Bat species richness and modelled distribution of bats in Ghana

by

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Disclaimer

This is not a traditional Master's dissertation with an outline of a single introduction, methods, results and discussion sections. Instead, the format of this dissertation has research chapters each having an introduction, methods, results, discussion and conclusion sections. The intention behind the said format is to submit each research chapter to scientific journals for publishing. There is also repetition within the thesis due to cross referencing of results between chapters.

Declaration

I, Emily N. Kudze declare that the work presented in this thesis, which I hereby submit for the degree Master of Science at the University of Pretoria, is my own work and has never been submitted for any degree or examination at any other tertiary institution, and that all the sources I have used or quoted have been acknowledged by complete reference.

Emily N. Kudze

Signature ________________________

Date ___________________________

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Summary

Bats are amongst the most diverse mammal group with over 1400 species; however, they are also understudied. Ghana, in West Africa, forms part of the Guinean Forest biodiversity hotspot which makes the country a diverse area. There has been little information about bat diversity, richness and distribution in Ghana for the last known publication on this topic was in Grubb et al. (1998). Forests are being degraded and depleted by the increase in human population and anthropogenic disturbances, such as climate and land-use changes. Wild stretches of forests are being converted to agricultural lands to help feed the ever-growing human population and to assist developing nations, like Ghana, sustain their economies. In the process animals, like bats, which are known to assist in seed dispersal, pollination and biological pest control, are being disturbed in their natural habitats.

This study investigated which of the agro-ecological zones in Ghana had the highest species richness and diversity (Alpha and Beta-diversity), and to determine which variables (climate or land-use) have influenced the distribution of bats in Ghana, using species distribution modelling (SDM). This study also aimed to identify which agro-ecological zone had a high modelled species richness.

The results showed that the Moist Semi-deciduous biotic zone was the most diverse in bat species. The Bray-Curtis dissimilarity index between agro-ecological zones, detailed that the Moist Semi-deciduous biotic zone is dissimilar to all the other agro-ecological zones, with high levels of richness. The SDM results also revealed that the land-use variable contributed to 31of the 42 models and determined that the modelled species richness estimate was highest in the Moist Semi-deciduous agro-ecological zone in Ghana.

Findings from this research point to the Moist Semi-deciduous zone of Ghana requiring further investigation, as the agro-ecological zone was predicted to have high species richness and diversity, thereby, indicating a high species richness. Agricultural sites and degraded forests

within the Moist Semi-deciduous zone of Ghana can likely have extensive effects on bat communities, therefore, mitigation of this land transformation to boost the regeneration of degraded forests, as well as assist in biological pest control. This would prevent the use of harmful pesticides that pose a threat, not only to the survival of bat species, but other wildlife as well.

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Chapter 1: General Introduction

The relationship between organisms and their distributional ranges has been a topic of discussion in ecology for decades (Diamond et al. 1976, Simberloff and Abele 1976, Simberloff et al. 1992, Boecklen 1997, Brashares et al. 2001). Any animal's environment can be categorized on two scales, namely, the macro-environment and micro-environment (Hogan et al. 2018). In an analogy by Hogan et al. (2018) and Rosenbaum et al. (2010), the micro-environment is likened to an open cage an animal dwells in, whereas the macro-environment is the housing space where the cage, with the animal inside, is kept. In other words, a micro-environment is the area immediately surrounding an animal or its primary living area (Rosenbaum et al. 2010, Hogan et al. 2018). An animal's environment has all the required resources necessary for their survival (Hogan et al. 2018). Destructive changes to animals' primary living areas can result in their dispersals or even extinction overtime (Corlett 2013, Hogan et al. 2018). Assessing species responses to variation in their macro- and micro-environments, can inform on the adaptability and survival of specific species and allow for sound management decisions to be made regarding any affected species (Guil et al. 2009). The environmental variables that can influence species distribution and extinction, hence, must be investigated in order to understand the probability of species' survival (Guisan and Zimmermann 2000). Evaluating environmental changes, such as climate change, land-use alterations and impact on species distribution, thus, can help identify priority areas (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Guisan et al. 2013).

According to Hogg and Wall (2011), transformations in the macro-environments of species are driven by larger-scale disturbances, such as temperature and land-use change; these have significant effects on species richness and diversity. For example, a study by Midgley et al.(2003) found that most Proteaceae species experience range contractions by range elimination; this shift in ranges was either related to land-use change or climate change. In micro environments, however, the distribution of species is driven by abiotic factors, such as temperature range and changes in light intensity (Hogg and Wall 2011). The pertinent question, therefore, is how organisms cope with the variation in their macro-environment (for example, climate and land-use changes), and micro-environment (e.g., moisture and coverage).

Natural factors, such as climate change throughout the years, have caused extreme seasonal changes and have caused range shifts in animal species (Svenning and Skov 2007). For example, small mammals migrate from unfavourable and unsuitable habitats to better habitats in response to long-term effects of change in climate (Brown and Yoder 2015). Extreme weather conditions such as wildfires have had an immediate impact on species, their distribution and in some instances, cause extinction of species (Baranowski et al. 2020). For instance, the wildfires in Australia caused a population decline in the grey-headed flying fox (*Pteropus poliocephalus*) (Dickman and Fleming 2002, Breed et al. 2010, Baranowski et al. 2020). Parmesan and Yohe (2003) suggest that extreme weather events, caused by climate change can be linked to changes in the body size, fitness and population dynamics of a species. Anthropogenic factors such as land-use changes have caused greater impact on species richness and distribution, than natural environmental changes (Brooks et al. 2002, Cooper-Bohannon et al. 2016). The anthropogenic transformations have been responsible for the loss of biodiversity due to soil and water degradation, and changes in microclimate and habitat loss (Pimm and Raven 2000, Foley et al. 2005). Historically, organisms have had to respond to constant environmental changes, either by adapting, migrating or going extinct (Moritz and Agudo 2013). These environmental changes, however, have been intermittent, with greater periods of no disturbance than those where disturbance is experienced. In recent times, however, the environmental changes have been more frequent and more intense, which have left species with less time to respond and fewer options for survival (Zerbo et al. 2016).

1.1 Land-use change

Over time, land-use change has drastically altered landscapes (Meyer and Turner II 1996). Meyer and Turner (1996) defined “land-use change” as a conversion from one land-use type to another. Human population increase and the demand for resources has stimulated land-use change for the purpose of agriculture and infrastructure development, in order to feed and house the growing human population (Newbold et al. 2015). This has resulted in loss of previously natural landscapes (Hooke 2012). According to Leridon (2020) the world’s population is set to increase to approximately 9.7 billion by 2050. Over the past 20 years, changes in landscapes have intensified due to higher demands for residential and agricultural lands and natural resources (Lipský 2006). In addition, land-use change results not only to ecological challenges, but economic challenges as well (Milà I Canals et al. 2007). With developing nations now becoming more developed, trade in agricultural products and mineral exports has increased (Schueler et al. 2011). Habitat degradation and fragmentation are directly linked to urbanisation and result in biodiversity losses and overall declines in wildlife (Saunders et al. 1991, Braimoh and Onishi 2007). A study by Braimoh (2004) indicates that 3% of the earth’s surface has been classified as urban, which means that the world’s human footprint has increased and is negatively impacting the natural environment. According to Mittermeier (2003), approximately 46% of global land remains pristine, whilst forest cover has been reduced from 50% to 30% (Vitousek et al. 1997). More recent studies, however, show that only a quarter of the land on earth is substantively free of human impact (WWF 2018).

Past studies have, extensively, documented the destruction of the Amazonian forests in South America, Guinean forests in Africa and the polar ice caps in Antarctica (Stuart et al. 1990, Chown et al. 2003). For instance, a study by Periago et al. (2015) detailed how the tagua *Catagonus wagneri* in the Argentine Chaco has disappeared from its original geographic range and its population is at a decline. Practices such as mining, agriculture and urbanisation have negatively affected global species richness (Biggs et al. 2008). Certain animal and plant species have been lost, despite increasing efforts to restore forests or initiatives to protect native biodiversity (Bullock et al. 2011). These initiatives include The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Convention on Biological Diversity (CBD) and The Millennium Development Goals (Bullock et al. 2011).

1.2 Effects of land-use change on Biodiversity in Ghana

Biological diversity, commonly known as 'biodiversity' is described by the Millennium Ecosystem Assessment (2005) as "diversity of genes, populations, species, communities and ecosystems in both terrestrial and aquatic ecosystems". Biodiversity hotspots are geographic regions that are biologically rich and have a high number of species (Brooks et al. 2002, Conservation International 2005, Pimm et al. 2014). Brooks et al. (2002) reported 34 recognised global biodiversity hotspots (Conservation International 2005, Baldwin 2009). Biodiversity hotspots have increased in number, although most have lost approximately 70% of their original terrestrial composition (Baldwin 2009, Deikumah and Kudom 2011, Pimm et al. 2014). Nine of the 34 biodiversity hotspots occur in Africa, and include the Guinean Forest which is located in the lowland regions of West Africa (Myers 2003, Conservation International 2005, Codjoe 2007, Brooks 2009).

