobiri Forest Reserve

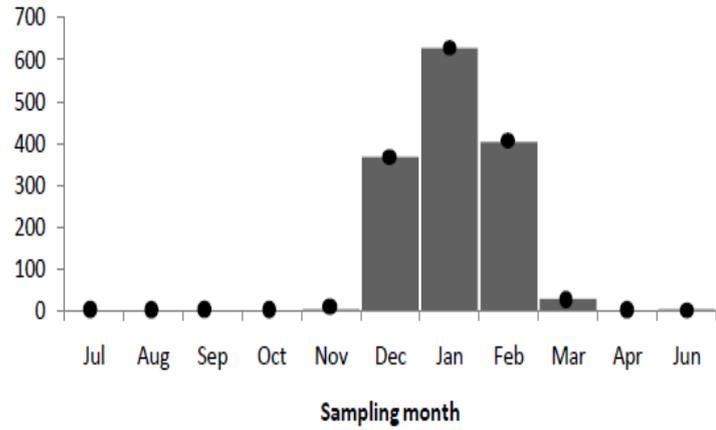


Figure 3.17 Temporal abundance of *Bicyclus funebris* in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve between December 2006 and November 2007

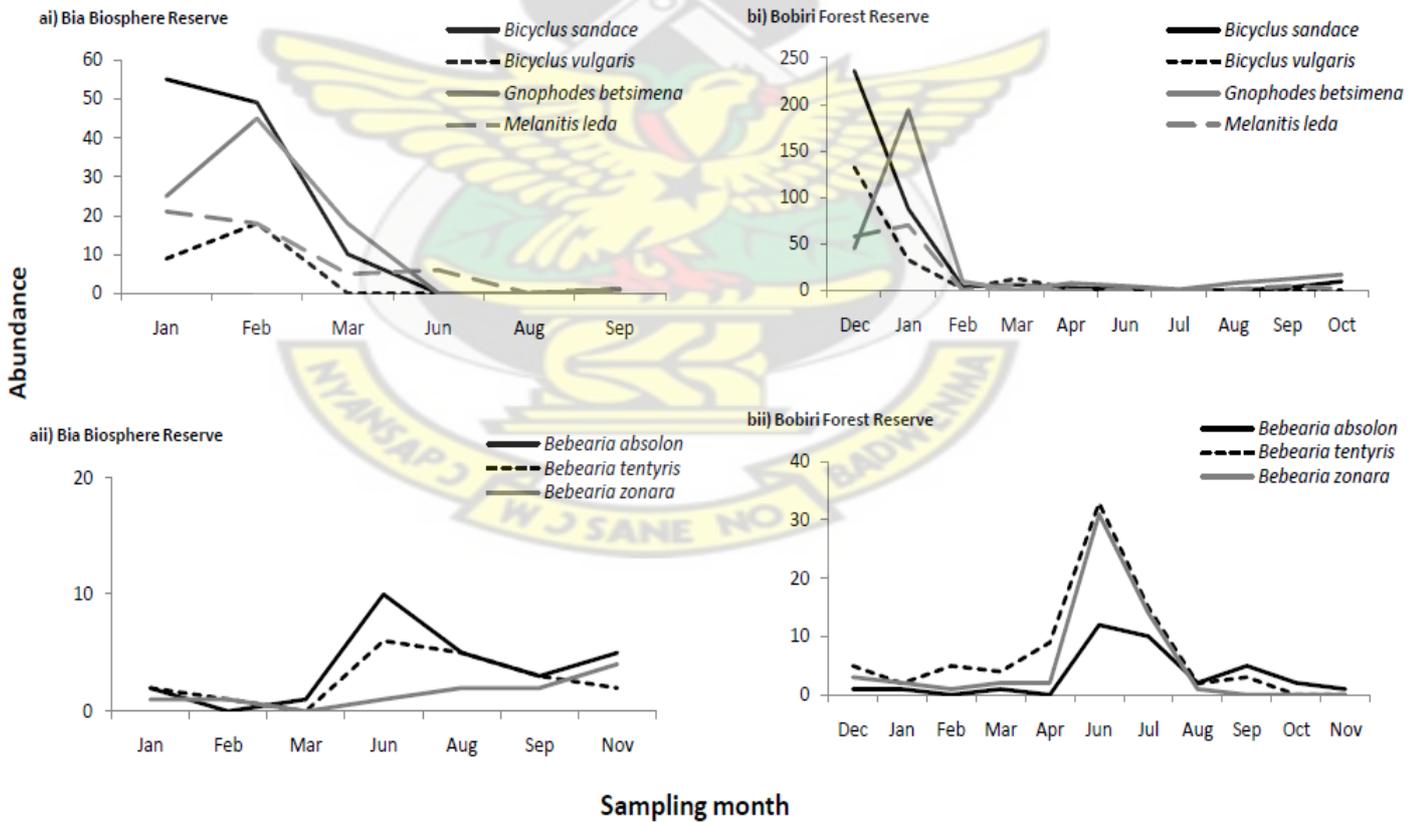


Figure 3.18 Temporal variations of some 'temporally abundant species' in a) Bia Biosphere Reserve and b) Bobiri Forest Reserve between December 2006 and November 2007.

3.4 DISCUSSION

3.4.1 Fruit-feeding butterfly species composition in Bia Biosphere Reserve and Bobiri Forest Reserve

Forty-five of the captured species were recorded for the first time in BIA, and five in BOB. This raised the number of species positively recorded and accepted for BIA (as in Larsen 2001) from 408 to 453; an 11% increase in its known butterfly richness. Larsen (2001) rarely used traps on his visits to BOB (personal communication) and this perhaps explains the high number of first-time-records in the present study. BOB, unlike BIA has been surveyed many times by both professional and amateur butterfly collectors. BOB is one of the well researched tropical forests in Africa, in terms of butterfly fauna (Larsen *et al.* 2007). The 140 and 90 species recorded in the present study (BIA and BOB respectively), represent more than half of the entire fruit-feeding butterfly guild known in Ghana (~170 species).

The butterfly biodiversity data presented in this study is the most species-rich of all fruit-feeding butterfly studies in the Afrotropics. Molleman *et al.* (2006), in a forest fragment in Uganda, found 94 species out of 34,308 trapped specimens over a 40-month sampling period (~4,576 trap days). Fermon *et al.* (2003) captured 103 species out of 2,189 sampled individuals between April and August (~204 trap days) in Côte d'Ivoire. The current study yielded 140 species from 2,764 individuals between August 2006 and June 2009 (~1,974 trap-days) in BIA. In BOB, I caught a total 4,782 individuals of 110 species in 11 months (~1,896 trap-days). Clearly the West African butterfly fauna may be richer than their counterparts in East Africa.

The absence of a species checklist in Fermon *et al.* (2003) makes it difficult to compare and contrast the butterfly species composition between Bia Biosphere

Reserve and Bossematié Forest (Côte d'Ivoire) which are just 40km apart. The likelihood that there will be much difference in butterfly species composition between the two forests is rather low. The environmental differences between these forests are low: both belong to the moist semi-deciduous forest zone (Hall & Swaine, 1976) with *Celtis* spp. and *Triplochiton* as the dominant flora, and receive an annual rainfall between 1200 and 1500 mm (as in Fermon *et al.* 2000).

Nevertheless, comparison of the data of the present study with Bossart *et al.* (2006) clearly shows that a larger proportion of Ghanaian fruit-feeding butterflies were sampled in the current study. In their survey in five relict sacred groves and a single larger forest reserve (Bobiri) in the moist semi-deciduous forest zone of Ghana, Bossart *et al.* (2006), using similar trapping methods captured a total of 6,836 individuals representing 79 species from five subfamilies. Only two (*Hallelesis halyma*, and *Cymothoe fumana*) of their species were not captured in this present study in BOB. Again, comparing the data of Bossart *et al.* (2006) to the study data from BIA, nine of their 79 species were not captured. Of these nine species, only six (*Charaxes varanes*, *Euphaedra inanum*, *Euphaedra cyparissa*, *Melanitis libya*, *Euriphene coerulea*, *Kallimoides rumia*) could be considered truly missing (false absences) in our data.

The other three species (*Junonia terea*, *Alcrea alciope*, *Ypthimomorpha itonia*) rarely visit fruits and are usually not considered 'true' fruit-feeders (Larsen 2005b). This is clearly evident also in the Bossart *et al.* (2006) data, where each of these species occurred in a single locality and as a singleton. *Melanitis libya* however, might not occur in Bia. As many as 54 individuals of its congeneric species in Ghana (*Melanitis leda*) were caught during the study. Fermon (2002) recorded 31

individuals of *Melanitis leda* and not a single individual of *Melanitis libya* in ~996 trap days in nearby Bossematié Forest. Larsen (2001) also never encountered *M. libya*.

Besides the obvious reason that BIA may be intrinsically more species rich than BOB and its surrounding sacred forests (Larsen *et al.* 2007) and the inclusion of the canopy strata in the current study might have widened the species pool, the modified trap could have also contributed to the high capture rate.

Preliminary results indicate that the modified trap used in this study has at least three times higher trap productivity (number of individuals collected per trap day) than the conventional van Someren-Rydon fruit-baited butterfly trap (see Chapter four for the full study).

3.4.2 Pattern of vertical stratification and its influence on rapid butterfly monitoring surveys.

The results revealed distinct differences in fruit-feeding butterfly biodiversity found in the understorey and forest canopy strata communities at all taxonomic levels. The understorey was dominated by Limenitidinae (*Euphaedra*, *Euriphene*, *Bebearia*) and Satyrinae which are known to feed exclusively on fruits (Larsen 2005b; Molleman *et al.* 2005) and are therefore more likely to visit baited traps. Characteristic of these species-groups is their short intermittent flap-and-glide flight along forest trails, making them more abundant in the understorey. In contrast, the canopy community was largely composed of robust, fast and agile *Charaxes* which can feed on food sources other than fruits (Molleman *et al.* 2005; Hamer *et al.* 2006) and are therefore relatively less susceptible to bait. As a result, there were generally more individuals and species at the understorey than at the forest canopy level. This finding is consistent with earlier vertical stratification studies in tropical forests

(DeVries *et al.* 1997; Devries & Walla 2001; Fermon *et al.* 2003; Molleman *et al.* 2006).

Another factor that might be maintaining the vertical stratification is a link between adult flight height and larval resource availability. The vast majority of Satyrinae are grass-feeders as larvae (Larsen 2005b) and most Limenitidinae utilize monocotyledon food plants mainly growing in the understorey. *Charaxes* larvae on the other hand, are known to feed mostly on leaves of tree species in many plant families (Larsen 2005b).

Satyrinae (*Bicyclus*, *Melanitis* and *Gnophodes*) were observed to have wider niche breadth than other understorey specialists as occasionally they could be captured in the canopy as well. The converse was more frequent for canopy dedicated species, which they were largely restricted to the canopy (Figure 3.8). On the whole, however, there was little overlap between the understorey and the canopy butterfly fauna in both BIA and BOB. Testament to this claim is that previous fruit-feeding butterfly surveys in West African forests that neglected the canopy strata (Oduro & Aduse-Poku 2005; Bossart *et al.* 2006) recorded very low numbers of Charaxinae and absolute absence of Apaturinae.

Distribution of rare and endemic species (which are usually the species of conservation concern) in the two strata communities followed the same taxonomic affiliation to trap heights and depended strongly on taxonomic group. West African rare and endemic (fruit-feeding butterfly) species such as *Bicyclus* (e.g. *B. ephorus*), *Euphaedra* (e.g. *E. ignota*), *Euriphene* (e.g. *E. simplex*) and *Bebearia* (e.g. *B. arcadius*) are restricted to the forest understorey. Rare and endemic *Charaxes* (*C. plantroui*, *C. bocqueti*) and *Neptis* (*N. strigata*, *N. paula*) species were, as expected, found at the forest canopy in both study areas.

However, unlike in the Neo-tropics (DeVries *et al.* 1997; DeVries *et al.* 1999), both the observed and expected species richness in Bia Biosphere Reserve were higher in the understory than in the canopy even after controlling for sample size. What accounts for these differences remains unclear. Factors driving vertical stratification in fruit-feeding butterflies could be more than food sources. Both ecological and evolutionary processes such as adaptation of behavioural traits, differences in microclimate (wind, temperature and light intensity; as alluded in DeVries & Murray 1999), and variations in vegetation structure and interaction with other species (Schulze *et al.* 2001) could be involved to some degree. It would be interesting to look in depth at how distribution of larval food plants also affect adult butterfly distribution.

The effect of vegetation structure on fruit-feeding butterflies' vertical stratification could not be established in this study, partly because the sample plots were so similar in structure in both the supposed secondary and primary forests. Bia was a forest reserve (with a certain level of timber harvest) for 36 years before becoming a National Park in 1974 (Lieberman *et al.* 1987). These past timber felling activities (selective logging) took place more than 30 years ago in the section of the reserve now referred to as a 'Resource Reserve'. It is suspected that the forest has recovered from the devastation of the selective logging and maybe be reaching its climax (Slik *et al.* 2002; Villela *et al.* 2006).

3.4.3 The influence of temporal variation on rapid butterfly monitoring surveys

In addition to vertical stratification differences, there was considerable temporal variation in trap capture rates; varying from 0.6 to 6.0 individuals per trap day in understory and from 0.05 to 2.5 at the canopy in BIA. Similar temporal

variation was also observed in BOB (Figure 3.11). Molleman *et al.* (2006) report even wider variation in capture rates in their three-year continuous trapping in a forest fragment in Uganda. Like earlier studies in African forests (Larsen 1979; Fermon 2000; Molleman *et al.* 2006), the temporal variation pattern did not seem to follow any apparent seasonal pattern.

However, grouping the sampling periods into 'dry' and 'wet' seasons suggested a subtle effect of seasonality on fruit-feeding butterfly composition. We found the fruit-feeding butterfly compositions in wet season months (June, August and September) to be similar to each other, just as January's biodiversity was to February in the dry season (Figures 3.11 and 3.15). The sudden increase and crash in numbers of fruit feeding butterflies at different trap heights during certain times of the year may as well be the result of direct seasonal effects on the dominant taxonomic group or species at each level.

A plausible factor underlying these observed temporal patterns in the understorey and the canopy could be the abundance of rotten fruit from fruiting forest trees. Although the effect of fruit falls was not directly assessed in the study, it is suspected that it might have affected the fruit-feeding butterfly temporal distribution in Bia Biosphere Reserve. The dominant understorey genera *Bicyclus*, *Bebearia*, *Euphaedra* and *Euriphene* feed extensively on fruit and may therefore be expected to be more abundant when forest tree fruit falls are at their peaks (Larsen 2005a). Several studies (e.g. Delampe *et al.* 1992; Chapman *et al.* 1999; McLaren & McDonald 2005) have demonstrated the positive feedback effect of rainfall on tree phenology. Both Lieberman (1982) and Chapman *et al.* (1999) observed that although fruiting and fruit falls occur throughout the year in most Afrotropical

forests, fleshy fruits were more abundant when the first wet season of the year is ending and the dry season is beginning.

This observation is consistent with the butterfly biodiversity data presented in the present study, which indicates a high abundance of fruit-feeding butterflies in January when the dry season is beginning in earnest and June when the first wet season of the year is ending. *Charaxes* on the other hand are versatile in their feeding behavior, feeding on a wide range of foods, from carrion (Hamer *et al.* 2006) through dung to fruits (Molleman *et al.* 2005). Therefore, they are less affected by the phenology of forest trees than the exclusive fruit-feeders.

Correspondingly, the mean daily number of individual *Charaxes* captured per trap in BIA increased by 30% in March (beginning of the first wet season of the year), when fruit falls were expected to be less and subsequently saw a drastic (>60%) decline in dedicated fruit-feeding butterfly abundance. There is a similar up-and-down population trend in BOB in the month of April. *Charaxes* increased by 20% (from 53 individuals in March to 63 in April) with dedicated fruit-feeding butterflies decreasing by about two-thirds (from 134 individuals in March to 46 in April). It is plausible that the climates of the two study areas differ slightly but that could not be established in the present study because specific rainfall data for BOB could not be obtained. The HOBO data loggers that were installed at each of the study location and programmed to take hourly temperature and relative humidity readings could not be communicate with the software for downloading its recorded data. However, unlike BOB, there was a regularly updated climatic database hosted by The European Commission for BIA and other National Parks in Africa (<http://www-tem.jrc.it/pa/>).

The above rationalization however cannot be used to explain the myriad temporal patterns exhibited by many individual species and groups of fruit-feeding butterflies. The interpretation of temporal patterns in butterflies is difficult and still remains enigmatic to most lepidopterists. Compensating for the effects due to temporal variation in rapid assessment programmes is not a simple one. One consequence of the limited sampling approach is the omission of peak activity periods for some nymphalid butterflies; a species may appear rare in samples when it is actually more abundant in the community at an earlier or later date. Notable among these temporally abundant species was *Bicyclus funebris*. As many as 95% of its total (154) individuals were captured in January and February alone in BIA. Only seven individuals of this seemingly abundant species were trapped in March and none in the remaining four sampling months (Figure 3.17a). In BOB, 98% of the total (1,387) of *Bicyclus funebris* individuals were also caught between December and February alone (Figure 3.17b). This was noticed as well for many other species, some of which are showed in Figures 3.16 and 3.17. The choice of appropriate sampling periods in Rapid Biodiversity Assessment (RBA) programme is therefore of prime importance.

It is worth stating that there is no substitute for long-term intensive sampling using a variety of techniques for estimating true diversity of a taxonomic group in a tropical forest (e.g. Stork *et al.* 2008; DeVries *et al.* 2009). However, rapid biodiversity assessment aims at finding differences among sites or trends in time that are relevant to conservation (Jost *et al.* 2010) with minimal effort, rather than total biodiversity (Magurran and Queiroz, 2010). Therefore, the aim of the present study, was to suggest minimal principles for RBA, realizing that with more data one can expect to reveal more subtle differences. In other words, the number of traps, bait type(s),

trap design and the number of trapping days will affect the power of RBA, but here the study is aiming at avoiding biases.

3.5 CONCLUSION

Trapping of fruit-feeding butterflies can be a practical method for assessing of biodiversity in West African forests. With the same conclusions emerging from similar studies carried out elsewhere, this study underlines the importance of taking temporal variation and vertical stratification into account when using fruit-feeding butterflies as a model system in Rapid Biodiversity Assessment in West-African forests. It is clear from the findings of the study that the 'when' (period of sampling) and 'where' (where we sample) attributes of a sampling strategy do affect RBA results. Detailed studies aimed at identifying which taxonomic groups of fruit-feeding butterflies enable the detection of changes in the environments, should be undertaken to evaluate further the relative importance of fruit-feeding butterfly guilds in RBA. Until those studies and their findings are available, completely neglecting the canopy strata in rapid butterfly biodiversity assessment programmes is not advisable. Again, in the light of evidence provided in the study, a useful recommendation to minimize the problems of precision associated with quick fruit-feeding butterfly surveys is always to conduct sampling both in the 'wet' and 'dry' seasons.

CHAPTER FOUR

Towards the development of an efficient rapid butterfly biodiversity monitoring framework in Ghana: on the use of bait- and trap-type for sampling butterflies

Abstract

Butterflies, especially those in the fruit-feeding guild, have proven to be potentially useful taxa for monitoring biodiversity trends in many parts of the world. As a means of widening species coverage, various authors have used different trap designs and baits in their sampling design. Here, the efficiencies of two types of traps and baits potentially useful for sampling fruit-feeding butterfly diversity in West African forests are evaluated for the first time. The two bait types included 1) mashed overripe banana fruit, and 2) palm wine mixed with mashed overripe banana fruit. The two trap types were 1) the conventional vanSomeren-Rydon baited trap, and 2) a novel trap made out of the IKEA children's toys storage basket ("MANIFANGST"). The study also investigated how the age of bait affects the type of species or species-group trapped. Results of the study showed that the novel trap type (with reduced entry/exit) performed thrice as much better than the conventional van Someren-Rydon, in terms of number of butterflies trapped per trap-day. Palm wine was found to be a useful bait 'add-in' as it functions to provide long range signals or volatile cues in directing butterflies to their food sources. Lastly, the present study provided evidence to support the hypothesis that, age of bait does affect both the numbers and types of butterflies trapped. It is therefore appropriate to identify a priori the focal butterfly taxa, before deciding on the duration of sampling.

4.1 INTRODUCTION

The interest in the use of fruit-feeding butterflies in developing biodiversity monitoring programs continues to soar in literature (Kremen 1994; Daily & Ehrlich 1995; Hill *et al.* 1995; Hughes *et al.* 1998; Fermon *et al.* 2000; Schulze *et al.* 2004; Veddele *et al.* 2005; Bobo *et al.* 2006; Benedick *et al.* 2007). As a result, practical approaches to the monitoring protocols have also varied widely among studies and countries. Different butterfly monitoring protocols have used different kinds of baits, traps and sampling designs, all with one common aim; to widen the species coverage of the sampling design. Interestingly, in each of these studies or countries, the choice of a sampling strategy, trap- or bait type is influenced largely by the local materials readily available for sampling butterflies. Such a decision does not only make a monitoring protocol cheaper but also easily implementable.

For instance, in tropical forests, banana fruits are frequently used as bait for sampling fruit-feeding butterflies (Nymphalidae) for two practical reasons: (i) banana fruits are affordable and obtainable all year round. This ensures that no bias is introduced into a temporal study by bait. (ii) the fragrance of banana (especially when overripe, mashed and allowed to ferment), can permeate the surrounding environment, attracting butterflies from reasonable distances (Hughes *et al.* 1998; Molleman *et al.* 2005).

Again, to effectively use nymphalids as bio-indicators, monitoring programs must aim at getting as many species or species-groups as possible in its sample pool by applying appropriate survey designs and methods. For instance, in the Neotropics molasses are sometimes added to banana bait to augment the potency of the bait to attract butterflies (Daily & Ehrlich 1995; Hughes *et al.* 1998; Horner-Devine *et al.* 2003). Although there is no available study that specifically investigates the effect of

molasses on species-turnover, it is a widely held belief that molasses increases species turnover in traps. Unfortunately, molasses are uncommon and relatively expensive in West Africa. The closest surrogate of this bait 'add-in' in West African is palm wine. Like banana, palm wine (fermented palm sap) is affordable, aseasonal and hence, obtainable all year round in West Africa where palm trees are common. The use and efficacy of palm wine as part of bait for sampling fruit-feeding butterflies (Nymphalidae) was evaluated for the first time in this study. The novel bait type used in the present study consisted of ripe mashed banana mixed with doses of palm wine.

I also designed a new fruit baited butterfly trap-type, made largely of local materials, and tested its efficiency against the conventional vanSomeren-Rydon baited trap (Rydon 1964). The basic difference between the two trap-types lay mainly in the amount of space provided as exit or entry for luring butterflies. The reduced entry space was intended to minimize the risk and rate of escape, once butterflies are lured into the trap. Again, compared to the old trap type, the new trap type was relatively easier to construct, lighter in weight, and most importantly, cheaper.

Lastly, I address as part of this study one of the most obvious but still unanswered questions associated with rapid butterfly biodiversity assessment programmes using bait-trapping technique by posing the question; how rapid should a rapid assessment of nymphalids be? While investigating this question, I also examined how age of bait influences the type of species or species-groups trapped and rapid biodiversity assessment (RBA) results in general.

4.2 MATERIALS AND METHODS

4.2.1 Description of Study Sites

The study was carried out in Bobiri Forest Reserve (BOB) between June and November 2007. BOB is located in the middle belt of Ghana and lies within the tropical moist semi-deciduous forest zone (Hall and Swaine, 1981), with a grid reference of latitude 6°25' N and longitude 2°40' W. The reserve could also be categorized into two forest blocks; primary (relatively undisturbed) and secondary (disturbed) forest blocks based on the past logging regimes (Figure 3.1). The primary forest constitutes portions of the forest adopted by the Forestry Research Institute of Ghana (FORIG) for research purposes several decades ago. The selected compartments for establishing the experimental plots were last logged at least 30 years ago. The secondary forest however comprises the production compartments which still carry out the orthodox timber production, and features few large trees and a dense understory.

4.2.2 Butterfly sampling

Butterflies were sampled using a total of four transects, spaced at least a kilometer for each other. Two transects were laid in the forest compartment adopted by the Forestry Research Institute of Ghana (FORIG) for research and putatively considered primary or 'undisturbed' forest. The remaining two transects were located within compartments, believed to be last logged at least 30 years ago and herein considered secondary forest. Six trap stations, distanced about 100m apart were demarcated on each transect. At each trap station, a fruit-baited trap was installed at about 0.1m from the forest floor for the quantitative butterfly biodiversity sampling.

4.2.3 Trap types

Two kinds of fruit-baited butterfly traps (both made of out of locally available materials) were used for this study. One trap type (hereafter referred to as Old-Trap type, or shorten OT) was modified from the conventional vanSomeren-Rydon trap (Rydon 1964) used by most researchers (e.g. DeVries 1987; DeVries 1988; Hughes *et al.* 1998; Fermon *et al.* 2003; Oduro & Aduse-Poku 2005; Bossart *et al.* 2006; Molleman *et al.* 2006) for sampling fruit-feeding butterfly communities in their natural habitats. OT consisted of a cylinder of black nylon netting (60 cm high and 32 cm in diameter) sewn onto a frame of two metal hoops, closed and covered by a transparent plastic sheet at the top to avoid baits being drenched by rains (see Figure 4.1A). the trap weighed ~0.50kg and had a space of about 10cm between the plywood base and the cylinder of nylon netting as an entrance for butterflies.



Figure 4.1 Types of fruit-baited used in the study. **A** is the Old-Trap type (OT) which was in the made and style of the conventional vanSomeren-Rydon trap. **B** is the (novel) New-Trap type (NT) smaller entrance/exit, made out of the IKEA children's toys storage basket.

The other trap type, hereafter called New Trap, shorten (NT) was made out of the IKEA children's toys storage basket (“MANIFANGST” see Figure 4.1B). NT weighed on average ~0.13 kilogram. It consisted of cylinders of viridian light coloured nylon netting (80 cm tall and 30 cm in diameter) sewn onto a frame of four plastic hoops. Like OT, NT was also covered by a transparent plastic sheet at the top, to keep rain water out of the bait. Between 1-1.5cm from the base of the trap, a slit of about 25cm was created to serve as the entrance for luring butterflies. The basic difference between NT and OT is the amount of space provided for butterflies entering the trap. The modified traps (NT) have only one slit opening at one side, as opposed to an opening around the whole circumference of the cylinder's base in the old trap design. Both trap types had a velcro-fastened slit on the side for removing trapped insects and small bait-holding plastic plates velcro-fastened at the bottom of the traps to prevent baits from being toppled over by wind.

4.2.4 Bait types

The two bait-types used in the study were (i) mashed ripe banana and (ii) mashed ripened banana mixed with palm wine. Palm wine is a whitish, effervescent, local alcoholic beverage produced by a spontaneous yeast-lactic fermentation of the sugary sap of palm trees. Mashed ripe banana has been the main type of bait used in trapping fruit-feeding butterflies in most ecological studies (e.g. Devries & Walla 2001; Rogo & Odulaja 2001; Fermon *et al.* 2005; Bossart *et al.* 2006; Molleman *et al.* 2006; Barlow *et al.* 2007b), hence it is referred to here, as the Old bait type (OB). The new bait type (NB) differed from OB, only by the addition of liberal doses of

palm wine (usually 1 litre: 8 litres of mashed banana). Baits were prepared at least 24 hours prior to setting the traps.

4.2.5 Experimental protocol

To evaluate the effect of both trap- and bait-types, an orthogonal sampling design was adopted and used. The design generated four possible pairwise bait- and trap-type combinations, namely; 1) New Trap - New Bait (NT-NB), 2) New Trap - Old Bait (NT-OB), 3) Old Trap - New Bait (OT-NB) and 4) Old Trap - Old Bait (OT-OB). Trap- and bait-type combinations (hereafter referred also as treatments) were allotted randomly to trap stations in the first month of sampling, such that each of the four possible pairwise combinations was represented at least once on each transect. In the subsequent sampling months, the arrangements of trap- and bait-types combinations at each trap station were systematically rotated as shown in Table 4.1.

The sampling period lasted for six weeks with sampling weeks at least four weeks (one month) from each other. Traps were inspected between 10.00 and 12.00 hours GMT daily after setting out the traps. Butterfly sampling continued for five consecutive days at each trap station during a sampling week. In total, the quantitative sampling protocol described generated a total of 761 trap-days, with one trap-day being equivalent to one trap sample per day (24 hours after setting out trap).

Bait eaten by rodents and traps heavily infested with ants were replaced or refreshed on the day of detection. Otherwise, all baits were refreshed every two days, using the original stock of bait prepared on the first day of the sampling week.

Trapped specimens were identified mostly in the field using available taxonomic treatises (e.g. D'Abrera 1997; Larsen 2005b). Specimens were identified to species-level and grouped into respective taxonomic units (putative species-groups, genus,

subfamily, family) following the proposed higher-level classification for Nymphalidae by Wahlberg *et al.* (2003).

Table 4.1 Arrangement of trap- and bait-types pairwise on four transects each with six trap stations in Bobiri forest reserve. OT and NT denote new and old trap type respectively. Likewise OB and NB refer to old and new bait types respectively.

Trap Position		Sampling month					
Transect	Trap Station	June	July	August	September	October	November
1	1	OT-NB	NT-OB	OT-OB	NT-NB	NT-NB	OT-OB
	2	NT-OB	OT-OB	NT-NB	NT-NB	OT-OB	OT-NB
	3	OT-OB	NT-NB	NT-NB	OT-OB	OT-NB	NT-OB
	4	NT-NB	NT-NB	OT-OB	OT-NB	NT-OB	OT-OB
	5	NT-NB	OT-OB	OT-NB	NT-OB	OT-OB	NT-NB
	6	OT-OB	OT-NB	NT-OB	OT-OB	NT-NB	NT-NB
2	1	NT-NB	OT-NB	OT-OB	NT-OB	OT-OB	NT-NB
	2	OT-NB	OT-OB	NT-OB	OT-OB	NT-NB	NT-NB
	3	OT-OB	NT-OB	OT-OB	NT-NB	NT-NB	OT-NB
	4	NT-OB	OT-OB	NT-NB	NT-NB	OT-NB	OT-OB
	5	OT-OB	NT-NB	NT-NB	OT-NB	OT-OB	NT-OB
	6	NT-NB	NT-NB	OT-NB	OT-OB	NT-OB	OT-OB
3	1	NT-NB	NT-OB	OT-OB	OT-NB	NT-OB	OT-NB
	2	NT-OB	OT-OB	OT-NB	NT-OB	OT-NB	NT-NB
	3	OT-OB	OT-NB	NT-OB	OT-NB	NT-NB	NT-OB
	4	OT-NB	NT-OB	OT-NB	NT-NB	NT-OB	OT-OB
	5	NT-OB	OT-NB	NT-NB	NT-OB	OT-OB	OT-NB
	6	OT-NB	NT-NB	NT-OB	OT-OB	OT-NB	NT-OB
4	1	NT-OB	NT-NB	OT-NB	OT-NB	OT-OB	NT-OB
	2	NT-NB	OT-NB	OT-NB	OT-OB	NT-OB	NT-OB
	3	OT-NB	OT-NB	OT-OB	NT-OB	NT-OB	NT-NB
	4	OT-NB	OT-OB	NT-OB	NT-OB	NT-NB	OT-NB
	5	OT-OB	NT-OB	NT-OB	NT-NB	OT-NB	OT-NB
	6	NT-OB	NT-OB	NT-NB	OT-NB	OT-NB	OT-OB

4.2.6 Data Analysis

EstimateS package (Colwell 2009) was used to compute all the biodiversity functions, estimators and indices. The means of two commonly used non-parametric abundance-based richness estimators (CHAO2, and JACK2) for datasets of small sample size were used to estimate the number of species of fruit feeding butterflies in the different trap and bait types. Details on the philosophy and computation of these estimators can be found in Magurran (2004) and Krebs (1999). Rarefaction was used to standardize and compare species richness computed from samples of different sizes. This was implemented in the EcoSim package (Gotelli & Entsminger 2009).

