Does Cocoa Farm Management Effect Bat Community Assemblages in Southern Cameroon?

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Image: *Rhinolophus alcyone*
Taken by A. Darling (Cameroon; Jan 2020)

Abstract

The Afrotropics are facing increasing pressures to intensify agricultural practises resulting from rising global demands for cash crops, such as cocoa. The intensification and conversion of cocoa farming from small-scale farms to large monocultures in West African countries is threatening the biodiversity of both flora and fauna. Cocoa landscapes have been known to support much of the biodiversity from the natural forests when grown in agroforestry systems. However, there exists little research and knowledge of African cocoa farms and their impact on animals, in particular on bats. The ecosystem services provided by bats within an environment are of high importance, hence studying their community composition is key in understanding how they are impacted by agricultural practices. Not only is it crucial to research how farming impacts bats themselves, it is also important to investigate how these impacts on bats could affect the ecosystem as a whole.

In the present study I will report the findings from a dataset of 800 bat individuals captured across 26 cocoa farms over a four-year period in Southern Cameroon. The abundance, richness and diversity were assessed, and the effects of farm management and seasonality were investigated. The total and insectivorous bat abundance and richness were negatively affected by an increase in management intensity. Seasonality affected total bat richness and frugivorous bat richness, with more species captured during the wet season. Additionally, frugivore abundance was positively correlated with forest cover within 5km of cocoa farms. Species such as *Hipposideros fuliginosus* were prominent in management intensity trends, whilst *Epomops franqueti* was a major species in forest cover trends. These findings support the concept that biodiversity is lowered when farm management is intensified and affects feeding guilds disproportionately. With increasing pressure to intensify cocoa agriculture, our results provide crucial conservation opportunities for bats and for promoting biodiverse cocoa landscapes that support healthy bat communities and thus healthier ecosystems.

Contents

3. Methodology

4. Results

4.1. Total Captures

4.2. Insectivores

4.3. Frugivores

5. Discussion

1. Introduction

The cocoa tree (*Theobroma cacao*) is a valuable crop to many tropical countries, where its pods are used in the production of chocolate. Within the last century, cocoa cultivation has expanded to over 50 countries, where 90% of the world's cocoa is grown on small-scale family farms (Lass, 2004; ICCO, 2017).

Global chocolate consumption is increasing by 2-3% per year and so the demand for cocoa is growing as a result; combining this with a rising human population, cocoa agriculture faces greater pressures than ever before (Lass, 2004). An increased demand for crops, such as cocoa, results in an increased demand for land, usually involving the partial or complete destruction of areas of natural forest (Schroth & Harvey, 2007). Traditionally, cocoa trees are planted under a thinned forest canopy in agroforestry systems, but full-sun plantations where the canopy is entirely removed are now becoming a more common practice as more crops can be planted in the same sized area of land. However, full-sun plantations, usually comprising of monocultures, risk the biodiversity and health of both wildlife and the environment and are eventually short-lived as a consequence of reduced soil quality over time (Nair, 1984). Cocoa agroforestry systems that maintain a diverse and structurally complex canopy conserve a considerable amount of the original biodiversity found in the natural forest, when compared to other agricultural land use systems (Rice & Greenberg, 2000; Duguma et al., 2001; Faria & Baumgarten, 2007; Nkrumah et al., 2017).

The conservation of biodiversity and agricultural production are often considered as mutually exclusive objectives; however, agroforestry systems have shown to host high biodiversity alongside high yields of crop production (Duguma et al., 2001; Faria et al., 2006; Sonwa et al., 2007). Agroforestry systems involve growing agricultural crops amongst shade trees where the level of ecosystem functioning within these systems are a result of the complexity and composition of the species of shade trees (Duguma et al., 2001). Within cocoa agriculture, shade systems can be used to define how a farm is managed; for example, in high-input and high-yielding farms, shade is often minimal or entirely absent, in comparison to lower yielding and low-intensity farms where almost full-shade is provided by thinned forest trees and additionally planted shade trees (Rice & Greenberg, 2000). Structurally complex shade canopies are able to provide wildlife with a comparable habitat to that of the original forest and can maintain connectivity between natural landscapes and agricultural systems (Faria et al., 2006). Across a range of taxa, reduced shade canopies within cash crop farms, including cocoa, results in lower plant and animal biodiversity, including lizards and frogs (Dixo, 2001), arthropods (Perfecto, 1996), birds (Greenberg et al., 1997) and bats (Estrada et al., 1993).

In cocoa agricultural landscapes, biodiversity of animals and plants is vulnerable to reduced forest cover, simplification of shade canopies and the conversion of cocoa agroforestry to other agricultural systems which cannot support an equally high biodiversity value (Schroth & Harvey, 2007). To conserve the current biodiversity within cocoa landscapes, and prevent further losses, it is vital to study the impact of farm management and how cocoa farmers can make their farms more biodiverse, without reducing their crop yields. If species richness and diversity are to be protected, as much of the natural forest habitats should be preserved within cocoa agricultural landscapes as possible, and the shade canopies should be restored both in diversity and structural complexity in order to enhance connectivity and availability of habitats (Faria, 2002).

Cocoa agriculture is one of the most prominent land uses in West Africa, where cocoa farming covers around 5-6 million hectares of land across four countries – Ghana, Côte d'Ivoire, Nigeria, and

Cameroon (FAO, 2017). Almost 70% of the world's cocoa supply is produced within these four countries but the effects of cocoa farming in West Africa is still vastly understudied (FAO, 2017).

Worldwide, Cameroon ranks fifth in the production of cocoa beans and cocoa is the country's third largest export, representing 12% of its total exports (OEC, 2017). In the forested region of Southern Cameroon, cocoa is commonly grown within complex agroforestry systems where it is grown together with native and exotic tree species (Sonwa et al., 2007). The Cameroonian government have recently released targets to triple the country's cocoa production by 2035, resulting in further pressure to increase the number of cocoa farms, in addition to converting and intensifying existing agroforestry systems to monocultures (Ordway et al., 2017). The consequences of such changes cannot be predicted unless the current cocoa agricultural systems are evaluated, in particular the impacts that they have on their associated wildlife and the contiguous environments. Thus, there is a crucial need for research within cocoa agricultural landscapes in Cameroon, along with other major cocoa producing West African countries, which are facing equally challenging pressures to intensify their systems to meet increasing demands.

The management of cocoa agroforests is important in maintaining a sustainable and profitable farm and not only involves the harvesting of cocoa beans but requires the control of diseases and pests, weeding and controlling shade coverage (Wessel, 1987). Shade cover plays a major role within cocoa agriculture and is considered to affect the cocoa plants' growth factors in regard to elements which influence photosynthetic processes and the incidence of pests, such as humidity, light intensity and temperature (Duguma et al., 2001). Recommendations suggest that shade trees should be managed to allow for 50-75% of light to reach the cocoa (Van Himme & Snoek, 2001). Cocoa agroforests, which have high shade coverage, thereby benefit both the agricultural production and the biodiversity of local wildlife by allowing for complex and diverse shade canopies to exist within these landscapes. (Harvey & González Villalobos, 2007)

Bats can be found within agricultural environments across the world and provide many benefits to both the farm and the surrounding ecosystem. Bats carry out necessary ecosystem services; for example, they play a crucial role in the pollination and dispersal of seeds and assist in controlling insect populations (Willig et al., 2007). Bats provide environmental benefits that are valuable to humans, and so can be classed as ecosystem service providers. Insectivorous bat species are beneficial as they regulate the numbers of arthropods and thereby prevent the over-consumption of plant matter by insects, including mass damage to crops. Since insectivorous bats can limit arthropod populations, they reduce the need for harmful chemicals and pesticides on crops, benefiting both the crops and the environment (Kalka et al., 2008). Within cocoa farms, DNA evidence has shown that bats also consume the main pest of cocoa plants, Brown Capsids (*Sahlbergella spp*.) (Powell & Welch, unpublished).

Bat species that are frugivores are also very beneficial to the environment as their consumption of fruit means that they disperse seeds, assisting in the distribution and growth of a variety of plants (Coutinho-Cunto & Bernard, 2012). Seeds dispersed by bats are vital in the process of renewing disturbed or damaged areas of natural forest. Over time, a seed bank of pioneer plants can be built up, allowing the growth of pioneer plants in the disturbed area, and eventually leading to the growth of a climax plant community (Altringham, 2011). Frugivorous and nectivorous bat species are also key pollinators to over 500 plant species worldwide, including valuable medicines and crops such as bananas and mangoes (Fleming et al., 2009).

The benefits that bats provide to agriculture and the neighbouring environments are critical for maintaining a healthy and functioning ecosystem, hence any changes in the abundance or diversity of species could cause adverse consequences for the entire ecosystem (Altringham, 2011). Various studies have shown that agroforestry systems can provide essential habitats for bats where natural forest is scarce or fragmented (Estrada & Coates-Estrada, 2001; Faria et al., 2006). Agroforestry landscapes are generally close to natural forest, allowing different landscapes to remain connected and so, facilitating the movement of animals. Numerous studies of animal diversity and agriculture have found that preserving the heterogeneity and connectivity between natural forest and areas of farming is crucial in the conservation of bats and other animal taxa, such as birds (Perfecto, 1996; Dixo, 2001; Greenberg et al., 1997; Estrada et al., 1993).