The forest of West Africa covers 11 countries, namely; Benin, Cameroon, Côte d'Ivore, Equatorial Guinea, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, Sao Tome and Principe and Togo (Küper et al. 2004), however, it has been damaged by deforestation, urbanisation and agriculture (Conservation International 2005). The Guinea Forest once covered an estimated area of about 680000 km^2, however, human influence has caused a 70% loss in forest cover resulting in various animal and plant species being declared either critically endangered or extinct (Leone 1996, Bakarr et al. 2001, McCullough et al. 2005, 2007). The forests of Ghana, although small, are host to several threatened and endemic species, making their conservation vital (Baldwin 2009, Deikumah and Kudom 2011, Pimm et al. 2014).

The upper portion of the Guinean Forest extends into Ghana, which is situated along the Gulf of Guinea in West Africa, covering approximately 239000 km^2 (McCullough et al. 2005, Codjoe 2007, Alo and Pontius 2008, Vordzogbe et al. 2009). The Ghanaian Republic has ten administrative regions and four bio-geographical zones: The Guinea-Congolian Zone (forest), the Guinea-Congolian/Sudanian transition zone (forest, savannah), Sudanian Zone (savannah) and the Sub-Sahelian Zone (woodland, savannah) (National Biodiversity Strategy for Ghana 2002). Portions of forest were cleared for cash-crop farming (such as cocoa) and mining (such as, gold and coal) (Thompson 1910, Hawthorne and Abu-Juam 1995). In an effort to reduce the deforestation rate, over 280 forest reserves were established in the early 1980s covering approximately 24000 km^2 (McCullough et al. 2007). However, this did not slow the deforestation down. Between 1990 and 2010 the deforestation rate in Ghana was reported to be 1.68% per year (Quacou 2016).

The human population of Ghana increased from 2.2 million to 4.1 million from 1921 to 1948 (Codjoe 2007). In 2010, a population of 24.6 million was reported for Ghana (Kayode et al. 2012). More land has had to be converted to agricultural croplands, and loss of forest currently measures at approximately 190000 km^2 (Attuquayefio and Fobil 2005, Ofori et al. 2013, Quacou 2016).. The conversion of these forests into agricultural land is causing local wildlife extinctions of animals, such as the Miss Waldron's red colobus (*Piliocolobus badius waldroni*) (Searchinger et al. 2008, Gockowski and Sonwa 2011, Ofori et al. 2012). There has been an approximate 20% loss of endemic species and terrestrial ecosystems in both Ghana's savannah and forest regions (Codjoe 2007, McCullough et al. 2007). Due to this loss, Ghana has committed to the African Forest Landscape Restoration Initiative in 2015 (WRI 2017). The aim of this initiative is to restore at least 1 million km^2 of degraded and deforested landscapes by 2030 (WRI 2017). In 2002, it was reported that 721 bird species, 225 mammalian species (13 of them fruit bats) and 221 species of amphibians and reptiles can be found in the savannah and forest regions in Ghana (National Biodiversity Strategy for Ghana 2002, Hackman 2014). Furthermore, according to the IUCN Red list, 29 mammalian species are threatened including five bat species, namely, *Eidolon helvum*, *Hipposideros jonesi*, *Otomops martiensseni*, *Mops petersoni* and *Scotonycteris ophiodon* due to habitat loss (Glenn 2006, Mickleburgh et al. 2010).

1.3 Bat species richness in Africa

Small mammals, such as bats, shrews and rodents, make up more than 60% of mammal diversity in the world, and are known to be biological indicators of ecosystem health (Jones et al. 2009, Happold and Happold 2013). Their small size allows them to survive in micro-habitats and broader climate ranges which makes them less affected by environmental changes and disturbance (Da Fonseca and Robinson 1990, Macdonald 2010). Small mammals play key ecological roles, such as assisting in the dissemination of plant products by consumption and the dispersal of plant material (Alain et al. 2006, Scott et al. 2010, Makundi and Massawe 2011). Bats are known to be good biological-status indicators because they are very sensitive to changes in the environment (Russo and Jones 2015). Some can adapt better to environmental changes than others. Jung et al. (2016) stated that specialized feeders are usually driven away by fragmented habitats as their sources of food and shelter are threatened (also see Russo and Ancillotto 2015). Furthermore, insectivorous bat species occupy a level in the trophic chain that makes them interact with the plant community, therefore, making them responsive to habitat changes (Russo and Ancillotto 2015, Russo and Jones 2015). Bats are essential components of a healthy ecosystem, because they are often able to act as biological pest-control agents, as many species are insectivorous, while fruit bats are known to assist in forest regeneration by dispersing seeds and organic matter (Monadjem and Fahr 2007*a*, Boyles et al. 2011).

Bats (Order: Chiroptera) can be categorised into two separate groups - megabats and microbats. Megabats are known to feed on ripe fruits, buds, flowers, pollen and nectar of trees. All African microbats are insectivorous; some eat arthropods, small terrestrial vertebrates and others eat nocturnal migratory birds (Happold and Happold 2013). Globally, there are approximately 1400 species of bats, and they account for about 20% of all mammal species (Monadjem et al. 2020, Simmons 2020); there are approximately 392 species of bats found in Africa (ACR 2020). The bats in Africa can be found in various vegetation types: 24% live exclusively in forests (rainforests, montane and riverine forests), 25% can be found in both forests and savanna, 28% exclusively in savanna, 7% in both savanna and arid zones, 4% exclusively in arid zones and about 2% are able to dwell in forest, savanna and arid habitats (Happold and Happold 2013).

1.4 Factors driving bat species distribution in Ghana

The distribution of bats has been negatively impacted by threats, such as hunting, as occurs in most central and West African countries (Ohemeng et al. 2017). Species like *Eidolon helvum* (African straw-coloured fruit bat) are consumed as bush meat (Fa and Brown 2009, Kamins et al. 2011, Carvalho et al. 2015). Disturbance to their roosting places, poor water quality, and the use of pesticides are some of the threats faced by bat species across Africa (Marshal and Mcwilliam 1982, Costa et al. 2018, Frick et al. 2019). Bats have been hunted by people out of fear, as, some bat species have been linked with diseases and may act as vectors of pathogens such as Ebola. (Messenger and Rupprecht 2003, Kamins et al. 2011) However, climate and land-use changes remain the biggest threats to bat distribution and survival (Vitousek et al. 1997, Mickleburgh et al. 2002).

In tropical forests, habitat fragmentation has resulted in major losses of natural landscapes and in the species that occupy these forests (Laurance et al. 2014, Banul et al. 2019). As deforestation rates increase, fragmentation rates follow suit (Wordley et al. 2017). The removal of bats from forest landscape results in slower regeneration of these disturbed landscapes, because species like fruit bats are integral in the forest regeneration process (Cosson et al. 1999). Agriculture has impacted pristine landscapes as more crops need to be planted to feed the growing human population (Cisneros et al. 2015*a*). This leads to the loss of native vegetation, which then affects insect populations, and negatively affects bat populations (Cisneros et al. 2015*b*). The removal of bats from agricultural landscapes reduces the number of natural pest-control agents as well, which causes farmers to use more insecticides, which further negatively affect other wildlife (Stechert et al. 2014, Russo and Jones 2015).

1.5 Species distribution modelling

Species assessments are imperative for adequate conservation planning of which species distribution modelling can be used to inform conservationists (Franklin and Miller 2010, Beaumont et al. 2016). Species distribution modelling (SDM) can be used to inform on threats and trends in a specific population (Akçakaya and Brook 2008, Franklin and Miller 2010). It is a systematic approach for conservation planning, as it can be used to predict present distributions, as well as any future threats to species range shifts (Qin et al. 2017).

Using methods like SDM, one can take species' occurrence data and environmental variables (climate and land use) and the model can accurately predict which variables influence the species' distribution (Elith and Graham 2009, Franklin and Miller 2010, Fithian et al. 2015, Akhter et al. 2017). SDM has been successful using maximum entropy (MaxEnt) (Elith et al. 2006, Schoeman et al. 2013). MaxEnt (Phillips 2017) uses modelling algorithms to predict distributions using eco-geographical variables as restrictions (Phillips et al. 2006, Franklin and

Miller 2010). SDMs have been used in West Africa to predict issues like - future climate's suitability for cocoa (*Theobroma cacao*) farming (Läderach et al. 2013), to predict plant species distribution (Amissah et al. 2014), seasonal habitat use by elephants (*Loxodonta africana*) (Ashiagbor and Danquah 2017) and modelling a spatial baseline for amphibians in West Africa (Penner et al. 2019). All these studies, either used climatic variables or land-use data and sometimes both in the analyses (Läderach et al. 2013, Amissah et al. 2014, Ashiagbor and Danquah 2017, Penner et al. 2019).