Individual abundances per trap- and bait-types were calculated as mean number of individuals per trap per day to correct for the slight variation in treatment numbers. Trap productivity or trapping success was calculated as the number of individual butterflies trapped per trap per day. The effects of bait- and trap-type on trapping success were evaluated using a generalized mixed-model, implemented in the R statistical package (R Development Core Team 2009). The mixed-effects model was used to avoid temporal pseudoreplication (repeated measurements) as measurements were taken from the same trap locations but at different sampling weeks (Bolker et al. 2009).

To identify species-groups (and species) level effects, a two tailed chi square-test was performed using a null hypothesis of equal proportions ($df = 1$, p -critical = 0.05). The chi square-test was also used to test the effect of sampling day (or age of bait) on trap productivity. All analyses were done using R (R Development Core Team 2009)

4.3 RESULTS

4.3.1 General Biodiversity

A total of 1,214 individuals, representing 64 butterfly species, were trapped during the entire study period (761 trap-days). All the trapped specimens belonged to the fruit-feeding butterfly guild (otherwise known as Nymphalidae) and came from 14 genera and five subfamilies (Table 4.2). Refer to Appendix 2 for the full list of species trapped. Majority of the trapped species and individuals (~95%) were from the Limentidinae and Satyrinae subfamilies. The remaining three subfamilies (Charaxinae, Nymphalinae and Heliconiinae) were marginally represented, constituting just 5% (61) of the total 1,217 individuals butterflies trapped. At the genus level, *Bicyclus*, *Euphaedra* and *Bebearia* alone constituted nearly two-thirds of the total number of species and individuals trapped. The number of individuals trapped per species ranged from one for eight species to 155 for *Bicyclus abnormis*, (Appendix 2).

4.3.2 Effect of bait and trap type on trapping success

As shown in Figure 4.2, the effect of trap type on trapping success was much stronger than, that of the bait type. There were generally higher numbers of individuals trapped with the newly designed traps (NT; 2.5 ± 0.17 , mean \pm SD) compared with the old traps types (OT; 0.7 ± 0.07). Even after correcting for both sample size and bait type, the number of individuals trapped per trap-day in NT (2.4) was on average three times greater than those recorded in OT (0.8). The numbers of individuals trapped using NB were consistently higher than OB, though the differences were not sometimes statistically significant. The GLMM model could

not reveal a significant interaction between the trap and bait types (GLMM, $p > 0.05$, Table 4.3).

Similar trends were observed when number of species (species richness) per trap-day was used as the response variable in similar analyses (Figure 4.2). Again, species richness per trap-day was at least thrice as high with NT, compared with (0.7 species per trap-day) for OT, after correcting for sample size and bait type. Like in the previous analyses, there were no significant interaction between bait and trap type (GLMM, $p > 0.05$).

Table 4.2 Number of fruit-feeding butterfly individuals caught per genus in Bobiri Forest Reserve Ghana, with categorization by bait and trap types.

Subfamily <i>Genus</i>	Abundance	Trap type			Bait type		
		% in NT ^a	F (X ² -test)	sign ^c	% in NB ^b	F (X ² -test)	sign
Limenitidinae							
<i>Bebearia</i>	276	81.9	112.2	***	58.7	8.3	**
<i>Eupahedra</i>	311	80.7	117.3	***	56.3	4.9	ns
<i>Euriphene</i>	88	79.5	30.7	***	50.0	0.0	ns
<i>Aterica</i>	35	91.4	24.0	***	54.3	0.3	ns
<i>Cymothoe</i>	2	50.0	0.0	ns	100.0	2.0	ns
<i>Catuna</i>	1	100.0	1.0	ns	100.0	1.0	ns
<i>Euryphura</i>	1	100.0	1.0	ns	0.0	1.0	ns
Satyrinae							
<i>Bicyclus</i>	316	71.8	60.3	***	53.5	1.5	ns
<i>Gnophodes</i>	106	73.6	23.6	***	59.4	3.8	ns
<i>Melanitis</i>	21	52.4	0.0	ns	61.9	1.2	ns
<i>Elymniopsis</i>	6	50.0	0.0	ns	66.7	0.7	ns
Charaxinae							
<i>Charaxes</i>	43	69.8	6.7	*	55.8	0.6	ns
<i>Palla</i>	5	80.0	1.8	ns	80.0	1.8	ns
Nymphalinae							
<i>Kallimoides</i>	2	100.0	2.0	ns	0.0	2.0	ns
Heliconiinae							
<i>Lachnoptera</i>	1	100.0	1.0	ns	0.0	1.0	ns

^a = percentage of the total individuals per genus caught using the new trap type

^b = percentage of the total individuals per genus caught using the new bait type

^c = Significance; *** at 0.001, ** at 0.005, * at 0.05

Table 4.3 Output of a generalized mixed model evaluating the effect of bait and trap types on number of individuals and species caught by baited traps in Bobiri Forest Reserve, Ghana

a) Predictor variable = Number Individuals per trap per day				
Random effects:		Variance		
Transect (Intercept)		0.14152		
TrapStation x Transect (Intercept)		0.04024		

Fixed effects:	Estimate	Std. Error	z-value	probability
(Intercept)	0.93240	0.13437	6.939	P<0.001
BaitType	-0.26582	0.06908	-3.848	P<0.001
Trap type	-1.16194	0.09320	-12.468	P<0.001
BaitType xTrap type	-0.07169	0.14310	-0.501	P=0.616

b) Predictor variable = Number Species per trap per day				
Random effects:		Variance		
Transect (Intercept)		0.086326		
TrapStation x Transect (Intercept)		0.026397		

Fixed effects:	Estimate	Std. Error	z-value	probability
(Intercept)	0.72688	0.11296	6.435	P<0.001
BaitType	-0.21452	0.07628	-2.812	P<0.001
Trap type	-1.04325	0.10032	-10.399	P<0.001
BaitType xTrap type	-0.06434	0.15201	-0.423	P=0.672

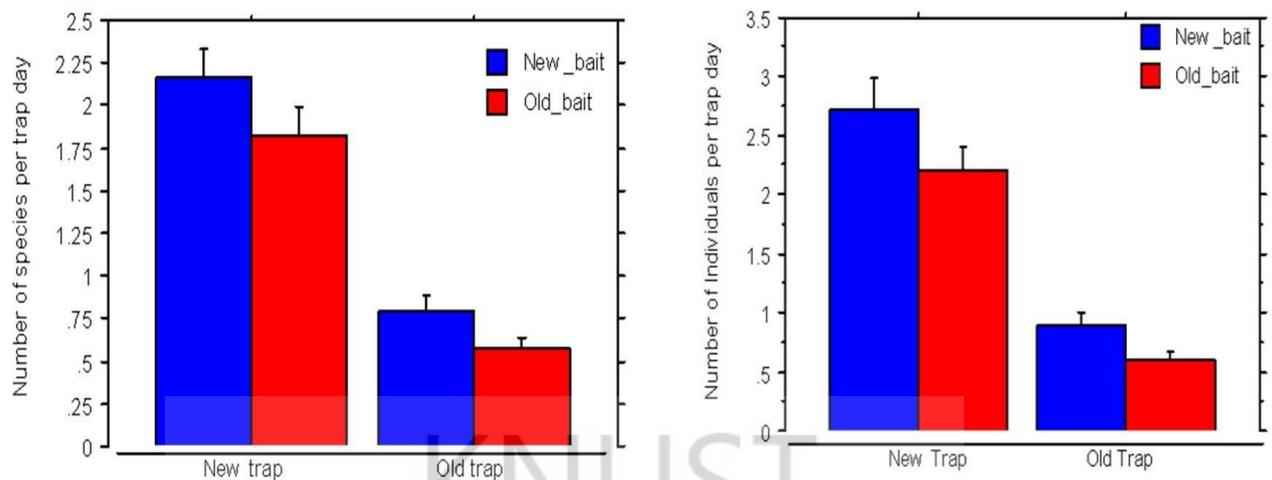


Figure 4.2 Number of species and individuals caught per treatment (bait and trap types pairwise)

4.3.3 Effect of sampling day on trap productivity

Generally, both species richness and individual abundances per trap-day were highest on the second or third days of sampling, depending on the kind of bait type used (Figure 4.3a). Using data pooled across the different species-groups and trap types, it was observed that traps baited with NB recorded the highest mean number of trapped individuals per trap-day (2.8 ± 0.5 ; mean \pm SD) on the second sampling days. The numbers in traps however declined steadily afterwards until its lowest (0.9 ± 0.2) on the last (sixth) sampling day (Figure 4.3a).

Using a similar pooled dataset, the mean highest number of individuals per trap-day (2.2 ± 0.4 ; mean \pm SD) captured using OB was highest on the third sampling day. Like NB, trapped individuals per sampling day declined steadily till it hit its lowest number on the last sampling day (Figure 4.3a). The average number of trapped individuals between NB and OB differed significantly in the first and second sampling days. NB recorded twice as many individuals per trap than OB in the first

two sampling days (chi-square test, $p=0.01$). Beyond the second sampling day, there were no significant differences in the trap productivity between the two bait types (chi-square test, $p>0.05$).

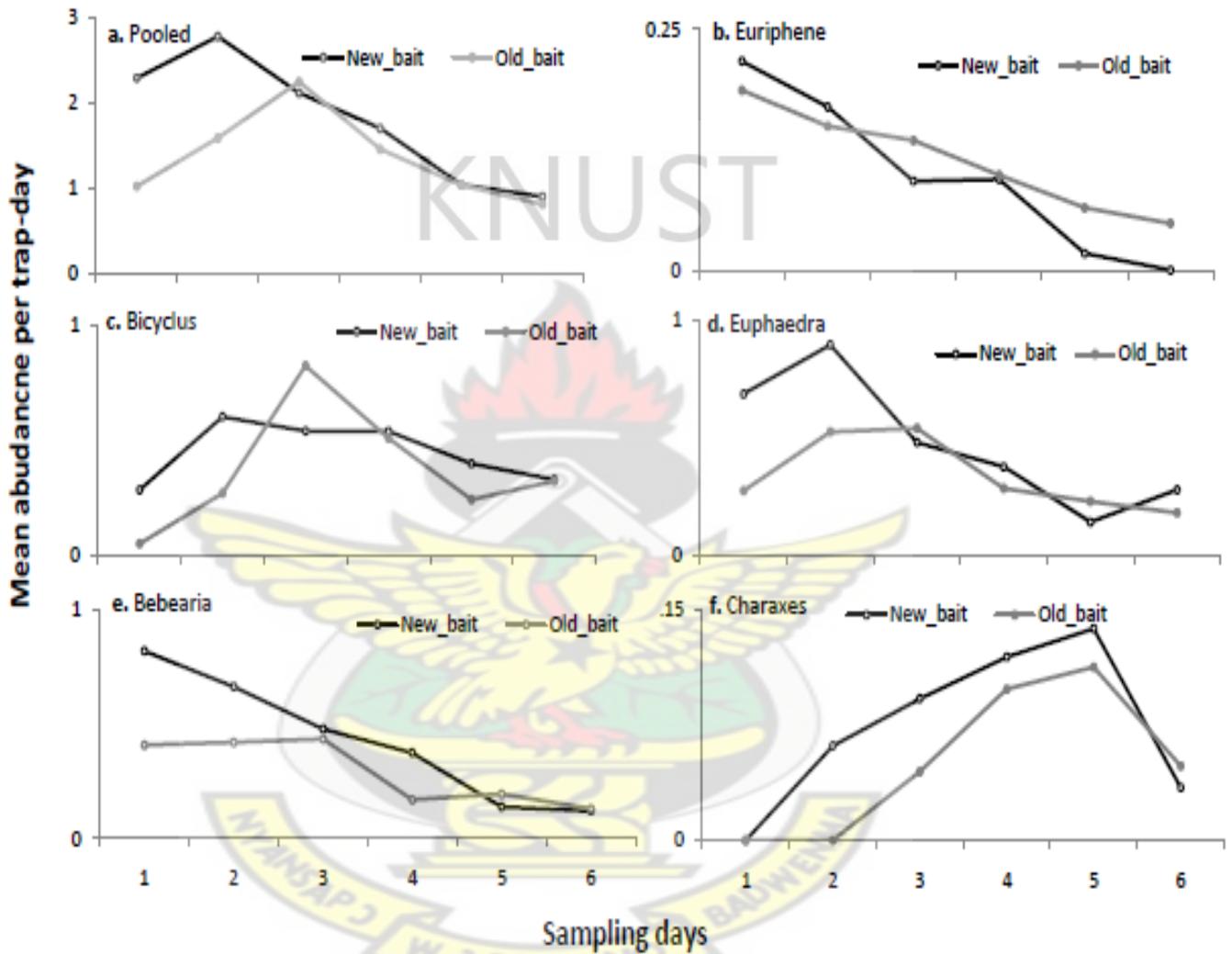


Figure 4.3 Response of different species groups to bait age, measured here as sampling days. **a) Pooled** represent the overall trend when all the species groups were pooled together as one sample. New bait and Old baits are the two types of baits used in the set up.

Further analyzing the effect of sampling day on trapping success at the genus level, I observed variation in individual species-groups' response to the age of bait (Figure 4.3b-f). The responses of the genera *Bebearia* and *Euriphene* to bait aging appeared similar. They both recorded their highest number of trapped individuals on the first sampling day and thereafter declined progressively, indicating a preference for fresh fruit bait (Figure 4.3b,e). The trend of *Bicyclus* abundance in trap. over the sampling days was very similar to the one observed when all the species-groups were combined or pooled (Figure 4.3c). However, in contrast to the trends described above for different species-groups, the number of individuals of the *Charaxes* and *Palla* species-groups trapped per sampling day, were highest on the fifth sampling day, when baits were putatively well advanced in age (Figure 4.3f).

4.4 DISCUSSION

The dataset of the present study contains almost all the key species-groups usually used as surrogate taxa for butterfly biodiversity monitoring studies in Afrotropical ecosystems. In Africa, these species-groups include mainly members of the Limenitidinae, Satyrinae and Charaxinae (Kremen 1994; Fermon *et al.* 2000; Rogo & Odulaja 2001; Bobo *et al.* 2006). Only three individuals (of two species; *Kallimoides rumia* and *Lachnoptera anticlia*) of the total 1,214 trapped individuals were not members of these three dominant subfamilies. Consequently, inferences drawn from this study could be applied to other African ecosystems, especially in the West African subregions, where these species-groups occur abundantly.

The results of the study clearly show that the new trap-type (NT) outperformed the old trap-type (OT) in terms of the number of individuals (and species) trapped per trap-day. On the average, the NT recorded three to four times more individuals per trap-day than OT (Figure 4.2). The basic difference between the two trap-types lies largely in the amount of space provided as entry for luring butterflies. The novel trap (NT) has only about a 25 x 10cm slit (opening) at only one side of its cylinder of nylon netting. Quite the opposite, the conventional van Someren-Rydon trap (OT) used in most similar studies (e.g. DeVries 1988; Oduro & Aduse-Poku 2005; Bobo *et al.* 2006; Bossart *et al.* 2006; Molleman *et al.* 2006; Bossart & Opuni-Frimpong 2009) has about a 10 cm space between the plywood at the base and the lower metal hoops holding the nylon nettings, serving as the exit or entry of butterflies lured.

The reduction in size of the exits of NT is suspected to have minimized the risk and rate of escape, once butterflies are lured into the trap. It is worth noting that the decrease in the entrance/exit size, did not necessarily affect the propensity of butterflies to enter traps. As was observed, butterflies after having detected the fruit bait, would go all round the trap till they find the trap's entry. Moreover, butterflies of all body sizes; small (e.g. *Bicyclus taenias*, *B. dorothea*), medium (e.g. *Bicyclus uniformis*, *Gnophodes betsimena*), and large (e.g. *Euphaedra harpalyce*, *Charaxes* species) were recorded in both trap types (Appendix 2). This further supports the belief that the entry size of NT did not unduly restrict large-bodied butterflies. An entry of 25 x 10cm is obviously large enough for even the largest African nymphalids to pass through (*personal observation* and *pers communication*, Torben B. Larsen).

The height of the NT might have also contributed to its relatively higher number of trapped individuals, compared to OT (NT was about 20cm taller than OT). Most nymphalids, by their flight behaviour, fly upwards after feeding, and this innate behavior forces trapped butterflies to settle at the upper portions of the trap is nylon netting. Higher trap heights means trapped species will fly higher up and this reduces the risk and rate of escape from the trap. Perhaps it will be useful to increase the height of traps in similar future research. One other practical advantage of the novel trap, compared to OT is the weight and ease of transport. NT was about four times lighter than the OT and this means four times as many NTs could be transported, compared to OT.

The present study found that age of bait did affect the number and kind of species-groups trapped. In other words, different species-groups respond differently to the age of bait (measured herein as sampling days). For instance, while *Bebearia* and *Euriphene* species seemed to prefer fresh bait and subsequently saw their numbers of individuals in traps decline after the first sampling day, *Charaxes* and *Palla* species showed a rather opposite trend (Figure 4.3). The results of the study showed that *Charaxes* and *Palla* prefer relatively older bait and this is apparent in their gradual increase in traps till the fifth sampling day. The observed trend is however, not contrary to what is known of the species group.

Charaxes and *Palla* are long known to prefer foul-scented food sources like rotten meat and carcasses (Larsen 2005b; Molleman *et al.* 2005; Hamer *et al.* 2006). The closest of the banana baits used in the study to these food sources would be a very old bait, prepared and allowed to ferment for over 120 hours. In their two-month study in Costa Rica on the use of fruit bait traps, Hughes *et al.* (1998) opine that variation in the number of trapped individuals is best explained by time of day

and not age of bait, except immediately after baiting. However, keeping the time of sampling (10:00-12:00 hours GMT) constant, it was established in the present study that age of bait can also account for some of the variations in fruit-feeding butterfly capture data.

Answering the question "how rapid should a rapid butterfly assessment be?" requires the knowledge of the species-groups, most relevant and effective in evaluating exogenous changes in ecosystems. At the moment further work is necessary to refine our knowledge on this. Until such studies and their results are made available, the reasonable approach is to target all nymphalids, as is currently the case in most monitoring protocols (e.g. Fermon *et al.* 2000; Rogo & Odulaja 2001; Aduse-Poku & Doku-Marfo 2007; Barlow *et al.* 2007a). Subsequently if the aim of the assessment is to target all frugivorous adult butterfly communities, then based exclusively on the results provided in this study, sampling needs not exceed two days (if palm wine is mixed with mashed banana and allowed to ferment for 24 hours) or three days (when only mashed banana fermented for 24 hours is used as bait) on the same location.

Beyond these recommended days, the number of trapped individuals decreased by 25 – 30%. One reason for the decline could be due to the reduction in the local population as sampling progressed in a sampling week. In the present study trapped specimens were collected for future curatorial project and for other studies (e.g. Aduse-Poku *et al.* 2009). Another plausible reason is the evaporation of alcohol, and other volatile fragrances which reduced baits cues, making them less attractive.

It is suspected that the palm wine in NB hastened the breakdown of sugars in the mashed banana fruits, and produced various aromatic organic acids and

alcohols at faster rates (Lasekan *et al.* 2007). Comparing the trends for the different bait-types (in Figure 4.3), one can speculate that addition of palm wine to mashed banana fruit might have sped up the fermentation process by 24 hours. Obviously, faster production of alcohol implies that bait will age and lose its attractiveness faster, as alcohol evaporates. This was exactly the case observed in the study. Traps baited with NB were more attractive in the first two sampling days but attractiveness generally declined thereafter. This makes NB ideal for use in rapid biodiversity assessment protocols where time is as important as the mission objective.

Palm wine, has a pH of about 3.6 and alcohol content of 3.3–4.0%, depending on the stage of fermentation (Lasekan *et al.* 2007). It contains a heavy suspension of yeast and bacteria, giving the wine a milky-white appearance (Uzochukwu *et al.* 1999). These microorganisms metabolize the sugars in the fresh wine within 36–48 hours and produce various organic acids and alcohols (Bassir 1962). In the present study, baits were prepared and allowed to ferment twenty-four hours before the setting of traps. This suggests that most of the various aromatic organic acids and alcohols in the palm wine-banana mix bait were produced during the first two days of sampling. Since fruit-feeding butterflies use these odours as cues for locating fruit (Dierks & Fischer 2008), it is expected that NB will be more attractive and hence productive (in terms of species turnover in traps) than OB, during the initial days of sampling and this is consistent with the results of the study (see Figure 4.2).

Generally, NB attracted more individuals (and species) compared to OB, (though not statistically significant for all the sampling days). The enhanced attraction of NB may be due to the presence of additional yeast and ethanol in the

Molleman et al. (2005) demonstrated that yeast solution alone can be useful in attracting fruit-feeding butterflies. Yeast and alcohol therefore function as long range signals or volatile cues in directing butterflies to their food sources (Dierks & Fischer 2008).

4.5 CONCLUSION

The present study has shown that a novel trap type (NT) with reduced entry/exit points performed thrice as much better than the conventional van Someren-Rydon, in terms of trap productivity. This, coupled with its light weight, makes this trap type preferable for rapid biodiversity assessment programmes where time and effort are important considerations. The study has also demonstrated the usefulness of adding palm wine to mashed banana fruits as bait for sampling fruit-feeding butterflies. Palm wine hastens the breakdown of sugars in the mashed banana fruits, which in turn accelerates the production of aromatic organic acids and alcohols. These organic compounds provided cues for butterflies in locating baited traps faster. Perhaps it is worth recommending that, similar future research should focus on working out the optimal concentrations of palm wine and mashed banana as bait for sampling butterflies. The study provided evidence that age of bait does affect both the number and kind of butterflies trapped. It is therefore appropriate to identify a priori the focal butterfly taxa, before deciding on the duration of sampling of RBA surveys. The study provides essential information on how to enhance butterfly RBA protocols in Ghana and West Africa.

CHAPTER FIVE

Assessing the use of fruit-feeding butterflies as indicators of habitat change in West African forests

Abstract

Although fruit-feeding butterflies are preferred surrogate taxa for monitoring biodiversity trends in many forest ecosystems, recent studies suggest that, not all fruit-feeding butterfly species groups are effective in detecting changes in habitat accurately. There is therefore the need for a conscious search for the actual "winners" and "losers" in the event of forest modification. Such information would undeniably provide a valuable guide to the interpretation of butterfly biodiversity data as indicators of changes in an ecosystem or environment. In this study, the value of fruit-feeding butterflies as indicators of habitat change was assessed at three taxonomic levels – species, genus and species-groups. The study was carried out between July 2006 and January 2007 on (habitat gradient) transects, running from a protected forest to neighboring cocoa farms. The study identified seven genera, six species-groups and 25 species as potentially useful indicators of habitat change. The study showed that species richness alone does not represent a powerful metric for monitoring degrees of forest disturbance. Rather, the relative abundances and complete assemblages of defined indicator taxa (based on both fidelity and specificity), were of a stronger indicative value. Considering the near lack of resources for biodiversity research in Ghana and West Africa, and the paucity of taxonomist experts, perhaps it is more useful to use higher level taxa (preferably at the genus and species-groups levels) as recognizable indicators in RBA design.

5.1 INTRODUCTION

Forests in West Africa are under increasing threat from logging and agricultural conversion. Forest destruction in the region remains among the highest in the world. For instance, the deforestation rates in Ghana and Nigeria are estimated at around 3% and 3.3% per annum respectively (IUCN 2006). The quest for a suitable monitoring scheme that would provide both conservationists and land-use managers quick hints on the changes of habitat quality in the region, is of prime importance.

The use of butterflies in such monitoring schemes allows patterns of diversity and environmental quality to be measured at scales that are often more meaningful than those measured using plants and vertebrates (Yen & Butcher 1997). Butterflies are more sensitive to environmental perturbations than plants and vertebrates owing to their rapid breeding rates and relatively short generation times (Kremen 1992; Thomas *et al.* 2004). Consequently, previous studies (e.g. Kremen 1994; Schulze *et al.* 2004; Thomas 2005; Barlow *et al.* 2007b) have demonstrated the utility of fruit-feeding butterflies as indicators of habitat disturbance.

However, there is growing evidence that not all fruit-feeding butterfly species groups can effectively be used as indicator taxa. For instance, canopy species groups (e.g. *Charaxes*, *Apatuopsis*) captured mostly in the forest canopy in good conditioned forest habitats are commonly trapped as well at the understorey in disturbed or opened forests (Fermon 2002; Fermon *et al.* 2003). There is therefore the need for a conscious search for the actual 'winners' and 'losers' in the event of forest modification. Such information would undeniably provide a valuable guide to the interpretation of (butterfly) biodiversity data as indicators of changes in an ecosystem or environment.

In the search for fruit-feeding butterfly taxa that can be used for monitoring habitat change accurately in West Africa, a study was carried out to assess the use of fruit-feeding butterflies as indicators of habitat change in West African forests at three taxonomic levels – species, genus and species-groups. The study was carried on habitat gradient transects, running from a protected forest (Bia National Park) through the forest boundary to neighboring cocoa farms.

5.2 MATERIALS AND METHODS

5.2.1 Description of Study Sites

The study was conducted in Bia National Park (BNP), located in the transitional zone between Moist Semi-deciduous and Evergreen forest. The area forms part of the vulnerable Upper Guinean rainforest (a strip of tropical moist forest stretching from Sierra Leone to Ghana), listed as one of the world's 25 biodiversity hotspots (Myers et al. 2000). It lies in the South Western part of Ghana ($06^{\circ}20'' - 06^{\circ}39''\text{N}$, $02^{\circ}58'' - 03^{\circ}13''\text{W}$) and shares a border with Côte d'Ivoire to the west. Bordering BNP are traditional cocoa farms grown under sparse trees. The ages of cocoa trees varied from 50 years to as young as two years.

5.2.2 Butterfly Sampling

The study covered four sampling periods between July 2006 and January 2007. The sampling protocol involved the use of line transects and fruit-baiting techniques. Butterfly traps were hung at about 10 cm above the forest floor and baited with mashed overripe banana fruits mixed with palm wine. Baits were prepared and allowed to ferment for 24 hours before the setting of traps. Two transects located about 1km from each other were used for the study. On each

transect, 17 trap-stations spaced at 50m from each other were installed for a quantitative butterfly diversity sampling. Each of the transects ran from the forest interior (through the forest boundary) into the bordering cocoa farms; such that 10 trap-stations were located within the National Park, one at the forest-cocoa farm boundary and six in the cocoa farms bordering the National Park. Traps were inspected daily during the sampling periods between 10.00 and 15.00 hours GMT. In total, the quantitative sampling protocol described generated a total of 596 trap-days. One trap-day is herein equivalent to one trap sample per day (24 hours after setting out trap).

5.2.3 Data Analysis

The EstimateS package (Colwell 2009) was used to compute the diversity and richness estimates. The Rarefaction technique, implemented in EcoSim, was used to standardize and compare species richness computed from samples of different sizes (Gotelli & Entsminger 2009). Patterns of species dominance or evenness were compared between habitats using species rank–abundance plots. Individual abundance per sampling period was calculated as the mean number of individuals per trap-day to correct for the variation in trap numbers in different habitats. The R package (R Development Core Team 2009) was used for the data analyses.

For the nymphalid community gradient study, species turnover between the different distinct land-use (habitat) communities (beta diversity) was first calculated using β (Wilson & Shmida 1984).

$$\beta = \frac{G + L}{2S}$$

where β = Beta diversity or species turnover; G = Species gained, L = Species lost and S = Mean species richness. This index uses only presence and absence data.

The species turnover is reflected by gain and loss of species along the environmental gradient and it provides an idea of the beta diversity (the overall diversity in the different habitat types). The Morisita-Horn index was also used to assess similarity of fruit feeding butterfly species composition among different trap stations in the forest, at the boundary and in the cocoa farms. This estimator quantifies species turnover in terms of both the identities and abundances of species and it is among the most robust estimators to sample size (Magurran 2004).

Potentially useful indicator taxa for intact or good conditioned forest and agriculturally-induced or open habitats like cocoa farms were identified using the Indicator Value (*IndVal*) method proposed by Dufrêne and Legendre (1997). This method assesses, for each taxon, whether it is a significant indicator of a particular habitat (forest or cocoa farm), based on the criteria of specificity to, and its frequency within, that habitat. The score of the *IndVal* represents the degree to which a given species or species-group is unique to a particular habitat type (Dufrêne & Legendre 1997). Species or species-groups with high *IndVal* are thus good indicator taxa because they are habitat specific and have a high probability of being sampled during monitoring (Cleary 2004).

The *IndVal* index is calculated as follows: For each species or species-group (or taxon) *i* in each site or habitat *j*, the product of *A_{ij}* and *B_{ij}* are computed. *A_{ij}* is mean abundance of a taxon *i* in the sites of habitat *j* compared to all groups in the study. *B_{ij}* is the relative frequency of occurrence of taxon *i* in the sites of habitat *j* (Dufrêne & Legendre 1997):

$$A_{ij} = \frac{N_{individuals_{ij}}}{N_{individuals_i}} \quad \text{and} \quad B_{ij} = \frac{N_{sites_{ij}}}{N_{sites_i}}$$

$$IndVal = A_{ij} \times B_{ij} \times 100$$

Where *IndVal* is the Indicator Value of the taxon *i* in site habitat *j*. In the formula for A_{ij} , which is a measure of specificity, $N_{individuals_{ij}}$ is the mean number of individuals of taxon *i* across sites of group *j*, while $N_{individuals_i}$ is the sum of the mean numbers of individuals of taxon *i* over all groups. A_{ij} is maximum when taxon *i* is only present in habitat *j*. In the formula for B_{ij} , which is a measure of fidelity (the degree to which a species is found only in a particular group), $N_{sites_{ij}}$ is the number of sites in cluster *j* where taxon *i* is present, while N_{sites_i} is the total number of sites in that habitat. B_{ij} is maximum when taxon *i* is present in all objects of habitat *j*. Final multiplication by 100 produces *IndVal* scores in percentage.