The responses of bats within in an environment can fluctuate throughout the year as a result of seasonal changes. In the tropics, seasonality is characterised by changes in precipitation and generally is divided into the 'wet' and 'dry' seasons (Janzen, 1967). In the Afrotropics, the dry season usually occurs between November and April (Proctor et al., 2007). It is the variation in rainfall that results in seasonal fluctuations in fruiting and flowering times and also causes peaks in fruit production during the wet season (Smythe, 1986). Ultimately, these peaks in fruit and flower abundance during the rainy months will affect the number of frugivorous and nectivorous bats that can be supported within an environment. The number of bat species which can be provided for may also differ between seasons as different species possess different dietary intakes and may be unable to gain their nutritional requirements in certain environments (Klingbeil & Willig, 2010). Insect abundance and diversity is also known to vary between seasons as a result of new leaf production in the wet season and changes in nutritional content of plant matter (Wolda, 1978). Therefore, insectivorous bat species may also differ in their relative abundances and species richness across the seasons due to changes in insect availability (Kalko et al., 1999). Studying bats across both the wet and dry seasons will provide a more extensive understanding of the bat communities within cocoa landscapes. Investigating seasonal differences in bat abundance, richness and diversity may provide more comprehensive information of how bats respond to changes in their food availability and distribution. Therefore, having knowledge of how bats respond to such changes may be useful in understanding how bats are responding to changes in the intensity of agricultural management. For example, an increase in intensification practises will likely impact the accessibility and distribution of bats' food sources and so understanding their responses to food-related changes could aid in developing mitigation strategies against the impacts of agricultural intensification.

The relationship between bats and agriculture has been studied in various parts of the world but there are few studies that investigate bats and cocoa agriculture, particularly in West Africa. There is continued pressure to intensify cocoa landscapes and clear further areas of land for farming, especially in major cocoa producing countries, such as Cameroon. Therefore, there is a crucial need for scientific research on the impacts of cocoa farming on biodiversity. As bats are of high ecological significance, it is vital that their response to changes within the environment, especially through anthropogenic actions, such as the clearance of natural forest and land conversion, is understood. Studying the effects of cocoa farming in Cameroon is also of significant importance environmentally, socially, and economically. Since around 70% of cocoa is produced in West African countries, the effects of cocoa landscapes need to be studied. Cocoa is a highly important cash crop in West Africa and the future sustainability of it is vital to the livelihoods of cocoa farmers and to the countries as a whole. Studying the impacts of cocoa farming on bat communities in Cameroon can aid in the creation of mitigation strategies that can optimise both the agricultural production and yields, as well as bat biodiversity.

2. Research Questions & Hypotheses

Data collected in Southern Cameroon from the dry and wet seasons (January-February and August-September, respectively) for 2017, 2018, 2019 and 2020 field seasons will be used to address the following questions:

1) Does cocoa farm management affect bat abundance, richness, or diversity?
2) Does seasonality have an effect on bat abundance, richness, or diversity?
3) What bat species or groups of species are influenced by cocoa farm management and/or seasonality?

My general hypothesis is that farm management, seasonality, and other investigated environmental conditions will affect bat communities. My predictions include:

1) Cocoa farm management will have a negative effect on bat abundance, richness, and diversity as percentage shade cover, which will be used as a proxy for farm management, is reduced.
2) Bat abundance, richness and diversity will be affected by seasonality, with an expected increase in these variables during the wet season.

3. Methodology

3.1. Data Collection

Bat mist-net captures were collected from cocoa farms in Southern Cameroon between 2016 and 2020 by the *Biodiversity Initiative* (B.I.) research team. I joined the B.I. team during the 2020 dry season fieldwork to collect data for the present study. Data were collected during both the dry (January-February) and wet (August-September) seasons. For the purposes of this investigation, data from the 2016 sample sites were excluded due to non-comparable shade cover measurements. A further two cocoa farm sites ("PAIJA001" and "MAMA") were excluded due to the presence of known bat roosts within the farm boundaries. Individuals not identified to species level, or species group (e.g. "*Hipposideros sp*.") were also omitted from analysis, as were recaptured individuals. The resulting dataset consisted of 800 individuals captured across 26 cocoa farms.

During data collection, one cocoa farm was visited per night of sampling and no repeat visits were carried out during the same field season. The same farms were visited each field season to provide necessary repeat visits to allow for suitable scientific analysis. *Figure 1* shows a map of the sampled cocoa farms which were located within 5 town areas (i.e. landscapes) in Southern Cameroon.

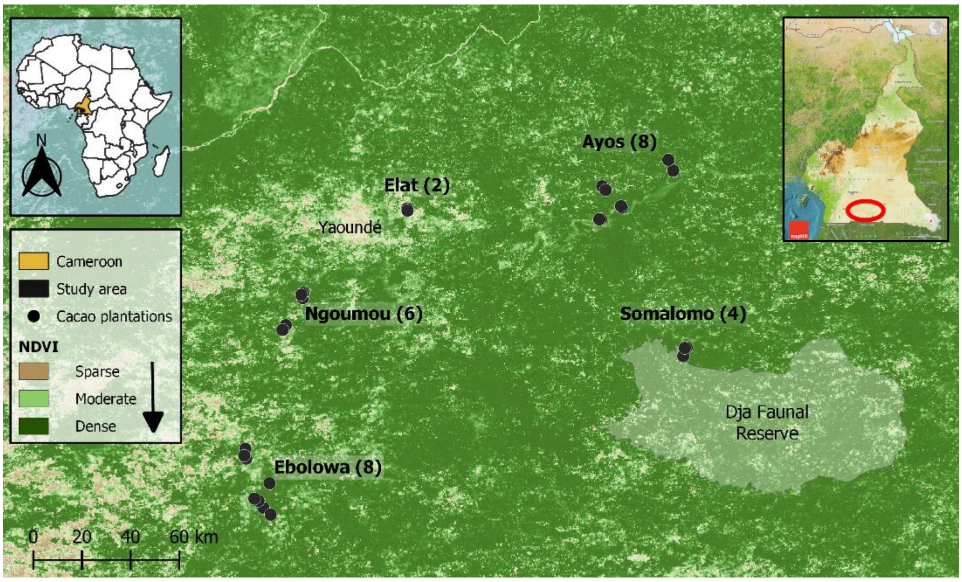

Figure 1 – Map of study sites in Cameroon. Each dot represents a cocoa farm within the 5 landscapes The number of farms visited in each town is shown by the number in brackets after the town name. *Figure 1* is an adaptation from a map created by Biodiversity Initiative researcher, Diogo Ferreira.
NDVI = Normalised Difference Vegetation Index.

Bats were surveyed through the use of mist-netting, of which 20 *Ecotone Nylon Mist Nets* (5 shelves, height 3.0m, length 12.0m) were used at every farm. The nets were placed in the centre of each farm in approximately two transect lines, situated away from the edges of the farms and therefore further away from any potential human disturbances such as roads. The nets were assembled during daylight hours - with the nets remaining closed - in order to collect environmental variables for each farm. At every farm site, a processing station, comprising of a table and chairs, was set up to provide an area to carry out measurements of captured bat individuals.

The nets were opened were opened for an average of 6 hours, between 18:30-00:30 per study night. After opening, nets were checked at regular intervals of 15-20 minutes. Once a bat was caught in the net, the net number, shelf of net and time of capture were recorded, and the bat was removed from the net. The bats were placed in cotton bags and taken to the processing station after the remaining net checks were completed. The bags holding the bats were hung on a line at the station and processed after finishing the subsequent net run.

Numerous measurements were taken for each bat captured. First, bats were weighed whilst in the bags using a *Pesola Spring Scale* (100g & 500g). The weight of the bag was noted once the bat had been removed, and so the weight of the bat could then be calculated. Using an *Ecotone Digital Calliper* (150mm), each bat's forearm, ear length and tail length were measured to the nearest 0.1mm. Several identification keys were used to identify bats to species or genus level (Monadjem et al., 2010; Happold & Happold, 2013; Cakenberghe & Seamark, 2018). The sex of each bat was noted, and their reproductive status was also recorded - pregnant, lactating, carrying young or non-reproductive for females and non-reproductive or the testes size was noted for males. The age of captured bats was assessed by examining the metacarpal- phalangeal joint in the wing and its extent of fusion. By illuminating the joint using a torch beneath a stretched wing, the growth plates of the joint become visible. As bats age, the growth plates undergo fusion and so adult individuals have more rounded joints than juveniles (Felten, 1973). For example, when illuminating the joint, if three bands of light were observed then the bat had not yet undergone fusion and the joints were straight, confirming that the bat was a juvenile. However, if only a single gap was observed in the joint then the joint was more rounded and had undergone fusion, therefore confirming the individual as an adult (Haarsma, 2008). Prior to release, photos of the wing and a wing punch were taken for each bat, to aid in identification purposes. For bats that use echolocation, individuals were recorded using a *Pettersson D1000X Ultrasound Detector* to also assist in species identification confirmation.

At each cocoa farm study site, environmental variables were documented, including GPS coordinates, shade cover (%) and tree composition data. Shade cover indicates the intensity of farm management; traditional shade farms tend to maintain a relatively undamaged forest canopy, whereas full-sun, intensive farms often cut back the canopy to allow sun exposure for the cocoa trees. The percentage of shade cover was assessed by using a camera, with a 'fish-eye' lens, attached to an extendable pole that then took photographs of the canopy from above the height of the cocoa trees (~12 metres). The photographs were taken from the centre of every second net of the transect, giving a distance of 24 metres between each photograph. The photographs were analysed using *ImageJ* software in which the images were converted to a black and white format where the black shade represented the vegetation within the image. The percentage shade cover was then calculated using the black shaded areas and an average of the percentage values extrapolated from all the images was then used to provide a single shade cover value for each farm. Tree composition data was also collected through the identification of trees that shaded the net lines of each cocoa farm.

Forest cover (%) was defined as the tree coverage within a 5km radius of every farm and is an indication of how damaged the landscape is that surrounds each farm. The values for forest cover were derived by uploading the GPS coordinates of the farms into *Google Earth Pro* and subsequently into *QGIS* (version 2.8.3). Using *MODIS Vegetation Continuous Fields (MOD44B)* which provide annual tree cover data (resolution of 250m), the appropriate MODIS layer was uploaded into QGIS and a 5km radius buffer was applied around each farm. An average tree cover percentage was then extracted from the pixels within the buffer. The work for obtaining forest cover values was carried out by Crinan Jarrett, a fellow B.I. researcher.