1.6 Purpose of this research

Information is lacking about the species of bats in Ghana and how they are affected by climate and land-use changes. The work of Grubb et al. (1998) titled, "The mammals of Ghana, Sierra Leone and The Gambia" provided the opportunity to assess the best-known distribution and diversity of bat species (Mammalia, Chiroptera) within Ghana. With little to no new information about the bat distribution in Ghana, SDM is the key to improving our knowledge and assisting in making informed management decisions on land use and how natural landscapes are transformed.

1.7 Objectives

- To identify which of the six agro-ecological zone reflects high species richness and relative abundance, and to assess alpha and beta diversity (**Chapter 2**). Also, to investigate community ecology assessments, such as bat-species abundance, diversity and richness in Ghana.
- To determine which eco-geographical variables (climate or land-use) contribute to the distribution of bats in Ghana (**Chapter 3**).

- To show the predicted area of distribution for the bats of Ghana using species distribution modelling (**Chapter 3**). The prediction of distribution can contribute to further research in these areas, and if necessary, conservation efforts to be focused on the areas identified to have a high predicted species richness.

1.8 Predictions

It was predicted that the Tropical Rain forest would be the agro-ecological zone with high species richness. It was also predicted that the land-use change variable would contribute the most to the distribution of bat species in Ghana than the climate change variable.

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Chapter 2: Ghana's bat species: which agro-ecological zone reflects high species richness and relative abundance?

2.1 Introduction

Natural landscapes have been modified through human-mediated activities, and, currently, about 77% of the terrestrial biosphere has been altered (Ellis et al. 2010). There has been an increase in forest loss in the tropics, as the demand for natural resources increases (Hansen et al. 2013, Fordham et al. 2018). The increase in human population has been a major driver in the rate of species extinction (Cisneros et al. 2015*a*). With this progression in the number of endangered species and extinction rates, it is critical that endemic and specialised species are studied in order to bolster conservation efforts (Jankowski et al. 2009). These endemic and specialist species have limited options, either, migration or adapting to new conditions (Cisneros et al. 2015*b*). Most of the earth's biodiversity is sustained by tropical ecosystems which, unfortunately, makes them vulnerable when the area is disturbed by land-use change (Laurance et al. 2014, Haddad et al. 2015). Some land-use changes include expansions in agricultural lands within these tropical ecosystems, with some croplands equalling the size of South America and grazing land equating to the size of Africa (Fargione et al. 2008, Laurance et al. 2014).

The effects of modifications on landscapes need to be investigated, and it is imperative to find the best way to conserve biodiversity across spatial scales, namely, from microhabitats to global landscapes (Schindler et al. 2013, García-Morales et al. 2016). It is necessary to have a link between collected data and diversity dynamics and illustrate how these mechanisms maintain diversity, both locally and regionally. Socolar et al., (2016) suggested that in order for conservation planning to occur, extensive biodiversity data are needed to inform decisions, such as purchasing of land and the management of it. This can be achieved through monitoring of species assemblages, focusing on species richness, composition and diversity (Ehrlén and Morris 2015). When a habitat has been transformed, it may lead to a loss of specialised species and an overall decline in species richness (Foley et al. 2005, Tscharntke et al. 2012).

Species diversity has been divided into different components - gamma, beta and alpha - (Socolar et al. 2016). Gamma-diversity is the species diversity of a large area, on global and regional scale; that is the diversity of an eco-region, nation or landscape (Crist et al. 2003). Lande (1996) reported that the total diversity (gamma) of an area could be divided into additional components representing diversity within the community (alpha) and between communities (beta). Alpha diversity is the diversity of a small area and can be expressed as species richness, whereas, beta diversity is used to describe the changes in species composition and abundance across environments (Koleff et al. 2008, Legendre 2008). Gamma, alpha and beta species diversity can be calculated using Shannon [$\sum p_i \ln(p_i)$] or Simpson's [$1 - \sum p_i^2$] indices of diversity, where p_i is the proportional abundance of species i for $i = 1$ to n total number of species in the sample (Crist et al. 2003).

Monitoring diversity and species richness at various spatial levels are common when assessing biodiversity (Crist et al. 2003). However, species richness can be a challenging variable to measure, as it cannot be estimated by observation (Chao et al. 2005). This is because the number of species observed is biased for the total species abundance of an assemblage (Chao et al. 2005, Watkins et al. 2006). Therefore, methods have been developed to estimate species richness and to account for this bias (Colwell et al. 2012). The types of data used for species richness studies are incidence data (when each group of species is detected in a sample or in its presence and absence data) and abundance data (how many times groups of species occur in a sample) (Gotelli and Colwell 2011).

Species richness is essential for conservation as the number of species in an assemblage is a natural index of the community's structure (Hepinstall et al. 2009, Nkrumah et al. 2017*b*). However, cumulative losses of specialised species, due to land transformation, can lead to reduced biodiversity (Karp et al. 2012, Tscharntke et al. 2012). Beta diversity is the variation in a community's composition among sites and is a vital index in understanding how ecological patterns of biodiversity are shaped (Whittaker 1972, Koh 2008). Beta diversity is said to decrease within transformed habitats such as agricultural fields and plantations, although, some species seem able to exploit fragmented habitats (Karp et al. 2012).

An example is how the contribution of neutral communities versus niche-based communities can be inferred from beta-diversity patterns (Püttker et al. 2015). Neutral (or stochastic) assembly is when the presences of species at a site is influenced by an ecological drift (Chase and Myers 2011). This infers that geographically distant sites should have dissimilar biological assemblages (Chase and Myers 2011). But in a niche-based or deterministic assembly, the local environment and species niche are determined by the absence or presence of a group of species (Chase and Myers 2011) . Implying that sites with similar environmental conditions will support similar biological communities (Chase and Myers 2011, Kraft et al. 2011). It is essential, however, to understand the processes driving the community, either to transformed land or natural habitats, especially, to inform process-based approaches to conservation.

The loss of biodiversity is prevalent in Africa, with its growing human populations and urbanisation (Seto et al. 2012, Laurance et al. 2014, Haddad et al. 2015). The land-use transformation has impacted the natural vegetation, especially, in tropical countries (Quagraine et al. 2017). Africa has lost parts of its land to commercial farming; countries, such as Madagascar are using approximately 453000 ha for a biofuel project and Ethiopia is using about 150000 ha for livestock (Karp et al. 2012). According to Karp et al. (2012), intense agricultural practices contribute to loss of species diversity, but the extent is unclear when done on a large scale. In West Africa, some countries fall within the Guinean forests, which provide a wide range of plant species to use for export (timber) and basic needs (construction material, food and medicine) (Nacoulma et al. 2011). The savanna biome is a vital ecosystem, especially in West Africa, as the land is mostly used for agricultural practices, grazing and logging (Nacoulma et al. 2011). The biome has been subjected to much anthropogenic exploitation as the human population increases, causing overuse of the savanna biome (Nacoulma et al. 2011, Zerbo et al. 2016).

The classification of agro-ecological zones in Africa is based on the combinations of the characteristics of vegetation, topography and climate (Happold and Lock 2014, Zerbo et al. 2016). In certain African countries, these agro-ecological zones are sub-divided into agro-ecological zones. This is usually determined by the climate, landform, soils and land-cover in the specific country, with a range of potentials and restrictions for land use (Happold and Lock 2014). In Ghana, there are six agro-ecological zones based on the climate and soil, as well as the natural vegetation. The six agro-ecological zones are the: Coastal Savannah, Guinean Savannah, Sudanese Savannah, Forest-Savannah Transitional, Tropical rain forest, and Moist Semi-deciduous Forest.

These agro-ecological zones have been fragmented and transformed, due to the growing human population of the country and the associated agricultural activities (Bossart et al. 2006, Asiedu 2015). Ghana is the second-highest cocoa (*Theobroma cacao*) exporter, with plantations all over the country. Agriculture also plays a significant role in the economy of the country, based on both subsistence and commercial farming (Asase and Tetteh 2010).

Large-scale farming is negatively impacting biodiversity; however several studies have demonstrated that these practices have value as they keep intermediate levels of biodiversity (Pimentel et al., 1992, Perfecto et al.,1996, Robertson & Swinton 2005). This is evident in the neo-tropics with some agro-ecosystems, such as the cocoa and plantain (*Plantago sp.*) (Phalan et al. 2011). These are garnering attention as the reservoirs of tropical biodiversity (Jarvis et al. 2010, Phalan et al. 2011). Phalan et al., (2011) showed that an agricultural land which had fragments of a forest, showed a diverse number of bird species and tree species. Similarly, the shaded cocoa farms have occasionally preserved native biota. This could be because, some of the agro-ecosystems share the same vegetation diversity and complexity as a natural-forest ecosystem (Nkrumah et al. 2017*b*). Complex structures like shaded canopies and agro-ecosystems can play vital roles in preserving portions of the original biodiversity (Addai and Owusu 2014, Asiedu 2015, Zampaligré and Schlecht 2018).