The indicator taxa analyses were implemented in R using the 'labdsv' package (Roberts 2009). Statistical significance was assessed using Monte Carlo randomization, also implemented in R. Following Cleary (2004), only taxon that were significant (at an α of <0.01) for both the *IndVal* Index and a 2-tailed chi-square test were considered significant.

5.3 RESULTS

5.3.1 General Biodiversity

A total of 1,337 individuals belonging to 88 species were trapped during the entire study period. All the individual butterflies but one (*Gamia bulchozi*) were fruit-feeders (nymphalids) belonging to six subfamilies of Nymphalidae ((Appendix 3; Table 5.1). *Gamia bulchozi* is a skipper and belongs to the Hesperidae family. Consequently, it was excluded from the subsequent data analyses. Nymphalid butterflies trapped during the study are summarized and grouped into their respective subfamilies and genera in Table 5.1.

Table 5.1 Number of fruit-feeding butterflies trapped in Bia National Park and bordering cocoa farms, grouped into subfamilies, genera and habitat types. The values in the parentheses are percentages of individuals of the genera trapped

Subfamily	Genus	Number of individuals		Number of species		
		Cocoa Farm	Forest	Cocoa Farm	Forest	% Shared
Limenitidinae						
	<i>Euphaedra</i>	21 (3.4)	148 (21)	7	17	41.2
	<i>Bebearia</i>	27 (4.4)	105 (15)	7	10	52.5
	<i>Euriphene</i>	1 (0.16)	89 (12.5)	1	8	12.5
	<i>Euryphura</i>	10 (1.6)	2 (0.28)	1	1	100
	<i>Aterica</i>	--	14 (2.0)	--	1	0.00
	<i>Catuna</i>	--	1 (0.14)	--	1	0.00
	<i>Cymothoe</i>	6 (0.97)	1 (0.14)	3	1	33.3
	<i>Harma</i>	3 (0.49)	--	1	--	0.00
	<i>Pseudacrea</i>	1 (0.16)	--	1	--	0.00
	<i>Pseudathyma</i>	2 (0.32)	--	1	--	0.00
Satyrinae						
	<i>Bicyclus</i>	463 (75)	244 (34)	15	18	65.0
	<i>Gnophodes</i>	26 (4.2)	67 (9.4)	2	2	100
	<i>Melanitis</i>	8 (1.30)	21 (3.0)	1	1	100
	<i>Elymniopsis</i>	8 (1.30)	2 (0.28)	1	1	100
	<i>Hallelesis</i>	--	3 (0.42)	--	1	0.00
Charaxinae						
	<i>Charaxes</i>	28 (4.5)	6 (0.84)	9	3	20.0
	<i>Palla</i>	7 (1.14)	7 (15.10)	2	1	50.0
Nymphalinae						
	<i>Salamis</i>	1 (0.16)	1 (0.14)	1	1	100
	<i>Hypolimnas</i>	1 (0.16)	--	1	--	0.00
	<i>Junonia</i>	1 (0.16)	--	1	--	0.00
Biblidinae						
	<i>Eurytela</i>	1 (0.16)	--	1	--	0.00
Heliconiinae						
	<i>Acraea</i>	1 (0.16)	--	1	--	0.00
TOTAL		623	711	58	68	42.5

The subfamilies with the highest representation in the pooled sample were Satyrinae (842 individuals of 25 species) and Limenitidinae (431 individuals of 45 species). With 10 *Charaxes* and two *Palla* species, the Charaxinae subfamily followed with 48 individuals. The most abundant species groups in the pooled sample were, in descending order of magnitude, *Bicyclus*, *Euphaedra*, *Bebearia*, *Euriphene* and *Charaxes* (Table 5.1). These five genera alone constituted

approximately 86% and 76% of the total number of individuals and species caught respectively.

5.3.2 Fruit-feeding butterfly composition in the different habitat types

Overall, 628 individuals of 58 fruit-feeding butterfly species were caught from the cocoa farm within the 586 trap-days. A total of 711 individuals belonging to 67 species were recorded from the trap stations in forest (Appendix 3). Species accumulation curves for the two habitat types did not reach an asymptote, suggesting further sampling effort would have yielded more species (Figure 5.1).

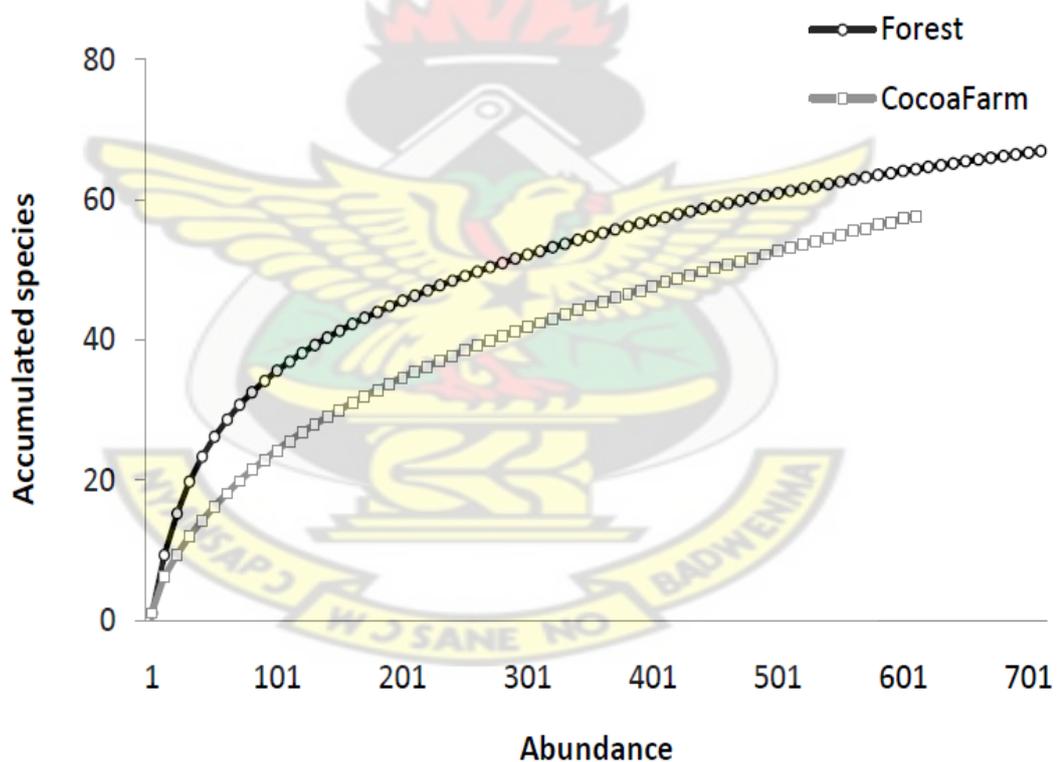


Figure 5.1 Sampled-based rarefaction curves for fruit-feeding butterflies in forest and cocoa farms in and around Bia Biosphere Reserve

There was considerable difference observed in the fruit-feeding butterfly composition in the different habitats. Butterflies trapped in the cocoa farm were largely (82%) Satyrinae. Further, *Bicyclus* alone made up 84% of the total (842 individuals) Satyrinae trapped in the cocoa farm. Investigating further to the species level, it came to light that about 88% of the total (463) *Bicyclus* individuals were of three species; *B. dorothea* (45%), *B. sandace* (29%) and *B. vulgaris* (14%, Appendix 3). *Bicyclus* and *Charaxes* contributed the largest numbers of species in the cocoa farms with 15 and nine species respectively.

Unlike in the cocoa farms, the individuals trapped in the forest were not only dominated by *Bicyclus* (34%) but also *Euphaedra* (21%), *Bebearia* (15%) and *Euriphene* (13%) species groups (Table 5.1). Species of these four genera alone constituted 80% of the total of 67 species trapped in the forest. Relative species abundance ranged from 233 individuals (for *Bicyclus dorothea*) to a single individual (for 28 species) in the cocoa farms. The highest relative species abundances in the forest was 51 (for *Gnophodes betsimena*). Twenty of the species recorded in the forest were singletons (i.e., represented by a single individual).

The forest fruit-feeding butterfly composition was richer and more diverse than in the cocoa farm (Figure 5.2 and Table 5.2). Samples from the cocoa farm were dominated by a few abundant species and many 'rare' species. Nearly half (48%) of the 58 species caught at the cocoa farms were represented by just a single individual (singleton) in the sample pool. In the forest sample, about a third (30%) of the species were singletons. Approximately two-thirds (67%, 414) of the all individuals trapped in the cocoa farms were of three commonest *Bicyclus* species (*B. dorothea*, *B. sandace* and *B. vulgaris*, Table 5.1). The three most abundant species (*Gnophodes*

betsimena, *Bicyclus funebris*, and *Euriphene gambiae*) accounted for only 20% of the total (711) individuals caught in the forest.

The relatively higher diversity of the fruit-feeding butterfly community in the forest is shown by the comparatively shallow gradient that characterized the slope of the graph in Figure 5.2. This indicates high evenness as the abundance of different species are similar. Tables 5.2 and 5.3 summarize the estimated species richness and diversity scores in the different habitats.

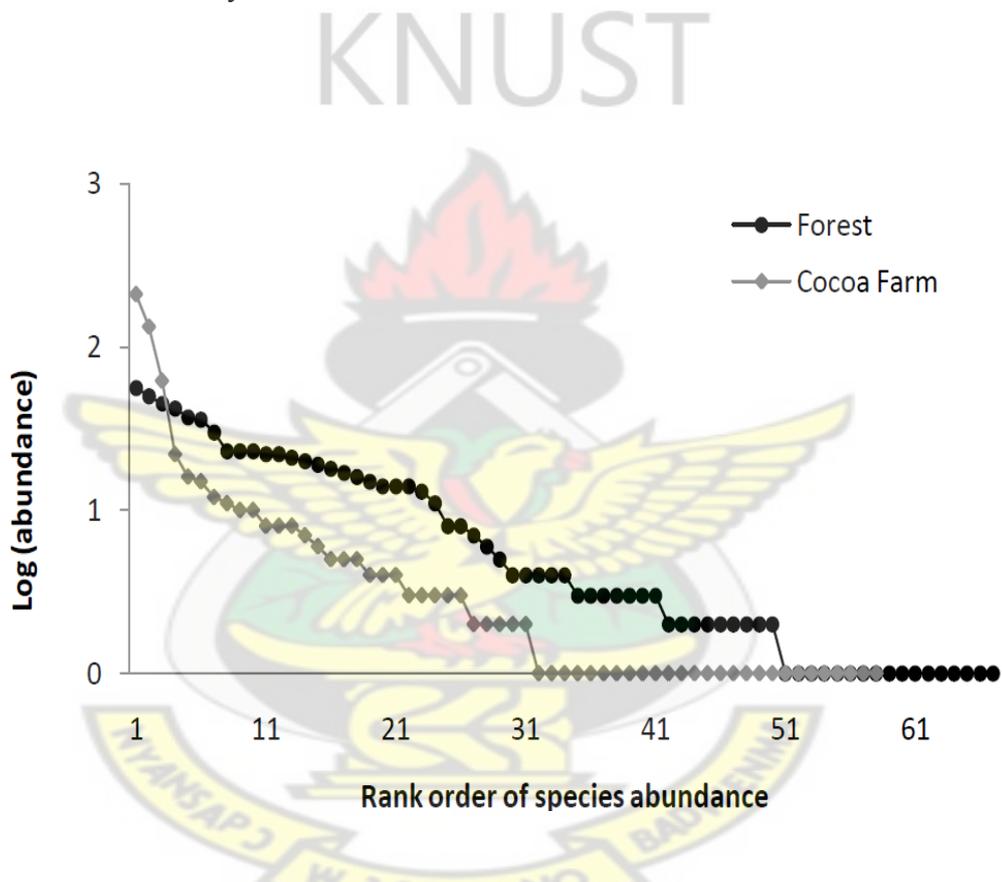


Figure 5.2 Rank-abundance distributions of fruit-feeding butterfly species in forest and cocoa farms in and around Bia Biosphere Reserve

Table 5.2 Estimated species richness and diversity (mean values with standard deviations in parentheses) for the different habitat types (Forest and Cocoa farm). Data from boundary trap stations BF and BC (do they need explanation/spelling out?) are added pooled with the forest and cocoa data respectively.

Habitat	Indv	Sobs	Trap ^a days	Estimated species richness								Computed species diversity				
				ICE	ACE	Chao1	Chao2	Jack1	Jack2	Bootstrap	MM	Alpha	Shannon	SHE	Simpson	Menhinick
Forest	711	68	335	89.1(5.0)	88.4 (4.3)	91.6 (14.3)	89.2 (12.5)	87.1 (5.8)	98.4 (6.1)	76.5 (2.2)	78.1	18.5 (1.3)	3.6 (0.01)	35.8 (0.5)	27 (0.4)	2.6
Cocoa	623	58	261	103 (5.9)	105 (5.9)	133 (42.9)	100 (21.6)	84.3 (6.5)	101 (4.1)	69.2 (2.4)	83.1	15.6 (1.2)	2.5 (0.02)	11.8 (0.3)	5.5 (0.1)	2.3

^aTrapday is calculated as the number of operational traps multiplied by the number of sampling days within a 'sampling week', Indiv = number of individuals, Sobs = number of observed species, ACE=Abundance-based coverage estimator, ICE = Incidence-based coverage estimator, Chao1= Chao 2 richness estimator, Chao 2 = Chao 2 richness estimator, Jack 1 = Jackknife first order richness estimator, Jack 2 = Jackknife second order richness estimator, Bootstrap=Bootstrap richness estimator, MM=Michaelis-Menten richness estimator, Alpha = alpha diversity, Shannon = Shannon diversity index, SHE= Shannon exponential index, Simpson = Simpson diversity index, Menhinick = Menhinick diversity index.

Table 5.3 Estimated species richness and diversity (mean values with standard deviations in parentheses) for the different habitat types (Forest, cocoa farm and the boundary between cocoa and forest).

Habitat	Indv	Sobs	Trap ^a days	Estimated species richness								Computed species diversity				
				ICE	ACE	Chao1	Chao2	Jack1	Jack2	Bootstrap	MM	Alpha	Shannon	SHE	Simpson	Menhinick
Forest	665	67	316	89.1 (5.0)	88.4 (4.3)	91.8 (14.3)	89.2 (12.5)	87 (5.8)	98.4 (6.1)	76.5 (2.2)	78.1	18.5 (1.3)	3.6 (0.01)	35.8 (0.5)	27 (0.4)	2.60
Boundary	89	28	19													
Cocoa	582	55	242	94.4 (8.3)	96.2 (6.5)	136 (48.7)	95.5 (21.5)	79 (6.4)	94.8 (4.8)	65.3 (3.3)	81	14.9 (1.2)	2.4 (0.06)	11.5 (0.7)	5.4 (0.2)	2.28

^aTrapday is calculated as the number of operational traps multiplied by the number of sampling days within a 'sampling week', Indiv = number of individuals, Sobs = number of observed species, ACE=Abundance-based coverage estimator, ICE = Incidence-based coverage estimator, Chao1= Chao 2 richness estimator, Chao 2 = Chao 2 richness estimator, Jack 1 = Jackknife first order richness estimator, Jack 2 = Jackknife second order richness estimator, Bootstrap=Bootstrap richness estimator, MM=Michaelis-Menten richness estimator, Alpha = alpha diversity, Shannon = Shannon diversity index, SHE= Shannon exponential index, Simpson = Simpson diversity index, Menhinick = Menhinick diversity index

A comparison of the trap stations within habitat types showed that the forest trap stations (F₁-F₁₀) all had relatively high diversities. The fruit-feeding butterfly communities at the cocoa farmland sites (C₁-C₇) were significantly less diverse. The Fisher's α and Menhinick diversities for the eight trap stations in the cocoa farmland ranged from 3.5 to 8.0 and 1.8 to 2.7 respectively, compared to 6.0 to 14.3 (using Fisher's α) and 3.1 to 4.2 (using Menhinick diversity index). In general, both (rarefied) species richness and (Menhinick's) diversity increased steadily with increasing distance to the forest interior (Spearman correlation, $R^2=0.74$, $p<0.001$ and $R^2=0.72$, $p<0.001$; Figure 5.3).

5.3.3 Species turnover along the Forest-Cocoa farm habitat gradient

As many as 38 species (representing 43% of the total species collected) were caught in both the forest and the cocoa farms. Species turnover among the different distinct habitat communities based on a species presence-absence matrix (β diversity) was 42%, suggesting a moderate overlap in species. The overall similarity between the forest and the cocoa farm using the Morisita-Horn similarity index was 31.5%. Comparing the similarity scores within the different habitats, the trap stations within the cocoa farms (C₁-C₇) were more similar in terms of fruit-feeding butterfly composition than those in the forest ((F₁-F₁₀; Table 5.4). On the average, there was a 92% species overlap between any two trap stations in the cocoa plot, with the highest similarity occurring between C₃ and C₆ (98%), and C₇ and C₆ (97%). The lowest pairwise similarity value in the cocoa farm was 83%, between C₆ and C₁. Within the forest, the similarity scores ranged from 84% (between F₅ and F₂) to 40% (F₈ and F₉). The mean species composition overlap within the forest trap stations was 65%; a relatively low score compared to the cocoa farm.

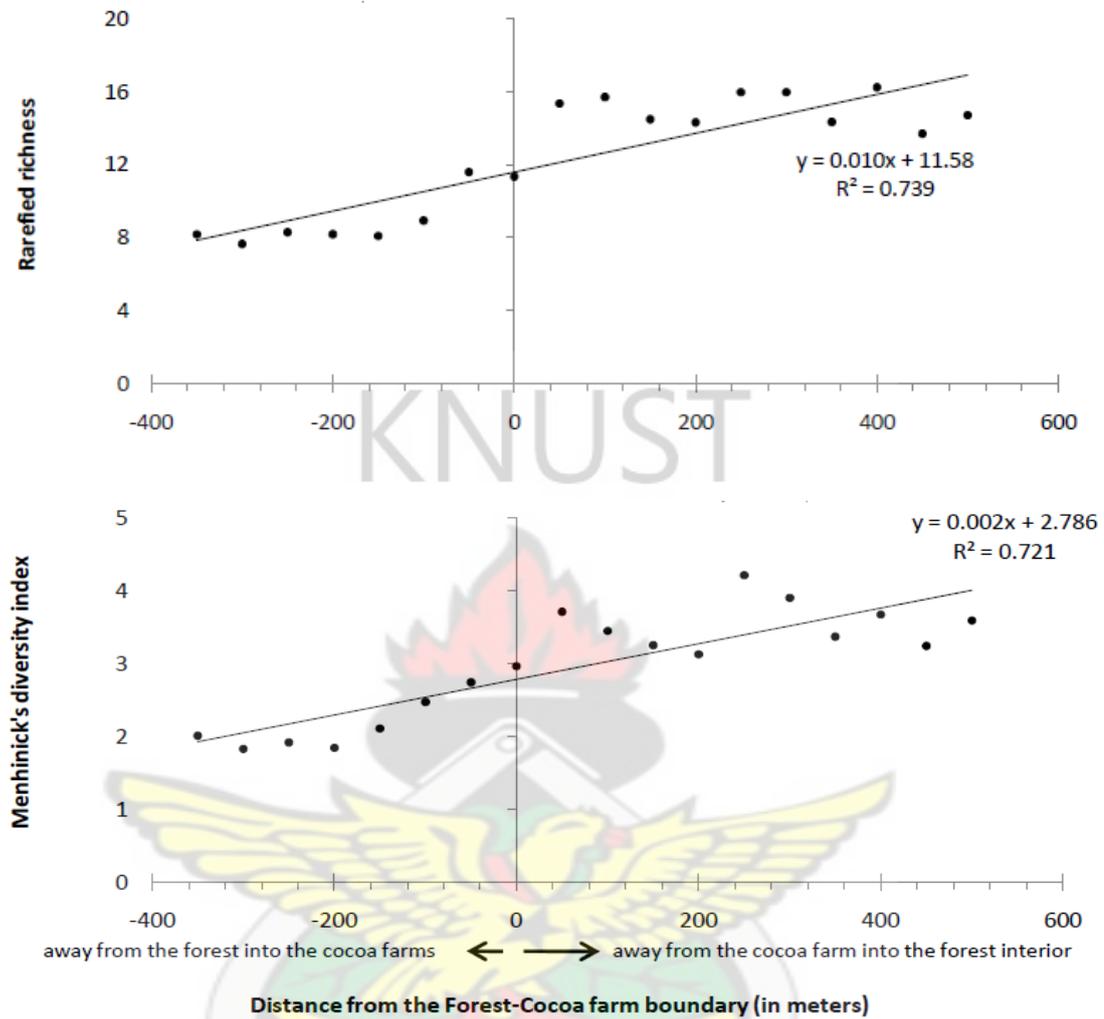


Figure 5.3 Regression of diversity and rarefied richness of trap stations from the forest-cocoa farm boundary. The negative values on the x-axis denote the distances of cocoa farm trap stations from forest edge, such that $C_1 = -50$ and $C_7 = -350$. i.e -300 means 300m inside the cocoa farm from the forest edge. Correspondingly, the positive values are the distances of forest trap stations from the forest-cocoa boundary (similarly $F_1 = 50$, and $F_{10} = 450$). Zero (0) on the x-axis denotes the boundary trap station between forest and the cocoa farm.

Table 5.4 Pairwise similarity scaling plot of fruit-feeding butterflies based on Morisita-Horn similarity scores (in colour range; green being the highest, yellow moderate and red the lowest) between trap stations in the Forest (F_1 - F_{10}), in the cocoa farm (C_1 - C_7) and at the forest-cocoa farm boundary (B) in Bia Biosphere Reserve

		Forest										Boundary	Cocoa farm						
		F_{10}	F_9	F_8	F_7	F_6	F_5	F_4	F_3	F_2	F_1	B	C_1	C_2	C_3	C_4	C_5	C_6	C_7
Forest	F_{10}	1																	
	F_9	0.449	1																
	F_8	0.428	0.403	1															
	F_7	0.677	0.773	0.508	1														
	F_6	0.595	0.59	0.565	0.698	1													
	F_5	0.695	0.599	0.43	0.735	0.763	1												
	F_4	0.627	0.648	0.444	0.744	0.74	0.785	1											
	F_3	0.582	0.587	0.502	0.632	0.683	0.619	0.808	1										
	F_2	0.679	0.558	0.496	0.768	0.801	0.836	0.804	0.743	1									
	F_1	0.667	0.613	0.465	0.784	0.783	0.795	0.778	0.711	0.841	1								
Boundary	B	0.412	0.295	0.166	0.22	0.418	0.291	0.212	0.151	0.169	0.199	1							
Cocoa farm	C_1	0.39	0.258	0.184	0.255	0.417	0.301	0.225	0.149	0.248	0.163	0.959	1						
	C_2	0.312	0.217	0.083	0.15	0.326	0.225	0.149	0.087	0.137	0.118	0.949	0.915	1					
	C_3	0.314	0.189	0.088	0.174	0.314	0.216	0.16	0.104	0.157	0.125	0.889	0.866	0.913	1				
	C_4	0.323	0.179	0.097	0.159	0.292	0.208	0.145	0.091	0.183	0.094	0.928	0.915	0.95	0.951	1			
	C_5	0.364	0.234	0.078	0.192	0.38	0.245	0.202	0.118	0.195	0.17	0.927	0.898	0.951	0.961	0.953	1		
	C_6	0.347	0.22	0.074	0.193	0.33	0.246	0.2	0.134	0.198	0.138	0.861	0.827	0.899	0.977	0.929	0.961	1	
	C_7	0.368	0.256	0.066	0.188	0.363	0.248	0.183	0.11	0.171	0.159	0.888	0.836	0.927	0.947	0.923	0.968	0.969	1

5.3.4 Identifying potentially effective bio indicator taxa

The *IndVal* method revealed four significant indicator species (*Bicyclus dorothea*, *B. sandace*, *B. safitza* and *B. vulgaris*) for an agricultural, open habitat (i.e., cocoa farm), and 21 significant indicator species for good condition forest (see Table 5.5 for the full list of species). At the genus level, there were six significant indicator genera (*Euphaedra*, *Aterica*, *Gnophodes*, *Melanitis*, *Bebearia* and *Euriphene*) of the forest habitat and one significant indicator genus (*Bicyclus*) of the cocoa farm or relatively disturbed habitat (Table 5.6). The abundance of *Euphaedra*, *Bebearia* and *Euriphene* per trap station decreased significantly with increasing distance from the forest edge into the cocoa farmland (Figure 5.4). The opposite was true for *Bicyclus*, which saw a rather considerable increase in its abundance with increasing distance into the cocoa farms (Figure 5.4).

Although *Bicyclus* was generally very abundant in the cocoa farms, its *IndVal* score for the cocoa farm habitat was disproportionately low (68%), compared to *Euphaedra* and *Euriphene*'s *IndVal* scores of 87% and 99% respectively, in the forest habitat; see Table 5.6). Further analyses of this genus level revealed an intriguing trend at the species-group level. Of the six species-groups with enough abundance (≥ 10 individuals) for the analysis, only one (*Bicyclus dorothea* species-group) was recovered as a significant indicator species-group for poor condition forest or open, disturbed habitats (Table 5.7). The remaining four *Bicyclus* species-groups (*sangmelinae*, *funnebris*, *angulosa*, *hewitsoni* and *safitza*) were rather recovered as good conditioned forest habitat indicators with high *IndVal* scores.

Table 5.5 List of potential indicator species (which significantly differentiated between the forest and the cocoa farm) with their indicator values (*IndVal*) and chi-squares scores

Species	Abundance		2-tailed chi-square		<i>IndVal</i>	
	Total	% in Forest	Chi-value	P-value	Forest	Cocoa farm
<i>Euriphene gambiae</i>	0	49	49.0	<0.001	100.00	0.00
<i>Euphaedra harpalyce</i>	1	37	34.1	<0.001	97.37	2.63
<i>Bebearia tentyris</i>	1	22	19.2	<0.001	95.65	4.35
<i>Bicyclus funebris</i>	15	48	17.3	<0.001	76.19	23.81
<i>Euphaedra phaethusa</i>	3	24	16.3	<0.001	88.89	11.11
<i>Euphaedra crockeri</i>	1	18	15.2	<0.001	94.74	5.26
<i>Bebearia phantasina</i>	0	15	15.0	<0.001	100.00	0.00
<i>Aterica galena</i>	0	14	14.0	<0.001	100.00	0.00
<i>Bicyclus abnormis</i>	3	21	13.5	<0.001	87.50	12.50
<i>Bicyclus sambulous</i>	1	16	13.2	0.001	94.12	5.88
<i>Bicyclus zinebi</i>	3	19	11.6	0.001	86.36	13.64
<i>Gnophodes chelys</i>	4	21	11.6	0.001	84.00	16.00
<i>Gnophodes bestimena</i>	22	50	10.9	0.002	69.44	30.56
<i>Bebearia sophus</i>	10	31	10.8	0.002	75.61	24.39
<i>Euriphene barombina</i>	1	13	10.3	0.003	92.86	7.14
<i>Euphaedra ceres</i>	8	26	9.5	0.004	76.47	23.53
<i>Euriphene simplex</i>	0	8	8.0	0.009	100.00	0.00
<i>Euphaedra medon</i>	5	17	6.5	0.021	77.27	22.73
<i>Bebearia zonara</i>	0	6	6.0	0.029	100.00	0.00
<i>Bicyclus sangmelinae</i>	1	8	5.4	0.039	88.89	11.11
<i>Melanitis leda</i>	8	20	5.1	0.047	71.43	28.57
<i>Bicyclus dorothea</i>	205	8	182.2	<0.001	3.76	96.24
<i>Bicyclus sandace</i>	128	35	53.1	<0.001	21.47	78.53
<i>Bicyclus vulgaris</i>	56	18	19.5	<0.001	24.32	75.68
<i>Bicyclus safitza</i>	10	0	10.0	0.003	0.00	100.00

Table 5.6 List of potential indicator genera (which significantly differentiated between the forest and the cocoa farm) with their indicator values (*IndVal*) and chi-squares scores

Genus	Abundance		2-tailed chi-square		<i>IndVal</i>	
	Total	% in forest	Chi-value	P-value	Forest	Cocoa farm
<i>Euphaedra</i>	164	87.80	93.76	<0.001	86.49	13.51
<i>Euriphene</i>	83	98.80	79.05	<0.001	98.72	1.28
<i>Bebearia</i>	123	79.67	43.33	<0.001	80.70	19.30
<i>Gnophodes</i>	97	73.20	20.88	<0.001	73.45	26.55
<i>Aterica</i>	14	100.0	14.00	<0.001	93.35	6.65
<i>Melanitis</i>	28	71.43	5.14	0.047	87.06	12.94
<i>Bicyclus</i>	659	32.47	80.97	<0.001	31.96	68.04

Table 5.7 List of potential indicator species-groups of the genus *Bicyclus* (which significantly differentiated between the forest and the cocoa farm) with their indicator values (*IndVal*) and chi-squares scores

Species-group	Abundance		2-tailed chi-square		<i>IndVal</i>	
	Total	% in forest	Chi-value	P-value	Forest	Cocoa farm
<i>sangmelinae</i>	26	96.2	22.15	<0.001	96.15	13.51
<i>funebri</i>	66	75.8	17.52	<0.001	75.76	1.28
<i>angulosa</i>	30	86.7	16.13	<0.001	86.67	19.30
<i>hewitsoni</i>	28	85.7	14.29	<0.001	85.71	26.55
<i>safitza</i>	10	0.00	10.00	<0.001	0.000	6.65
<i>dorothea</i>	489	17.2	210.72	<0.001	17.18	82.82

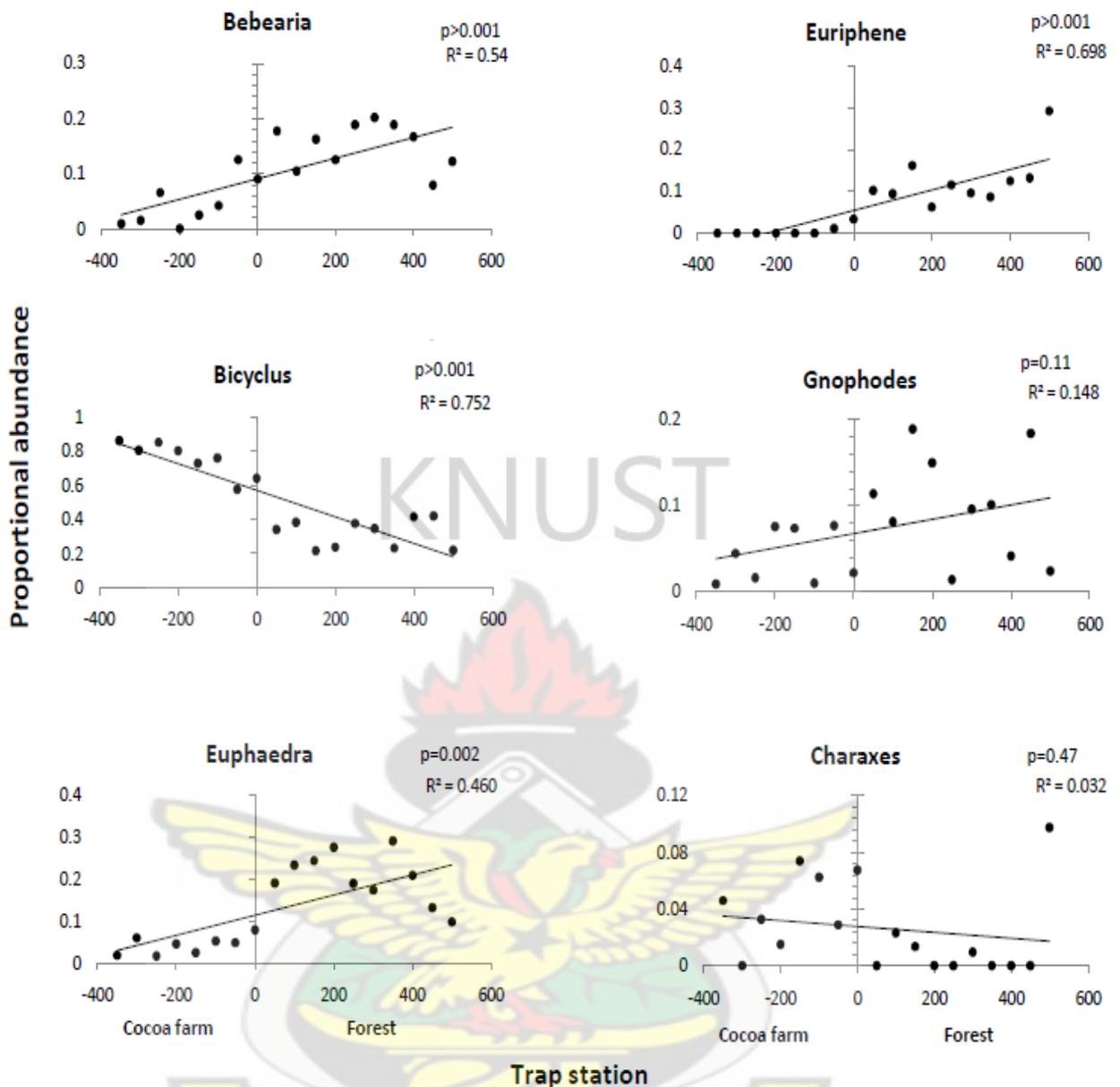


Figure 5.4 Between and within habitat comparison of the abundance of *Bebearia*, *Euphaedra*, *Euriphene*, *Bicyclus*, *Charaxes* and *Gnophodes* genera. The negative values on the x axis denote the distance of Cocoa farm trap stations from forest edge, such that $C_1 = -50$ and $C_7 = -350$. Correspondingly, the positive values are the Forest trap stations from the forest-cocoa farm boundary (similarly $F_1 = 50$, and $F_{10} = 450$). Zero (0) on the x axis denotes the boundary trap station between forest and the cocoa farm.