3.2. Statistical Analysis

The data were initially analysed in *Microsoft Excel* to calculate mean values for bat abundance, species richness and species diversity. Abundance being the number of bat individuals captured per study night and richness as the number of species captured per night. Species diversity was calculated using *Simpson's Index of Diversity* (1 – *D*) in which the index values range from 0-1 - the greater the value, the greater the sample diversity (Magurran & McGill, 2011).

The data were then uploaded and analysed in *R* (version 1.2.5). All required packages were loaded, and the data was organised. Generalised Linear Mixed Models with 'AD Model Builder' (glmmADMB) were used to investigate the effect of numerous variables on bat community assemblages, including shade cover, forest cover and season. The glmmADMBs were used to account for the negative binomial distribution of the data. Negative binomial was used because the count data was over-dispersed and Poisson distribution did not fit. Total abundance, species richness and diversity were used as response variables. The abundance and richness of different feeding guilds were calculated using the 'dplyr' package and the resulting frugivore and insectivore abundance and richness were also used as response variables. There was limited data for nectarivores and carnivores to carry out analysis for these guilds, so we excluded those from analyses. The global model was created first and was the most complex, in which the variables and interactions were included. To account for repeat visits, 'Site' (i.e. farm) was included as a random effect and interactions between shade cover and forest cover, and forest cover and landscape, were included. The global model also contained season, shade cover, forest cover, landscape, and year as explanatory variables and additionally, an offset of the net hours to account for any differences in sampling effort was included. Following a stepwise process of elimination and on inspection of the summary output that provided p-values, the least significant variable was removed from subsequent models.

Likelihood ratio tests (LRTs) were carried out to test for the model of best fit, where the more complex model is compared to the simpler model. Once a significant p-value ($p<0.05$) was obtained, the more complex model of the two in comparison was selected as the model of best fit. This process was carried out for each of the response variables.

3.3. Ethics Statement

During data collection, the welfare of the bats was of highest priority and individuals were handled with the upmost care. Prior to data collection, correct and safe handling techniques for both the bat and handler were revised and were reviewed whenever necessary in the field. Animal care approval was provided by Durham University.

The study sites were located in family-owned cocoa farms and consent was obtained from the owners prior to sampling. Obtaining permission was attained through the collaboration with the International Institute for Tropical Agriculture (IITA) and the Congo Basin Institute (CBI).

No license was required for this study to take place.

4. Results

4.1. Total Captures

4.1.1. Total Abundance

From the 800 captures used for analysis, we recorded 28 species: 66% were insectivores (n =526), 26% were frugivores (n=208) and 8% nectarivores (n =66). The most common species was *Rhinolophus alcyone* (17% of total captures), followed by *Hipposideros ruber* (16% of total captures) and *Epomops franqueti* (15% of total captures). Four bat species were represented by only a single capture.

The best fit model explaining the variation in total abundance of bat individuals included landscape and shade cover as significant variables (LRT: χ^2= 4.742; df = -1, p= 0.02943).

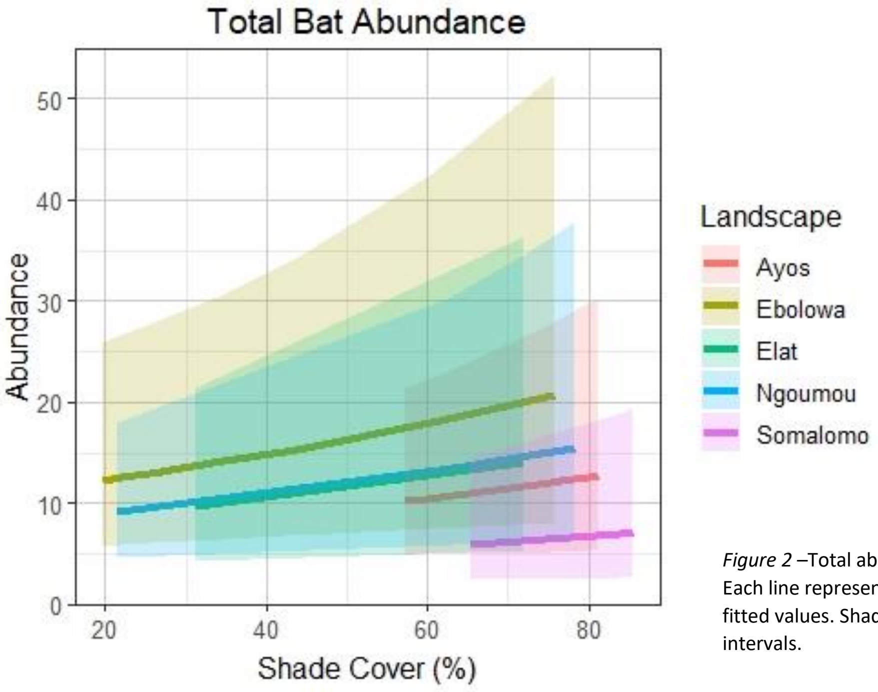

Figure 2 –Total abundance of bats by percent shade cover. Each line represents a landscape and has been plotted using fitted values. Shading corresponds to 95% confidence intervals.

There is a positive relationship between percent shade cover and total abundance (*Figure 2*). In landscapes where a full range of shade cover is available, for example in Ebolowa, bat abundance increases by 43% when shade cover increases from 20% to 76%.

4.1.2. Total Richness

The best fit model contained season, landscape and shade cover as significant variables in explaining the variation in total richness of bat species (LRT: χ^2= 5.364; df = -1, p= 0.02056).

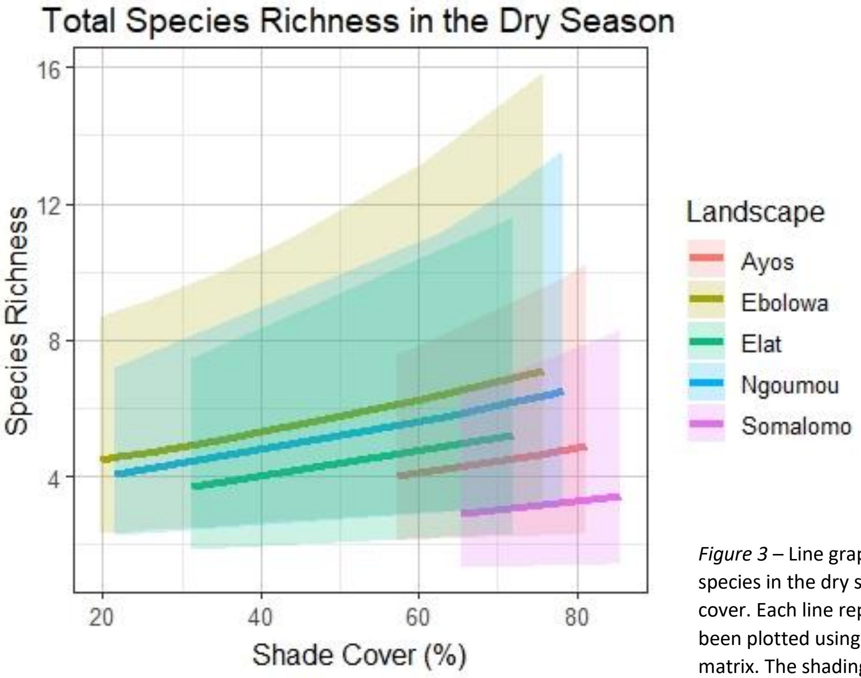

Figure 3 – Line graph showing the total richness of bat species in the dry season across varying percentages of shade cover. Each line represents the 5 study landscapes and has been plotted using fitted values generated from a prediction matrix. The shading corresponds to 95% Confidence Intervals. The graph highlights that at lower shade coverage, species richness is also lower relative to the landscape.

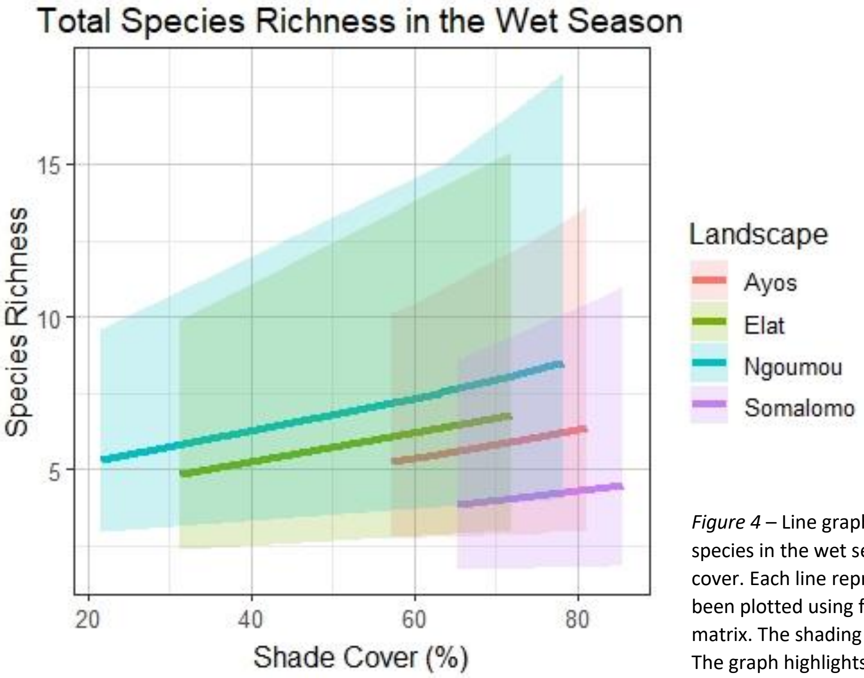

Figure 4 – Line graph showing the total richness of bat species in the wet season across varying percentages of shade cover. Each line represents the 5 study landscapes and has been plotted using fitted values generated from a prediction matrix. The shading corresponds to 95% Confidence Intervals. The graph highlights that at lower shade coverage, species richness is also lower relative to the landscape. No data exists for Ebolowa during the wet season and so is not included in the graph.