Bats are the second-largest mammalian order, they are found all over the world especially in tropical ecosystems, such as the ones found in Ghana (Simmons 2005). They possess both frugivorous and insectivorous species, hence, they are known to regulate ecological processes through insect predation, seed dispersal and pollination (Weber and Fahr 2007, Kunz et al. 2011, Costa et al. 2018). insectivorous bats act as biological pest control (Jung et al. 2016, Maas et al. 2016, Starik et al. 2018, Weier et al. 2018). Insectivorous bats have economic importance in the agricultural industry, with an estimated value of $22.9 billion, annually (Boyles et al. 2011). Bats can consume, approximately, 25-50% of their body mass (Russo and Ancillotto 2015, Russo and Jones 2015). Despite their importance, there is still very little data on their species abundance, composition and diversity in the agro-ecosystems of Africa (Nkrumah et al. 2017*b*). These species need monitoring in order to understand the community of bats found in these agro-ecological zones of Ghana.

This study aimed to identify the agro-ecological zones in Ghana with the highest bat abundance and species richness. In this study: i) abundance data rather than presence and absence data were used to calculate species richness (alpha diversity) within each agro-ecological zone and ii) the diversity between each of the agro-ecological zones (beta diversity) was measured.

Improved knowledge on bat community assemblages and diversity can inform on policy and management strategies, as well as conservation efforts.

2.2 Methods and materials

2.2.1 Study area

The Republic of Ghana (5°5′39″N and 10°54′38″N latitudes, 0°05′04″E and 3°14′12″W longitudes) is approximately 239000 km^2 (Gumma and Pavelic 2013). Ghana borders Côte d'Ivoire to the west, Burkina Faso to the north and Togo to the east (Figure 2.1). The country has ten administrative regions and three biotic zones (Savannah, Transitional zone and Forest) (Appiah et al. 2014). These zones were then sub-divided into six agro-ecological zones based on the climate and soil as well as the natural vegetation in the country (National Biodiversity Strategy for Ghana 2002, Appiah et al.,2014). The six agro-ecological zones are the Savannah (Sudan, Guinea and Coastal), Forest-Savannah Transitional Zone, the Moist Semi-deciduous Forest zone and the Rain Forest zone (Figure 2.1). The Guinean and Sudanese Savannah are located along the northern part of Ghana, with Guinea in a more north-easterly direction (Wongnaa and Awunyo-Vitor 2019). Both cover about 125430 km^2 with a tropical climate and wooded grassland vegetation (Asiedu et al. 2019, Wongnaa and Awunyo-Vitor 2019). These zones experience long periods of a dry climate, with the dry seasons occurring between October/November and April/May and the rainy seasons between May and October (Wongnaa and Awunyo-Vitor 2019). Temperatures range from 27 to 35°C and a rainfall pattern that is unimodal with an average annual rainfall of 950 - 1300 mm during the rainy season (Addai and Owusu 2014, Asiedu et al. 2019, Atiah et al. 2019, Wongnaa and Awunyo-Vitor 2019). The Coastal Savannah biotic zone is different from the other savannahs as it has two peaks in rainfall, namely, July and September to October (Wongnaa and Awunyo-Vitor 2019). The annual rainfall in the Coastal Savannah is bimodal and can range between 800 – 900 mm (Addai and Owusu 2014, Atiah et al. 2019). The Forest-Savannah Transitional zone is located in the middle of Ghana and is a boundary between the forest and savannah (Addai and Owusu 2014, Wongnaa and Awunyo-Vitor 2019). Furthermore, because of its position, this zone experiences mixed weather patterns, with the climate being semi-equatorial and having a savannah, woodland and forest belt vegetation (Addai and Owusu 2014, Atiah et al. 2019, Wongnaa and Awunyo-Vitor 2019). With its bimodal rainfall, the zone can experience up to 1300 mm of rain annually and an annual temperature of approximately 26°C (Addai and Owusu 2014). Most of Ghana's forest is Moist Semi-deciduous, covering about 66000 km^2 and the Tropical Rain forest only covering about 633 km^2 (Addai and Owusu 2014, Wongnaa and Awunyo-Vitor 2019). The area is situated at the southern part of Ghana, with the rainforest more to the south-west; it has a semi equatorial climate and is wet most of the year (Atiah et al. 2019). The forests have a bimodal rainfall pattern, with rainfall of 1600 -1800 mm annually and temperatures of up to 26.4°C (Addai and Owusu 2014, Atiah et al. 2019).

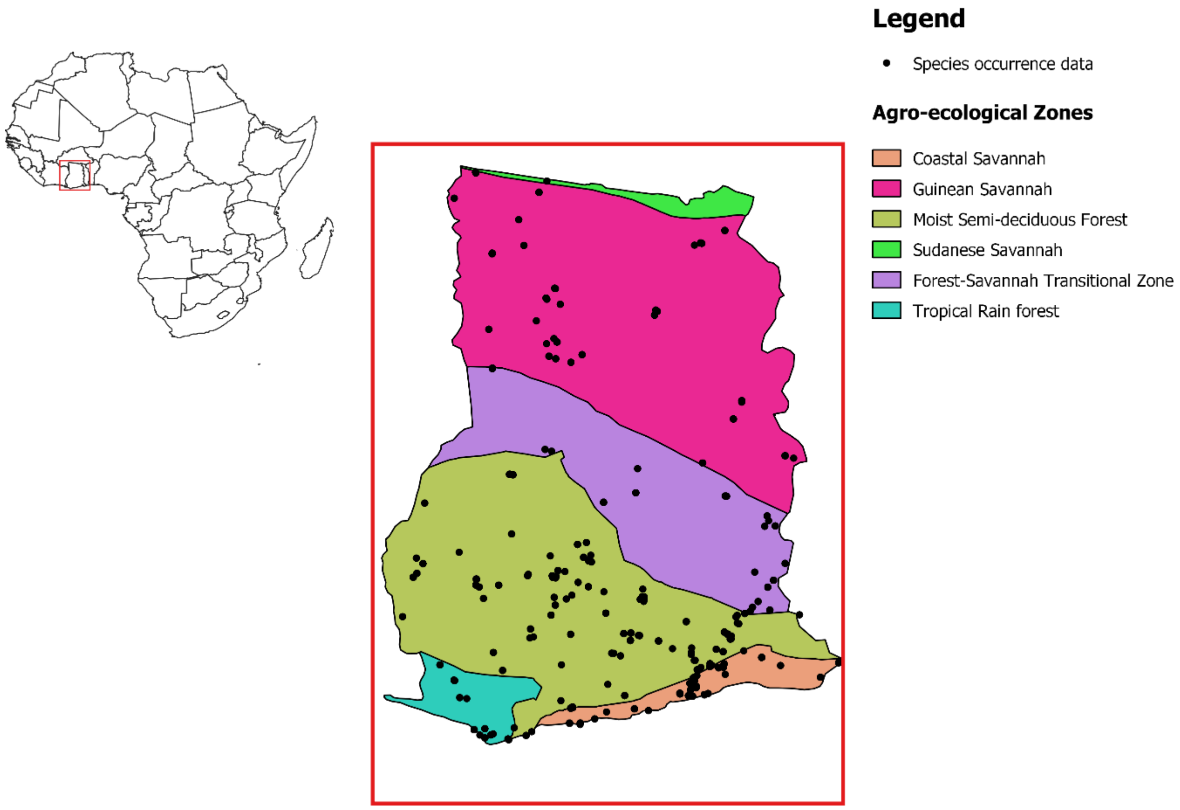

Figure 2.1: Map of the study area, Ghana, showing the six agro-ecological zones (Coastal Savannah, Guinean Savannah, Moist Semi-deciduous forest, Sudanese Savannah, Forest-Savannah Transitional zones and the Tropical Rain forest), and occurrence records of 96 bat species.

2.2.2 Data Collection

Data on species occurrence were collected from the African Chiropteran Report (ACR) 2018 (ACR 2018). The ACR (2018) provides very comprehensive information on bats in Africa complied by the African Bats NPC. ACR's database comprises of bat occurrence data, collected from literature and museum databases, like The American Museum of Natural History (AMNH), The British Museum of Natural History (BMNH) and The Field Museum of Natural History (FMNH) specifically on the African continent (ACR 2018). To assess which agro-ecological zone the different species covered, the species' occurrence records were converted to data points using ArcMap analysis tools from the software ArcGIS version 10.2.2 (ESRI 2014). Data on the agro-ecological zones of Ghana were downloaded from WWF eco-regions map (https://worldwildlife.org/pages). ArcGIS was used to calculate a geometric intersection of the input features (point, line or polygon) and identity features (polygon). The input feature that intersects with the identity feature will get the attributes of those identity features (ESRI 2014). In this case, the species data points (input feature) were overlapped with the agro-ecological zones of Ghana (identity feature) to identify which biotic zone each species data point belongs to.