5.4 DISCUSSION

Although both the number of observed species (Table 5.2 and 5.3) and richness estimated by rarefaction (Figure 5.1) were higher in the forest compared to the cocoa farm, six species richness estimators (ICE, ACE, Chao1, Chao2, Jack and MM) indicated a higher (though not always significant) richness in the cocoa farm (Table 5.2 and 5.3). The inconsistency in richness is explained as an artifact of the estimators, owing to high numbers of rare species in the assemblages, especially in the cocoa farm. In the current study, almost (48%) of the species trapped in the cocoa farm were represented by just a single individual (singleton), compared to 29% in the forest. I suspect the high number of singletons and other 'unique' species (with less than three total individuals in the entire data pool) in the cocoa farm might have led to an overestimation of the habitat richness by some of these estimators. Poulin (1999) tested the performance of three richness estimators and concluded that Chao and Jackknife methods were imprecise, relative to bootstrapping, if the assemblage contained many rare species. Bootstrapping indicated a significantly higher richness (76.5 ± 2.2 , Mean \pm SD) in the forest, compared to 69.2 ± 2.4 in the cocoa farm (Table 5.2 and 4.12).

Taxon diversity was generally higher in the forest, compared to the cocoa farm (Figure 5.2). The relatively high species richness and diversity in the forest, compared to the cocoa farm is in consonance with the nested subset principle (Patterson 1987) which states that species comprising a depauperate insular biota are a proper subset of those in richer habitat, ranked by species richness. This is evidenced by the fact that almost two-thirds (64%) of the species caught from the cocoa farm were recorded in the forest farm as well. All the 21 'cocoa species' not captured in the forest in the present study, were caught in the larger-scale spatio-

temporal survey of fruit-feeding butterflies in the forest (see chapter 3 and Appendix 1).

The forest is apparently more heterogeneous than the cocoa farm in terms of structure, composition and floral diversity. According to the habitat heterogeneity hypothesis (MacArthur & MacArthur 1961), a more structurally complex and heterogeneous habitat offers more niches and/or 'microhabitats' (e.g. shaded areas, light gaps and edges) and therefore supports a greater number of species than a homogenous simple structured habitat like a cocoa farm. Accordingly, the fruit-feeding butterfly communities in the cocoa farm were particularly similar to each other, with significantly higher (0.92 ± 0.04 , Mean \pm SD) mean pairwise similarity among the seven cocoa farm trap stations, compared to 0.65 ± 0.13 in the forest (Table 5.4). Many studies have also showed significant decline in both species richness and diversity with increasing habitat modification (Lawton *et al.* 1998; Schulze *et al.* 2004; Veddeler *et al.* 2005; Barlow *et al.* 2007b).

There were considerable shifts in ecological composition of the fruit-feeding butterfly fauna in the two defined habitats, indicating an influence of habitat modification on butterfly fauna. Results of the present study show that forest species (e.g. *Euriphene*, *Euphaedra*, *Bebearia*) were conspicuously replaced by species adapted to disturbed habitats (e.g. *Bicyclus*) as one moves from the forest to the cocoa farm on the habitat gradient (Figure 5.4). There were also relatively higher abundance of *Charaxes* and *Cymothoe* in the cocoa farm than in the forest. The concept of beta diversity, or the rate of change in species composition along a habitat gradient, has been applied to many studies (Beck *et al.* 2002; Fermon 2002; Bobo *et al.* 2006; Bossart & Opuni-Frimpong 2009), which indicate that the presence of a species at a given place may be related to several factors such as resource availability

for adult and larval host-plants, microclimatic condition, behavioural traits and interactions with other species.

Although some of these factors were not directly measured in the present study, it is suspected that some of them could have influenced the observed ecological shift. The plausibility of these factors regulating the distribution of butterfly fauna is discussed below. First, one of the important elements influencing the response of butterflies to disturbance is the degree of host-plant specificity (Koh *et al.* 2004). Many studies, including the current study reported an increase in Satyrinae (e.g. *Bicyclus*) with increased forest disturbance (Daily & Ehrlich 1995; Fermon *et al.* 2005; Figures 4.20 and 4.21). Increased disturbance leads to an increase in monocotyledonous annual plants on which the larvae of most Satyrinae depend (Fermon *et al.* 2000; Larsen 2005b). Satyrinae generally feed on grasses and unlike many of the relatively more specialized forest species (e.g. *Euriphene*, *Euphaedra*, *Bebearia*), are capable of dispersing into agricultural landscapes. For many Nymphalinae species, several feed on plant species of a mature forest understorey (Larsen 2005b). This matrix might constitute a real barrier (Fermon *et al.* 2000), consequently, species similarity between both sampling sites in the forest and cocoa farm was very low (see Table 5.4).

The differences in the canopy cover, light penetration and level of habitat disturbance lead to the differences in butterfly faunal composition (DeVries 1988; Hill *et al.* 2001; Schulze *et al.* 2001). There exist appreciable differences in light intensity, or penetration, microclimatic temperature and relative humidity in the forest and the 'unshaded' cocoa habitats. The relatively warmer microclimate and higher intensity of perturbation in the cocoa farm lead to high abundance of 'sun-loving' species like *Bicyclus dorothea*, *B. sandace* and *B. vulgaris*. Birket-Smith

(1970) tested the behaviour of *Euphaedra* spp. in relation to temperature, humidity and light and found that a lower relative humidity and higher temperature cause heliophobia and makes species return to the shade after a few minutes. The response of *Euphaedra* to differences in microclimates is no different from *Bebearia* and *Euriphene* (Larsen 2005b). Consequently, these species groups were found almost exclusively in the forest (Figure 5.4, Table 5.5 – 5.7, Appendix 3).

The strong difference in light levels between the two habitats (owing to the absence or near lack and presence of canopy cover in the cocoa and forest habitats respectively) is likely to have disrupted the distinct vertical stratification that existed within the fruit-feeding butterfly assemblage, causing canopy flyers like *Charaxes* and *Cymothoe* to visit the forest floor more frequently (Fermon *et al.* 2000; Hill *et al.* 2001). As expected, high abundances of *Charaxes* and *Cymothoe* were found in the cocoa farm, compared to the forest (see Table 5.1).

High levels of congruency have been found in responses of butterflies to habitat disturbance (Beccaloni & Gaston 1995; Cleary 2004). Although other authors have also reported lower levels of congruence in higher taxonomic groups (Lawton *et al.* 1998; Barlow *et al.* 2007b), high levels of congruence were found between richness and diversity of some of the species-groups and habitat disturbance (see Figure 5.3). The results of the taxon indicator value (*IndVal*) analyses revealed some species, genera and species-groups as significant indicator taxa of forest and more open habitats. Most of the forest indicator species were *Euriphene*, *Euphaedra* and *Bebearia*. *Bicyclus* were generally indicators of disturbed open habitats and this is consistent with results of previous studies. In Cameroun, Bobo *et al.* (2006) found high abundance of *Bicyclus sandace* and *B. vulgaris* in disturbed (cocoa and coffee farmlands) habitat and a significantly lower abundance in the natural forests. This

means that these species are good as indicator taxa of disturbed open habitats in Ghana but West Africa as a whole.

However, the use of *Bicyclus* as an indicator taxon of disturbed open habitats in any monitoring protocol should be approached with caution. As observed, aside the *dorothea* species-group, (which in Ghana consist of *Bicyclus sandace*, *B. vulgaris* and *B. dorothea* species), all the other remaining *Bicyclus* species-groups were identified as a potential indicators of good-quality forest (Table 5.7). The most apparent factor distinguishing *dorothea* and the four other *Bicyclus* species-groups evaluated in the present study is body size. The estimated forewing span of a typical species of the *dorothea* group is about 19mm (Larsen 2005b). The estimated forewing span of a typical species of the *safitza* group is about 24mm (Larsen 2005b). A similar forewing span is quoted for *funebria* and a slightly longer (25mm) span for the *sangmelinae* species-groups (Larsen 2005b). The forewing spans of a typical species of *angulosa* and *hewitsoni* species-groups are estimated as 23mm and 33mm respectively. It can therefore be inferred from the results of this study that relatively larger bodied-sized *Bicyclus* prefer forest habitats, where there is appreciable shade to prevent desiccation. Therefore, caution should be taken in the use of *Bicyclus* as indicators of disturbed open habitats. The genus *Bicyclus* contains species with varying habitat preferences and functional roles, and as a result individual species' responses can be masked by analysis at higher taxonomic levels (Table 5.6 and 4.14c). Clearly, the *dorothea* species group with its excessive dominance (489 out of the total *Bicyclus* 659 individuals), masked the individual species' responses of the other four species-groups which made up only ~25% of the total *Bicyclus* individuals trapped in the study.

Changes in the relative abundances of these indicator species could give a quick hint of the impact of a management decision on biodiversity, allowing adjustment options in space and/or time (Brown 1991; McGeoch 1998; Marcio Uehara-Prado et al. 2007; Dornelas et al. 2009). Compared to other insect groups, butterflies are generally easier to identify to species. However species-level identification of some butterfly groups are very challenging, especially in the field. This is obviously a disincentive for rapid monitoring programmes, where results are needed quickly to evaluate the changes in habitat structure and composition, in response to natural factors and human activity or management practices (McGeoch 1998; Lovell *et al.* 2007). Considering this taxonomic impediment and the high congruence of the indicator genera to habitat change or disturbance in this study, it is perhaps more useful to develop monitoring programmes that are based on genus and/or species-group level identification. The advantage of using higher taxonomic levels in surveys is that costs could be substantially reduced as the time-consuming task of identifying specimens to species level becomes unnecessary (Oliver & Beattie 1996).

5.5 CONCLUSION

The study showed that species richness alone does not represent a powerful metric for monitoring degrees of forest disturbance. Rather, relative abundance and complete assemblages of butterfly taxa with high indicator (*IndVal*) values were more informative and discrete, and hence better metrics for evaluating habitat quality or human-induced disturbance. The results of the study indicated that monitoring butterflies could provide a quick guide to biodiversity management even on a smaller scale and over shorter periods (see also Kremen 1994; Beccaloni & Gaston 1995; Fermon *et al.* 2000).

Considering the near lack of resources for biodiversity research in Ghana and West Africa, and the paucity of taxonomist experts, it may be more useful to use higher level taxa (preferably at the genus and sub-genus levels) as the recognizable indicators in RBA design. Fortunately, most of the fruit-feeding butterflies in Ghana could be identified and sorted out into genus and species-groups, even in flight. Trained forestry and wildlife technicians would be able to carry out simple monitoring programmes. Results of these pilot studies will provide information on the changes in the ecosystem and also help identify priority areas for more in-depth (species-level) studies.



CHAPTER SIX

Empirical evaluation of neutral theory in fruit-feeding butterfly (Lepidoptera: Nymphalidae) assemblages in three forest fragments in Africa

Abstract

The unified neutral theory of biodiversity and biogeography is gradually gaining status as a quantitative null model for explaining macro-ecological patterns in ecological (meta)communities. The theory assumes that differences between members of an ecological community of trophically similar species are "neutral," or irrelevant to their success. In this study, the relative contribution of neutral processes in shaping fruit-feeding butterfly assemblages in three forest fragments in Africa are empirically evaluated using both direct (confronting the neutral model to species abundance data) and indirect approaches (testing the predictions of neutral theory against species-specific data). The species-specific data consisted of six morphological traits, biogeographic distributions and phylogeny. Direct data were obtained by sampling butterflies using banana baited traps set at the forest canopy and the understorey. The results indicated a clear consistency in the kind of species or species-groups found at either the canopy or understorey in the three studied communities, suggesting that fruit-feeding butterfly assemblages are vertically structured by species' (habitat) preferences. Furthermore, there were significant correlations between some flight-related morphological traits and species abundance at the forest canopy, but not in the understorey. Neutral theory's contribution to explaining the species abundance data lies largely in identifying dispersal limitation as a key process regulating fruit-feeding butterfly community structure.

6.1 INTRODUCTION

6.1.1 Background of the study

It is almost a universal law that in each ecological community, there exist only a few abundant species and many rare species (Magurran 2004; McGill *et al.* 2007; Krebs 2009). The consistency of these patterns among many taxonomic groups suggests that they have been produced in conformity with a set of basic principles rather than by accident (Hubbell 2001; McGill *et al.* 2007; Krebs 2009). The crucial question however is: what factors or processes regulate these community structure patterns? This question has long fascinated ecologists and remains open even today (Chesson 2000; Hubbell 2001; Magurran 2004; Gaston & Chown 2005; McGill *et al.* 2007; Krebs 2009). With the current rate of global biodiversity decline, the need to understand the processes that determine and sustain biodiversity is urgent. Two main but contrasting hypotheses have been proposed to explain the observed patterns of richness, abundance and distribution of species on a single trophic level.

The first is the classical adaptive niche apportionment hypothesis which explains the observed biodiversity patterns as the end products of inter-specific competition and niche differentiation of coexisting species amidst resource diversity (Tilman 1999; Chesson 2000). The other hypothesis is the neutral theory of biodiversity (Caswell 1976; Hubbell 1997; 2001) which explains the species abundance, distribution and diversity patterns by assuming individuals of all trophically similar species to be ecologically equivalent. Thus, all individuals regardless of their species identity are identical in their niche requirement and have the same per capita birth and death rates. This assumption clearly challenges the classical niche apportionment held by ecologists for many decades. Some studies have indeed demonstrated that species differ in their life history properties (Mazer

1989; Chown & Nicolson 2004) and that competition is commonly observed among species in nature (Kohler 1992; Tilman 1994, 1999), but the key question is: how much do these differences contribute to determining community structure? (Gravel *et al.* 2006; Leibold & McPeck 2006; Adler *et al.* 2007). Neutral theory emphasizes dispersal limitation as the key ecological process that fashions species abundance distributions and other biodiversity patterns. Although critics of neutral theory have questioned the reality of its assumptions (e.g. patently ignoring species-specific traits like habitat preferences, physiological tolerances, and dispersal abilities), the model has been demonstrated to fit empirical data rather well (Hubbell 2001; Condit *et al.* 2002; Olszewski & Erwin 2004; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* in press) and in some cases better than all other relative species abundance models (Volkov *et al.* 2003) but see (McGill 2003).

6.1.2 Assumption and mechanisms of neutral theory

Neutral theory assumes very little about community dynamics and hence offers a simple representation of ecological community structure. It is intriguing to see how well we can predict the patterns of ecological communities with minimal assumptions. The theory is gradually gaining status as a quantitative null model for ecological community structure (Alonso *et al.* 2006; Hubbell 2006; Leibold & McPeck 2006; Zillio & Condit 2007; Ellwood *et al.* 2009, but see McGill *et al.* 2006). Neutral theory in its simplest, spatially-implicit form models population dynamics at two community levels (hierarchical model): a local community and a metacommunity. The local community consists of co-occurring assemblages of trophically similar species that (potentially) compete for the same or similar resources in a localized area. The metacommunity is the larger (regional) pool of

species from which species are assembled at random in the local community (Hubbell 2001). The metacommunity is maintained by the balance between speciation and extinction. Stochastic ecological processes of birth, death and immigration are assumed to operate at the local community level. The local community is connected to the larger regional pool of species (metacommunity) through dispersal, analogous to classical island biogeography (MacArthur & Wilson 1967). Hubbell's neutral model requires just two parameters to characterize an ecological community. One parameter is the fundamental biodiversity number θ which summarizes the speciation process in the metacommunity and is a function of both the metacommunity size (J_M) and the rate (v) at which new species arise at random when an individual mutates to become a new species, a process assumed to be similar to mutation of alleles in genetics. The mathematical relationship is

$$\theta = \frac{v(J_M - 1)}{1 - v}.$$

Stated otherwise, θ is the number of species arising per generation via speciation in the regional community (Jabot & Chave 2009).

The other fundamental parameter is the migration parameter m which measures the probability of migration or dispersal from the metacommunity into a local community when an individual leaves the local community (via death). The range of m is between zero and one. Low values of m suggest that the local community receives few immigrants from the metacommunity and so it is 'dispersal limited'. When there is no dispersal limitation, $m = 1$. However, the probability of a new recruit being derived locally or via immigration from the metacommunity is also partly dependent on the number of individuals in the local community (J_L).

Therefore a new parameter, fundamental immigration number (I) is used in place of m , when data are combined from multiple samples across the metacommunity

(Etienne 2007). The relation is, $m = \frac{I}{(I + J_L - 1)}$, such that as m approaches 1, I

approaches infinity.

I is often interpreted as the number of potential immigrants competing with local individuals for a vacant position in the local community (Etienne & Olf 2004; Etienne 2007). In other words, I measures the magnitude of recruitment limitation which encompasses both dispersal and establishment limitations (Jabot *et al.* 2008). Low I values suggest either high dispersal limitation, or high establishment limitation or high limitation in both dispersal and establishment.

6.1.3 Evaluating Neutral theory

Nearly all evidence in support of neutral theory is restricted to sessile (space-limited) species like trees (Hubbell 2001; Condit *et al.* 2002; Latimer *et al.* 2005; Etienne *et al.* 2006; Perry *et al.* 2009) and brachiopods (Olszewski & Erwin 2004). Compared to mobile organisms, sessile species generally lack the luxury of deciding where they and their offspring should occur in an ecological system, making lottery effects of establishment more plausible. This perhaps makes species-level traits such habitat preference and tolerance less relevant, apparently satisfying the requirements of neutral theory. To fully appreciate the strengths and weaknesses of neutral theory as a universal model, we must as well evaluate the model and its predictions in more mobile organisms. Butterfly communities represent useful ecological systems within which we can evaluate the neutral model in mobile organisms. Butterflies are by far the best known and most-studied larger group of organisms apart from plants and vertebrates. Both ecological and evolutionary information such as species habits, habitat preference, host plants, geographical

distribution, and phylogeny of most species groups are readily available for use in the evaluation of the model and testing of its predictions.

Almost all studies (e.g. Hubbell 2001; Condit *et al.* 2002; Volkov *et al.* 2003; Latimer *et al.* 2005; Perry *et al.* 2009) attempting to empirically evaluate neutral theory followed three standard steps; 1) they estimate the key model parameters (θ , and m or I) from samples of the species abundances and 2) then use the estimated parameter values to generate either ecological patterns or artificial communities. 3) The actual test of neutral theory then involved the comparison of the predicted ecological patterns or communities with those of the real biological surveys. McGill *et al.* (2006, 2007) however cautions that this approach should be only a preliminary step of evaluating a model, because as they argue, many theories based even on conflicting assumptions can produce similar patterns of species abundance.

Other appropriate methods of evaluating a theory are to empirically test the predictions of the theory using both real biological sample data and our knowledge of the ecological system. For instance, neutral theory assumes that species-level traits have no impact on their overall abundance in the local community. The theory asserts that abundance in a local community is determined entirely by ecological drift and in the strict interpretation of neutrality specific traits such as body size should not correlate with abundance in a local community. Likewise, species-level traits like habitat preferences, physiological tolerances and dispersal abilities should be uncorrelated with abundance in a local community. These are predictions that can easily be evaluated in butterfly assemblages using our knowledge of the system and independent species-specific data (as in Fargione & Tilman 2006; Harpole & Tilman 2006).

Most neutral models assume that ecological communities are always saturated and in equilibrium; it is only when an individual dies, that a new recruit can enter the system (Hubbell 2001). The new recruit (regardless of its species identity) is chosen at random (comparable to genetic drift in population genetics). The probability of a species replacing a dead individual in a local community is therefore proportional to its abundance in the local community or, in the case of immigration, in the metacommunity (Etienne & Olf 2004). In effect, the abundant species become more abundant over time. With drift as the sole determinant of species abundance in an ecological community, neutral theory predicts that older species-groups or lineages would have more individuals than younger ones by virtue of being in the metacommunity relatively longer.

6.1.4 Specific objectives

Here neutral model is empirically evaluated in fruit-feeding butterfly (Lepidoptera; Nymphalidae) assemblages in three forests fragments in Africa. The specific objectives of this study were to:

1. fit the standard neutral model to multiple samples of butterfly abundances and test the predictions or inferences of the model parameter estimates with independent data obtained using methods other than neutral theory sampling formulae.
2. assess the similarities and differences of fruit-feeding butterfly composition and assemblage structure at two different (vertical) habitats. Neutral theory ignores species-specific habitat preferences. If indeed the structure of the fruit-feeding butterfly community is determined entirely by

stochastic processes of birth, death, speciation and extinction, then we expect to find no differences in species composition in the canopy and understory.

3. explore the relationship between species abundance and morphological traits like forewing span, thoracic size and abdominal length. If ecological drift is the sole determinant of abundance in the local community then none of these species-specific traits should be correlated with abundance.
4. evaluate the relationship between species abundance and age of species and species groups estimated from phylogenetic data. A strict interpretation of neutral theory posits that older species-groups will be more abundant than younger ones.

6.2 MATERIALS & METHODS

6.2.1 Description of Study Areas

The study was conducted in three protected forests in Africa (Figure 6.1); two in Ghana (Bia National Park and Bobiri Forest Reserve) and one (Kibale National Park) in Uganda. Bia National Park (BIA) is found in the southwestern part of Ghana and borders the forests of Côte d'Ivoire to the west. BIA (06°20' N 06°39' W) covers a total area of 304 km², and lies in a transitional zone between moist semi-deciduous and moist evergreen zone and forms part of the upper Guinea rainforest - one of the Conservation International's global biodiversity hotspots (Myers 2000). Bobiri Forest Reserve (BOB) is located in the middle belt of Ghana and lies within the moist semi-deciduous forest zone. BOB (6°25' N, 2°40' W) is about 50 km² and mainly managed for timber production. The distance between BIA and BOB is about 200 km. Kibale National Park (KIB) is located in Western Uganda and at least 3,500

km from BOB and BIA. KIB ($0^{\circ}35' N$, $20^{\circ}39' W$) lies in a transition between lowland rain forest and submontane forest. It is generally classified as a moist evergreen forest and covers an area of 560 km^2 . It is comprised of mature forest, swamp, grassland, plantation and secondary forest (Butynski 1990).

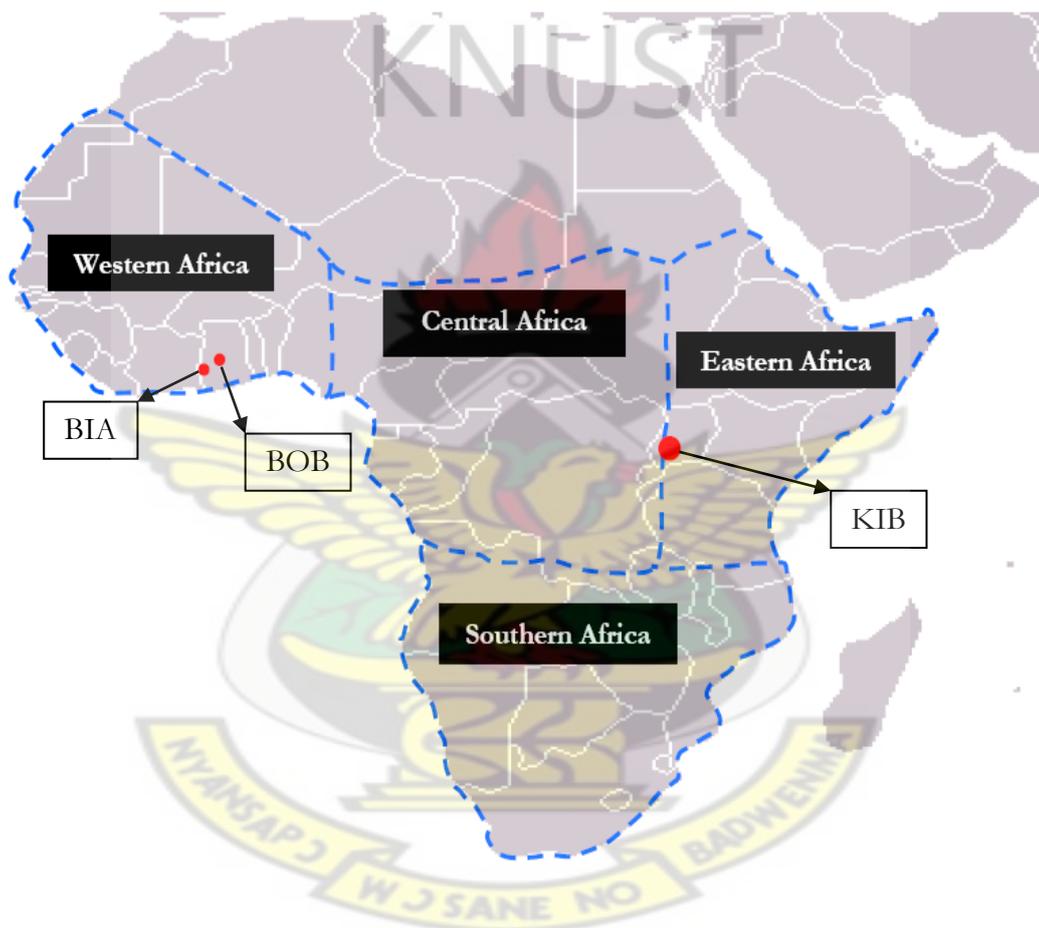


Figure 6.1 Map of Africa showing the geographical locations of three study areas; BOB (Bobiri forest reserve, Ghana), BIA (Bia National Park, Ghana) and KIB (Kibale National Park, Uganda). The dashed lines denote the biogeographical boundaries in Africa based on previous butterfly zoogeographical studies (Carcasson 1964, Larsen 2005b).

6.2.2 Butterfly sampling

Butterflies were sampled using fruit-baited traps which ensured that the sampled butterflies were generally from the fruit-feeding butterfly guild (Nymphalidae). However, the bait trapping techniques are not without potential biases; the method might provide a biased representation of fruit-feeding butterflies in the sampled communities (Hughes *et al.* 1998). There may be some fruit-feeding butterflies that are never lured into baited traps. Even among those likely to be trapped, some probably would be more strongly attracted than others. The relative abundances of species caught may not accurately reflect the relative abundances of fruit-feeding species in the local community.

However, other techniques such as the use of butterfly nets or visual surveys restrict the sampled butterflies to more or less low flying, conspicuous, and not-too-fast flying species groups, which may not necessarily be closely-related phylogenetically and in niche requirements. The fruit-baited trapping technique generally lures members of the fruit-feeding butterfly guild (Daily & Ehrlich 1995; DeVries *et al.* 1999; Fermon *et al.* 2000; DeVries & Walla 2001; 2003; Oduro & Aduse-Poku 2005; Molleman *et al.* 2006; Aduse-Poku 2008). This is in line with Hubbell's (2001) neutral ecological community; where trophically similar, sympatric species in a local area compete for the same or similar resources. Bait trapping also makes it possible to compare species assemblage structures between sites without correcting for the collector's skills and experience.

Traps were baited with mashed bananas mixed with palm wine. Sampling of fruit-feeding butterflies was done on transects. In Ghana, six trap stations were established on each transect (four in each local community) at ~100m intervals. At each trap station, two fruit-baited traps were installed; one at the forest canopy and the

other at the understorey. Canopy traps were suspended between 20m and 30m above ground level using thin nylon ropes running over branches of emergent trees, such that they could be serviced directly when the nylon ropes were lowered. The understorey traps were set between 0.1m and 0.2m above the forest floor. Traps were inspected and re-baited continuously every 24 hours for five consecutive days in each month for one year. Bait eaten by rodents and other mammals and traps heavily infested with ants were replaced or refreshed on the day of detection. Otherwise, all baits were refreshed every two days, using the original stock of bait prepared on the first day.

Some trap stations could not be used at certain times of the sampling period because their canopy traps were either pushed down by falling tree branches, heavy rainstorms or got stuck in the tree canopy branches during sampling. In such cases, abundance data from the corresponding understorey traps were also discarded to correct for sample effort between the two strata. In total, the quantitative sampling protocol described generated a total of 1,974 and 1,812 trap-days in BIA and BOB respectively. For details of the experimental setup in KIB, I refer to Molleman (2006), which in principle did not differ much from the set up in Ghana. The sampling in KIB spanned over three-year period and yielded a total of 6,952 trap-days.