The total species richness varied seasonally, with an average increase of 21.8% in richness during the wet season. *Figure 3* highlights the species richness of the total bat captures during the dry season at all 5 landscapes along a varying shade coverage gradient. It can be observed that as shade cover increases, total species richness also increases and is relative to landscape. Ngoumou shows an increase from 21.5% shade cover to 78.3% where the fitted values for species richness rises from 4 species to 7 species.

Figure 4 shows total species richness in the wet season with increasing shade cover. No data were recorded for Ebolowa during the wet season, therefore the farms within this landscape cannot be compared between seasons. The other 4 landscapes show the same trends as the dry season whereby increasing shade cover increases the species richness of the sampled bat community. Species richness is overall higher in the wet season than in the dry season. For example, the cocoa farm at 72% shade in Elat has a species richness of 7 species in the wet season, whereas there are only 5 species found in the same farm during the dry season.

4.1.3. Total Diversity

The null model was the best fitting model for the diversity of total bat captures. No significant variables were associated with explaining the variation in bat diversity. The *Simpson's Index of Diversity* may not be accounting for species at relatively low captures and as diversity indices depend on both species richness and evenness there may be discrepancies due to the species with only one or few captures.

4.2. Insectivores

4.2.1. Insectivore Abundance

Model selection and LRTs determined that the model of best fit contained landscape and shade cover as significant variables in explaining the variation in abundance of insectivorous bat individuals (LRT: χ^2= 27.66; df = -4, p= 1.462 x 10^{-5}).

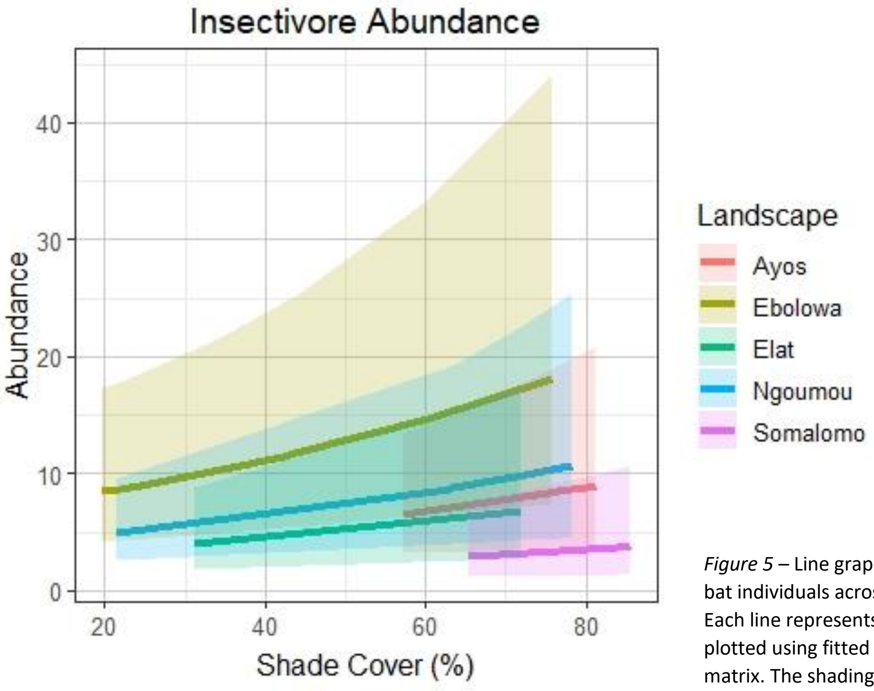

Figure 5 – Line graph showing the abundance of insectivorous bat individuals across varying percentages of shade cover. Each line represents the 5 study landscapes and has been plotted using fitted values generated from a prediction matrix. The shading corresponds to 95% Confidence Intervals. The graph highlights that at lower shade coverage, insectivore abundance is also lower relative to the landscape.

There is a positive relationship between percentage shade cover and abundance of insectivores, with higher abundances being found at higher shade percentages (*Figure 5*) The relationship between abundance and shade cover is relative to landscape and can be observed in the increase in fitted values for insectivore abundance in all landscapes. For example, in Ayos, the abundance of insectivores rises from 7 to 9 bats which coincides with the shade cover increasing from 57.2% to 81.2%.

4.2.1. Insectivore Richness

The best fit model explaining the variation in richness of insectivorous bat species included landscape and shade cover as significant variables (LRT: χ^2= 14.804.; df = -4, p= 0.005125).

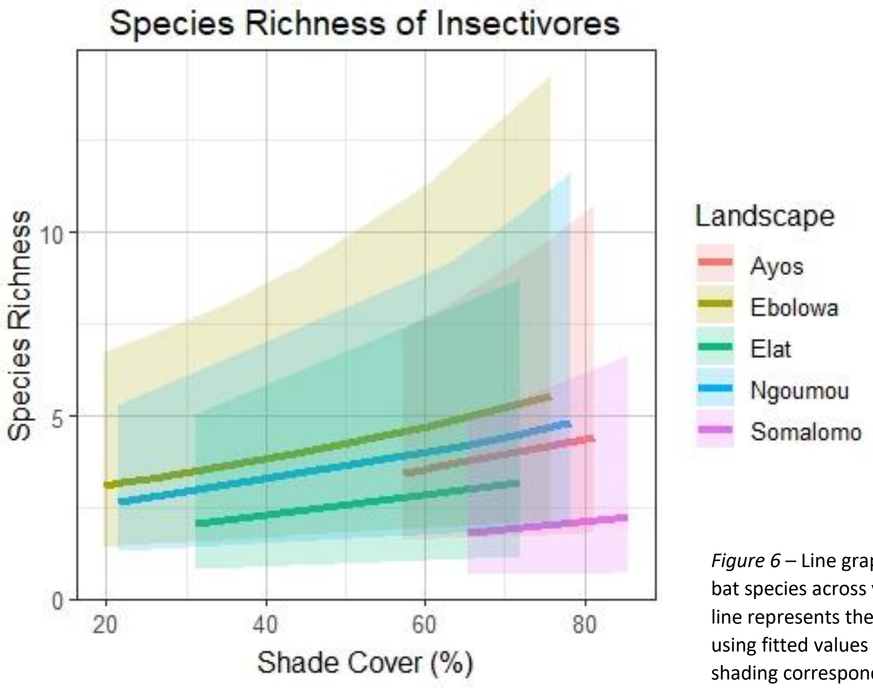

Figure 6 – Line graph showing the richness of insectivorous bat species across varying percentages of shade cover. Each line represents the 5 study landscapes and has been plotted using fitted values generated from a prediction matrix. The shading corresponds to 95% Confidence Intervals. The graph highlights that at lower shade coverage, insectivore richness is also lower relative to the landscape.

The relationship between the richness of insectivorous bat species and shade cover within the various landscapes can be seen in *Figure 6* above. A positive trend exists between shade cover and species richness and is relative to landscape. The linear relationship can be viewed in the increase from 19.6% to 75.7% in Ebolowa where species richness increases from 3 to 6 insectivore species.

4.2.3. Insectivore Diversity

The null model was accepted as the best fitting model for the diversity of insectivore captures. No significant variables were associated with explaining the variation in insectivore diversity.

4.2.4. Insectivore Species Trends

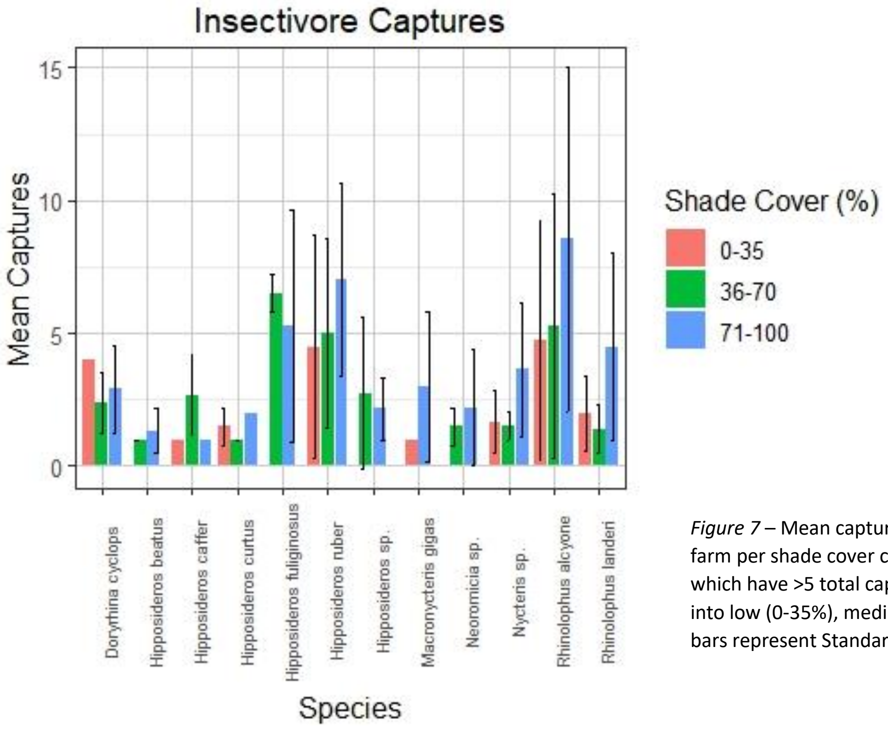

Figure 7 – Mean captures of insectivorous bat species per farm per shade cover category. The graph shows species which have >5 total captures. Shade cover categories divided into low (0-35%), medium (36-70%) and high (71-100%). Error bars represent Standard Error.