2.2.3 Data analyses

a. Species abundance

Data on species abundance was obtained by calculating how many bat species data points overlapped a specific biotic zone.

b. Alpha diversity

To estimate the species richness of the different agro-ecological zones of Ghana, the program EstimateS 8.2.0 was used (Chao et al. 2005). EstimateS uses abundance data and calculates rarefied estimated species richness, as Chao1 values for each biotic zone (Chao et al. 2005). Non-parametric species-richness estimators estimate the bat-species richness within each biotic zone: Chao1 for abundance data and Chao2 for incidence data. EstimateS also has the option to calculate the two known indices for diversity - Shannon's diversity index. The estimated species richness, per agro-ecological zones, was compared using the estimated Chao1 values obtained. To determine whether the species richness differed among the agro-ecological zones, the asymmetrical 95% confidence intervals (CI) of Chao1 were used (Lande 1996). Since the species' richness is now estimated using the frequency of a species occurrence within a sample, Chao1 has become the most used index (Chiu and Chao 2016). Alpha diversity is defined as the species richness at a sampling unit, therefore, for this study, an alpha diversity value was obtained for each biotic zone.

c. Beta-diversity

Beta-diversity was calculated within the respective agro-ecological zones (Sudanese Savannah, Guinean Savannah, Coastal Savannah, Forest-Savannah Transitional, Moist Semi-deciduous Forest and the Rain Forest zone). There are different indices for beta diversity - Jaccard-Sørensen or Bray-Curtis; these measure the (dis)similarity between assemblages (Beck et al. 2013). The Bray-Curtis dissimilarity index was used in this study as it allowed for the inclusion of abundance and not just the presence or absences data for the different agro-ecological zones. This index provides values ranging between 0 and 1, with a value closer to 1 indicating a high level of dissimilarity between sites and a value closer to 0 indicating that sites have similar species (Ricotta 2017). The analysis for beta diversity was conducted in the R programming environment (R Core Team 2013) using the vegan package (Oksanen 2013).

2.3 Results

In total, 96 species from 4898 species records across five different agro-ecological zones in Ghana (Figure 2.1) were analysed, with no species record from the Sudanese Savannah agro-ecological zone. The agro-ecological zone with the most species was the Moist Semi-deciduous forest (n = 72), followed by Coastal Savannah (n = 48), Transitional zone (n = 44), Guinean Savannah (n = 42) and the Tropical Rain forest recording the least number of species (n = 27) (Figure 2.3b). However, when it came to species abundance, Coastal Savannah had the most occurrence records (n = 1844) followed by Moist Semi-deciduous forest (n = 1554), Guinean Savannah (n = 630), Transitional zone (n = 536) and Tropical Rain forest (n = 334) (Figure 2.3a). Upon further investigation, there were eight species that occurred in all 5 agro-ecological zones. These were *Micropteropus pusillus* (n = 397), *Epomops franqueti* (n = 336), *Hipposideros ruber* (n = 76), *Megaloglossus azagnyi* (n = 71), *Doryrhina cyclops* (n = 70), *Hipposideros fuliginosus* (n = 66), *Hypsignathus monstrosus* (n = 39), *Macronycteris gigas* (n = 21) (Figure 2.2). On the other hand, 29 species occurred exclusively in at least one of the agro-ecological zones, except in the Tropical Rain Forest. These were in the Moist Semi-deciduous forest (n = 16), Guinean Savannah (n = 6), Coastal Savannah (n = 6), Transitional zone (n = 1) (Table 2.1).

a. Alpha diversity

The estimated levels of species richness which the Chao1 identified, were the Moist Semi-deciduous forest ($Chao1_{\text{Moist Semi-deciduous forest}}$ = 110), followed by the Transitional zone ($Chao1_{\text{Transitional zone}}$ = 58), Coastal Savannah ($Chao1_{\text{Coastal Savannah}}$ = 54), Guinean Savannah ($Chao1_{\text{Guinean Savannah}}$ = 47) and, finally, the agro-ecological zone with the lowest estimated species richness was the Tropical rain forest ($Chao1_{\text{Tropical Rain forest}}$ = 42) (Table 2.2). Using other estimates for species richness, it showed that Moist Semi-deciduous forest was indeed the agro-ecological zone with the highest species richness and that Tropical rain forest did have the lowest species richness. The Shannon index for diversity calculated that the Moist Semi-deciduous forest was high in species richness and, it was more diverse than the other agro-ecological zones with an index value of 3.26. The Transitional zone with 3.17 index value, was the second most diverse agro-ecological zone (Table 2.2).

b. Beta diversity

The Bray-Curtis index value for dissimilarity (0.758) between the agro-ecological zones, suggests a high levels of dissimilarity between the agro-ecological zones (Table 2.3). The zones that had some similarity or a low-dissimilarity index value was the diversity between Guinean Savannah and Transitional zone (β_{bray} = 0.664) (Table 2.3). In contrast, the agro-ecological zones that had a high- dissimilarity index value were Guinean Savanna and Tropical Rain forest (β_{bray} = 0.925) (Table 2.3).

Table 2.1: Bat species occurring exclusisvely in Four agro-ecological zones in Ghana (Coastal Savannah (n = 6), Guinean Savannah (n = 6), Moist Semi-deciduous Forest (n = 16), Forest-Savannah Transitional Zone (n = 1)).

Coastal Savannah	**Guinean Savannah**	**Moist Semi-deciduous Forest**	**Forest-Savannah Transitional**
Epomophorus labiatus	*Chaerephon chapini*	*Casinycteris ophiodon*	*Pipistrellus inexspectatus*
Epomophorus wahlbergi	*Coleura afra*	*Chaerephon russatus*	
Pipistrellus hesperidus	*Otomops martiensseni*	*Glauconycteris beatrix*	
Rhinopoma microphyllum	*Pipistrellus rusticus*	*Glauconycteris superba*	
Scotoecus albofuscus	*Rhinolophus denti*	*Hipposideros jonesi*	
Taphozous mauritianus	*Taphozous nudiventris*	*Hypsugo musciculus*	
		Kerivoula lanosa	
		Kerivoula phalaena	
		Mops (Mops) trevori	
		Mops (Xiphonycteris) petersoni	
		Pseudoromicia brunnea	
		Nycteris intermedia	
		Nycteris nana	
		Rhinolophus fumigatus	
		Scotophilus nucella	
		Taphozous perforatus	

Table 2.2: Recorded species richness and abundance (individuals recorded), abundance-based richness estimators, percentage of predicted richness observed and Shannon diversity 96 of bat species in Ghana, across five agro-ecological zones (Guinea Savannah Coastal Savannah, Forest-Savannah Transitional, Moist Semi-deciduous Forest and the Rain Forest Zone) using Abundance-based coverage estimator (ACE), Confidence Interval (CI).

Agro-ecological zones	Observed Species	Individuals observed	Chao 1 Mean	Chao 1 95% CI Lower Bound	Chao 1 95% CI Upper Bound	ACE Mean	Shannon diversity
Coastal Savannah	48	1844	53.79	49.33	73.26	52.5	2.48
Guinean Savannah	42	630	47	43.22	62.57	47	2.58
Moist Semi-deciduous forest	72	1554	110	84.24	190.02	110	3.26
Forest-Savannah Transitional zone	44	536	57.75	47.4	99.55	57.75	3.17
Tropical Rain forest	27	334	42	30.5	91.24	42	2.39

Table 2.3: Beta diversity values (β_{bray}) for 96 bat species between five agro-ecological zones (Guinea Savannah Coastal Savannah, Forest-Savannah Transitional, Moist Semi-deciduous Forest and the Rain Forest Zone) (Bray-Curtis dissimilarity) between agro-ecological zones and the mean Bray-Curtis index value for dissimilarity in Ghana.