Specimens were identified to species and grouped into respective taxonomic units (putative species-groups, genus, subfamily, family) following the proposed higher-level classification for Nymphalidae by Wahlberg *et al.* (2003).

6.2.3 Estimating neutral model parameters

I first partitioned the species abundance dataset into three, to reflect the three local communities; namely BIA, BOB and KIB. I then aggregated the data across the three local communities to form (one 'combined' but not lumped sample (as local community identities were maintained in the sample) and (b) three samples of pairs of 'combined' local communities; i.e., BIA & BOB, BIA & KIB, BOB & KIB. I estimated the neutral model parameters (θ and I) for each of the four samples using maximum likelihood estimation (MLE) neutral sampling formulae for multiple samples with varying dispersal limitation (Etienne 2009b, a). Like the previous sampling formulae (Etienne 2005, 2007), these sampling formulae assume point mutation as the speciation process and model local communities as spatially separated samples (spatially implicit model). Unlike the previous frameworks (Etienne 2005, 2007), however, Etienne's (2009b) sampling formula allows for the estimation of model parameters even when the samples (in this particular case local communities) have different degrees of dispersal (recruitment) limitation. Also, novel in its utility is its ability to compute the (standard) errors in the model parameter estimates.

The sampling formula provides an expression of the probability ($P[D|\theta, I, J]$) of observing a particular species abundance dataset D , given the neutral model parameters, (θ, I) and the number of individuals in the sample (J). I implemented the computation of the neutral model parameters estimates in PARI/GP (<http://pari.math.u-bordeaux.fr/>) using a code (or algorithm) provided in Etienne (2009a, b). Using different starting values, I re-ran the optimization algorithm at least four times for each 'combined sample' to find the global likelihood optimum. For each of the four 'combined samples' I further partitioned the data into canopy and

understorey to reflect the two sampled stratum communities and estimated the model parameter values for each stratum community. For this study, I evaluated Hubbell's neutral model in fruit-feeding butterflies at two metacommunity scales: the 'Ghana' metacommunity scale (when only BIA and BOB samples were considered) and the 'Africa' metacommunity (when all the local communities are considered).

6.2.4 'Exact' test of neutrality

The second stage of the direct model evaluation employed Etienne's (2007, 2009b) 'exact' test of neutrality. This is a general test of neutrality that does not require an alternative (usually niche-based) model for its evaluation. The test simply involves a comparison of the realized configuration with the probabilities of artificial configurations generated using the model parameter estimates (Etienne 2007). To implement this test, I simulated 1,000 artificial communities using the model parameters (θ, I) and sample size vector of the observed data (J). I then computed for the real data and each of the 1,000 simulated communities the log-likelihood and the dissimilarity (Bray-Curtis) between local community pairs.

To assess the extent to which the neutral model mimics the observed data, I compared the log-likelihood value of the real dataset to the frequency distribution of simulated communities' log-likelihood values. I performed a similar comparison test with the Bray-Curtis values to assess the extent to which the observed species turnover departs from those expected under neutrality. I concluded that the observed community is highly unlikely to be structured by neutral processes, if the probability of the real data is significantly smaller than most of the artificial datasets (Etienne 2007). If, however, the observed is similar to the artificial communities, then I cannot reject neutrality as a plausible driver of the observed biodiversity pattern.

6.2.5 Species distributional range data

The recruitment limitation parameter estimates (m or I) of the neutral model informs us about the migration tendencies in the different local communities. Differences in I between local communities for instance, suggest either that the local communities differ in the ease with which they are reached by dispersal (e.g. hindrance due to presence of physical barriers) or that they differ in the relative success of dispersers versus residents in establishing at the local community (Jabot *et al.* 2008). Either way, we would expect to find more individuals or species with relatively wider distributional range (high dispersal abilities) with high I values local communities, compared with those with low I values. To impartially evaluate the plausibility of the migration tendencies, suggested by the neutral model, I obtained independent distributional range information of the sampled species using available taxonomy treaties (Larsen 1991, 2005; Ackery *et al.* 1995; D'Abrera 1997; Larsen 2005b; Williams 2008).

Based on previous biogeographical studies (Carcasson 1964 ; Larsen 1991, 2005) of afro-tropical butterflies, the present distribution of the sampled species were partitioned into four zoogeographical regions; Western Africa (W), Central Africa (C), Eastern Africa (E), Southern Africa (S) as indicated in figure 6.1. These delineations did not necessarily follow on the sub-regional political boundaries. Here, Western Africa is bordered by the Sahara in the north, the Atlantic Ocean in the west and south and Western Nigeria and Niger River in the east (as in Larsen 2005b). Central Africa stretches from eastern Nigeria to the western border of Uganda, down to the upper portions of Angola and Zambia. Eastern Africa covers areas from main Uganda to the Indian Ocean in the east and from Sudan and Eritrea in the north to northern portions of Mozambique. Stretching from main Angola and Zambia to the

Indian Ocean in the east and Atlantic Ocean in the west is the Southern Africa region. Madagascar and all surrounding lesser islands were included as part of southern Africa. The zoogeographical distributional range of each sampled species was scored between one and four based on its present distribution on the entire African continent. A score of one denotes species occurring in only one of the four biogeographical regions in Africa outlined above. A score of four denotes species distributed in all four zoogeographical regions.

6.2.6 Assessing species composition and community structure

The null hypothesis of no difference between the species abundance distribution of the canopy and understorey communities was tested using a two-sample Kolmogorov–Smirnov test (Magurran 2004). The Morisita-Horn index was used to assess similarity in species composition between the fruit-feeding butterfly populations at the canopy and understorey. This index is considered among the most robust quantitative beta diversity estimators (Magurran 2004). It quantifies species turnover in terms of both the identities and abundance of species. The index value ranges from 0 (when no species is shared between the compared communities, a and b) to 1 (when the compared communities comprise the same species in identical proportions). The Morisita-Horn index (C_{mH}) is calculated as;

$$C_{mH} = \frac{2 \sum_{i=1}^s (n_{ai} \times n_{bi})}{(d_a + d_b) \times (N_a \times N_b)} \quad \text{where} \quad d_b = \frac{\sum_{i=1}^s n_{bi}^2}{N_b^2}, \quad d_a = \frac{\sum_{i=1}^s n_{ai}^2}{N_a^2}$$

and

s = total number of species at both sites

N_a = the total number of individuals of all species collected at site a

N_b = the total number of individuals of all species collected at site b

n_{ai} = the number of individuals of the i th species collected at site a

n_{bi} = the number of individuals of the i th species collected at site b

and, in the denominator, there are two terms summed that are defined as:

The classical Sørensen index (Sørensen 1948; Magurran 2004) was used to further explore the species turnover. Unlike Morisita-Horn, the Sørensen index (C_s) is simple to calculate and interpret, and based on incidence rather than abundance data:

$$C_s = \frac{2x}{2x + y + z}$$

where x = number of species present in both communities, y = number of species found in community A but not in community B, and z = number of species found in community B but not in community A. All biodiversity indices were computed using the EstimateS software (Colwell 2009).

6.2.7 Morphometric data

Samples of 62 species of butterflies were caught with banana baited traps for morphological measurements at Kibale National Park. Morphological data were supplied by Freerk Molleman. For each individual, five easily obtainable morphological parameters of the fruit feeding butterflies taken from banana baited traps were measured: 1] Wing length L_W (forewing base to apex), 2] Wing width W_W (distance between the leading and trailing edge of the forewing), 3] Thoracic length L_T (section between the head and abdomen), 4] Thoracic width W_T (distance between forewing bases) and 5] Abdomen length L_A . Except for L_T and W_W which were measured with a ruler, all other morphological parameters were measured using a pair of Venier calipers, after which specimens were released. Means of the morphological

measurements were calculated for each species, with between 2 and 333 individuals per species (Mean = 34; SD=56). Besides the five direct morphological measurements, I also characterized wing shapes using the ratio of the Wing length to its width (L_W/W_W). Species (e.g. *Euphaedra medon*, *E. preussi*, *E. christyi*) that exhibited strong sexual dimorphism in their morphological structures were excluded from the allometric analysis.

Prior to the regression analyses all data were \log_{10} -transformed to improve normality. Analyses were done separately for the canopy and understorey communities and for the lumped community. The effects of variation in any of the species-level morphological traits between species on the overall abundance were done in two phases: First, I performed a simple regression analysis to find the strength of the relationship between each of each of the morphological traits and species abundance (at the canopy, understorey and when canopy and understorey data are lumped). The second phase involved multivariate linear regression analyses.

However, due to high collinearity in morphological traits some variables were condensed into single factors. For instance, thoracic stoutness (W_T/L_T) was used as a combined effect of thorax length and thorax width. Likewise, wing shape (L_W/W_W) indexed the forewing parameters. Multivariate linear regression analysis was used to evaluate the extent to which variation in overall species abundance could be explained by a combination of the morphological traits (wing shape, thoracic stoutness and abdomen length). Model selection (towards a final model) was done by stepwise backward elimination of factors using the Akaike information criterion (AIC). All analyses were performed with the R software (R Development Core Team 2009).

6.2.8 Phylogenetic data

Estimated ages of species and species-groups (clades) were obtained from a recent phylogenetic study based on five gene regions and 144 exemplar taxa of the Charaxinae subfamily (Aduse-Poku *et al.* 2009). Detailed species-level (age-calibrated) phylogenetic hypotheses are currently available for only these groups of Nymphalidae in Africa. Consequently, this part of the neutral model evaluation was restricted to the Charaxinae members (of *Charaxes*, *Palla* and *Euxanthe* genera) in the samples. Spearman rank correlation was used to test whether the age of a (Charaxinae) species has any effect on its overall abundance in a local community.

6.3 RESULTS

6.3.1 Species abundance, richness and diversity patterns

In all, a total of 39,856 individuals representing 201 butterfly species were captured from the three locations. All specimens but three were positively identified to species level (Appendix 1). Butterflies captured came from 37 genera and eight subfamilies; all members of the Nymphalidae family. Table 6.1 summarizes the abundance, richness and sampling efforts at each local community. Bia National Park (BIA) was by far the species richest (139), despite being the community with the fewest sampled individuals. Species abundances at the understory were generally (four to six-fold) higher than at the forest canopy. I also recorded a little more species (109) at the understory than at the canopy level (75).

Table 6.1 Number of individuals and species captured in each local community. Pooled data resulted from lumping of the forest canopy and understorey data. Understorey and Canopy denotes that each vertical stratum community data is considered separately. Trap-days are calculated as the number of traps installed at a locality multiplied by the number of times sampled. One trap-day is equivalent to one trap sampled for a day (within 24 hours after setting out trap).

Summary statistics	Data set								
	Pooled			Understorey			Canopy		
	KIB _{POL}	BIA _{POL}	BOB _{POL}	KIB _{UND}	BIA _{UND}	BOB _{UND}	KIB _{UND}	BIA _{CAN}	BOB _{CAN}
Abundance	32,310	2,764	4,782	27,960	2,187	4,151	4,350	577	631
Richness	94	139	111	90	109	90	75	59	54
Trap-days	6,952	1,974	1,812	3,476	987	906	3,476	987	906

6.3.2 Fruit-feeding butterfly community structure as predicted by the neutral model

The resultant neutral model parameter estimates (θ , I) of the study hinted at two kinds of ecological communities depending on the scale of metacommunity considered. On a 'Ghana' metacommunity scale (i.e. when only Bia and Bobiri samples are considered), the θ and I estimates suggested a closed ecological system with low regional diversity (low θ) and low dispersal (recruitment) limitation (high I). In contrast, on the 'Africa' metacommunity scale (i.e. 'combined' sample of the three local communities), the parameter estimates depicted a system of high regional diversity (high θ) and strong dispersal (recruitment) limitation (low I) (Table 6.2), as expected from the large spatial separation of the samples. There were considerable and sometimes significant differences in the degree of recruitment limitations among the three local communities. Recruitment parameter estimates for BIA (I_{BIA}) were consistently the highest, regardless of the metacommunity scale looked at. I_{KIB} values on the other hand were always the lowest in all its 'combined' samples (Table 2). Between Bobiri and Bia (i.e. within the 'Ghana' metacommunity), I_{BIA} values were nearly three times higher than I_{BOB} .

Comparing the two forest strata communities within the 'Ghana' metacommunity, the model parameter estimates suggest relatively less recruitment limitation (higher I values) at the canopy compared to the understorey (Table 2). In contrast the fundamental biodiversity number was twice as high at the understorey (42.3) than at the canopy (20.7). θ estimates were also higher (but not statistically significant) at the understorey for the BOB-KIB and BIA-KIB pair wise samples. There were however no clear trends in the recruitment parameter estimates between the canopy and understorey when all the three local communities are 'combined' ('Africa' metacommunity).

Table 6.2 Neutral parameter estimates for samples from three local fruit-feeding butterfly communities (BOB [Bobiri forest reserve], BIA [Bia National Park], and KIB [Kibale National Park], using Etienne (2009) sampling formulae for multiple samples with varying degrees of dispersal limitation. J and S are the number of individuals and species respectively in each local community denoted as BOB=Bobiri Forest Reserve, Ghana; BIA=Bia National Park, Ghana; KIB=Kibale National Park, Uganda. I_{BIA} , I_{BOB} and I_{KIB} are the recruitment parameter estimates for BIA, BOB and KIB respectively. P_{MLE} and P_{BC} are the probabilities that the log-likelihoods and Bray-Curtis indices of the model simulated communities deviate significantly from the observed community.

Data set	Sample size and species richness		Maximum likelihood parameter estimates					Neutrality Test	
	J	S	θ	I_{BOB}	I_{BIA}	I_{KIB}	Loglik	P_{MLE}	P_{BC}
<i>Pooled</i>									
BOB + BIA + KIB	(4782, 2764, 32310)	(111, 139, 94)	96.1 ± 10.1	47.3 ± 6.63	97.0 ± 14.8	17.3 ± 2.0	-1079.4	0.478	--
BOB + BIA	(4782, 2764)	(111, 140)	49.5 ± 5.31	91.9 ± 13.6	324.6 ± 80.8		-516.5	0.473	0.651
BOB + KIB	(4782, 32310)	(111, 94)	171.9 ± 27.6	29.4 ± 3.60		16.6 ± 2.0	-572.7	0.536	0.746
BIA + KIB	(2764, 32310)	(140, 94)	185.0 ± 27.8		51.2 ± 6.30	16.0 ± 1.9	-561.4	0.369	0.229
<i>Understorey</i>									
BOB + BIA + KIB	(4151, 2187, 27960)	(90, 109, 90)	101.0 ± 11.8	30.1 ± 4.26	55.5 ± 8.23	16.7 ± 2.0	-909.0	0.638	--
BOB + BIA	(4151, 2187)	(90, 109)	42.3 ± 5.09	69.7 ± 11.8	212.2 ± 54.3		-424.5	0.936	0.796
BOB + KIB	(4151, 27960)	(90, 90)	179.1 ± 32.3	21.2 ± 2.71		15.6 ± 1.9	-493.9	0.674	0.770
BIA + KIB	(2187, 27960)	(109, 90)	200.7 ± 35.1		34.3 ± 4.36	15.1 ± 1.8	-477.9	0.558	0.229
<i>Canopy</i>									
BOB + BIA + KIB	(631, 577, 4351)	(54, 59, 75)	73.9 ± 10.8	28.8 ± 5.90	33.5 ± 6.77	18.3 ± 2.5	-455.9	0.634	--
BOB + BIA	(631, 577)	(54, 59)	20.7 ± 3.18	126.2 ± 36.6	293.1 ± 171		-183.0	0.473	0.651
BOB + KIB	(631, 4351)	(54, 75)	142.8 ± 31.5	18.8 ± 3.32		16.8 ± 2.4	-242.5	0.815	0.331
BIA + KIB	(577, 4351)	(59, 75)	147.1 ± 31.5		21.7 ± 3.71	16.6 ± 2.3	-241.4	0.802	0.558

Kibale is ~3,500 km from Bia and Bobiri so that BIA-KIB and BOB-KIB multi-sample pairs are approximately equidistant. As would be expected of a metacommunity structured by dispersal limitation or distance decay, the estimates of equidistant pairs were fairly similar (Table 6.2).

6.3.3 Neutrality Test

The 'exact' test of neutrality suggested that, based on the species abundance vector datasets I cannot reject neutrality and/or dispersal limitation as a plausible explanation for the structure of fruit-feeding butterfly communities observed in the three forest fragments (Table 6. 2). Indeed, the neutral model of the present study did mimic the observed data most of the time based on the position of the observed likelihood relative to the frequency distribution of the simulated likelihoods. This was true when the strata communities were analyzed separately (Figure 6.2A-D, i-ii) and when they were pooled (Figure 6.2A-D, iii). Likewise, the observed species turnover (measured as Bray-Curtis) did not depart significantly from those expected under neutrality at the 'Ghana' metacommunity scale (at the canopy [observed=36.6%, mean simulated=31.7%, $p=0.651$], understory [obs=56.6%, mean sim=52.9%, $p=0.796$] and pooled [obs=52.4%, mean sim=49.4%, $p=0.651$]). The situation was not different when the metacommunity was extended from 'Ghana' to 'Africa' to include the sample from Kibale (Figure 6.2 B-D; Table 6.2).

6.3.4 Evaluating the plausibility of the migration tendencies suggested by the neutral model

The high I_{BIA} values suggest that either Bia is relatively easier to reach by dispersal (i.e., less hindrance due to few or no physical barriers) or that it is easier for

dispersers to establish themselves in Bia. The latter is more plausible and I evaluated this using my knowledge of the ecological system. Bia is part of a large tract of forest, called the Upper Guinea rainforest that stretches from Ghana to Western Sierra Leone. Migration of individuals to Bia (local community) from the metacommunity (which in the case can be assumed to include that forest continuum) is much easier than to Bobiri which is about 150km away from the Upper Guinea rainforest.

The neutral model parameters (m , I) also suggested less dispersal and/or recruitment limitation in the canopy compared to the understorey. In other words, it is relatively easier for dispersers or immigrants to establish in the canopy than in the understorey. To evaluate the plausibility of this I compared the abundance of individuals with different distribution ranges in the canopy and understorey stratum communities. The results of the distributional range analysis were consistent with those expected under neutrality. There were more individuals of species with wider distributional ranges (score 3 and 4) at the canopy compared to the understorey (Figure 6.3) both in Bia and in Bobiri. However, when the metacommunity was extended from 'Ghana' to 'Africa' the neutral model parameter estimates suggested a rather different trend. The parameter estimates suggested two possibilities; (i) either there are more potential immigrants (thus less dispersal limitation) at the understorey or (ii) the rate of dispersal limitation is about the same in both the canopy and understorey. This neutrally suggested trend conflicted with the independent distributional range data.

6.3.5 Community structure and habitat preference of fruit-feeding butterflies

It was observed that considerable differences existed in both the structure and composition of fruit-feeding butterfly assemblages found at the two stratum

communities. On the average, there was ~52% overlap in species (measured as Sørensen index) and ~11% overlap in species composition (measured by Morisita-Horn) between the understorey and canopy strata communities. The similarity values were relatively lower (~half the average) in Ghana than in the Kibale samples. The species abundance distribution patterns in the forest understorey were significantly different from those observed at the canopy. This was true for all the three sampled locations ($D=0.1809$, $p=0.003$; $D=0.2513$, $p<0.001$; $D=0.1809$, $p=0.003$ at KIB, BIA and BOB respectively).

When the canopy and understorey samples were analyzed separately, I found no significant difference between the patterns of species abundance distributions in the two local communities in Ghana. When either BIA or BOB was contrasted with KIB in the separate stratum analysis, I observed significant differences in the fruit-feeding butterfly community structures in understorey but not in the canopy. Although there were no substantial differences at the canopy between the three study sites, the two communities in Ghana (BOB and BIA) were more similar than when either of the two was contrasted with KIB, as expected because of distance decay.

The composition of species in the canopy and understorey communities was strikingly different at all taxonomic levels: subfamily, genus and species. There was an apparent consistency in the kind of fruit-feeding butterfly species or species-groups found at the canopy versus the understorey (Figure 6.4). Generally, the understorey fruit-feeding butterfly community was composed mainly of members of the Limenitidinae, Nymphalinae and Satyrinae subfamilies. The Limenitidinae subfamily is composed of genera like *Bebearia*, *Catuna*, *Euphaedra* and *Euriphene* which were predominately captured at the forest understorey.

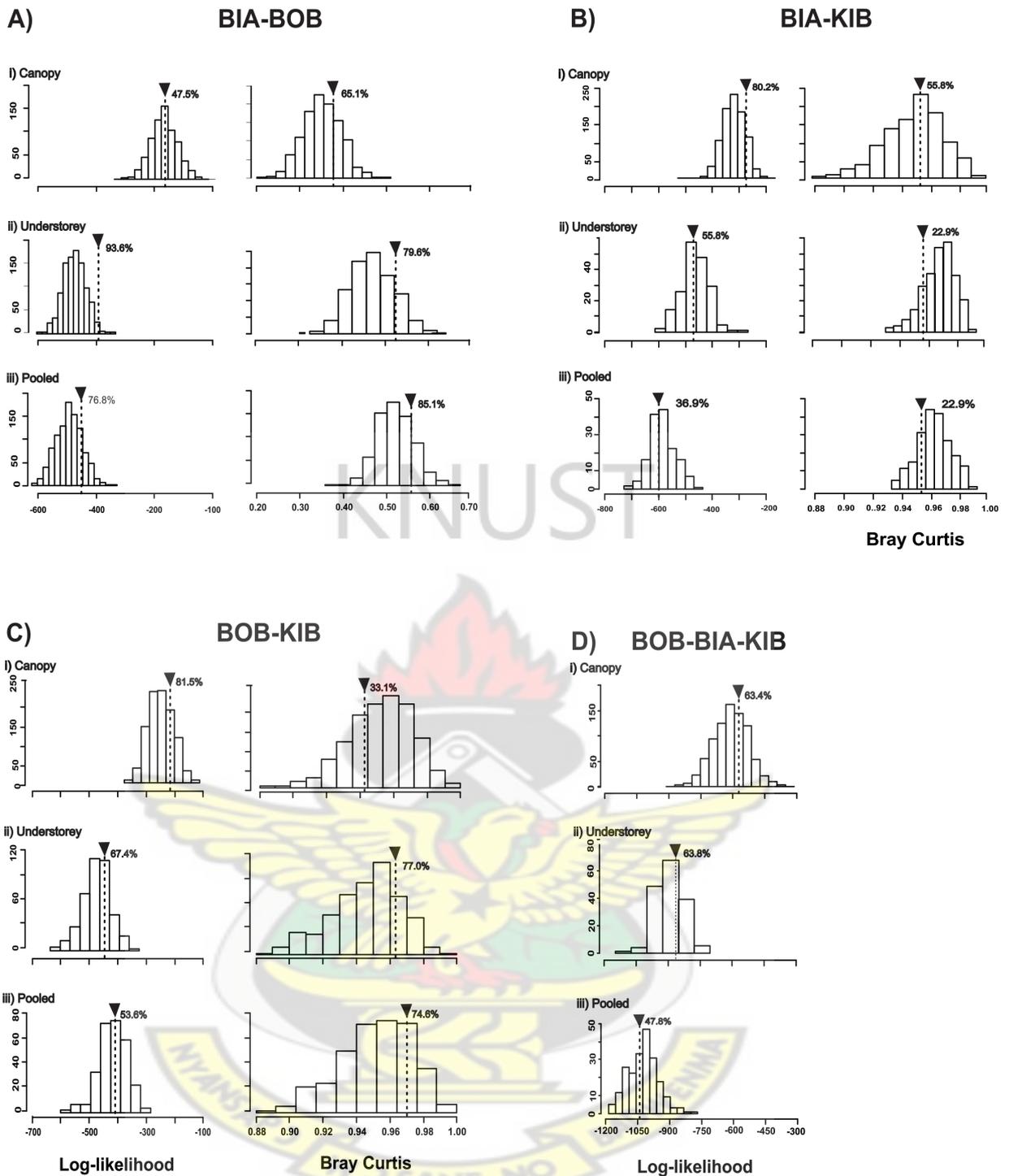


Figure 6.2 Test of departure from neutrality using the Etienne's (2007, 2009) 'exact' test of neutrality formulae. The test simply involved a comparison of the realized configuration with the probabilities of 1000 artificial configurations generated using the model parameter estimates in Table 6.2. The arrow indicates the position of the observed data in relation to the simulated neutral communities. Values besides the arrow show the percentage of simulated communities with values less than the observed. Understorey and Canopy denotes that each vertical stratum community data is considered separately. Pooled is when the forest canopy and understorey data are lumped.

Of the total Limenitidinae individuals sampled in KIB, 7,821 were from the understorey and only 398 (<5%) were captured at the forest canopy. Not even a single of the nearly 2,000 individuals (comprising 56 species) of these four genera was captured at the canopy during the entire sampling periods in Bobiri Forest Reserve and Bia National Park, Ghana (Figure 6.4).

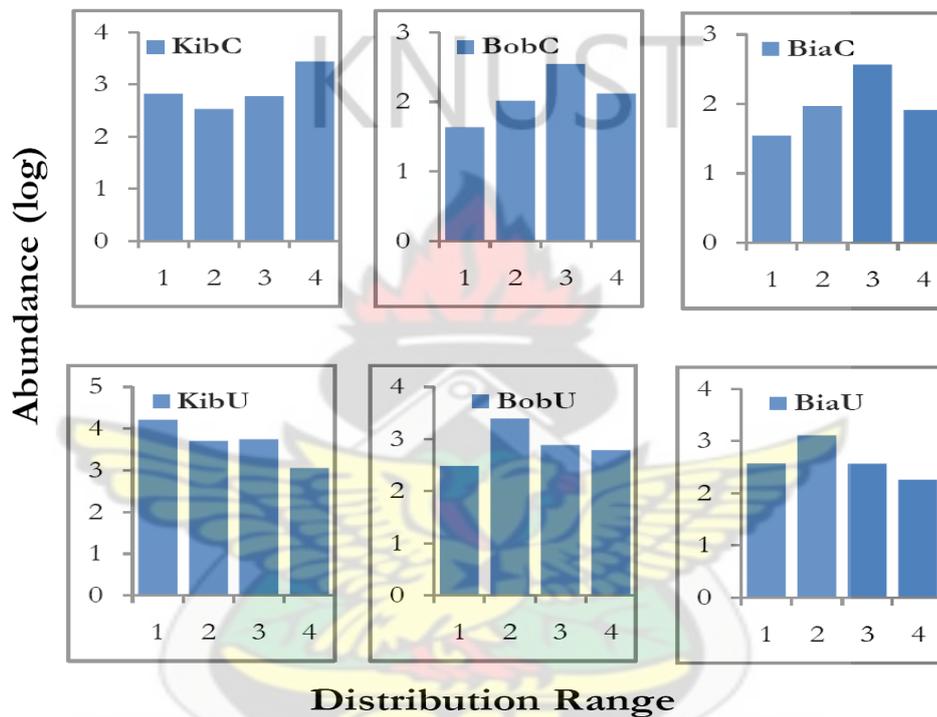


Figure 6.3 Histogram of the (log) abundance of individuals with different distributional range. A score of one on the 'Distribution range' axis denotes species occurring in only one of the four categorized zoogeographical regions in Africa. Score four species are those distributed in all zoogeographical regions

A similar and even more entrenched pattern was exhibited by members of the Satyrinae subfamily. This species-group contributed the largest (~62%; 21,061

individuals) to the overall understorey species abundance pool. Only 4% of the total Satyrinae individuals trapped were recorded from the forest canopy.

In contrast, the canopy was preferred largely by the Charaxinae (*Charaxes* and *Palla*), Apaturinae, Libytheinae and Biblidinae subfamilies (Figure 6.4). For instance, of the total 958 Charaxinae recorded in Ghana, an overwhelming 83% were trapped at the canopy (Figure 6.4b, c). The relative abundances of the *Charaxes* and *Eurytela* species were a bit different among the strata communities in Kibale National Park. The Apaturinae subfamily on continental Africa is constituted by a single species, *Apaturopsis cleocharis*. As many as 64 individuals of this species were recorded in Ghana and all were from the canopy. In KIB, of the total 138 *A. cleocharis* individuals trapped, 27 (20%) were from the understorey.

6.3.6 Relationship between morphological traits and species abundance

The simple regression analyses revealed a significant relationship between some morphological characters and species abundances at the forest canopy. There was a significant relationship between (fore)wing measurements and abundance of 'canopy' species (Figure 6.5a, b). The combined descriptor index of the forewing, which I termed 'wing shape' (ratio of forewing length to forewing width) did correlate positively with species' abundance at the canopy ($F_{1, 50} = 5.042$; $R^2=0.092$; $P=0.029$).