Figure 7 highlights the mean captures of insectivorous bat species per farm within three shade cover categories – 0-35% (low), 36-70% (medium) and 71-100% (high). The species represented in *Figure 7* have 5 or more total captures within the dataset; *Figure 12* in *Appendix 8.2* shows all insectivorous bat species, including those with fewer than 5 total captures.

As with the trends seen in the insectivore abundance analysis (*Figure 5*), the mean captures increase as shade cover increases for each species. However, for *Doryrhina cyclops*, the mean captures are at their highest within 0-35% shade. Several species are not recorded in 0-35% shade, including *Neoromicia sp.* and several *Hipposideros* species, most prominent being that of *Hipposideros fuliginosus*. Further analysis using model selection and LRTs indicate that *Hipposideros fuliginosus* may be one of the species driving the trend between insectivores and shade cover as the models yield similar results to the insectivore abundance model (see *Appendix 8.1*).

Rhinolophus species (*R. alcyone* & *R. landeri*) show a considerable increase in mean captures in 71-100% shade when compared to the lower shade cover categories, as does *Nycteris sp.* The additional analysis, summarised in *Appendix 8.1*, does not indicate that *Rhinolophus* species play a major role behind the trend in insectivore abundance, despite the sizeable increase from low and medium shade to high shade cover as seen above (*Figure 7)*.

4.3. Frugivores

4.3.1. Frugivore Abundance

The model of best fit contained landscape and forest cover as significant variables in explaining the variation in the abundance of frugivorous individuals (LRT: $\chi^2= 11.11$; df = -4, p= 0.02536).

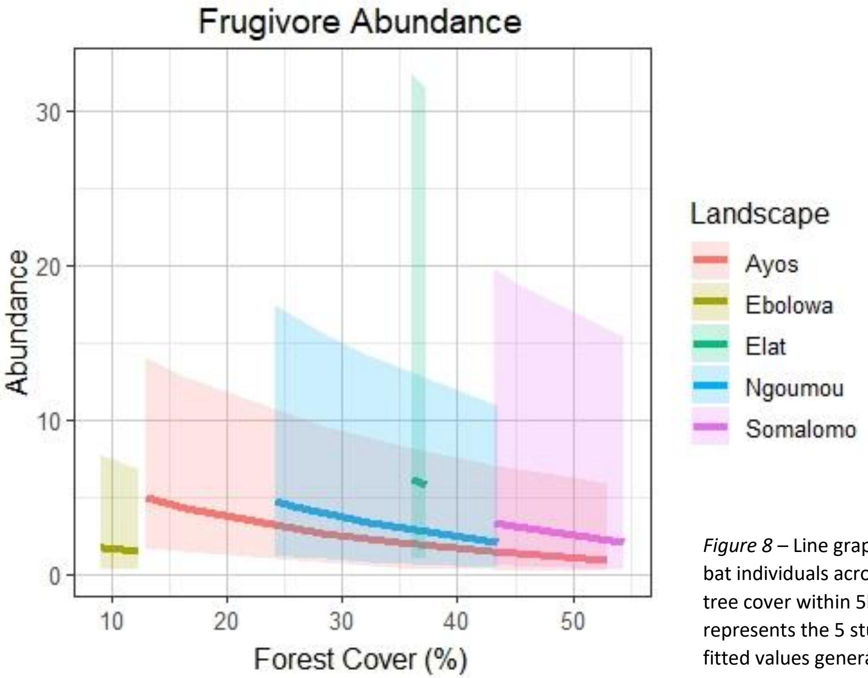

Figure 8 – Line graph showing the abundance of frugivorous bat individuals across varying percentages of forest cover (% tree cover within 5km radius of each farm). Each line represents the 5 study landscapes and has been plotted using fitted values generated from a prediction matrix. The shading corresponds to 95% Confidence Intervals. The graph highlights that at higher forest coverage, frugivore abundance decreases relative to landscape

Figure 8 highlights the abundance of frugivorous bat individuals within the five landscapes in varying forest cover. Forest cover is the percentage of tree coverage within a 5km radius of each cocoa farm. There is a negative relationship between frugivore abundance and forest cover, relative to landscape, where a rise in percentage cover results in reduced abundance. For example, in Ayos the fitted values for the abundance of frugivores decreases from 5 at 13% forest coverage to 1 at 53.1% cover.

4.3.2. Frugivore Richness

Model selection and LRTs showed that the model of best fit contained season, landscape and shade cover as significant variables in explaining the variation in the richness of frugivorous bat species (LRT: χ^2= 4.0522; df = -1, p= 0.04411).

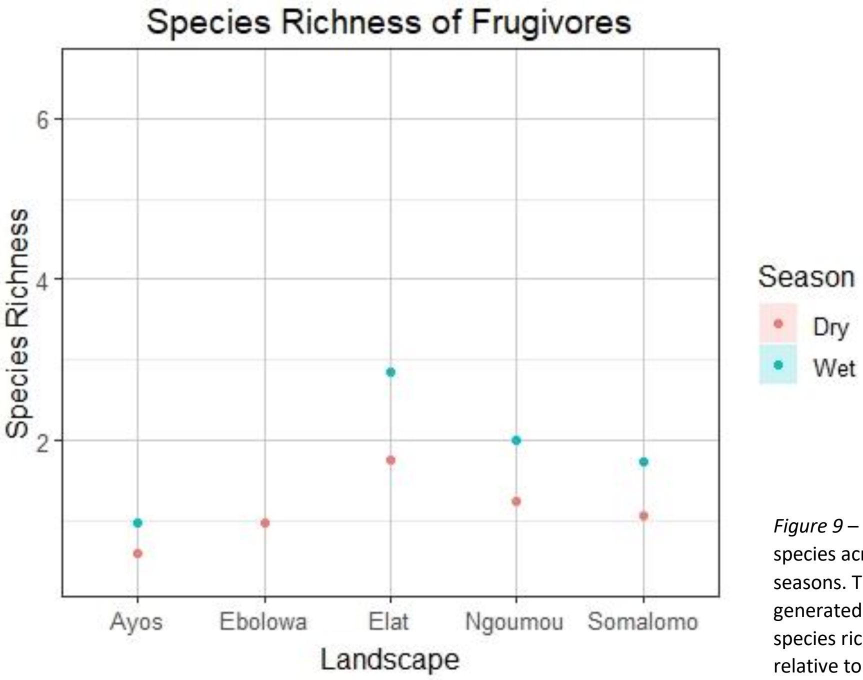

Figure 9 – Scatterplot showing the richness of frugivorous bat species across the 5 study landscapes in the wet and dry seasons. The graph has been plotted using fitted values generated from a prediction matrix. The graph shows that the species richness of frugivores increases during the wet season relative to landscape.

The species richness of frugivores varied seasonally, with an increase in richness during the wet season in all landscapes except Ebolowa, where data is not available. *Figure 9* highlights the richness of frugivorous bat captures during both the wet and dry seasons. It can be observed that species richness increases from the dry to the wet season and is relative to landscape. The points on the graph are the fitted values for richness and the greatest increase between seasons can be observed in Elat where the number of species increases from 1.8 to 2.9.

4.3.3.Frugivore Diversity

The null model was accepted as the best fitting model for the diversity of frugivore captures. No significant variables were associated with explaining the variation in frugivore diversity.

4.3.4. Frugivore Species Trends

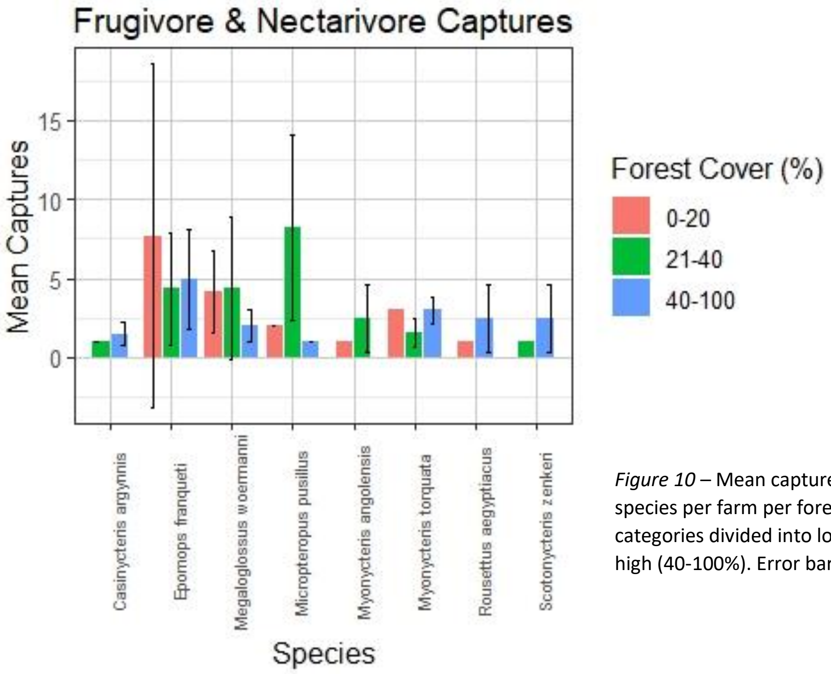

Figure 10 – Mean captures of frugivorous and nectivorous bat species per farm per forest cover category. Forest cover categories divided into low (0-20%), medium (21-40%) and high (40-100%). Error bars represent Standard Error.

Figure 10 represents the mean captures per farm of all frugivorous species and the nectarivore, *Megaloglossus woermanni*, within three forest cover categories – 0-20% (low), 21-40% (medium) and 40-100% (high). The most commonly captured frugivore species, *Epomops franqueti* (n=123) which represents 59% of the frugivore captures, appears to be one of the species responsible for the trends in frugivore abundance and forest cover. *E. franqueti* shows an increase in mean captures when forest cover is low (0-20%) and further analysis using LRTs and model selection find that this species produces the same results as the frugivore abundance model (refer to *Appendix 8.1*). Additionally, the comparison of *Figure 8* (Section 4.3.1) and *Figure 11*, which can be found in *Appendix 8.2*, show that the trends found between forest cover and frugivore abundance, compared to that of forest cover and *E. franqueti* abundance follow the same negative linear relationship.