Agro-ecological zones	**β_{bray} Index value**
Coastal savanna ~ Guinean savanna	0.707
Coastal savanna ~ Moist Semi-deciduous forest	0.723
Coastal savanna ~ Transitional zone	0.822
Coastal savanna ~ Tropical rain forest	0.831
Guinean savanna ~ Moist Semi-deciduous forest	0.739
Guinean savanna ~ Transitional zone	0.664
Guinean savanna ~ Tropical rain forest	0.925
Moist Semi-deciduous forest ~ Transitional zone	0.686
Moist Semi-deciduous forest ~ Tropical rain forest	0.689
Transitional zone ~ Tropical rain forest	0.795
Mean β_{bray}	**0.758**

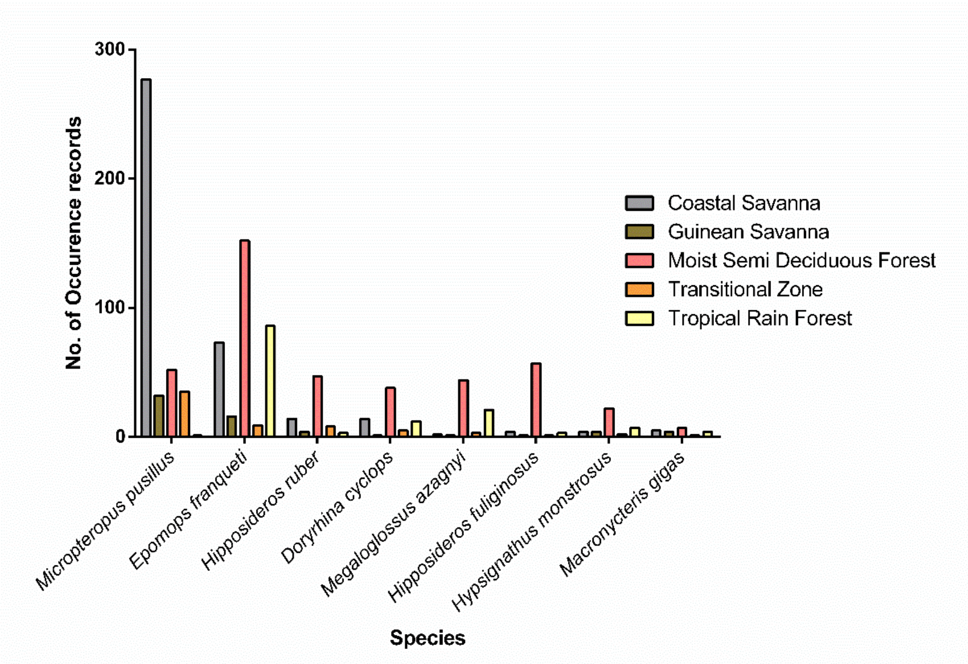

Figure 2.2: Eight bat species (*Micropteropus pusillus* (n = 397), *Epomops franqueti* (n = 336), *Hipposideros ruber* (n = 76), *Megaloglossus azagnyi* (n = 71), *Doryrhina cyclops* (n = 70), *Hipposideros fuliginosus* (n = 66), *Hypsignathus monstrosus* (n = 39), *Macronycteris gigas* (n = 21) occurring across all five agro-ecological zones (Coastal Savannah, Guinean Savannah, Moist Semi-deciduous Forest, Forest-Savannah Transitional and Tropical Rain Forest Zone) in Ghana.

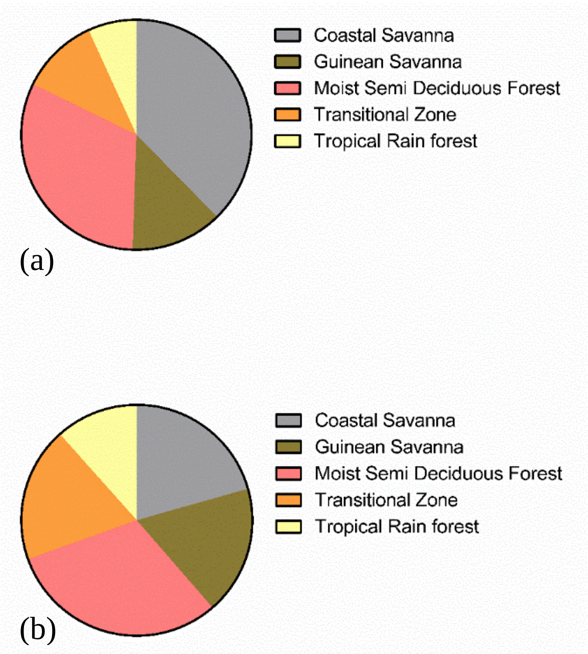

Figure 2.3: (a) Bat species abundance across the five agro-ecological zones in Ghana: Coastal Savannah (37.64%), Guinean Savannah (12.86%), Moist Semi-deciduous Forest (31.73%), Forest-Savannah Transitional (10.94%) and Tropical Rain Forest (6.82%)); (b) Bat species richness using presence and absence data ((Coastal Savannah (20.60%), Guinean Savannah (18.03%), Moist Semi-deciduous Forest (30.90%), Forest-Savannah Transitional (18.88%) and Tropical Rain Forest (11.59%)).

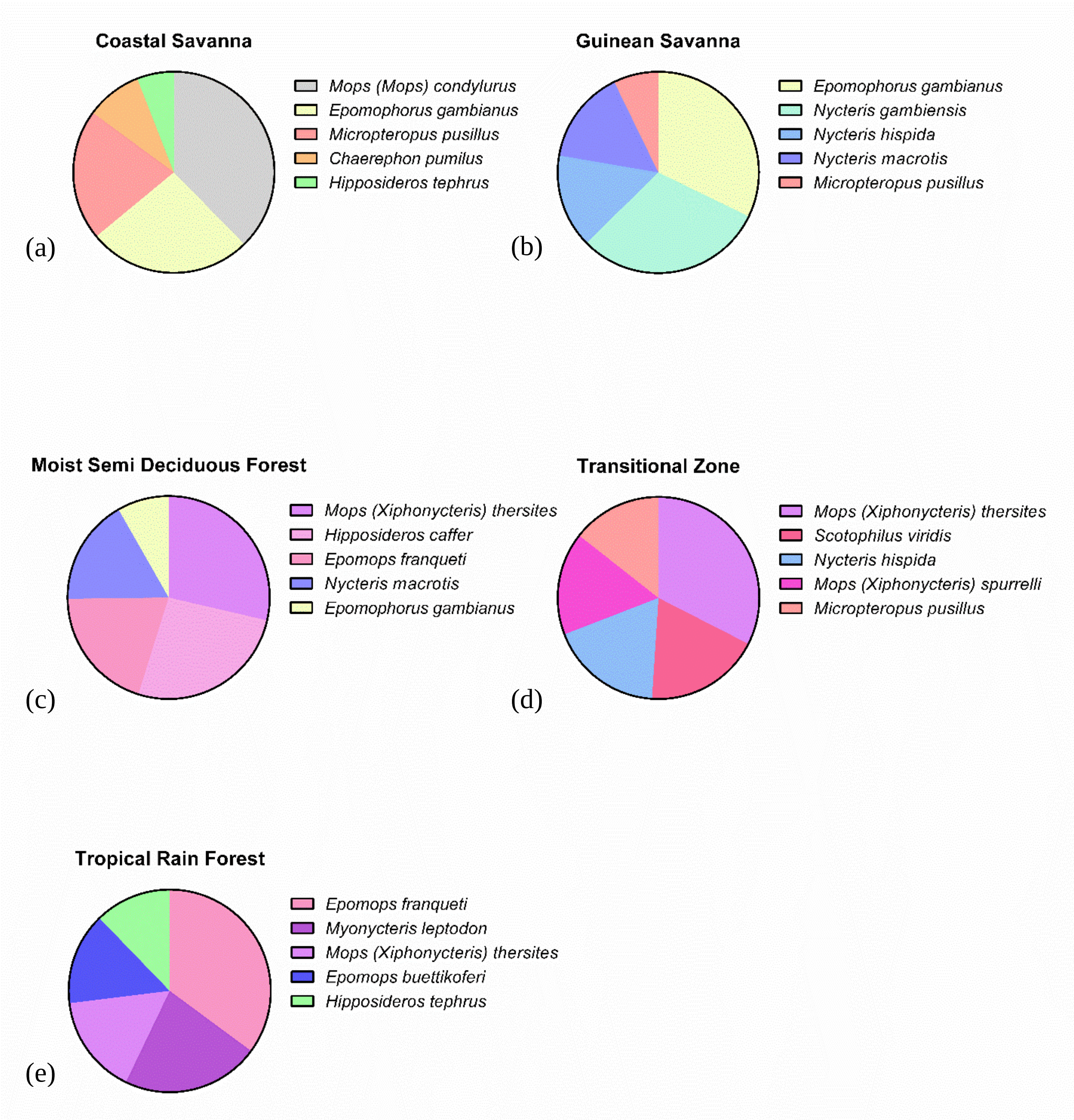

Figure 2.4: Top five bat species (species abundance) across five agro-ecological zones in Ghana: (a) **Coastal savannah** (*Mops (Mops) condylurus* (37.67%), *Epomophorus gambianus* (26.33%), *Micropteropus pusillus* (21.08%), *Chaerephon pumilus* (8.98%), *Hipposideros tephrus* (5.94%)) (b) **Guinean savannah** (*Epomophorus gambianus* (32.21%), *Nycteris gambiensis* (30.41%), *Nycteris hispida* (15.09%), *Nycteris macrotis* (15.09%), *Micropteropus pusillus* (7.21%)), (c) **Moist Semi-deciduous forest** (*Mops (Xiphonycteris) thersites* (28.61%), *Hipposideros caffer* (26.25%), *Epomops franqueti* (19.95%), *Nycteris macrotis* (16.93%), *Epomophorus gambianus* (8.27%)) (d) **Transitional zone** (*Mops (Xiphonycteris) thersites* (32.51%), *Scotophilus viridis*(18.52%), *Nycteris hispida* (18.11%), *Mops (Xiphonycteris) spurrelli* (16.46%), *Micropteropus pusillus* (14.40%)), (e) **Tropical rain forest** (*Epomops franqueti* (35.10%), *Myonycteris leptodon* (22.04%), *Mops (Xiphonycteris) thersites* (15.92%), *Epomops buettikoferi* (14.96%), *Hipposideros tephrus* (12.24%)).