A similarly significant but negative relationship was also observed between 'canopy' species abundance and the length of the abdomen. ($F_{1, 50} = 6.674$; $R^2=0.118$; $P=0.013$). There were however no such clear (linear) relationships between the measured thoracic characters (thoracic length, –width and –stoutness) and abundance

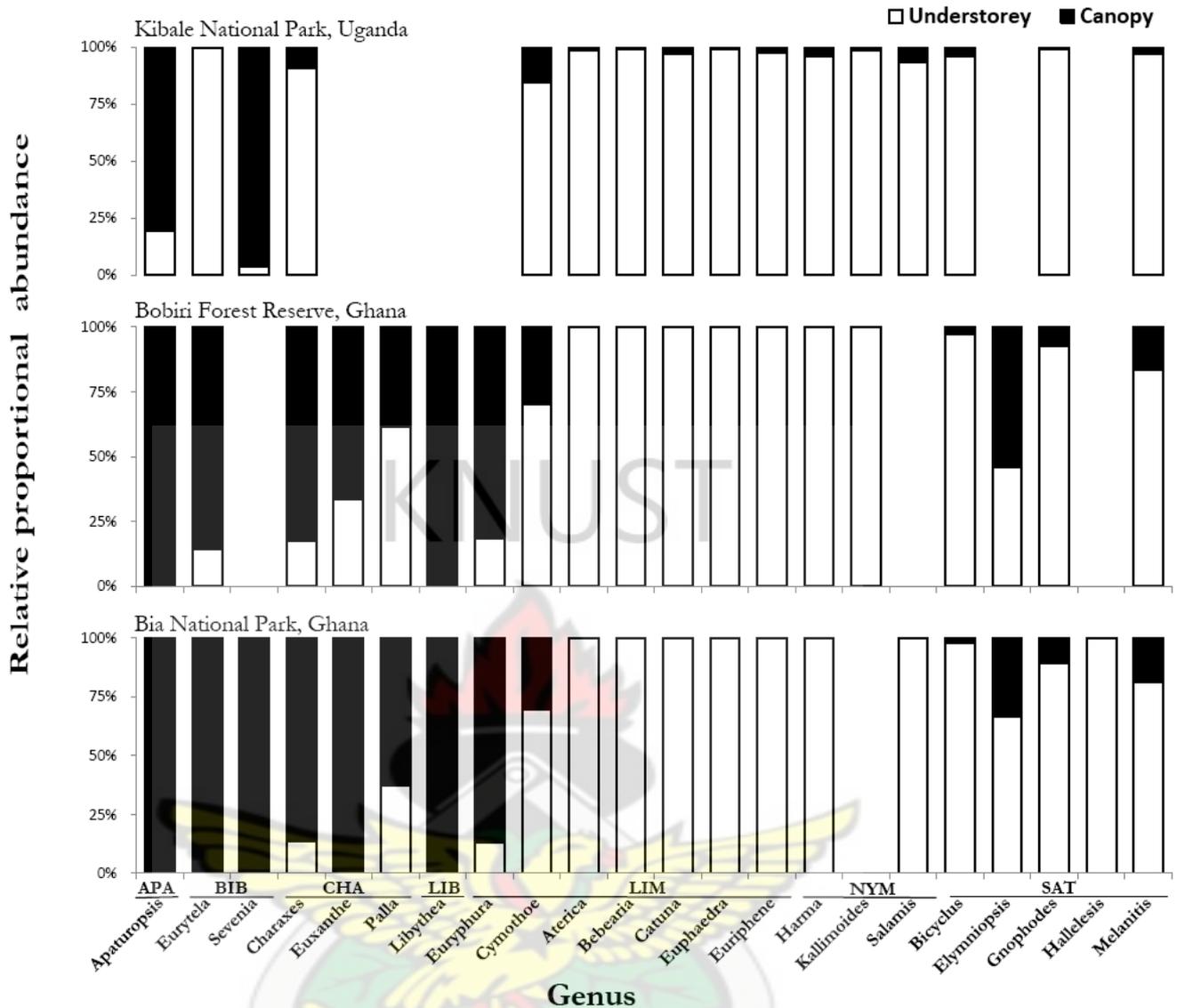


Figure 6.4 Bar chart of relative percentage proportional abundance of fruit-feeding butterfly genera and subfamilies at the forest canopy and understory in three protected forests in Africa: Kibale National Park (KIB), Uganda, Bobiri Forest Reserve (BOB), Ghana, Bia National Park (BIA), Ghana. The shortened subfamily names in full means; APA = Apaturinae, BIB = Biblidinae, CHA = Charaxinae, LIB = Libytheinae, LIM = Limenitidinae, NYM = Nymphalinae, SAT = Satyrinae. A gap on the genus axis means that no member of the genus was captured at that particular local community.

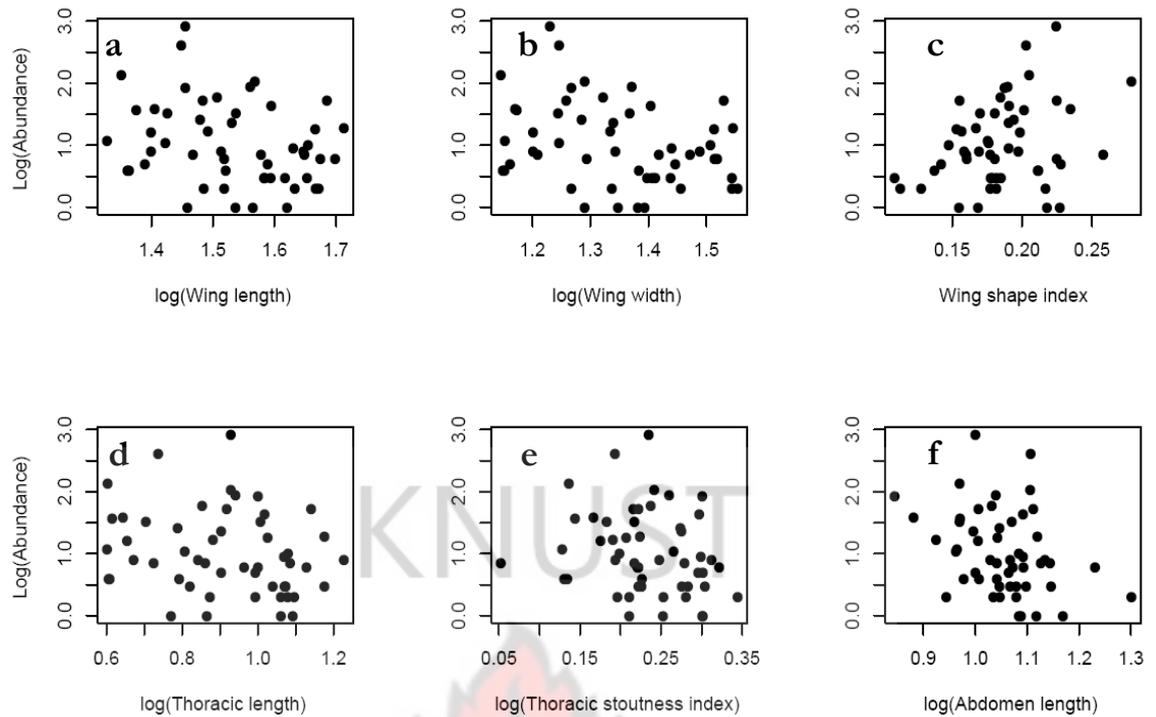


Figure 6.5 The relationship between species abundance at the canopy and six measured morphological traits (wing length, wing width, wing shape index, thoracic length, thoracic stoutness index, abdomen length) of fruit-feeding butterflies in Kibale National park. The P and r values are the probabilities and strengths (coefficient) of correlation. Bolded P and r values denote significant association between species abundance and the measured morphological trait (on the x axis).

at the canopy. Also, I found no evidence of association between the measured morphological traits and abundance at the understorey and when the data was pooled across the strata communities (Table 6.3). The multiple stepwise regression analysis retained wing shape and abdomen as the best predictor of species abundance at the canopy ($F_{2, 49} = 4.662$; $P=0.014$; $Y= 2.646 + 4.35[\log.wing\ ratio] + 2.31[\log.adomen\ length]$) with the model explaining $\sim 16\%$ of the variations in abundance among species at the canopy.

Table 6.3 Linear regression model fitted to the relationship between species abundance and six measured morphological characters of fruit-feeding butterflies in Kibale National Park, Uganda. β_0 = intercept, β_1 = slope, r = correlation coefficient. Significance relationships are in bold and asterisk*. ns means no significant relationship

Dataset	Species specific traits ^a	Test statistics			Regression equation		Significance	
		df	F-stat	r	β_0	β_1	P-value	sign
<i>Canopy</i>	Wing length (L_W)	50	4.151	-0.277	3.725	-1.763	0.047	*
	Wing width (W_W)	50	5.476	-0.314	3.297	-1.687	0.023	*
	Wing shape (L_W/W_W)	50	5.042	0.303	-0.106	6.096	0.029	*
	Thoracic length (L_T)	50	2.778	-0.229	1.827	-0.882	0.102	ns
	Thoracic width (L_w)	50	1.894	-0.191	1.629	-0.892	0.175	ns
	Thoracic stoutness (L_W/L_T)	50	2.347	-0.212	0.234	-2.390	0.132	ns
	Abdomen length (L_A)	50	6.674	-0.334	4.051	-2.877	0.013	*
<i>Understorey</i>	Wing length (L_W)	60	0.486	-0.090	2.9781	-0.6731	0.489	ns
	Wing width (W_W)	60	0.988	-0.127	3.0468	-0.8179	0.324	ns
	Wing shape (L_W/W_W)	60	2.388	0.196	1.0521	4.8579	0.128	ns
	Thoracic length (L_T)	60	1.109	-0.135	2.4968	-0.6081	0.297	ns
	Thoracic width (L_w)	60	1.496	-0.156	2.5211	-0.8564	0.226	ns
	Thoracic stoutness (L_W/L_T)	60	0.022	-0.019	2.0129	-0.2578	0.882	ns
	Abdomen length (L_A)	60	1.228	-0.142	3.451	-1.421	0.272	ns
<i>Pooled</i>	Wing length (L_W)	60	0.284	-0.069	2.7977	-0.5009	0.596	ns
	Wing width (W_W)	60	0.780	-0.113	2.9807	-0.7073	0.381	ns
	Wing shape (L_W/W_W)	60	2.792	0.211	1.091	5.088	0.100	ns
	Thoracic length (L_T)	60	0.515	-0.092	2.3967	-0.4047	0.476	ns
	Thoracic width (L_w)	60	0.707	-0.108	2.4167	-0.5756	0.404	ns
	Thoracic stoutness (L_W/L_T)	60	0.007	-0.011	2.0669	-0.1373	0.935	ns
	Abdomen length (L_A)	60	1.886	-0.175	3.828	-1.702	0.175	ns

^a All the morphological data were \log_{10} -transformed to improve normality

6.3.7 Relationship between species age and abundance

There was no apparent relationship between the estimated 'age' of species or species groups and abundance (Figure 6. 6). The Spearman rank correlation confirmed no significant relationship between the variables at all the three local communities (Kibale [Spearman's rho=-0.037, d.f=18, P=0.876]; Bia [r =0.055, d.f=31, P=0.761]; Bobiri [r =-0.082, d.f=28, P=0.667]). Again, I also found no evidence in support of older species or species-groups being more abundant than younger ones. Rather there were even some relatively young (<6Mya) species groups (e.g. *C. etheocles* group) which were more abundant than older (>20Mya) species groups like *C. zingha*, *Palla* and *Euxanthe* (Figure 6.7).

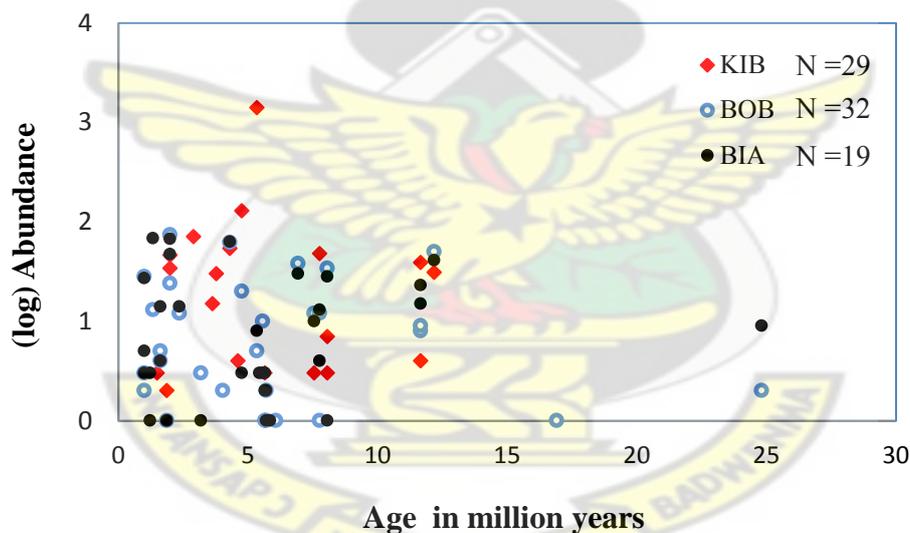


Figure 6.6 The relationship between species' ages and abundance in the three local communities: BOB (Bobiri forest reserve), BIA (Bia National Park), and KIB (Kibale National Park). N denotes the number of sampled Charaxinae species. Estimated ages of species and species-groups (clades) were obtained from a recent phylogenetic study based on five gene regions and 144 exemplar taxa of the Charaxinae subfamily (Aduse-Poku *et al.* 2009).

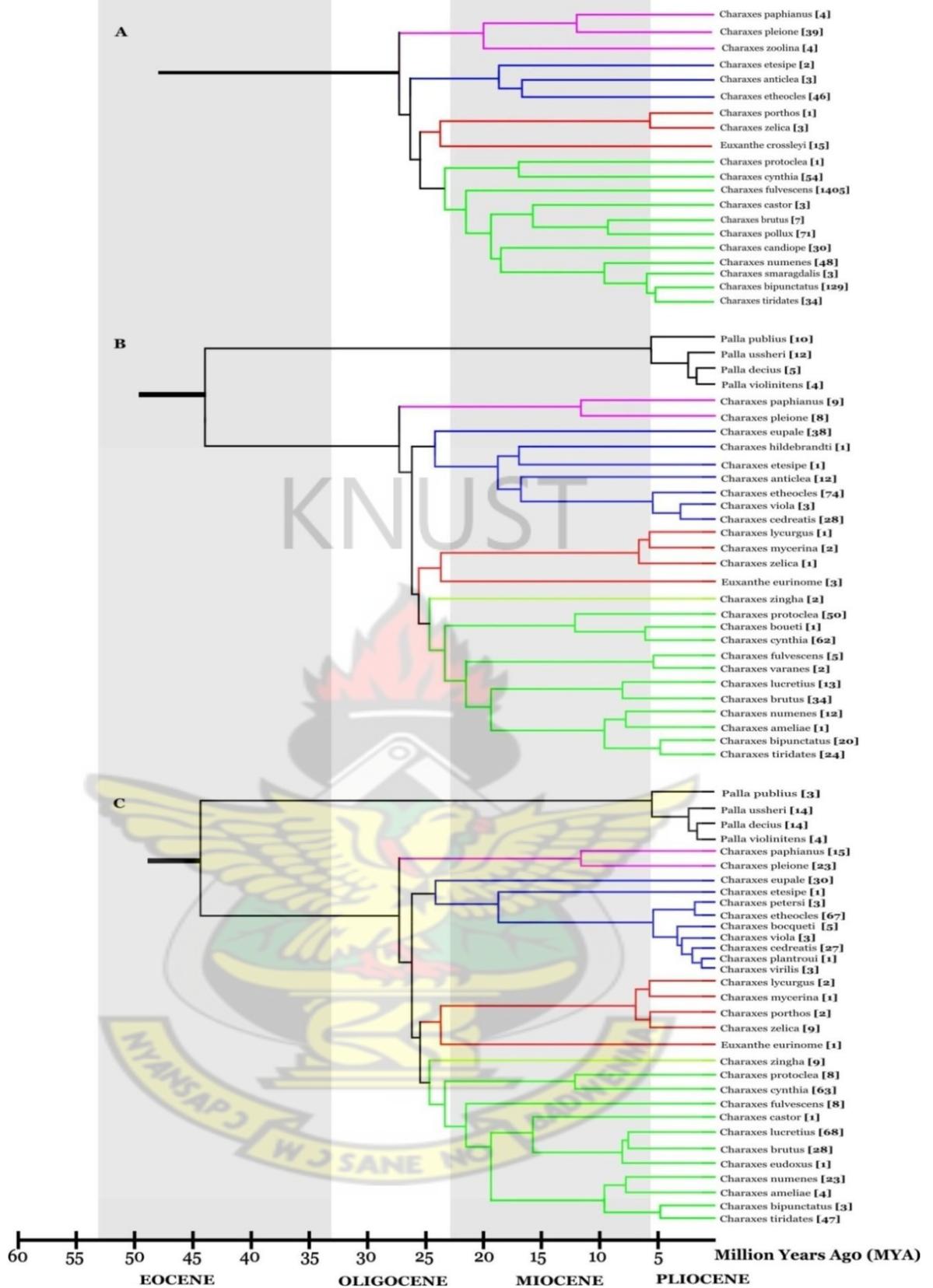


Figure 6.7 Bayesian phylogenetic topology of *Charaxes*, *Euxanthe* and *Palla* genera. The original tree (in Aduse-Poku *et al* 2009) was constructed using 5 gene regions of 144 Charaxinae exemplar taxa. Here the tree is pruned to include only exemplar species found in (a) Kibale National Park, Uganda (b) Bobiri Forest Reserve, Ghana and (c) Bia National Park, Ghana. Numbers in square brackets after species name are the species abundances.

6.4 DISCUSSION

The results present clear and strong evidence of niche differentiation among fruit-feeding butterfly assemblages. The apparent consistency in the kind of species or species-groups found at either the canopy or understorey in the three study communities suggests that fruit-feeding butterfly assemblages are largely structured by species' vertical (habitat) preference. If at all, neutral theory therefore should only be applied to understorey or canopy separately. Similarly, species composition in the understorey was too different between Ghana and Kibale to justify considering them together in a single metacommunity. In the canopy, this is warranted.

The understorey fruit-feeding butterfly community was chiefly composed of members of Limenitidinae, Nymphalidae and Satyrinae subfamilies with the *Euphaedra*, *Bicyclus*, *Bebearia*, *Catuna* and *Euriphene* being the dominant genera. Members of these genera were either completely absent in the canopy, or scarcely represented (Figure 6.4). The forest canopy stratum species were mainly members of the Charaxinae (*Charaxes* and *Palla*), Apaturinae and Biblidinae subfamilies. Previous long-term vertical stratification studies report of similar distinct differences in fruit-feeding butterfly faunal composition between the forest canopy and understorey in Africa and even in Asia and the Neotropics (Beccaloni 1997; DeVries *et al.* 1999; DeVries & Walla 2001; Schulze *et al.* 2001; Veddeler *et al.* 2005).

A probable link between adult flight height and larval resource (host plant) availability is mostly cited as the main factor maintaining the vertical stratification in fruit-feeding butterfly assemblages (Beccaloni 1997; Schulze *et al.* 2001; Janz *et al.* 2006). The vast majority of Satyrinae are grass-feeders as larvae (Larsen 2005b) and most Limenitidinae utilize monocotyledonous food plants mainly growing at the forest understorey. The larvae of the dominant 'canopy species-groups' (*Charaxes*,

Palla and *Apaturopsis*) are known to feed mostly on leaves of tree species in many families (Larsen 2005b).

Factors maintaining the vertical stratification in fruit-feeding butterflies could be more than food sources; both ecological and evolutionary processes such as differences in microclimate (wind, temperature and especially light intensity as in DeVries *et al.* (1999), variations in vegetation structure, interaction with other species (Schulze *et al.* 2001) and adaptation of behavioral traits could be involved to some degree. For instance, I found a significant relationship between some morphological traits (e.g. forewing length, forewing width, wing shape, abdominal length) and species abundance when the canopy data were analyzed separately. Incidentally, the morphological characters that correlated significantly with species abundance at the canopy level are strongly related to butterfly flight behavior (Betts & Wootton 1988; Chai & Srygley 1990; Srygley 1990; Dudley & Srygley 1994; Berwaerts *et al.* 2002; Jantzen & Eisner 2008; Bonte & Van Dyck 2009).

Results of the present study indicate that species with long, slender wings (high wing ratio) tend to have higher frequencies at the canopy than those with low wing ratio (Figure 6.5c). Long, slender winged butterflies are known to be associated with swift and erratic flight patterns (Betts & Wootton 1988; Chai & Srygley 1990). This flight behavior makes such butterflies less susceptible to key butterfly predators like birds who find it hard to predict the flight paths of their prey. I conjecture that this anti-avian-predatory strategy is a fitness advantage at the canopy and perhaps a plausible explanation for the positive correlation between wing shape and abundance.

Species with relatively shorter abdominal length were generally more frequent at the forest canopy (Figure 6.5f). Shorter abdominal bodies are associated with fast flying butterflies (Chai & Srygley 1990) in the same direction but perhaps

not at the same strength as high wing ratio. Although in principle, the body of a butterfly is composed of the head, thorax and the abdomen, the latter contributes most to the overall body length. Consequently long abdominal length makes a butterfly's body relatively longer and that increases their risk of being captured by their body (abdomen) by their key predators such as birds. Because the original intent of the morphological data was not to investigate flight-related issues, certain key flight morphological parameters (e.g. body mass, wing area = total area of both pairs of fore- and hind wings when overlapped in natural configuration) were not measured. These are essential parameters for computing two key aerodynamic indexes (i) aspect ratio which is four times the ratio of squared forewing length to wing area and (ii) wing loading (mass/wing area), used in investigating butterfly flight behavior and mechanisms (Srygley & Dudley 1993; Srygley 2004). I am therefore unable to directly relate flight performance to species abundance.

However, the results do suggest an indirect relationship, which offers us some room to speculate that flight morphological traits would impact on overall species abundance at the canopy; at least the results suggest that flight-related traits are of some relevance in determining which species or species-group does well at the forest canopy. Extending the above rationalization to the understory, the inferred fitness advantages would presumably be of less relevance or of no importance at the forest understory. As expected, none of the measured species-level morphological traits show a significant relationship with species abundance in the understory (Table 6.3). There were also no significant relationships between the measured morphological traits and species abundance when the canopy and the understory data were pooled. This underscores the importance of analyzing the two strata communities separately before combining them.

The 'exact' test of neutrality as a plausible explanation for the observed butterfly community assemblages did not lead to rejection of the model. On the one hand, this is consistent with the findings that abundance did not correlate with many traits (and even none in the understory or combined data sets). On the other hand, we need to keep in mind that the test is conservative because it may yield false negatives but rarely false positives (Etienne 2007): in the latter case, neutral theory is rejected with much confidence. Of course, failure to reject the neutral theory does not necessarily mean that the observed biodiversity pattern is generated by neutral processes. Indeed, two empirical studies (Purves & Pacala 2005; Walker 2007) demonstrate how non-neutral processes can generate neutral patterns. The test as described by McGill *et al* (2006) is a single theory test and provides a weak mode of inference. Stronger tests, as they advocate, should involve contrasting multiple plausible hypotheses and empirical testing of the predictions of neutral theory using both real biological sampled data and our knowledge of the ecological system. Nevertheless, the 'exact' test of neutrality still remains useful in developing explanations for biodiversity community structure and assemblages (Leigh 2007). Failure to reject theory (based on the 'exact' test of neutrality) prompts us look for plausible alternative explanations for the observed biodiversity pattern, other than niche apportionment.

A plausible candidate for a key process determining butterfly community assemblages in the local communities is dispersal limitation. The results suggest lowest dispersal limitation (highest number of potential immigrants) in BIA, compared to the two other sampled local communities. BIA forms part of the Upper Guinea rainforest, which is a large tract of rainforest extending from south-western Ghana to western Sierra Leone. Dispersal or migration of individuals or species from the metacommunity (which in this case can be assumed to include the forest

continuum) into BIA is intuitively much easier than to BOB, which is about 150 km from the Upper Guinea rainforest and exists as an isolated forest 'island' surrounded by a highly altered landscape matrix. This explains the high I_{BIA} values and high richness and diversity in BIA compared to BOB.

Likewise, the migration tendencies at the different (vertical) stratum levels suggested by the neutral model were consistent with our knowledge of the system. There are more individuals (of species) with wider distributional ranges at the canopy than at the forest understorey (Figure 6.3). This trend is also intrinsically linked to the life properties of species found in the different vertical stratum communities. Most canopy 'dedicated' species are robust in body structure, have strong flight muscles, and are powerful in flight (Larsen 2005b). These life history properties enable them to disperse long distances (good dispersers). Consequently, an alternative explanation for the high abundance of wider-ranged species at the canopy is simply because most 'canopy species' are able to fly across long distances and hence are better dispersers.

However, extending the metacommunity from 'Ghana' to 'Africa' to include KIB as one of its local communities makes the parameter estimates less informative for evaluating the ecological meaning of the neutral model estimates for the different local communities. The neutral model parameter (I and θ) estimates for the different local communities were frequently not significantly different from each other at the 'Africa' metacommunity level (Table 6.2). Unlike in the 'Ghana' metacommunity, the neutrally predicted dispersal tendencies in the 'Africa' metacommunity were largely at variance with the trends proposed by the independent species distributional range analysis. At the 'Africa' metacommunity scale, the neutral model parameter estimates suggested less dispersal limitation (although not always significant) at the

understorey, compared to the forest canopy. This contradicts our independent knowledge of the system which indicates a rather opposite trend; more individuals (of species) with wider distributional ranges at the canopy than at the forest understorey (Figure 6.3).

The meltdown in the neutral model parameter estimates' information as the metacommunity extends from 'Ghana' to 'Africa' to include KIB as one of its local communities is explained as follows: First, KIB and the two local communities in Ghana (BIA and BOB) may not belong to the same metacommunity. It is unclear at what distance apart, two samples can be said to belong to the same metacommunity. Etienne (2007) without quoting distances advises that, samples treated as local communities should be separated by distances longer than the typical dispersal of the studied taxa but at the same time, close enough to belong to the same metacommunity. Information on butterfly dispersal distance is currently unavailable but certainly a distance of 3,500km is above the typical.

The other plausible explanation for the information meltdown is that the neutral model of the present study is plainly false. It is worth noting here that falsifying neutral model in the current study applies only to the specific form of the neutral model used to estimate the model parameters. The neutral theory of the present study assumes point mutation as the speciation process and modeled local communities as spatially separated samples (spatially implicit model).

Spatially implicit neutral models are convenient to model but biologically unrealistic (McGill *et al* 2006) as it assumes a fictitiously huge panmictic source pool, which is completely immune of the changes occurring at the local community owing to its large size. Spatially explicit model are more representative of what pertains in nature. There are no clear boundaries separating local communities from

the metacommunity as assumed in the implicit models. However, spatially explicit models (e.g. Chave & Leigh 2002; Rosindell & Cornell 2007) are extremely demanding mathematically and less tractable (Leigh 2007; Etienne 2007).

Again, different modes of speciation, other than point mutation, have been shown to produce different neutral models (Etienne *et al.* 2007b). Perhaps it will be useful in future studies, to empirically evaluate neutral theory in biodiversity assemblages under models of varying modes of speciation and metacommunity assumptions. The plausibility of the different neutral model parameters can then be tested using independent datasets and our knowledge of the system.

Clearly, differences in the life properties of fruit-feeding butterfly species do matter in determining their overall abundance and diversity in ecological communities, contrary to what neutral theory posits. Butterflies, unlike sessile organisms like trees and brachiopods, are mobile organisms and apparently have the luxury of deciding where they and their offspring should occur in an ecological system. They do this by making use of their species-specific traits like habitat preferences, tolerance, flight behaviors and dispersal abilities.

Based on the evidence provided in the current study, the vertical structure of fruit-feeding butterfly assemblages is largely caused by niche differentiation. Neutral theory can still be used to understand community structure in each of these strata separately, especially in terms of dispersal limitation. It is interesting to note that even though the individuals in different strata hardly mix, this can in principle actually be modeled in a 3D spatially explicit models, by setting vertical dispersal distance to a very low value relative to horizontal dispersal distance.

CHAPTER SEVEN

7. SUMMARY, GENERAL DISCUSSION & RECOMMENDATIONS

7.1 Broad Study Objective 1: Development of efficient and reliable Rapid Biodiversity Assessment (RBA) protocol for monitoring Ghanaian forests; using fruit-feeding butterflies as the model system

7.1.1 Summary of Results

The first individual study of this thesis (Chapter 3) underscored the importance of taking into account the effects of temporal and vertical stratification when using fruit-feeding butterflies as a model system in Rapid Biodiversity Assessment in Ghanaian forests. It is clear from the findings of the study that the 'when' (period of sampling) and 'where' (where we sample) attributes of a sampling strategy do affect RBA results. The choice of appropriate sampling design in RBA is therefore of prime importance. Detailed studies aimed at identifying which taxonomic groups of fruit-feeding butterflies do well in detecting changes in the environments should be undertaken to evaluate further the relative importance of fruit-feeding butterfly guilds in RBA. Until those studies and their findings are available, completely neglecting the canopy strata in rapid butterfly biodiversity assessment programs is not advisable. Again, in the light of evidence provided in the study, a useful recommendation to minimize the problems of precision associated with quick fruit-feeding butterfly surveys is always to conduct sampling both in the 'wet' and the 'dry' seasons.

The results of the second study (in Chapter 4) showed that the new trap type (NT, with reduced entry/exit) performed better than the conventional van Someren-

Rydon. This, coupled with its light weight, makes this trap type preferable for rapid biodiversity assessment programs where time and effort are important constraints. The study also revealed that palm wine can act as a useful bait 'add-in' in rapid biodiversity monitoring programs that use fruit-feeding butterflies as the surrogate taxa. Palm wine in baits functions as long range signals or volatile cues in directing butterflies to their food sources. It therefore increases bait attractiveness and subsequently the trap's productivity. Lastly, the present study provides evidence to support that age of bait does affect both the number and kind of butterflies trapped. It is therefore appropriate to identify a priori the focal butterfly taxa, before deciding on the duration of sampling of rapid butterfly diversity survey.

The third study (in Chapter 5) identified seven genera, six species-groups and 25 species as potentially useful indicators of habitat change. The result of the study indicated that monitoring butterflies could provide a quick guide to biodiversity management even on a smaller scale. The study further demonstrated that species richness alone does not represent a powerful metric for monitoring degrees of forest disturbance. Rather the relative abundances of species of defined indicator taxa (based on both fidelity and specificity), were of a much more indicative value. The study identified the following genera; *Euriphene*, *Bebearia*, *Aterica*, *Gnophodes*, *Melanitis* and *Euphaedra* as effective indicator taxa of good conditioned forest habitats. On the converse, small bodied-sized *Bicyclus* (mostly of the *dorothea* species-groups) were identified as effective indicator taxa of disturbed habitats. The relatively large bodied-sized *Bicyclus* (of the *sangmelinae*, *funnebris*, *angulosa*, *hewitsoni* and *safitza* species-groups) were rather recovered as potentially useful indicator taxa of good conditioned forest habitat indicators.

7.1.2 Proposed biodiversity monitoring frameworks: Towards the development of efficient RBA in Ghana (and West Africa)

Currently, the majority of the few available RBA protocols that use fruit-feeding butterflies as the focal taxon in African forests do not involve trapping or observation in the forest canopy. Most of these protocols (e.g. Fermon *et al.* 2000; Rogo & Odulaja 2001; Larsen 2005a; Oduro & Aduse-Poku 2005) are of short duration, usually not spanning more than a season. The few relatively longer surveys (e.g. Bossart *et al.* 2006; Bossart & Opuni-Frimpong 2009) that cover the two main seasons in tropical Africa also neglect the canopy strata, but see Molleman *et al.* (2006). Other protocols like Aduse-Poku & Doku (2007) and Fermon *et al.* (2003) involve canopy trapping but covered only one season.

The value of efficient RBAs for developing countries like Ghana cannot be overemphasized. Global defaunation, deforestation and extinction have reached unprecedented rates and resources available for long term inventories remain severely limited or nonexistent. Larsen (2008) showed that effectively no butterflies have as yet become completely extinct in West Africa, though many have disappeared from much of their previous areas of occurrence. Further monitoring of these and many other biodiversity features will demand continued RBAs. Therefore the search for an efficient yet cost-effective, sustainable and easily implementable biodiversity assessment program to identify conservation priority sites in Ghana (and West Africa) for formal protection should be given priority attention.

Based exclusively on the findings of the first three minor studies of this thesis, two kinds of RBA frameworks are proposed for monitoring forests in Ghana

(and West Africa). These are; 1) Species and taxonomic surrogacy and 2) All species approach.