Micropteropus pusillus shows a notable increase in mean captures within 21-40% forest cover when compared to the other forest cover categories. *M. pusillus* only has 39 captures so further analysis using LRTs could not be carried out for this species alone.

The nectarivore, *M. woermanni*, was also included in *Figure 10* and shows a decrease in mean captures when forest cover increases above 40%. There is minimal variation between mean captures and low and medium forest cover for *M. woermanni*.

5. Discussion

In this study we determined that farm management, using percentage shade cover as a proxy, has a negative effect on bat abundance and richness of the total sampled community and insectivorous bat species but has no effect for frugivorous bat species. Seasonality had an effect on frugivorous bat species, with greater abundance and richness during the wet season. Additionally, the landscape of where the farms (i.e. village area) were located was a significant variable for all abundance and richness models. We found no effect of farm management and season on the diversity of the sampled bat communities.

Our findings are of particular importance given the current situation within Cameroon, and other West African nations, of increasing agricultural intensification. The results of this study highlight the need for cocoa landscapes to be managed at lower intensities in which shade canopies are preserved and as much of the natural forest is maintained as possible, thus supporting more abundant and species rich bat communities.

5.1. Farm Management & Shade Cover

Shade plays a significant role in cocoa farming and can indicate how intensively a farm is managed, with high intensity farms generally having minimal shade cover and low intensity farms with higher shade coverage. Following this, our sampled farms with higher shade cover suggest that they are of low intensity and possess a greater complexity of shade canopy. The abundance and richness of insectivorous bat species were negatively affected by reduced shade cover (i.e. higher intensity of farm management), with further analysis showing that species such as *Hipposideros fuliginosus* may be one of the focal species responsible for these findings. Insectivores, such as *H. fuliginosus*, feed on a diet of primarily large flying insects including moths and beetles which have been shown to reduce in species richness, diversity, and evenness in cocoa farms with reduced strata of shade trees (Toana et al., 2014). The stratification of a habitat refers to the layering of vegetation and so the strata of a landscape can be indicative of cocoa farm management – more strata layers infer a lower intensity farm. In Toana et al.'s study, the number of arthropods significantly decreased when the strata of the shade trees decreased from two layers of shade canopy, comprising of both forest and fruit trees, to one strata layer of planted Candlenut trees (*Aleurites moluccanus*). The abundance of arthropods decreased further in full-sun cocoa farms with no shade, as did arthropod richness, diversity, and evenness. A reduction in arthropods within cocoa landscapes will have consequences for insectivorous bats that rely on a variety of insects to gain their complete nutritional requirements (Altringham, 2011). Reduced arthropod availability coincides with reduced insectivorous bat abundance and species richness as the full-sun cocoa farms will be unable to provide enough food for high numbers of bats and will also be unable to provide the variety of arthropod species that some bat species consume. Therefore, cocoa farms with little, or no shade canopies may be unable to support sufficient arthropod populations and so are unable to support abundant and species rich bat communities which ultimately indicates that they cannot maintain ecosystem equilibrium (Perfecto, 1996).

On the other hand, cocoa farms and agroforests that have complex shade canopies can support a wealth of food sources for both insectivores and frugivores. Often within shaded cocoa landscapes, fruit trees are planted for additional income or personal use for the farmers and these are often plants that provide fleshy fruits or nectar which are appealing to bats, for example *Citrus* spp. (Harvey & González Villalobos, 2007). Within agroforests, native trees are also allowed to regenerate over time and species such as those in the *Ficus* and *Piper* genera are also major food sources to frugivorous bats (Fleming, 1991). Insects are also abundant within cocoa agroforests as the floristic diversity and structure of the habitat provides a suitable environment for a diverse arthropod community.

The results from the present study suggest that since shade did not significantly affect the abundance and richness of frugivorous species, the reduction in insectivorous bat species with reduced shade cover is more likely linked to changes in food availability and dietary requirements rather than other factors such as roost availability or possible increased predation risks by raptors and owls (Fenton et al., 1994). The diversity and abundance of arthropods is influenced by shade cover which subsequently impacts the assemblage of bats that can be supported whereas fruit availability has not been shown to be directly associated to reductions in shade cover of the cocoa farms (Toana et al., 2014; Marino & Landis, 1996).

At higher shade coverage, there are a greater number of bats and species of bats captured within these landscapes. High levels of bat abundance and species richness within cocoa agroforestry landscapes can be attributed to various factors. Although when compared to the natural forest, cocoa agroforests have reduced plant diversity and lower tree density, they maintain structurally complex canopies. A diverse canopy provides essential roosting sites and feeding perches for bats and therefore can support an extensive range of species, including forest-dependent species (Estrada et al., 1997). The canopy of agroforests is simplified and thus more open than the comparative natural forest and it is thought that this may aid bat flight, resulting in greater numbers of bats being captured within these landscapes (Faria et al., 2006). Insectivorous bats require greater manoeuvrability in their flight patterns in comparison to frugivorous species due to their feeding habitats and so a relatively diverse but simplified canopy may be beneficial to insectivorous bat species (Vaughan, 1970). Several *Hipposideros* species were captured more frequently in medium shade cover (36-70%) than the other shade categories, including *H. fuliginosus* and *H. caffer.* Medium shade cover may be optimal to the flight patterns of such species as a reduction in dense vegetation, such as that found in high shade cover (71-100%), may enhance foraging techniques, including aerial captures and surface gleaning (Wright, 2009). Another species which may be aided by reduced vegetation and shade is *Doryrhina cyclops*, which had its highest number of captures in low shade cover (0-35%). Unlike other insectivorous species, *D. cyclops* seems to benefit from reduced shade cover which may be attributed to its fast flight, but poor manoeuvrability and so reduced shade and clutter may also assist in its flight patterns (Happold & Happold, 2013).

Cocoa agroforestry maintains relatively biodiverse and complex shade canopies that have been shown to host abundant, rich, and diverse communities of various taxa, including arthropods (Perfecto, 1996), birds (Greenberg et al., 1997) and bats (Estrada et al., 1993). Studies of bats within cocoa agroforests have found that agroforestry landscapes are capable of supporting equally species rich bat fauna as natural forest or at least a vast majority of the existing forest community. For example, Faria et al. (2006) found that in cocoa agroforests in Brazil the bat communities were richer and more diverse than the surrounding forests, whereas Estrada & Coates-Estrada (2001) showed that in Mexico, 71% of the bat species from the natural forest were supported in agroforest landscapes. Studies such as these imply that bats can benefit from the habitats and resources available within cocoa agroforests and thus it can be assumed that these habitats present numerous opportunities for bat conservation within agricultural landscapes.

5.2. Landscape & Forest Cover

Landscape was a significant variable for explaining the variation in the total abundance and richness of the sampled bat community, as well as for insectivore and frugivore abundance and richness, independently. The five landscapes - Ayos, Ebolowa, Elat, Ngoumou & Somalomo - varied in numerous conditions such as the size area of the town, degree of urbanisation, the size of human population, and the proximity to natural forested areas and environmental features such as rivers and waterways. Additionally, the cocoa farms varied in distance from the towns and so human activity around the farms also varied. In terms of bats, the landscape of the farms may influence their abundance and species richness through human disturbance and resulting factors such as roost availability, food availability and the amount of agricultural land and forested land within the area.

The surrounding forest cover of the cocoa farms was also considered in the present study, where the percentage of forest coverage within a 5km radius was investigated. Forest cover was found to negatively affect the abundance of frugivores and from further analysis it is thought that the most commonly captured frugivore species, *Epomops franqueti*, is one of the species that is predominantly influenced by the percentage of tree cover within the surrounding 5km (*Appendix 8.1* & *8.2*). *E. franqueti* is one of the larger frugivorous bat species in Cameroon and studies show that unlike other frugivorous bat species, it is rare for them to travel extensive distances from their roost site meaning that they generally feed and live within the one area (Adeyanju et al., 2019). However, *E. franqueti* travels further distances from their roosting sites when there is human disturbance within the area (Amponsah-Mensah, 2017). Our findings show that as forest coverage within 5km of the cocoa farms increased, the abundance of captured *E. franqueti* decreased which could be indicative of this species remaining within the area of their roost in more forested areas than in cleared agricultural landscapes. Bats such as *E. franqueti* have particular roosting requirements, such as tree height and canopy coverage, so a more diverse and connected landscape will offer more optimal roosting conditions for these bats compared to cocoa farms (Adeyanju et al., 2019).

Another frugivorous species, *Micropteropus pusillus,* has prominent trends with forest cover, with a marked increase in mean captures in medium forest cover (21-40%). *M. pusillus* is known to roost in dense vegetation, thereby a higher forest coverage would indicate a more preferential habitat for roosts (Jones, 1972). *M. pusillus* feeds on fruits which can be commonly found in cocoa farms, including bananas and fruits from the *Ficus* genus, it also prefers to forage at low heights (Marshall & McWilliam, 1982; Owen-Ashley & Wilson, 1988). The increase in mean captures of *M. pusillus* at farms where the surrounding forest cover is 21-40% is possibly the result of the species roosting within the forested areas and then utilising the fruit trees which are frequently planted in cocoa farms. Additionally, cocoa farms often have a lower canopy height than that of the surrounding forest, and so the cocoa farms provide ideal foraging conditions for *M. pusillus*. The medium forest cover may result in an increase of captures of M. pusillus as at low forest coverage (0-20%) the surrounding area may not be able to support the species roosting requirements and at high forest coverage (40-100%) the environment may support a greater diversity of plant species, including preferred fruits and flowers.