2.4 Discussion

In this study, it was found that the Moist Semi-deciduous forest had the highest species richness, and when it came to species diversity, it was the most diverse biotic zone, whereas the Tropical Rain forest had the lowest species richness and was the least diverse biotic zone. The Forest-Savannah Transitional zone had the second highest Chao1 value and Shannon diversity index and, although, the Coastal Savannah agro-ecological zone had more individual observed bat species, it was not as diverse. In Ghana, the majority of the forest cover is represented by Moist Semi-deciduous forest and with most frugivorous bat species in west Africa attracted to forest canopy, it might explain the high diversity and richness in this agro-ecological zone (Muscarella and Fleming 2007, García-Morales et al., 2016).

Furthermore, due to most agricultural lands in Ghana being located in the Moist Semi-deciduous forest, insectivorous bats could also be driven to inhabit the forest because of the variety of insects available (Maas et al. 2013). The 5 bat species that had the most recorded occurring in the Moist Semi-deciduous biotic zone, comprised of two frugivorous and three insectivorous bats (*Epomops franqueti*, *Epomorphorus gambianus*, *Nycteris macrotis*, *Hipposideros caffer*, *Mops* (*Xiphonycteris*) *thersites*). According to Happold and Happold (2013), these 5 species are all distributed around the rainforests of West Africa, particularly, in the lowland forests. It was also expressed that these species preferred woodland, savanna and grassland habitats (Happold and Happold 2013). A study done by Tom-Dery et al.(2013) found that approximately 20 different mammal species surroundings were recorded in a plantation in the Semi-deciduous forest; out of those, three were indeed fruit bats. The authors concluded that the presence of these mammals in and around the plantations, in the forest did assist in seed dispersion in the area (Tom-Dery et al. 2013, Chanthorn et al. 2018). With the insectivores bats, they might persist in this agro-ecological zone as they can still cross over to savanna matrices to forage and find food in other habitats, although, not necessarily, staying in the Rain forest (Fenton et al. 1990, Fenton and Simmons 2015).

This study found that, according to the dissimilarity index, Moist Semi-deciduous agro-ecological zone was dissimilar to all other agro-ecological zones, showing heterogeneity in this particular zone. According to Fahr and Kalko (2011), diversity increases with habitat heterogeneity when looking at beta diversity. The habitat heterogeneity hypothesis suggests that complex habitats should provide more niches and diverse ways to exploit resources, therefore, increasing the number of species in an area (Cramer and Willig 2002). Taking the habitat heterogeneity hypothesis into consideration for this study, the Moist Semi-deciduous agro-ecological zone should exhibit this habitat heterogeneity as it showed high species diversity (Schoeman et al. 2013, Lewin et al. 2016, Deikumah et al. 2017). Although this may be true for certain animal species (avian fauna) this may not be the case for mammals (Schoeman et al. 2013, Lewin et al. 2016, Deikumah et al. 2017). Considering that the Moist Semi-deciduous forests of Ghana have natural forests and plantations surrounding the forest, it could be that, different species of bats occupy different parts of the forest (Kerr and Packer 1997, Fahr and Kalko 2011). While habitat similarity should influence community similarity, habitat similarity decreases as fragmentation increases (Dormann et al. 2007). This situation instead favours the dominance of generalist species rather than specialist ones. Bats found in Ghana's agro-ecological zones have adapted to not only the agro-ecological zones but the land-use transformations within these zones (Nkrumah et al. 2017*b*, da Silva et al. 2018, Shapiro et al. 2020).

For this study, eight bat species were present in all five agro-ecological zones. These were *Micropteropus pusillus*, *Epomops franqueti*, *Hipposideros ruber*, *Megaloglossus azagnyi*, *Doryrhina cyclops*, *Hipposideros fuliginosus*, *Hypsignathus monstrosus* and *Macronycteris* *gigas*. Species such as *Micropteropus pusillus* and *Hipposideros ruber* are known to survive in a variety of agro-ecological zones (Manga Mongombe et al. 2019). This corroborates a study by Waghiiwimbom et al.(2020) who found the abundance of *Hipposideros ruber* and *Micropteropus pusillus* across all their three studies in the savannah, forest and farmlands. These results, however, contrast those obtained by Fahr (1996), which found 69% of *M. pusillus* in Ivory Coast's savannah. Of the 29 bat species that were exclusively present in at least one agro-ecological zone apart from the Tropical Rain Forest, most are driven by the abundance of roosting sites and availability of food resources (Happold and Happold 2013, ACR 2018). For example, *Epomophorus labiatus*, *Pipistrellus hesperidus* and *Pipistrellus rusticus* are known to dwell in, either, open savannah or Guinean Savannah (Happold and Happold 2013, ACR 2018). Species such as *Glauconycteris Beatrix*, *Glauconycteris superba* and *Kerivula phalaena* are known to occupy both Moist and Tropical forest agro-ecological zones similar to the results obtained in this study (Happold and Happold 2013, ACR 2018). *Casinycteris ophiodon*, was identified in this study to occupy the Moist Semi-deciduous zone. However, Happold and Happold (2013) described these as specialist species that dwelled in Tropical Rain Forests and are, therefore, prone to threats such as deforestation and forest fragmentation. It is assumed that the 29 bat species found exclusively in a specific agro-ecological zone are specialist feeders. Whereas species like *Hipposideros jonesi*, known to be scattered across different agro-ecological zones are generalist feeders (Happold and Happold 2013). It may seem that species found in all the agro-ecological zones show resilience to disturbances, those found exclusive agro-ecological zones are not all necessarily restricted in that agro-ecological zone (Bellamy and Altringham 2015, Waghiiwimbom et al. 2020).

There has not been much information or documentation on the species composition of forests in Ghana (Vordzogbe et al. 2009, Pappoe et al. 2010). However, human activities still threaten the biological diversity of the forests in Ghana and other parts of Africa (Vordzogbe et al.

2009). About 20-25% of forests in Ghana have been under forest reserve since the 1920s, and 90% have been in the management of forest services in the country (Addo-danso 2016). It can be assumed that these forests would be protected against destructions. However, with timber contributing to 6% of Ghana's Gross domestic profit (GDP) and a combination of poor planning and weak governmental policies there will always be a decrease in pristine forests in Ghana (Appiah-Opoku 2001, Blay et al. 2008). The strengthening in government policies and proper planning can assist in reinforcing the rules and policing the usage of plant species for timber production, in the country. These plantations form part of the roosting sites for bat species, although, it was seen that only a few of the study species need the forests to survive, namely, *Casinycteris ophiodon*, *Glauconycteris Beatrix*, *Glauconycteris superba* and *Kerivoula phalaena* (Happold and Happold 2013). These species are threatened by deforestation, forest fragmentation and even the use of pesticides (Happold and Happold 2013, Stechert et al. 2014, ACR 2018). Bat species in this study, belonging to Molossidae, Vespertilionidae and Hipposideridae are suspected to be generalist and would occupy agro-ecological zones that have abundant food resources, as well as foraging and roosting sites (Maas et al. 2016, Costa et al. 2018, Starik et al. 2018). They have therefore, adapted to disturbed areas and agricultural lands (Fenton et al. 1990, Maas et al. 2016, Costa et al. 2018, Starik et al. 2018).

Multiple studies have shown and assessed how bats do assist in the regeneration of forests and plant species, in general (Lopez-Hoffman et al. 2010, Kunz et al. 2011, Reilly et al. 2015). Phalan et al. (2011) studied the concept of land-sharing (integrating conservation and food production) in Ghana. They concluded that since most of Ghana's farmlands have fragments of forest, more food could be produced if Ghana implemented a land-sharing program (Phalan et al. 2011). A study by Waghiiwimbom et al., (2020), found that bats species that usually occupy man-made structures and buildings were underrepresented in their survey. They further noted that with the degradation of forests, forest-adapted species, such as *Hipposideros ruber*, find suitable habitats that resemble a natural forest vegetation (Waghiiwimbom et al. 2020). The same could be said for this study, seeing as specimen records from museum databases were used, this reflects a sampling bias (Jensen et al. 2017, Phillips et al. 2017, Støa et al. 2018). Using database records has its pros and cons, as certain species could be under-represented. Therefore, it is very possible that collectors accessibility to collection sites in the different agro-ecological zones were limited (Phillips et al. 2017). The cons about using database specimens records means the accuracy of species distribution and relative abundance could be skewed (Jensen et al. 2017, Phillips et al. 2017, Gomes et al. 2018). One does need to be aware of the limitations and bias. Collection databases are now a very important source of biodiversity information (Støa et al. 2018). Furthermore, different species and locations should be well and equally represented but this is not the case.