7.1.2.1 Species and Taxonomic Surrogacy

The species surrogacy approach entails the use of taxonomic levels higher than species such as genus, tribes, subfamilies, families, order, etc. (Ward & Larivière 2004). This is the original RBA approach proposed by Oliver and Beattie (1993). Taxonomic surrogacy is similar to species surrogacy in approach except that the former uses what has come to be known as recognisable taxonomic units (RTUs) also known as morphospecies (MSP) or operational taxonomic units (OTUs). RTUs act as a surrogates for species-level identification (Beattie & Oliver 1994).

These RBA frameworks are proposed in situations where there are no trained butterfly specialists (taxonomists). Unfortunately, this is likely to be the case in most developing countries. The third study (in Chapter 5) demonstrated that some species-groups (at genus and sub-genus levels) could serve as potentially useful indicators for monitoring the quality of forest habitats. The study identified fruit-feeding butterflies of the genera *Euphaedra*, *Euriphene*, *Bebearia* and *Aterica* are potential indicator taxa of good quality forests in Ghana (see Table 5.5 and 5.6; Figure 5.4). As indicators of disturbed or 'poor quality' forest habitats, the study identified the *dorothea* species-groups (of the genus *Bicyclus*) as potentially useful taxa (see Table 5.7).

There are approximately 100 species of *Euphaedra*, *Euriphene*, *Bebearia*, *Aterica* and *Bicyclus* in Ghana alone (Larsen 2006). This species richness is high enough for meaningful synthesis and interpretation of biodiversity trends. Species-level identification of specimens of these genera would pose significant challenges for

non-specialist taxonomists (also known as parataxonomists). Species of these genera often form real cryptic complexes with possible hybrids between species. As a result, their species-level identification sometimes confuses even specialist taxonomists. However, the sorting of specimens of these genera into morphospecies (as in genera or species-groups) is undeniably easier, since individual putative species-groups are distinctive enough, not to be confused (Larsen 2005b). The relative abundances and diversities of these focal species-groups could be used as the metric of evaluating the quality or state of the habitat. Changes in the relative abundances of these indicator species could give a quick hint of the impact of a management decision on biodiversity, allowing adjustment options in space and/or time.

The results of Study 1 (in Chapter 3, Figure 3.8; Appendix 1) revealed that effectively all the potential indicator taxa groups (i.e. *Euphaedra*, *Euriphene*, *Bebearia*, *Aterica* and *Bicyclus*) identified for this approach, are distributed at the forest understorey and are abundant both in the wet and dry seasons. Accordingly, to maximize the efficiency of the taxonomic surrogacy approach in Ghana (and West Africa, in general), sampling could be restricted to the forest understorey, but with the caveat that some impacts confined to the canopy layer may not be detected early enough, or at all. Moreover, sampling period should be designed such that it covers both the dry and wet seasons.

The second study (in Chapter 4, Figure 4.3) showed that when using the bait-trapping technique, spot sampling at the same location (or trap station) need not exceed two continuous days (if palmwine is mixed with mashed banana and allowed to ferment for 24 hours) or three days (when only mashed banana fermented for 24 hours is used as bait). The target species groups (i.e. *Euphaedra*, *Euriphene*, *Bebearia*, *Aterica* and *Bicyclus*) in this kind of approach generally prefer fresh fruit

bait (see Figure 4.3). The new and improved trap type used in chapter 4 (Figure 4.1B) is highly recommended for this proposed framework for these few reasons. (i) they are relatively lighter in weight compared to the old trap type and this makes their transport to the field easier, (ii) they are cheaper to construct (cost effective), and (iii) they are more productive in terms of species and abundances turnover in traps (Table 4.3, Figure 4.2).

7.1.2.2 All species approach

This RBA approach aims at identifying all trapped specimens to species-level. The all-species approach is recommended in situations where butterfly specialists or taxonomists are available to identify specimens to species level. In this RBA framework, all fruit-feeding butterflies are targeted in the sampling design. Imperatively, apart from sampling both in the wet and dry seasons, trapping should also be done at both the forest understorey and canopy. The novel bait (mashed banana mixed with palm wine) and the new trap type (Figure 4.1B) used in chapter 4 are recommended for this approach to enhance species turnover in traps.

Following the recommendation of the third study of this thesis (Chapter 5), the efficiency of this approach could be enhanced by sampling not more than two continuous days (if palmwine is mixed with mashed banana and allowed to ferment for 24 hours) or three days (when only mashed banana fermented for 24 hours is used as bait) at the same trap location. However, to widen the species coverage to include species of the *Charaxes* and *Apaturopsis* genera, foul-scented food sources like rodent carcasses could be used as bait in some traps (see Figure 4.3f and Section 4.4 for discussion on this). Compared to the Species and Taxonomic surrogacy approach, the All Species approach is more discrete and finer scaled, because it involves

relatively more taxa or measurable units. The rich ecological and evolutionary information currently readily available for most fruit-feeding species could be used in drawing inferences about the condition or state of habitat or forest under study.

The above two proposed biodiversity monitoring frameworks are practicable in Ghana and West Africa, even in the face of limited resources and personnel for monitoring forests. It is however expected that, the proposed protocols would be enhanced as our knowledge of Ghanaian or West African butterflies improves.

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7.2 Broad Study Objective 2: Empirical evaluation of neutral theory in mobile organisms; using fruit-feeding butterflies as the model system

Study 4 (Chapter 6) showed that clearly differences in the life properties of fruit-feeding butterfly species do matter in determining their overall abundance and diversity in ecological communities, contrary to what neutral theory posits.

Butterflies, unlike sessile organisms (like trees and brachiopods) are mobile organisms and apparently have the luxury of deciding where they and offspring should occur in an ecological system. They do this by making use of their species-specific traits like habitat preferences, tolerance, flight behaviors and dispersal abilities.

Based on the evidence provided in the current study, the vertical structure of fruit-feeding butterfly assemblages is largely caused by niche differentiation. Neutral theory can still be used to understand community structure in each of these strata separately, especially in terms of dispersal limitation. It is interesting to note that even though the individuals in different strata hardly mix, this can in principle

actually be modeled in a 3D spatially explicit model, by setting vertical dispersal distance to a very low value relative to horizontal dispersal distance.

To my knowledge, Chapter 6 represent the first attempt to empirically evaluate neutral theory in mobile organism assemblages using both direct (confronting neutral model to real species abundance data) and indirect approaches (testing the predictions of neutral theory against independent datasets and our knowledge of the system). It has been shown that using species abundance data alone in investigating the factors or processes regulating biodiversity community structures and patterns can be informative, but is not sufficient. To fully develop a universal neutral model to explain species assemblages, neutral theoreticians must look beyond species abundance data and consider including other useful ecological and evolutionary information such as the phylogeny and species distributional range data into the already available sampling formulae. I believe that it is useful to develop such models using well-studied ecological systems such as butterfly communities where information such as species traits, habitat preference, host plants, geographical distribution, and phylogeny of most species groups are readily available for use in the evaluation of the model and testing of the model predictions.

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APPENDICES

Appendix 1 List of trapped species and their relative abundances in Bobiri Forest Reserve and Bia Biosphere Reserve, with stratum categorization

Subfamily Species	Study area									
	Bobiri Forest Reserve					Bia Biosphere Reserve				
	Relative abundances		Chi-square test			Relative abundances		Chi-square test		
	Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d	Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d
Apaturinae										
<i>Apaturoopsis cleochares</i>	51	100	51.0	***	c	13	100	13.0	***	c
Biblidinae										
<i>Byblia anvatarata</i>	1	0.00	1.00	ns	bu	--	--	--	--	--
<i>Eurytela dryope</i>	4	75.0	1.00	ns	b	1	100	1.00	ns	bc
<i>Eurytela hiarbas</i>	3	100	3.00	ns	bc	1	100	1.00	ns	bc
<i>Neptidopsis ophione</i>	1	100	1.00	ns	bc	1	0.00	1.00	ns	bu
† _{BIA} <i>Sevenia occidentarium</i>	--	--	--	--	--	2	100	2.00	ns	bc
Charaxinae										
<i>Charaxes ameliae</i>	1	100	1.00	ns	bc	4	100	4.00	ns	bc
† _{BIA} <i>Charaxes anticlea</i>	12	91.7	8.33	**	c	10	100	10.0	**	c
<i>Charaxes bipunctatus</i>	20	90.0	12.8	***	c	3	66.7	0.33	ns	b
† _{BIA} <i>Charaxes bocqueti</i>	2	100	2.00	ns	bc	5	100	5.00	*	c
<i>Charaxes boueti</i>	1	100	1.00	ns	bc	--	--	--	--	--
† _{BIA} <i>Charaxes brutus</i>	34	100	34.0	***	c	28	92.9	20.6	***	c
† _{BIA} <i>Charaxes castor</i>	--	--	--	--	--	1	100	1.00	ns	bu
† _{BIA} <i>Charaxes cedreatis</i>	28	100	28.0	***	c	27	100	27.0	***	c
<i>Charaxes cynthia</i>	62	67.7	7.81	ns	b	63	71.4	11.6	**	c
† _{BIA} <i>Charaxes etesipe</i>	1	100	1.00	ns	bc	1	100	1.00	ns	bc
<i>Charaxes etheocles</i>	74	97.3	66.2	***	c	67	95.5	55.5	***	c
† _{BIA} <i>Charaxes eudoxus</i>	--	--	--	--	--	1	100	1.00	ns	bc
<i>Charaxes eupale</i>	38	100	38.0	***	c	30	100	30.0	***	c
† _{BIA} <i>Charaxes fulvoscens</i>	5	0.0	5.00	*	u	8	12.5	4.50	*	u
<i>Charaxes hildabrandti</i>	1	100	1.00	ns	bc	--	--	--	--	--
<i>Charaxes lucretius</i>	13	69.2	1.92	ns	b	68	95.6	56.5	***	c
† _{BIA} <i>Charaxes lycurgus</i>	1	100	1.00	ns	bc	2	100	2.00	ns	bc
† _{BIA} <i>Charaxes mycerina</i>	2	100	2.00	ns	bc	1	100	1.00	ns	bc
<i>Charaxes numenes</i>	12	91.7	8.33	**	c	13	84.6	6.23	*	c
† _{BIA} <i>Charaxes paphianus</i>	9	100	9.00	**	c	15	86.7	8.07	**	c
† _{BIA} <i>Charaxes petersi</i> ^{WV}	--	--	--	--	--	3	100	3.00	ns	bc
† _{BIA} <i>Charaxes plantroui</i> ^{WV}	--	--	--	--	--	1	100	1.00	ns	bc
<i>Charaxes pleione</i>	8	100	8.00	**	c	23	95.7	19.2	***	c
† _{BIA} <i>Charaxes porthos</i>	--	--	--	--	--	2	100	2.00	ns	bc
<i>Charaxes protoclea</i>	50	36.0	3.92	ns	b	41	56.1	0.61	ns	b
<i>Charaxes tiridates</i>	24	91.7	16.7	***	c	47	89.4	29.1	***	c
<i>Charaxes varanes</i>	2	0.00	2.00	ns	bu	--	--	--	--	--
† _{BIA} <i>Charaxes viola</i>	3	100	3.00	ns	bc	3	100	3.00	ns	bc
† _{BIA} <i>Charaxes virilis</i>	--	--	--	--	--	3	100	3.00	ns	bc
† _{BIA} <i>Charaxes zelica</i>	1	100	1.00	ns	bc	3	100	3.00	ns	bc
† _{BIA} <i>Charaxes zingha</i>	2	100	2.00	ns	bc	9	66.7	1.00	ns	b
† _{BIA} <i>Euxanthe eurinome</i>	3	66.7	0.33	ns	b	1	100	1.00	ns	bc
† _{BIA} <i>Palla decius</i>	5	20.0	1.80	ns	b	14	71.4	2.57	ns	b
† _{BIA} <i>Palla publius</i>	10	80.0	3.60	ns	b	3	66.7	0.33	ns	b
<i>Palla ussheri</i>	12	8.30	8.33	**	u	14	42.9	0.29	ns	b
<i>Palla violinitens</i>	4	50.0	0.00	ns	b	4	100	4.00	ns	bc
Satyrinae										
<i>Bicyclus abnormis</i> ^{WV}	226	15.9	105	***	u	127	7.90	90.2	***	u

Subfamily	Species	Study area									
		Bobiri Forest Reserve					Bia Biosphere Reserve				
		Relative abundances		Chi-square test			Relative abundances		Chi-square test		Cat ^d
Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d	Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c			
† _{BOB} , † _{BIA}	<i>Bicyclus auricruda</i>	2	0.00	2.00	ns	bu	8	0.00	8.00	**	u
	<i>Bicyclus dorothea</i>	19	0.00	19.0	***	u	66	3.00	58.2	***	u
† _{BIA}	<i>Bicyclus ephorus</i>	--	--	--	--	--	8	0.00	8.00	**	u
	<i>Bicyclus evadne</i>	1	0.00	1.00	ns	bu	10	0.00	10.0	**	u
	<i>Bicyclus funebris</i>	1403	1.10	1340	***	u	154	0.60	150	***	u
	<i>Bicyclus ignobilis</i>	--	--	--	--	--	2	0.00	2.00	ns	bu
† _{BIA}	<i>Bicyclus istaris</i>	9	33.3	1.00	ns	b	3	0.00	3.00	ns	bu
	<i>Bicyclus madetes</i>	69	0.00	69.0	***	u	23	0.00	23.0	***	u
† _{BOB} , † _{BIA}	<i>Bicyclus maesseni</i> ^{ww}	--	--	--	--	--	4	50.0	0.00	ns	b
	<i>Bicyclus mandanes</i>	--	--	--	--	--	5	0.00	5.00	ns	bu
	<i>Bicyclus martius</i>	68	0.00	68.0	***	u	16	0.00	16.0	***	u
	<i>Bicyclus nobilis</i>	--	--	--	--	--	3	0.00	3.00	ns	bu
† _{BIA}	<i>Bicyclus procora</i>	34	0.00	34.0	***	u	29	0.00	29.0	***	u
	<i>Bicyclus safitza</i>	46	6.50	34.8	***	u	6	0.00	6.00	ns	bu
	<i>Bicyclus sambulous</i>	--	--	--	--	--	61	0.00	61.0	***	u
	<i>Bicyclus sandace</i>	443	2.30	404	***	u	127	0.80	123	***	u
	<i>Bicyclus sangmelinae</i>	25	0.00	25.0	***	u	69	1.40	65.1	***	u
	<i>Bicyclus taenias</i>	29	0.00	29.0	***	u	44	0.00	44.0	***	u
	<i>Bicyclus uniformis</i>	2	0.00	2.00	ns	bu	--	--	--	--	--
	<i>Bicyclus vulgaris</i>	193	0.50	189	***	u	32	3.10	28.1	***	u
	<i>Bicyclus xeneas</i>	68	7.40	49.5	***	u	27	11.1	16.3	***	u
	<i>Bicyclus zinebi</i> ^{ww}	10	20.0	3.60	ns	b	115	0.00	115	***	u
	<i>Elymniopsis bammakoo</i>	24	54.2	0.17	ns	b	6	33.3	0.67	ns	b
	<i>Gnophodes betsimena</i>	380	6.10	294	***	u	99	15.2	48.1	***	u
	<i>Gnophodes chelys</i>	62	16.1	28.5	***	u	41	0.00	41.0	***	u
	<i>Hallelesis halyma</i> ^{ww}	--	--	--	--	--	21	0.00	21.0	***	u
	<i>Melanitis leda</i>	183	14.8	90.9	***	u	54	18.5	21.4	***	u
	<i>Melanitis libya</i>	7	57.1	0.14	ns	b	--	--	--	--	--
Libytheinae											
	<i>Libythea labdaca</i>	14	100	14.0	***	c	3	100	3.00	ns	bc
Limenitidinae											
	<i>Aterica galene</i>	51	0.00	51.0	***	u	42	0.00	42.0	***	u
	<i>Bebearia abesa</i>	3	0.00	3.00	ns	bu	2	0.00	2.00	ns	bu
	<i>Bebearia absolon</i>	35	0.00	35.0	***	u	26	0.00	26.0	***	u
	† _{BIA} <i>Bebearia arcadius</i> ^{ww}	--	--	--	--	--	7	0.00	7.00	*	u
	<i>Bebearia carce</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	† _{BIA} <i>Bebearia carshena</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Bebearia cocalia</i>	8	0.00	8.00	**	u	25	0.00	25.0	***	u
	<i>Bebearia demetra</i>	2	0.00	2.00	ns	bu	6	0.00	6.00	*	u
	<i>Bebearia laetitia</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	† _{BOB} , † _{BIA} <i>Bebearia lucayensis</i>	8	0.00	8.00	**	u	2	0.00	2.00	ns	bu
	† _{BIA} <i>Bebearia maledicta</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Bebearia mandinga</i>	6	0.00	6.00	*	u	6	0.00	6.00	*	u
	<i>Bebearia mardania</i>	13	0.00	13.0	***	u	24	0.00	24.0	***	u
	† _{BIA} <i>Bebearia oxione</i>	2	0.00	2.00	ns	bu	2	0.00	2.00	ns	bu
	<i>Bebearia paludicola</i>	7	0.00	7.00	*	u	17	0.00	17.0	***	u
	<i>Bebearia phantasina</i>	21	0.00	21.0	***	u	24	0.00	24.0	***	u
	<i>Bebearia sophus</i>	29	0.00	29.0	***	u	81	0.00	81.0	***	u
	<i>Bebearia tentyris</i>	78	0.00	78.0	***	u	19	0.00	19.0	***	u
	<i>Bebearia zonara</i>	56	0.00	56.0	***	u	11	0.00	11.0	**	u
	<i>Catuna angustatum</i>	--	--	--	--	--	2	0.00	2.00	ns	bu
	<i>Catuna crithea</i>	2	0.00	2.00	ns	bu	2	0.00	2.00	ns	bu
	<i>Catuna oberthueri</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Cymothoe caenias</i>	13	69.2	1.92	ns	b	4	100	4.00	ns	bc
	<i>Cymothoe coccinata</i>	--	--	--	--	--	1	100	1.00	ns	bc

Subfamily	Species	Study area									
		Bobiri Forest Reserve					Bia Biosphere Reserve				
		Relative abundances		Chi-square test			Relative abundances		Chi-square test		
Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d	Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d		
† _{BIA}	<i>Cymothoe egesta</i>	25	0.00	25.0	***	u	20	0.00	20.0	***	u
	<i>Cymothoe fumana</i>	--	--	--	--	--	3	0.00	3.00	ns	bu
	<i>Cymothoe jodutta</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Cymothoe indet?</i>	1	0.00	1.00	ns	bu	--	--	--	--	--
	<i>Cymothoe lurida</i>	3	33.3	0.33	ns	b	--	--	--	--	--
† _{BIA}	<i>Cymothoe mabillei</i> ^{ww}	32	40.6	1.13	ns	b	14	57.1	0.29	ns	b
	<i>Cymothoe sangaris</i>	3	0.00	3.00	ns	bu	--	--	--	--	--
	<i>Euphaedra B217</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Euphaedra B301</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Euphaedra ceres</i>	86	0.00	86.0	***	u	89	0.00	89.0	***	u
† _{BIA}	<i>Euphaedra cf tenebrosa</i> ^{en}	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Euphaedra crockeri</i> ^{ww}	--	--	--	--	--	41	0.00	41.0	***	u
† _{BIA}	<i>Euphaedra diffusa</i>	--	--	--	--	--	4	0.00	4.00	ns	bu
	<i>Euphaedra edwardsii</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Euphaedra eleus</i>	--	--	--	--	--	3	0.00	3.00	ns	bu
	<i>Euphaedra eupalus</i> ^{ww}	11	0.00	11.0	**	u	2	0.00	2.00	ns	bu
† _{BIA}	<i>Euphaedra francina</i> ^{ww}	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Euphaedra gausape</i> ^{ww}	2	0.00	2.00	ns	bu	6	0.00	6.00	*	u
	<i>Euphaedra harpalyce</i>	26	0.00	26.0	***	u	78	0.00	78.0	***	u
	<i>Euphaedra hebes</i>	4	0.00	4.00	ns	bu	7	0.00	7.00	*	u
† _{BIA}	<i>Euphaedra ignota</i> ^{en}	--	--	--	--	--	3	0.00	3.00	ns	bu
	<i>Euphaedra janetta</i>	4	0.00	4.00	ns	bu	8	0.00	8.00	**	u
† _{BIA}	<i>Euphaedra mariachristinae</i> ^{en}	--	--	--	--	--	4	0.00	4.00	ns	bu
	<i>Euphaedra medon</i>	100	0.00	100	***	u	32	0.00	32.0	***	u
† _{BIA}	<i>Euphaedra minuta</i> ^{en}	3	0.00	3.00	ns	bu	3	0.00	3.00	ns	bu
† _{BIA}	<i>Euphaedra modesta</i> ^{en}	--	--	--	--	--	4	0.00	4.00	ns	bu
	<i>Euphaedra perseis</i> ^{ww}	--	--	--	--	--	9	0.00	9.00	**	u
	<i>Euphaedra phaethusa</i> ^{ww}	48	0.00	48.0	***	u	61	0.00	61.0	***	u
	<i>Euphaedra sarcoptera</i>	5	0.00	5.00	*	u	3	0.00	3.00	ns	bu
† _{BOB} ; † _{BIA}	<i>Euphaedra splendens</i>	1	0.00	1.00	ns	bu	2	0.00	2.00	ns	bu
† _{BIA}	<i>Euphaedra themis</i>	43	0.00	43.0	***	u	3	0.00	3.00	ns	bu
	<i>Euphaedra xypete</i>	3	0.00	3.00	ns	bu	10	0.00	10.0	**	u
† _{BIA}	<i>Euphaedra zampa</i> ^{ww}	--	--	--	--	--	5	0.00	5.00	*	u
	<i>Euriphene amicia</i>	1	0.00	1.00	ns	bu	1	0.00	1.00	ns	bu
	<i>Euriphene ampedusa</i>	--	--	--	--	--	7	0.00	7.00	*	u
	<i>Euriphene aridatha</i>	26	0.00	26.0	***	u	13	0.00	13.0	***	u
† _{BOB}	<i>Euriphene atossa</i>	2	0.00	2.00	ns	bu	15	0.00	15.0	***	u
	<i>Euriphene barombina</i>	70	0.00	70.0	***	u	38	0.00	38.0	***	u
	<i>Euriphene gambiae</i>	21	0.00	21.0	***	u	151	0.00	151	***	u
† _{BIA}	<i>Euriphene incerta</i>	1	0.00	1.00	ns	bu	3	0.00	3.00	ns	bu
	<i>Euriphene simplex</i> ^{ww}	37	0.00	37.0	***	u	33	0.00	33.0	***	u
	<i>Euryphura chalcis</i>	33	81.8	13.4	***	c	46	87.0	25.1	***	c
	<i>Harma theobene</i>	15	0.00	15.0	***	u	6	0.00	6.00	*	u
† _{BIA}	<i>Neptis paula</i>	--	--	--	--	--	1	100	1.00	ns	bc
† _{BIA}	<i>Neptis strigata</i>	--	--	--	--	--	1	100	1.00	ns	bc
	<i>Pseudacraea eurytus</i>	2	50.0	0.00	ns	b	1	0.00	1.00	ns	bu
† _{BIA}	<i>Pseudacraea lucretia</i>	10	40.0	0.40	ns	b	10	100	10.0	**	c
† _{BIA}	<i>Pseudathyma falcata</i>	--	--	--	--	--	1	0.00	1.00	ns	bu
	<i>Pseudathyma sibyllina</i>	1	100	1.00	ns	bc	1	100	1.00	ns	bc
	<i>Pseudoneptis bungandensis</i>	1	0.00	1.00	ns	bu	--	--	--	--	--
Nymphalinae											
	<i>Antanartia delius</i>	1	100	1.00	ns	bc	2	100	2.00	ns	bc
	<i>Hypolimnas anthedon</i>	--	--	--	--	--	1	100	1.00	ns	bc
	<i>Hypolimnas salmacis</i>	3	0.00	3.00	ns	bu	2	0.00	2.00	ns	bu
	<i>Junonia terea</i>	1	0.00	1.00	ns	bu	--	--	--	--	--
	<i>Kallimoides rumia</i>	5	0.00	5.00	*	u	--	--	--	--	--

Subfamily Species	Study area									
	Bobiri Forest Reserve					Bia Biosphere Reserve				
	Relative abundances		Chi-square test			Relative abundances		Chi-square test		
Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d	Total ^a	% in Canopy ^b	F(χ^2 -test)	Sig ^c	Cat ^d	
Heliconiinae										
<i>Salamis cacta</i>	--	--	--	--	--	4	0.00	4.00	ns	bu
<i>Lachnoptera anticleia</i>	1	0.00	1.00	ns	bu	--	--	--	--	--

†_{BIA} = First-time-record for Bia Biosphere Reserve, †_{BOB} = First-time-record for Bobiri Forest Reserve
^{ww} = West African endemics, ^{en} = Ghanaian endemics

^aTotal number individuals of the species caught. ^bPercentage of the total individual of the the species caught at the canopy. ^cSignificant level; ***= <0.001, ** = <0.01; * = <0.05

^dspecies categorization; c = canopy species, u = understory species, b = both strata, bc = only caught at the canopy but not statistically significant, bu = only caught at the understory but not statistically significant

Appendix 2 Species and number of individuals of fruit-feeding butterfly recorded using the different bait and trap types

Subfamily Species	Relative ^a abundance	Bait type				Trap type			
		New Bait	Old Bait	χ^2 value	Sign ^b	New Trap	Old Trap	χ^2 value	Sign ^b
Limenitidinae									
<i>Aterica galene</i>	35	19	16	0.26	ns	32	3	24.03	***
<i>Bebearia abesa</i>	2	2	--	2.00	ns	1	1	0.00	ns
<i>Bebearia absolon</i>	44	23	21	0.09	ns	40	4	29.45	***
<i>Bebearia cocalia</i>	7	6	1	3.57	ns	3	4	0.14	ns
<i>Bebearia demetra</i>	2	1	1	0.00	ns	1	1	0.00	ns
<i>Bebearia lucayensis</i>	12	8	4	1.33	ns	9	3	3.00	ns
<i>Bebearia mandinga</i>	7	2	5	1.29	ns	7	--	7.00	*
<i>Bebearia mardania</i>	13	5	8	0.69	ns	10	3	3.77	ns
<i>Bebearia oxione</i>	4	4	--	4.00	ns	4	--	4.00	ns
<i>Bebearia paludicola</i>	7	2	5	1.29	ns	6	1	3.57	ns
<i>Bebearia phantasina</i>	14	8	6	0.29	ns	11	3	4.57	ns
<i>Bebearia sophus</i>	27	13	14	0.04	ns	21	6	8.33	**
<i>Bebearia tentyris</i>	82	53	29	7.02	*	65	17	28.10	***
<i>Bebearia zonara</i>	55	35	20	4.09	ns	48	7	30.56	***
<i>Euphaedra perseis</i>	1	1	--	1.00	ns	--	1	1.00	ns
<i>Euphaedra ceres</i>	115	62	53	0.70	ns	95	20	48.91	***
<i>Euphaedra eupalus</i>	12	7	5	0.33	ns	9	3	3.00	ns
<i>Euphaedra harpalyce</i>	22	12	10	0.18	ns	18	4	8.91	**
<i>Euphaedra hebes</i>	2	2	--	2.00	ns	1	1	0.00	ns
<i>Euphaedra janetta</i>	3	--	3	3.00	ns	3	--	3.00	ns
<i>Euphaedra medon</i>	84	50	34	3.05	ns	70	14	37.33	***
<i>Euphaedra phaethusa</i>	26	19	7	5.54	*	20	6	7.54	**
<i>Euphaedra sarcoptera</i>	7	6	1	3.57	ns	5	2	1.29	ns
<i>Euphaedra themis</i>	34	15	19	0.47	ns	25	9	7.53	**

Subfamily	Species	Relative abundance	Bait type				Trap type			
			New Bait	Old Bait	Chi-value	Sign	New Trap	Old Trap	Chi-value	Sign
	<i>Euphaedra xypete</i>	5	1	4	1.80	ns	5	--	5.00	*
	<i>Euriphene amicia</i>	3	--	3	3.00	ns	--	3	3.00	ns
	<i>Euriphene aridatha</i>	23	14	9	1.09	ns	21	2	15.70	***
	<i>Euriphene atossa</i>	1	--	1	1.00	ns	--	1	1.00	ns
	<i>Euriphene barombina</i>	12	10	2	5.33	*	10	2	5.33	*
	<i>Euriphene gambiae</i>	11	4	7	0.82	ns	8	3	2.27	ns
	<i>Euriphene incerta</i>	5	2	3	0.20	ns	4	1	1.80	ns
	<i>Euriphene simplex</i>	33	14	19	0.76	ns	27	6	13.36	***
	<i>Catuna crithea</i>	1	1	--	1.00	ns	1	--	1.00	ns
	<i>Cymothoe caenias</i>	1	1	--	1.00	ns	--	1	1.00	ns
	<i>Cymothoe fumana</i>	1	1	--	1.00	ns	1	--	1.00	ns
	<i>Euryphura chalcis</i>	1	--	1	1.00	ns	1	--	1.00	ns
Satyrinae										
	<i>Bicyclus abnormis</i>	143	79	64	1.57	ns	101	42	24.34	***
	<i>Bicyclus dorothea</i>	3	1	2	0.33	ns	2	1	0.33	ns
	<i>Bicyclus funebris</i>	12	5	7	0.33	ns	8	4	1.33	ns
	<i>Bicyclus istaris</i>	5	1	4	1.80	ns	5	--	5.00	*
	<i>Bicyclus madetes</i>	12	7	5	0.33	ns	10	2	5.33	*
	<i>Bicyclus martius</i>	17	14	3	7.12	*	13	4	4.76	ns
	<i>Bicyclus procora</i>	26	19	7	5.54	*	22	4	12.46	***
	<i>Bicyclus sandace</i>	30	13	17	0.53	ns	20	10	3.33	ns
	<i>Bicyclus sangmelinae</i>	43	18	25	1.14	ns	26	17	1.88	ns
	<i>Bicyclus taenias</i>	1	--	1	1.00	ns	1	--	1.00	ns
	<i>Bicyclus uniformis</i>	1	1	--	1.00	ns	1	--	1.00	ns
	<i>Bicyclus vulgaris</i>	4	1	3	1.00	ns	3	1	1.00	ns
	<i>Bicyclus xeneas</i>	17	9	8	0.06	ns	14	3	7.12	*
	<i>Bicyclus zinebi</i>	2	1	1	0.00	ns	1	1	0.00	ns
	<i>Elymniopsis bammakoo</i>	6	4	2	0.67	ns	3	3	0.00	ns
	<i>Gnophodes betsimena</i>	78	44	34	1.28	ns	57	21	16.62	***
	<i>Gnophodes chelys</i>	28	19	9	3.57	ns	21	7	7.00	*
	<i>Melanitis leda</i>	21	13	8	1.19	ns	11	10	0.05	ns
Charaxinae										
	<i>Charaxes cynthia</i>	7	4	3	0.14	ns	5	2	1.29	ns
	<i>Charaxes etheocles</i>	1	--	1	1.00	ns	1	--	1.00	ns
	<i>Charaxes fulvescens</i>	3	1	2	0.33	ns	--	3	3.00	ns
	<i>Charaxes lucretius</i>	1	1	--	1.00	ns	1	--	1.00	ns
	<i>Charaxes numenes</i>	1	1	--	1.00	ns	1	--	1.00	ns
	<i>Charaxes protoclea</i>	30	17	13	0.53	ns	22	8	6.53	*
	<i>Palla publius</i>	1	1	--	1.00	ns	1	--	1.00	ns
	<i>Palla ussheri</i>	4	3	1	1.00	ns	3	1	1.00	ns
Nymphalinae										
	<i>Kallimoides rumia</i>	2	--	2	2.00	ns	2	--	2.00	ns
Heliconiinae										
	<i>Lachnoptera antidia</i>	1	--	1	1.00	ns	1	--	1.00	ns

^aTotal number individuals of the species caught during the study

^bSignificant level; ***= <0.001, ** = <0.01; * = <0.05, ns = non significant

Appendix 3 Species and number of individuals of fruit-feeding butterfly recorded at each trap station in the forest and cocoa farm habitats.