The reduced abundance of frugivores and of *E. franqueti* in cocoa farms with higher percentages of forest cover, suggest that there are less bats using the cocoa farms for feeding sites or flight paths. Higher forest cover has a greater amount of tree coverage and lower volumes of cleared land, implying that there is more natural forest and/or low intensity shaded farms within the area. The increased availability of tree coverage and likely the greater biodiversity of vegetation can support a healthy community of bats and so, bat species are less inclined to use cocoa landscapes where fruit trees are less abundant or diverse. However, some bat species, such as *M. pusillus*, may in fact benefit from the planted fruit trees within cocoa farms and the lower canopy heights, providing that the surrounding forest cover can support their natural roosting sites.

Forest cover was also found to significantly affect some insectivorous bat species on additional investigation (*Appendix 8.1*). For example, *Hipposideros* species, both common and rare, had a positive relationship with forest cover and increased in abundance in farms with greater surrounding forest cover. *Figure 13* in *Appendix 8.2* highlights that *Hipposideros fuliginosus* shows large increases in mean captures when forest cover increases. An increase in forest cover may increase connectivity between cocoa farms and natural forest and so this could allow bats to travel between the two landscape types and use both environments for feeding and roosting. *Hipposideros* species are less particular about their roosting sites, in comparison to *E. franqueti*, and will use hollow trees, caves and old buildings, which means that they are not as restricted to roosting in specific conditions (Wright, 2009).

However, *Figure 13* also indicates that the only *Hipposideros* species to not follow a positive trend with forest cover is *Hipposideros ruber. H.ruber* decreases in captures when forest cover increases, with the highest number of this species being captured within farms that have a surrounding 0-20% forest cover. Among insectivorous bats it is rare to show preference for a single foraging habitat type and often it is the availability and distribution of its prey which determines where a bat focuses its foraging (Nkrumah et al., 2016). The use of a certain habitat type by insectivorous bats is therefore strongly liked to prey availability (Kusch et al., 2004). Thus, cocoa agroforest landscapes that provide a complex habitat, which increase insect abundance and diversity, in areas where the surrounding forest cover is low, will be attractive to bat species such as *H. ruber. H. ruber* has also shown to prefer highly cluttered environments to forage in and agroforestry landscapes may support this preference when surrounding forest cover is low (Shnitzler & Kalko, 2001). The differences between species within the *Hipposideros* genus indicate the importance of carrying out more species-specific research on how different species are influenced by environmental changes such as forest clearances and farm intensification.

Studying the surrounding forest coverage of the cocoa landscapes is important in understanding the associated bat assemblages, in particular the abundance of species such as *E. franqueti* and *H. ruber* where a negative relationship exists between abundance and forest cover. Reducing the forest coverage of an area may result in more bats using agricultural landscapes for feeding and roosting which could lead to a crowding effect and increased inter and intra-specific competition, which ultimately could result in reduced fecundity and the breakdown of populations (Estrada et al., 1993).

5.3. Season

Our study aimed to find out if seasonality had an effect on bat abundance, richness or diversity and the results partly conformed to the prediction where species richness was found to increase during the wet season for total captures and frugivores. Further investigation using model selection and LRTs indicate that the abundance of rarer species with the inclusion of the nectarivore *Megaloglossus woermanni*, were also positively affected by season, with an increase in relative abundance in the wet season (see *Appendix 8.1*).

In the tropics, seasonality is defined by differences in precipitation and it has been shown that variations in the timing and length of precipitation can alter the phenology of flowering, fruiting, and leaf production of tropical plants (Janzen, 1967; MacArthur, 1972). Fruit abundance generally peaks when rainfall is at its peak during the wet season, this results in there being fewer fruits available for frugivorous species in the dry season (Smythe, 1986). The results of the present study find that bat species richness and frugivore richness increases during the wet season which is likely a response to the seasonal fluctuations in fruit availability and abundance. Within natural forest landscapes, the effects of the dry season are likely buffered due to high shade cover, dense vegetation and efficient soil binding and cycling (Beer et al., 1997). In comparison, agroforests, although structurally complex, may not be as efficient in providing the same protection from seasonal changes that occur in the dry season, such as limited rainfall and increased heat stress (Lin, 2007). Therefore, bats may be more inclined to use natural forest habitats as opposed to cocoa landscapes, where conditions during the dry season are not as harsh.

Cocoa agroforests often contain planted and natural trees that produce fruits or flowers that are attractive to bats. Many of these plant genera such as *Ficus*, peak in fruiting during the wet season and so various frugivorous bat species can be found within cocoa landscapes. In contrast, during the dry season there are fewer fruits available to frugivores so there is a reduction in the species captured within cocoa landscapes as many bat species will be sourcing their food elsewhere (Ramos-Pereira et al., 2010). Many *Ficus* trees tend to have a clustered distribution and produce large amounts of fruit at different times to each other, where fruit is only available for relatively few days. The fruiting pattern of plants such as *Ficus*, therefore could cause influxes in the number of bats and number of species captured within cocoa landscapes during fruiting peaks (Klingbeil & Willig, 2010).

The rarer captured frugivorous species, with the addition of the nectivorous bat *Megaloglossus woermanni,* are significantly affected by seasonality, increasing in abundance in the wet season. An increase in abundance may be related to the increased availability of more fruit and flower types within cocoa farms that can support a greater number of bat species and bat numbers than in the dry season. Species that are rarely captured may become more prevalent during the wet season as they may be restricted to areas where food is more readily available in the dry season. However, with a greater abundance and diversity of food in the wet season, the rare species may utilise the increased food accessibility in cocoa landscapes.

Additional analysis, using LRTs, found no seasonal effects for insectivorous bat species (*Appendix 8.1*). Seasonality may not have had an effect on insectivorous bats as insect abundance and/or diversity may not fluctuate to the same extent as fruit abundance. Whilst fruiting patterns show strong peaks within the wet season it is possible that the seasonal variations in insect abundance are less pronounced within cocoa landscapes. During the dry season when insect availability is reduced and more dispersed, it is thought that insectivorous bats travel greater distances and exploit additional habitat types to meet their nutritional needs (Klingbeil & Willig, 2010). Therefore, the abundance and richness of insectivorous bat species may not show seasonal changes in cocoa landscapes as bats will still use the farms for foraging and flight paths but may spend less time within these environments when food availability and distribution is reduced.

5.4. Conclusion

Farm management, using shade cover as a proxy, does indeed affect bat community assemblages, specifically the abundance and richness of insectivorous bat species. A reduction in shade cover, and therefore an increase in management intensity, results in lower total and insectivorous bat abundance and species richness. Secondly, we aimed to find out if seasonality had an effect on the sampled bat communities within cocoa farms to which we found there was a significant relationship between species richness and season. Total species richness and frugivorous richness increased during the wet season. Additionally, forest cover, i.e. the percentage of tree cover within a 5km radius of each cocoa farm, was also a significant variable in explaining variation in frugivore abundance whereby increasing forest cover resulted in a reduced abundance of frugivores in the cocoa farms.

The final aim of the present study was to discover which species or groups of species were driving the trends presented in the total captures, insectivore and frugivore abundance and richness models. Various different conclusions were drawn from this additional analysis, including species such as *Hipposideros fuliginosus* being prominent in shade cover trends, *E. franqueti* being a principal species in forest cover trends and rare frugivore captures, including *Megaloglossus woermanni,* being key in seasonal trends in species richness.

This investigation is one of the first studies to show that cocoa farm management has an effect on bat community assemblages in West Africa and therefore the findings of this study are important in expanding on the limited research and knowledge that exists for bats and cocoa farms in Africa. The increasing global demands for cocoa and resulting rising pressure to intensify cocoa practices are threatening biodiversity of both flora and fauna, particularly in West Africa. The results produced by this study emphasise the need for cocoa agroforests and farms managed at lower intensities in comparison to full-sun monocultures. By promoting cocoa agroforestry and the practise of preserving shade canopies and natural forest, both the biodiversity of the cocoa landscape and of the associated wildlife including bats can be conserved, and the optimal cocoa yields can still be obtained.

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8. Appendices

8.1. Summary of Models of Best Fit

(Y) = trend exists; (+) = positive trend; (-) = negative trend; (N) = no trend

Model	LRT Output	Landscape	Shade	Forest Cover	Season	Landscape* Forest Cover
Total abundance	χ^2= 4.742; df = -1, p= 0.02943	Y	+	N	N	N
Total richness	χ^2= 5.364; df = -1, p= 0.02056	Y	+	N	+	N
Insectivore abundance	χ^2= 27.66; df = -4, p= 1.462×10^{-5}	Y	+	N	N	N
Insectivore richness	χ^2= 14.80.; df = -4, p= 0.005125	Y	+	N	N	N
Frugivore abundance	χ^2= 11.11; df = -4, p= 0.02536	Y	N	-	N	N
Frugivore richness	χ^2= 4.0522; df = -1, p= 0.04411	Y	N	N	+	N
H.ruber & R.alcyone	χ^2= 10.864; df = -3, p= 0.01248	Y	N	N	N	N
H.ruber & H.fuliginosus	χ^2= 10.634; df = -3 p= 0.01388	Y	+	+	N	N
All Hipposideros species	χ^2= 10.382 ; df = -4 p= 0.03446	Y	N	+	N	Y
All insectivores (excluding H.ruber & R.alcyone)	χ^2= 7.034; df = -1 p= 0.007998	N	+	N	N	N
All insectivores (excluding H.ruber)	χ^2= 4.196; df = -1 p= 0.04052	Y	+	N	N	N
All insectivores (excluding R.alcyone)	χ^2= 9.788; df = -1 p= 0.001757	Y	+	N	N	N
D.cyclops, Nycteris sp., & H.fuliginosus	χ^2= 5.225; df = -1 p= 0.02226	Y	+	+	N	N
D.cyclops & Nycteris sp.	-	N	N	N	N	N
Rare insectivore species (25 captures or less)	-	N	N	N	N	N
Rare species (25 captures or less)	χ^2= 10.155; df = -4 p= 0.0379	Y	N	+	+	Y
E.franqueti	χ^2= 9.305; df = -1 p= 0.002285	Y	N	-	N	N
All frugivores & M.woermanni (excluding E.franqueti)	χ^2= 4.6792; df = -1 p= 0.03053	Y	N	N	+	N
All frugivores (excluding E.franqueti)	χ^2= 14.658; df = -4 p= 0.005465	Y	N	N	N	N

Table 1 - Table summarising the significant variables of the abundance models of best fit for various species and groups of species. The table also includes the total abundance and richness models, as well as the insectivore and frugivore abundance and richness models which can be seen in detail in Section 4 (Results).

8.2. Additional Graphs

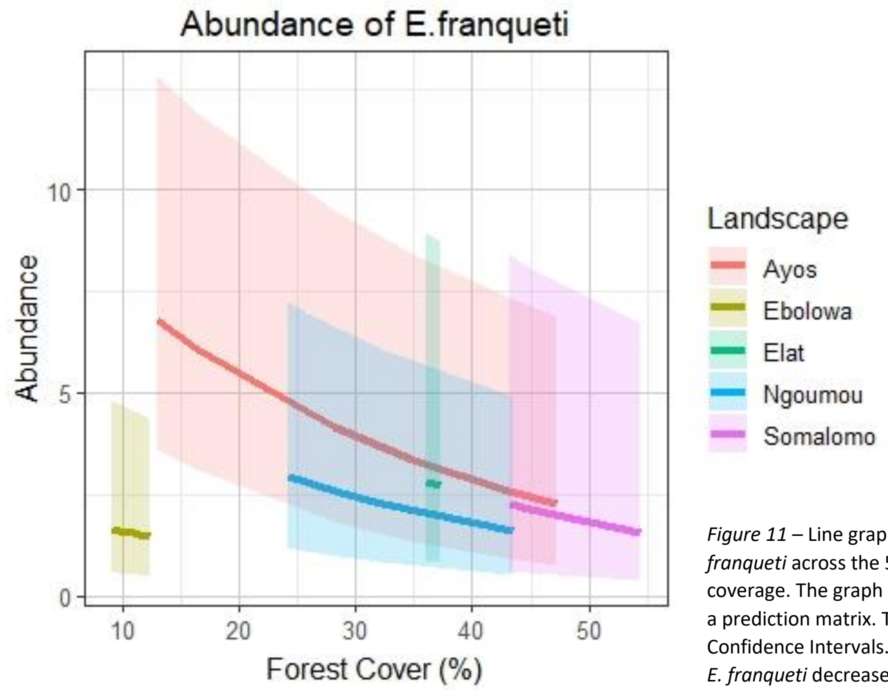

Figure 11 – Line graph showing the abundance of *Epomops franqueti* across the 5 study landscapes in increasing forest coverage. The graph has been plotted using fitted values from a prediction matrix. The shading corresponds to 95% Confidence Intervals. The graph shows that the abundance of *E. franqueti* decreases as forest cover increases.

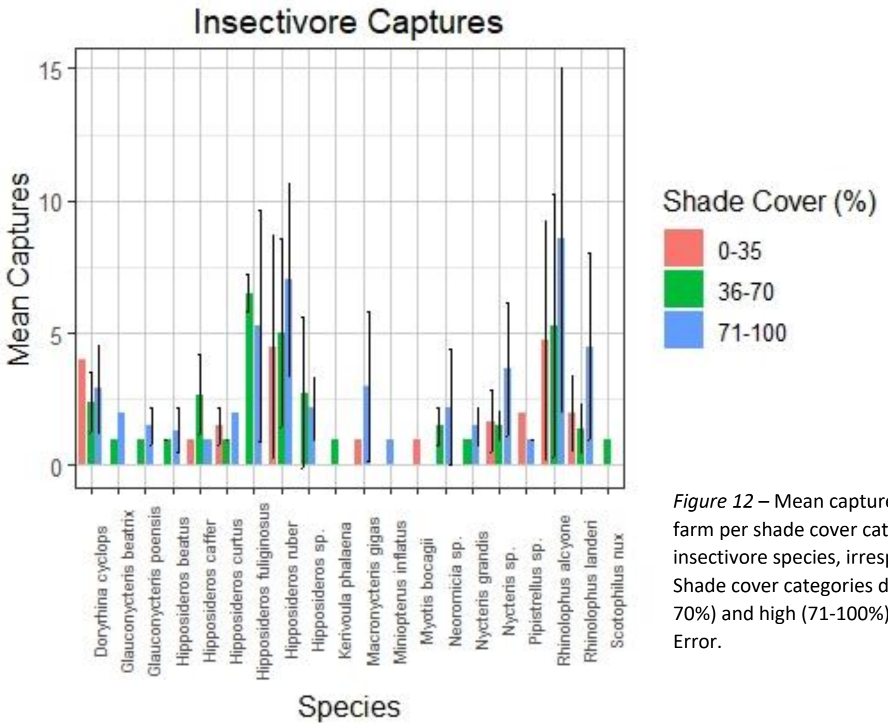

Figure 12 – Mean captures of insectivorous bat species per farm per shade cover category. The graph shows all insectivore species, irrespective of number of total captures. Shade cover categories divided into low (0-35%), medium (36-70%) and high (71-100%). Error bars represent Standard Error.

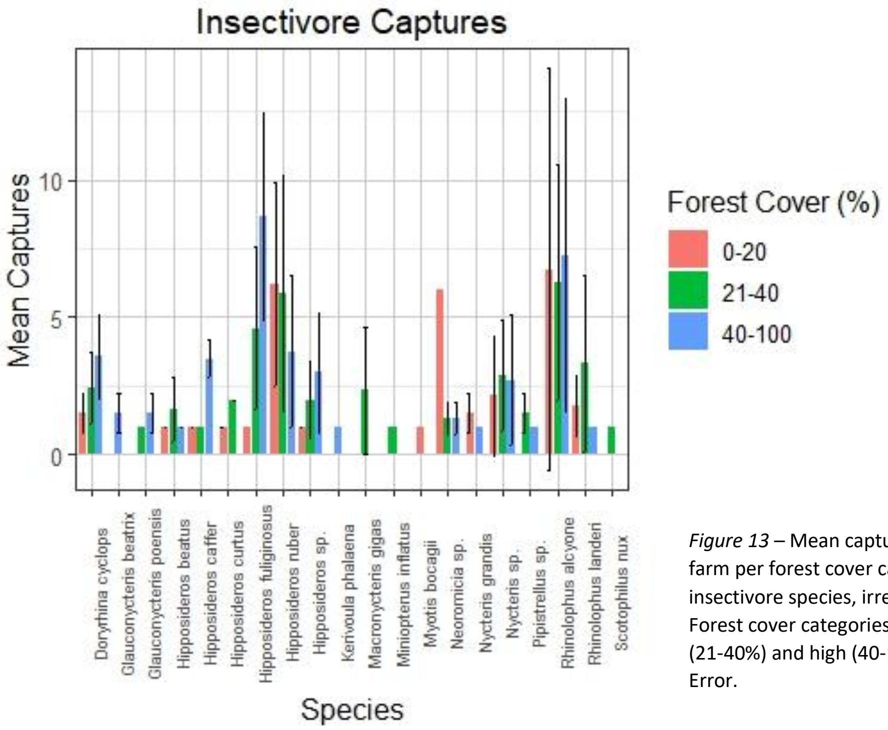

Figure 13 – Mean captures of insectivorous bat species per farm per forest cover category. The graph shows all insectivore species, irrespective of number of total captures. Forest cover categories divided into low (0-20%), medium (21-40%) and high (40-100%). Error bars represent Standard Error.

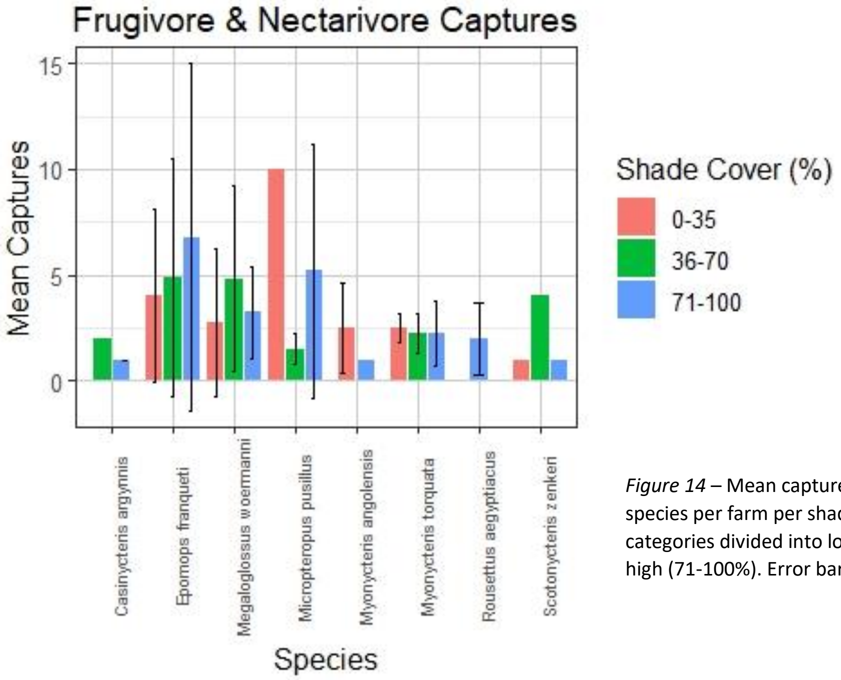

Figure 14 – Mean captures of frugivorous and nectivorous bat species per farm per shade cover category. Shade cover categories divided into low (0-35%), medium (36-70%) and high (71-100%). Error bars represent Standard Error.