Subfamily Species	Forest										Boundary	Cocoa farm							Total			
	F ₁₀	F ₉	F ₈	F ₇	F ₆	F ₅	F ₄	F ₃	F ₂	F ₁	F _{total}	B	C ₁	C ₂	C ₃	C ₄	C ₅	C ₆		C ₇	C _{total}	
Heliconiinae																						
<i>Acraea alciope</i>	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	1	
Limenitidinae																						
<i>Aterica galene</i>	2	--	--	2	4	1	2	--	2	1	14	--	--	--	--	--	--	--	--	--	14	
<i>Beberia abesa</i>	--	--	--	1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	1	
<i>Beberia absolon</i>	--	1	1	1	5	1	--	2	--	1	12	1	2	2	--	--	--	--	--	4	17	
<i>Beberia areadius</i>	2	--	--	--	--	--	--	--	1	1	4	--	--	--	--	--	--	--	--	--	4	
<i>Beberia carshena</i>	--	--	--	--	--	--	--	1	--	--	1	--	--	--	--	--	--	--	--	--	1	
<i>Bebearia cocalia</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	1	1	
<i>Beberia mardania</i>	--	1	--	--	2	--	--	--	--	1	4	1	4	1	--	--	1	1	--	7	12	
<i>Beberia paludicola</i>	--	--	--	--	2	--	--	--	--	--	2	1	2	--	--	--	--	--	--	2	5	
<i>Beberia phantasina</i>	--	--	1	3	1	1	--	2	3	4	15	2	--	--	--	--	--	--	--	--	17	
<i>Beberia sophus</i>	2	1	1	3	3	6	5	2	4	4	31	3	5	--	1	--	3	--	1	10	44	
<i>Beberia tentyris</i>	2	--	--	1	1	4	5	5	2	2	22	--	--	--	1	--	--	--	--	1	23	
<i>Beberia zonara</i>	--	--	1	--	3	1	--	--	--	1	6	--	--	--	--	--	--	--	--	--	6	
<i>Catuna crithea</i>	--	--	--	--	--	--	--	--	1	--	1	--	--	--	--	--	--	--	--	--	1	
<i>Cymothoe egesta</i>	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	1	--	1	--	2	3	
<i>Cymothoe fumana</i>	--	--	--	--	--	--	--	--	--	--	--	--	1	2	--	--	--	--	--	3	3	
<i>Cymothoe mabiliei</i>	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	1	
<i>Euphaedra ceres</i>	1	--	1	1	2	2	5	7	5	2	26	3	3	1	2	--	--	1	1	8	37	
<i>Euphaedra crockeri</i>	1	--	--	2	2	2	5	2	3	1	18	--	--	1	--	--	--	--	--	1	19	
<i>Euphaedra diffusa</i>	--	1	--	--	--	1	--	--	--	--	2	--	--	--	--	--	--	--	--	--	2	
<i>Euphaedra edwardsii</i>	1	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	1	
<i>Euphaedra eleus</i>	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	1	
<i>Euphaedra francina</i>	--	--	1	--	1	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	2	
<i>Euphaedra gausape</i>	--	--	--	--	--	1	1	1	1	--	4	--	--	--	--	--	--	--	--	--	4	
<i>Euphaedra harpalyce</i>	5	3	--	9	1	3	3	3	4	6	37	1	--	--	--	--	1	--	--	1	39	
<i>Euphaedra hebes</i>	--	1	--	1	1	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	3	
<i>Euphaedra janetta</i>	--	--	--	--	--	--	--	1	--	--	1	--	--	--	--	--	--	--	--	--	1	
<i>Euphaedra mariaechristinae</i>	--	--	--	--	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	1	
<i>Euphaedra medon</i>	--	1	1	3	4	1	--	2	4	1	17	1	--	1	1	2	--	1	--	5	23	
<i>Euphaedra minuta</i>	--	--	--	--	--	1	1	--	--	--	2	--	--	--	--	--	--	--	--	--	2	

Subfamily	Forest											Boundary	Cocoa farm							Total	
	Species	F ₁₀	F ₉	F ₈	F ₇	F ₆	F ₅	F ₄	F ₃	F ₂	F ₁		F _{total}	B	C ₁	C ₂	C ₃	C ₄	C ₅		C ₆
<i>Euphaedra modesta</i>	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	1	--	1		2
<i>Euphaedra phaethusa</i>	--	--	2	3	5	1	5	1	3	4	24	1	--	--	--	1	--	1	1	3	28
<i>Euphaedra sarcoptera</i>	--	--	--	1	--	1	1	--	--	--	3	--	1	--	--	--	--	--	1		4
<i>Euphaedra xypete</i>	--	--	--	--	--	--	1	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Euphaedra zampa</i>	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Euriphene amicia</i>	--	--	--	--	--	1	1	--	--	--	2	--	--	--	--	--	--	--	--		2
<i>Euriphene ampedusa</i>	--	--	--	--	--	--	3	1	1	--	5	--	--	--	--	--	--	--	--		5
<i>Euriphene aridatha</i>	--	--	--	--	--	1	--	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Euriphene atossa</i>	--	--	--	--	--	--	--	2	1	--	3	1	--	--	--	--	--	--	--		4
<i>Euriphene barombina</i>	1	1	1	2	2	2	--	1	1	2	13	--	1	--	--	--	--	--	--	1	14
<i>Euriphene gambiae</i>	6	1	1	3	10	4	6	7	5	6	49	2	--	--	--	--	--	--	--		51
<i>Euriphene incerta</i>	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Euriphene simplex</i>	--	2	1	1	2	--	--	2	--	--	8	--	--	--	--	--	--	--	--		8
<i>Euryphura chalcis</i>	--	--	--	--	--	--	1	--	--	1	2	--	1	1	1	1	--	2	2	8	10
<i>Harma theobene</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	1	--	--	--	3	3
<i>Pseudacrea hostilia</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	1	1
<i>Pseudathyma sibyllina</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	1	1
Satyrinae																					
<i>Bicyclus abnormis</i>	1	3	2	5	2	1	2	3	1	1	21	--	--	1	--	--	1	1	--	3	24
<i>Bicyclus auricruda</i>	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Bicyclus dorothea</i>	--	--	--	--	2	3	--	--	--	3	8	29	34	35	31	27	22	23	33	205	242
<i>Bicyclus ephorus</i>	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Bicyclus funebris</i>	2	5	--	6	8	7	6	3	7	4	48	--	4	4	--	--	3	1	3	15	66
<i>Bicyclus ignobolis</i>	--	--	--	1	1	--	--	--	1	--	3	--	--	--	--	--	--	--	--		3
<i>Bicyclus istaris</i>	--	--	--	--	--	--	--	--	1	--	1	--	1	--	--	--	--	--	--	1	2
<i>Bicyclus madetes</i>	1	1	--	--	2	2	--	1	3	1	11	--	--	--	1	1	--	--	3	5	16
<i>Bicyclus mandanes</i>	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--		1
<i>Bicyclus martius</i>	--	--	--	--	2	--	--	--	--	--	2	--	--	--	--	1	--	--	--	1	3
<i>Bicyclus procora</i>	--	--	--	--	2	1	--	--	--	--	3	--	--	--	--	1	--	--	--	1	4
<i>Bicyclus safitza</i>	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	2	1	--	5	10	10
<i>Bicyclus sambulous</i>	--	1	3	1	3	1	1	3	2	1	16	1	--	1	--	--	--	--	--	1	18
<i>Bicyclus sandace</i>	2	2	1	4	6	5	4	--	5	6	35	11	10	15	23	12	15	22	31	128	174
<i>Bicyclus sylvicolus</i>	--	--	--	--	--	1	--	--	--	--	1	--	--	--	--	--	--	--	--		1
<i>Bicyclus taenias</i>	--	2	--	--	1	1	1	2	2	5	14	3	1	1	--	4	2	2	4	14	31

Subfamily Species	Forest										Boundary	Cocoa farm							Total		
	F ₁₀	F ₉	F ₈	F ₇	F ₆	F ₅	F ₄	F ₃	F ₂	F ₁	F _{total}	B	C ₁	C ₂	C ₃	C ₄	C ₅	C ₆		C ₇	C _{total}
<i>Bicyclus xeneas</i>	--	--	--	--	1	--	--	--	2	1	4	--	--	1	--	--	--	--	--	1	5
<i>Bicyclus zinebi</i>	4	--	3	1	2	2	1	2	3	1	19	1	2	--	--	--	1	--	--	3	23
<i>Elymniopsis bammakoo</i>	--	--	--	--	--	--	1	1	1	1	2	1	2	1	--	1	2	--	1	7	10
<i>Gnophodes betsimena</i>	1	7	1	6	6	3	9	8	4	5	50	1	7	1	4	5	1	3	1	22	73
<i>Gnophodes chelys</i>	--	--	--	1	4	--	3	6	3	4	21	1	2	--	2	--	--	--	--	4	26
<i>Hallelesis halyma</i>	1	1	--	--	--	1	--	--	--	1	3	--	--	--	--	--	--	--	--	--	3
<i>Melanitis leda</i>	1	1	1	4	4	2	2	1	3	2	20	2	4	1	--	--	--	2	1	8	30
Charaxinae																					
<i>Charaxes anticlea</i>	--	--	--	--	--	--	--	1	--	--	1	--	--	--	--	--	--	--	--	--	1
<i>Charaxes brutus</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	2	3	3
<i>Charaxes cynthia</i>	--	--	--	--	1	--	--	--	--	--	1	--	1	3	--	--	--	--	1	5	6
<i>Charaxes etheocles</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	1	1
<i>Charaxes lucretius</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	--	2	2
<i>Charaxes paphianus</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	1	1
<i>Charaxes protoaclea</i>	1	--	--	--	--	1	--	--	2	--	4	4	2	2	1	1	--	--	1	7	15
<i>Charaxes tiridates</i>	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	1	2
<i>Charaxes varanes</i>	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	1
<i>Charaxes zingha</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	1	1
<i>Palla ussheri</i>	1	--	--	1	--	1	1	1	1	--	6	3	2	--	1	--	--	--	1	4	13
<i>Palla violinitens</i>	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	1
Biblidinae																					
<i>Eurytela dryope</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	1	1
Nymphalinae																					
<i>Hypolimnias salmactis</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	1	1
<i>Junonia terea</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	1	1
<i>Salamis cacta</i>	1	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	1	1	2
Overall																					
Abundance	41	38	24	69	105	69	80	74	86	79	665	89	104	94	81	66	61	67	109	582	1,336
Observed richness	23	20	18	28	40	35	28	28	32	33	67	28	28	24	19	15	15	15	21	55	88
Menhinick diversity	3.6	3.2	3.7	3.4	3.9	4.2	3.1	3.3	3.5	3.7	2.6	3.0	2.7	2.5	2.1	1.8	1.9	1.8	2.0	2.3	2.4

Notes: F₁-F₁₀ are the forest trap stations with increasing distance (100m interval) from the forest boundary (B) into the forest interior. C₁-C₇ are the cocoa farm trap stations with increasing distance from the forest boundary (B) into the cocoa farmland.

Appendix 4 Species and number of individuals of fruit-feeding butterfly recorded at the understory (under.) and the canopy strata in each local community

Subfamily Species	Kibale National Park			Bia Biosphere Reserve			Bobiri Forest Reserve		
	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a
Apaturinae									
<i>Apaturopsis cleochares</i>	27	111	138	--	13	13	--	51	51
Biblidinae									
<i>Ariadne enotrea</i>	55	26	81	--	--	--	--	--	--
<i>Ariadne pagenstecheri</i>	5	1	6	--	--	--	--	--	--
<i>Byblia anvatar</i>	--	--	--	--	--	--	1	--	1
<i>Eurytela dryope</i>	3	3	6	--	1	1	1	3	4
<i>Eurytela hiarbas</i>	590	842	1,432	--	1	1	--	3	3
<i>Neptidopsis ophione</i>	83	39	122	1	--	1	--	1	1
<i>Sevenia boisduvalli</i>	58	1,542	1,600	--	--	--	--	--	--
<i>Sevenia occidentali</i>	1	46	47	--	2	2	--	--	--
<i>Sevenia umbrina</i>	8	105	113	--	--	--	--	--	--
Charaxinae									
<i>Charaxes ameliae</i>	--	--	--	--	4	4	--	1	1
<i>Charaxes anticlea</i>	3	--	3	--	10	10	1	11	12
<i>Charaxes bipunctatus</i>	77	52	129	1	2	3	2	18	20
<i>Charaxes bocqueti</i>	--	--	--	--	5	5	--	2	2
<i>Charaxes boueti</i>	--	--	--	--	--	--	--	1	1
<i>Charaxes brutus</i>	4	3	7	2	26	28	--	34	34
<i>Charaxes candiope</i>	20	10	30	--	--	--	--	--	--
<i>Charaxes castor</i>	--	3	3	--	1	1	--	--	--
<i>Charaxes cedreatis</i>	--	--	--	--	27	27	--	28	28
<i>Charaxes cynthia</i>	52	2	54	18	45	63	20	42	62
<i>Charaxes etesipe</i>	2	--	2	--	1	1	--	1	1
<i>Charaxes etheocles</i>	13	33	46	3	64	67	2	72	74
<i>Charaxes eudoxus</i>	--	--	--	--	1	1	--	--	--
<i>Charaxes eupale</i>	--	--	--	--	30	30	--	38	38
<i>Charaxes fulvescens</i>	1387	18	1405	7	1	8	5	--	5
<i>Charaxes hildabrandti</i>	--	--	--	--	--	--	--	1	1
<i>Charaxes lucretius</i>	--	--	--	3	65	68	4	9	13
<i>Charaxes lycurgus</i>	--	--	--	--	2	2	--	1	1
<i>Charaxes mycerina</i>	--	--	--	--	1	1	--	2	2
<i>Charaxes numenes</i>	42	6	48	2	11	13	1	11	12
<i>Charaxes paphianus</i>	3	1	4	2	13	15	--	9	9
<i>Charaxes petersi</i>	--	--	--	--	3	3	--	--	--
<i>Charaxes plantroui</i>	--	--	--	--	1	1	--	--	--
<i>Charaxes pleione</i>	22	17	39	1	22	23	--	8	8
<i>Charaxes pollux</i>	63	8	71	--	--	--	--	--	--
<i>Charaxes porthos</i>	--	1	1	--	2	2	--	--	--
<i>Charaxes protoclea</i>	29	2	31	18	23	41	32	18	50
<i>Charaxes smaragdalis</i>	2	1	3	--	--	--	--	--	--
<i>Charaxes tiridates</i>	15	19	34	5	42	47	2	22	24
<i>Charaxes varanes</i>	--	--	--	--	--	--	2	--	2
<i>Charaxes viola</i>	--	--	--	--	3	3	--	3	3
<i>Charaxes virilis</i>	--	--	--	--	3	3	--	--	--
<i>Charaxes zelica</i>	1	2	3	--	3	3	--	1	1
<i>Charaxes zingha</i>	--	--	--	3	6	9	--	2	2
<i>Charaxes zoolina</i>	--	4	4	--	--	--	--	--	--
<i>Euxanthe crossleyi</i>	9	6	15	--	--	--	--	--	--
<i>Euxanthe eurinome</i>	--	--	--	--	1	1	1	2	3
<i>Palla decius</i>	--	--	--	4	10	14	4	1	5

Subfamily Species	Kibale National Park			Bia Biosphere Reserve			Bobiri Forest Reserve		
	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a
<i>Palla publius</i>	--	--	--	1	2	3	2	8	10
<i>Palla ussheri</i>	--	--	--	8	6	14	11	1	12
<i>Palla voilinitens</i>	--	--	--	--	4	4	2	2	4
Heliconiinae									
<i>Lachnoptera anticlia</i>	109	60	169	--	--	--	1	--	1
<i>Phalanta eurytis</i>	26	7	33	--	--	--	--	--	--
<i>Phalanta phalantha</i>	30	171	201	--	--	--	--	--	--
Libytheinae									
<i>Libythea labdaca</i>	--	--	--	--	3	3	--	14	14
Limnitiidae									
<i>Aterica galene</i>	344	6	350	42	--	42	51	--	51
<i>Bebearia abesa</i>	--	--	--	2	--	2	3	--	3
<i>Bebearia absolon</i>	28	--	28	26	--	26	35	--	35
<i>Bebearia arcadius</i>	--	--	--	7	--	7	--	--	--
<i>Bebearia barce</i>	--	--	--	1	--	1	--	--	--
<i>Bebearia carshena</i>	--	--	--	1	--	1	--	--	--
<i>Bebearia cocalia</i>	--	--	--	25	--	25	8	--	8
<i>Bebearia demetra</i>	--	--	--	6	--	6	2	--	2
<i>Bebearia laetitia</i>	--	--	--	1	--	1	--	--	--
<i>Bebearia lucayensis</i>	--	--	--	2	--	2	6	--	6
<i>Bebearia maledicta</i>	--	--	--	1	--	1	--	--	--
<i>Bebearia mandinga</i>	--	--	--	6	--	6	6	--	6
<i>Bebearia mardania</i>	--	--	--	24	--	24	13	--	13
<i>Bebearia oxione</i>	--	--	--	2	--	2	2	--	2
<i>Bebearia paludicola</i>	--	--	--	17	--	17	7	--	7
<i>Bebearia phantasina</i>	--	--	--	24	--	24	21	--	21
<i>Bebearia sophus</i>	249	2	251	81	--	81	29	--	29
<i>Bebearia tentyris</i>	--	--	--	19	--	19	78	--	78
<i>Bebearia zonara</i>	--	--	--	11	--	11	56	--	56
<i>Catuna angustatum</i>	--	--	--	2	--	2	--	--	--
<i>Catuna crithea</i>	207	7	214	2	--	2	2	--	2
<i>Catuna oberthueri</i>	--	--	--	1	--	1	--	--	--
<i>Cymothoe caenias</i>	1	2	3	--	4	4	4	9	13
<i>Cymothoe coccinata</i>	--	--	--	--	1	1	--	--	--
<i>Cymothoe egesta</i>	--	--	--	20	--	20	25	--	25
<i>Cymothoe fumana</i>	--	--	--	3	--	3	--	--	--
<i>Cymothoe herminia</i>	525	90	615	--	--	--	--	--	--
<i>Cymothoe hobarti</i>	92	52	144	--	--	--	--	--	--
<i>Cymothoe jodutta</i>	--	--	--	1	--	1	--	--	--
<i>Cymothoe lurida</i>	416	43	459	--	--	--	2	1	3
<i>Cymothoe mabillei</i>	--	--	--	6	8	14	19	13	32
<i>Cymothoe sangaris</i>	--	--	--	--	--	--	3	--	3
<i>Cymothoe spp.A</i>	--	--	--	--	--	--	1	--	1
<i>Euphaedra alacris</i>	1,344	9	1,353	--	--	--	--	--	--
<i>Euphaedra B217</i>	--	--	--	1	--	1	--	--	--
<i>Euphaedra B301</i>	--	--	--	1	--	1	--	--	--
<i>Euphaedra ceres</i>	--	--	--	89	--	89	86	--	86
<i>Euphaedra cf tenebrosa</i>	--	--	--	1	--	1	--	--	--
<i>Euphaedra christyi</i>	301	5	306	--	--	--	--	--	--
<i>Euphaedra crockeri</i>	--	--	--	41	--	41	--	--	--
<i>Euphaedra diffusa</i>	--	--	--	4	--	4	--	--	--
<i>Euphaedra edwardsii</i>	165	3	168	1	--	1	--	--	--
<i>Euphaedra eleus</i>	--	--	--	3	--	3	--	--	--

Subfamily Species	Kibale National Park			Bia Biosphere Reserve			Bobiri Forest Reserve		
	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a
<i>Euphaedra eupalus</i>	--	--	--	2	--	2	11	--	11
<i>Euphaedra eusemoides</i>	240	--	240	--	--	--	--	--	--
<i>Euphaedra francina</i>	--	--	--	1	--	1	--	--	--
<i>Euphaedra gausape</i>	--	--	--	6	--	6	2	--	2
<i>Euphaedra harpalyce</i>	647	7	654	78	--	78	26	--	26
<i>Euphaedra hebes</i>	--	--	--	7	--	7	4	--	4
<i>Euphaedra hollandi</i>	18	1	19	--	--	--	--	--	--
<i>Euphaedra ignota</i>	--	--	--	3	--	3	--	--	--
<i>Euphaedra janetta</i>	--	--	--	8	--	8	4	--	4
<i>Euphaedra kakamega</i>	35	1	36	--	--	--	--	--	--
<i>Euphaedra mariachristinae</i>	--	--	--	4	--	4	--	--	--
<i>Euphaedra medon</i>	1725	19	1744	32	--	32	100	--	100
<i>Euphaedra minuta</i>	--	--	--	3	--	3	3	--	3
<i>Euphaedra modesta</i>	--	--	--	4	--	4	--	--	--
<i>Euphaedra perseis</i>	--	--	--	9	--	9	--	--	--
<i>Euphaedra phaethusa</i>	--	--	--	61	--	61	48	--	48
<i>Euphaedra preussi</i>	269	5	274	--	--	--	--	--	--
<i>Euphaedra sarcoptera</i>	--	--	--	3	--	3	5	--	5
<i>Euphaedra splendens</i>	--	--	--	2	--	2	1	--	1
<i>Euphaedra themis</i>	--	--	--	3	--	3	43	--	43
<i>Euphaedra uganda</i>	339	3	342	--	--	--	--	--	--
<i>Euphaedra xypete</i>	--	--	--	10	--	10	3	--	3
<i>Euphaedra zaddachi</i>	154	3	157	--	--	--	--	--	--
<i>Euphaedra zampa</i>	--	--	--	5	--	5	--	--	--
<i>Euriphene amicia</i>	--	--	--	1	--	1	1	--	1
<i>Euriphene ampedusa</i>	--	--	--	7	--	7	--	--	--
<i>Euriphene aridatha</i>	--	--	--	13	--	13	26	--	26
<i>Euriphene atossa</i>	--	--	--	15	--	15	2	--	2
<i>Euriphene barombina</i>	--	--	--	38	--	38	70	--	70
<i>Euriphene gambiae</i>	--	--	--	151	--	151	21	--	21
<i>Euriphene incerta</i>	--	--	--	3	--	3	1	--	1
<i>Euriphene lucayensis</i>	--	--	--	--	--	--	2	--	2
<i>Euriphene ribensis</i>	69	2	71	--	--	--	--	--	--
<i>Euriphene saphirina</i>	7	--	7	--	--	--	--	--	--
<i>Euriphene simplex</i>	--	--	--	33	--	33	37	--	37
<i>Euryphura chalcis</i>	4	7	11	6	40	46	6	27	33
<i>Harma theobene</i>	570	23	593	6	--	6	15	--	15
<i>Neptis paula</i>	--	--	--	--	1	1	--	--	--
<i>Neptis strigata</i>	--	--	--	--	1	1	--	--	--
<i>Pseudacraea clarckii</i>	--	1	1	--	--	--	--	--	--
<i>Pseudacraea eurytus</i>	1	--	1	1	--	1	1	1	2
<i>Pseudacraea lucretia</i>	70	107	177	--	--	--	6	4	10
<i>Pseudacraea semire</i>	1	--	1	--	--	--	--	--	--
<i>Pseudathyma falcata</i>	--	--	--	1	10	11	--	--	--
<i>Pseudathyma sibyllina</i>	--	--	--	--	1	1	--	1	1
<i>Pseudoneptis bungandensis</i>	--	--	--	--	--	--	1	--	1
Nymphalinae									
<i>Antanartia delius</i>	40	84	124	--	2	2	--	1	1
<i>Antanartia dimorphica</i>	11	11	22	--	--	--	--	--	--
<i>Hypolimnias anthedon</i>	3	1	4	--	1	1	--	--	--
<i>Hypolimnias monteironis</i>	2	--	2	--	--	--	--	--	--
<i>Hypolimnias salmacis</i>	5	--	5	2	--	2	3	--	3
<i>Junonia stygia</i>	58	11	69	--	--	--	--	--	--
<i>Junonia terea</i>	--	--	--	--	--	--	1	--	1

Subfamily Species	Kibale National Park			Bia Biosphere Reserve			Bobiri Forest Reserve		
	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a	Under.	Canopy	Abund ^a
<i>Junonia westermanni</i>	12	5	17	--	--	--	--	--	--
<i>Kallimoides rumia</i>	369	5	374	--	--	--	5	--	5
<i>Kamilla ansorgei</i>	2	--	2	--	--	--	--	--	--
<i>Protogoniomorpha parhassus</i>	6	2	8	--	--	--	--	--	--
<i>Protogoniomorpha temora</i>	3	--	3	--	--	--	--	--	--
<i>Salamis cacta</i>	58	4	62	4	--	4	--	--	--
Satyrinae									
<i>Bicyclus abnormis</i>	--	--	--	117	10	127	190	36	226
<i>Bicyclus auricruda</i>	576	37	613	8	--	8	2	--	2
<i>Bicyclus buea</i>	350	12	362	--	--	--	--	--	--
<i>Bicyclus campinus</i>	16	--	16	--	--	--	--	--	--
<i>Bicyclus campus</i>	4	--	4	--	--	--	--	--	--
<i>Bicyclus dentatus</i>	74	4	78	--	--	--	--	--	--
<i>Bicyclus dorothea</i>	--	--	--	64	2	66	19	--	19
<i>Bicyclus ephorus</i>	--	--	--	8	--	8	--	--	--
<i>Bicyclus evadne</i>	--	--	--	10	--	10	1	--	1
<i>Bicyclus funebris</i>	18	--	18	153	1	154	1,387	16	1,403
<i>Bicyclus golo</i>	700	16	716	--	--	--	--	--	--
<i>Bicyclus graueri</i>	1,067	8	1,075	--	--	--	--	--	--
<i>Bicyclus ignobilis</i>	--	--	--	2	--	2	--	--	--
<i>Bicyclus istaris</i>	59	--	59	3	--	3	6	3	9
<i>Bicyclus madetes</i>	--	--	--	23	--	23	69	--	69
<i>Bicyclus maesseni</i>	--	--	--	2	2	4	--	--	--
<i>Bicyclus mandanes</i>	826	33	859	5	--	5	--	--	--
<i>Bicyclus martius</i>	--	--	--	16	--	16	68	--	68
<i>Bicyclus mesogena</i>	368	8	376	--	--	--	--	--	--
<i>Bicyclus mollitia</i>	1,790	415	2,205	--	--	--	--	--	--
<i>Bicyclus nobilis</i>	--	--	--	3	--	3	--	--	--
<i>Bicyclus procora</i>	--	--	--	29	--	29	34	--	34
<i>Bicyclus safitza</i>	4	--	4	6	--	6	43	3	46
<i>Bicyclus sambulos</i>	45	1	46	61	--	61	--	--	--
<i>Bicyclus sandace</i>	--	--	--	126	1	127	433	10	443
<i>Bicyclus sangmelinae</i>	--	--	--	68	1	69	25	--	25
<i>Bicyclus sebetus</i>	122	1	123	--	--	--	--	--	--
<i>Bicyclus smithi</i>	9,524	135	9,659	--	--	--	--	--	--
<i>Bicyclus taenias</i>	--	--	--	44	--	44	29	--	29
<i>Bicyclus uniformis</i>	--	--	--	--	--	--	2	--	2
<i>Bicyclus vulgaris</i>	1	--	1	31	1	32	192	1	193
<i>Bicyclus xeneas</i>	--	--	--	24	3	27	63	5	68
<i>Bicyclus zinebi</i>	--	--	--	115	--	115	8	2	10
<i>Elymniopsis bammakoo</i>	--	--	--	4	2	6	11	13	24
<i>Gnophodes betsimena</i>	103	--	103	84	15	99	357	23	380
<i>Gnophodes chelys</i>	955	7	962	41	--	41	52	10	62
<i>Gnophodes grogani</i>	97	4	101	--	--	--	--	--	--
<i>Hallelesis halyma</i>	--	--	--	21	--	21	--	--	--
<i>Henotesia peitho</i>	32	4	36	--	--	--	--	--	--
<i>Melanitis ansorgei</i>	4	--	4	--	--	--	--	--	--
<i>Melanitis leda</i>	96	3	99	44	10	54	156	27	183
<i>Melanitis libya</i>	--	--	--	--	--	--	3	4	7
Overall									
Abundance	27,960	4,350	32,310	2,187	577	2,764	4,151	631	4,782
Observed richness	90	75	94	109	59	139	90	54	111

^aAbund = relative abundance of the species in the entire data pool in the local community.

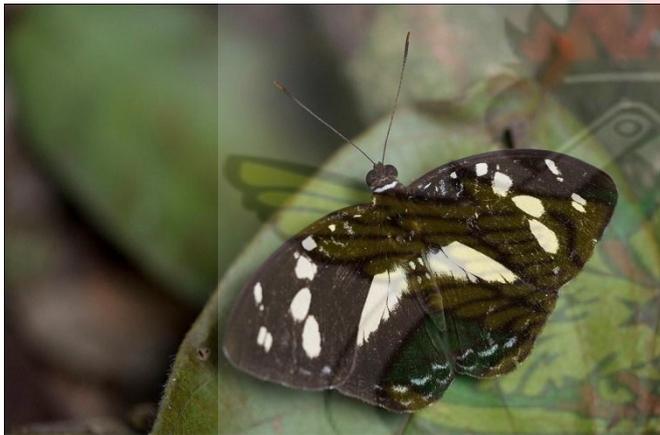
Appendix 5 Photographs of some fruit-feeding butterflies caught during the study



Euphaedra splendens ghanaensis Hecq & Joly, 2004



Bicyclus safitza Hewitson, 1851



Aterica galena galene Brown, 1776



Kallimodies rumia rumia Doubleday, 1849



Euphaedra medon medon Linné, 1766



Euriphene barombina Aurivillius, 1894