The current study concluded that it is possible the Moist Semi-deciduous forest is the richest and the most diverse agro-ecological zone in Ghana. With most of Ghana's forests under forest reserves, of which a portion is being managed by forestry services (Hilson and Nyame 2006). This study recommends that policymakers strengthen the law, so that there would be more vigilance around the farming and harvesting of plants, in these forests. This study's results showed that according to data used, the Tropical Rain forest had the lowest species diversity and richness. However, this could just mean there was under-representation due to sampling bias. As this study used specimen database records rather than in person collection records. With no added information, one cannot know how and why certain species were caught in specific agro-ecological zones rather than others. With the knowledge that there are certain species that rely extensively on natural Tropical Rain forests (*Casinycteris ophiodon* and *Mops (Xiphonycteris) petersoni*) means that the government would be aware that the lack of these forests could result in the disappearance of these species. *Mops (Xiphonycteris) petersoni* is near threatened, according to the IUCN red data list (2009) (Mickleburgh et al. 2010). A concept like land-sharing, would assist in the conservation of bat species in the area, and the bats could, in turn, assist as biological pest controllers and seed dispersers. These results also revealed that more studies and surveys need to be conducted to expand on the knowledge of bat species in Ghana, thereby, identifying other threats that may affect the distribution and diversity of bats in the country.

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Chapter 3: Species Distribution Modelling (SDM) of the bat species of Ghana: using climate and land-use variables

3.1. Introduction

Bats (Order: Chiroptera) contain species that are frugivores, nectarivores, carnivores and insectivores to name a few (Simmons 2020) and are significant contributors to biological diversity, with over 1400 species worldwide (Simmons 2020). They provide a variety of ecosystem services, for example, they are active biological control agents as they can consume between 25-50% of their body weight in insects (Boyles et al. 2011, Kunz et al. 2011). Globally, the economic value of bat predation in the agro-ecosystems is approximately 47% the value of annual production (Boyles et al. 2011, Maas et al. 2016, Linden et al. 2019, Weier et al. 2020). Furthermore, the fruit and nectar-feeding bats act as seed dispersers and pollinators (Fujita and Tuttle 1991, Ghanem and Voigt 2012). A reduction in their numbers could mean reduced-ecosystem functioning and loss of plant species that are reliant on seed dispersal (Danell et al. 2006, Laurance et al. 2012, Corlett 2013). Being primarily insect feeders and contributing to key processes in plants, bats are vulnerable to specific environmental changes that affect plant growth and insect populations (Mickleburgh et al. 2002, Jones et al. 2009). This makes bats essential biological indicators as they are greatly influenced by environmental changes; they express the impact of such changes in their population sizes, behaviour, and diversity (Brook 2008, Jones et al. 2009, Sherwin et al. 2013). Bat are affected both directly and indirectly by environmental changes, like land-use and climate changes (Jones et al. 2009). Like other species, bats use climatic cues to assist with activity patterns in terms of foraging, breeding, hibernation, and migration (Brook 2008, Pretorius et al. 2020*a*, *b*, Weier et al. 2020). Therefore increased global variations in temperature and rainfall can significantly affect bats (Brook 2008, Sherwin et al. 2013).

Climate change (defined here as the change over time in variables such as precipitation, temperature, and wind) has had a notably negative effect on biodiversity (Malcolm et al. 2006, de Chazal and Rounsevell 2009). Fluctuations in temperature, in conjunction with the destruction of natural ecosystems can turn a favourable habitat into an unfavourable environment for many variations of fauna and flora (Dixon et al. 1996, Anglaaere et al. 2011, Anand et al. 2018). The shift in climate, in particular temperature, has altered many ecosystems, including tropical forests and their biodiversity (Torres et al. 2014). This is because when extreme temperature variations occur, the distributional range of a species can shift (Talib and Randhir 2017, Asiedu et al. 2019). If species have adapted to a colder climate and experience warmer temperatures, this can result in species' losses in previously favourable ecosystems (Sultaire et al. 2016, Wauchope et al. 2017).

Land-use changes (defined here as the alteration of the biophysical characteristics of earth's surface and subsurface) has a notably negative impact on biodiversity as a direct result of habitat loss and fragmentation (Meyer and Turner II 1996, Mantyka-Pringle et al. 2014). Studies have, usually, assessed the impact of climate change and land-use change separately (Midgley et al. 2003, Vinet and Zhedanov 2011). Previously, the majority of studies focused on the effects of climate change on biodiversity, while land-use effects were not as heavily researched (de Chazal and Rounsevell 2009). Recently, however, studies have incorporated the mixed effects of climate change and land-use to determine the extent of both their impact on the natural environment (Collingham et al. 2004, Thuiller 2004, de Chazal and Rounsevell 2009).

When biodiversity becomes threatened, its results can be seen through loss of food, shelter, and an increased risk in predation (Pimm and Raven 2000, Schipper et al. 2008). The term "defaunation" has recently been used to describe this phenomenon which is seen mainly in tropical and subtropical regions (Sanderson et al. 2002, Wilkie et al. 2011). Defaunation is defined as the loss of animals from an ecological community and unlike extinction, it includes declines in both species richness and abundance (Corlett 2013, Harrison et al. 2013, Periago et al. 2015). Tropical and subtropical biomes are usually the most affected (Torres et al. 2014).

Africa is an under-studied continent when it comes to the effects of climate and land-use changes and its impacts on species distribution (Parmesan and Yohe 2003, Sala et al. 2008, Norris et al. 2010). The continent is rich in biodiversity (Lee et al. 2011), and has eight of the 34 biodiversity hotspots in the world - the Succulent Karoo, Madagascar, and the Indian Ocean Islands, Horn of Africa, Guinean Forests of West Africa, Eastern Afromontane, Coastal Forests of Eastern Africa, the Cape Floristic Region and the Maputaland-Pondoland Albany (Brooks et al. 2002, Küper et al. 2004, Lee et al. 2011). Unfortunately, these biodiversity hotspots are under constant anthropogenic threats (Brooks et al. 2002). For instance, in the forests of West Africa, cash crops, such as cocoa (*Theobroma cacao*) and maize (*Zea mays*) are the primary agricultural outputs which have resulted in rapid deforestation rates (Holbech 2005, 2009).

Ghana, is a west African country with forests that are host to several threatened and endemic species (Yeboah 1998, Hill and Curran 2003). These forests are fragmented, disappearing and are being converted for agricultural purposes causing local plant and animal extinction (Searchinger et al. 2008, Gockowski and Sonwa 2011). With the rapid human population growth and urbanization, as at 2010, about 58000 km^2 of Ghana's forest area had been converted for economic benefits (Norris et al. 2010). Hundred and twenty four species of bats have been identified in Ghana (Hackman 2014), six of which are near-threatened – according to the IUCN Red List *Hipposideros abae* (Aba roundleaf bat), *Nycteris intermedia* (Intermediate slit-faced bat), *Hipposideros jonesi* (Jones's roundleaf bat), *Otomops martiensseni* (Large-eared free-tailed bat), *Scotonycteris ophiodon* (Pohle's fruit bat) and

Tadarida demonstrator (Mongalla free-tailed bat) (Mickleburgh et al. 2010) . *Epompos buettikoferi* (Buettikofer's epauletted fruit bat) is of conservation concern as they are endemic to the West African forests in Ghana (Stuart et al. 1990).

Despite the high bat species diversity in Ghana, there have been very few bat surveys (Grubb et al. 1998, Yeboah 1998, Hayman et al. 2012, Anti et al. 2015). These studies have usually been conducted in forest reserves, national parks, or specific areas of interest. For example, the Rapid Assessment program sponsored by Conservation International focused on high priority areas for mammal conservation in Ghana (Decher and Fahr 2005, McCullough et al. 2005, 2007). Historical surveys and bat research include those of - Rosevear's (1965) (*The bats of West Africa)*, Hayman and Hill's (1971) identification manual, a bat survey by Holbech (1999), and the 45-year-old study done by (Jeffrey 1975). There has not, however, been a published survey on the bats of Ghana since the 1998 publication by Grubb and co-authors titled - *Mammals of Ghana, Sierra Leone, and The Gambia* (Grubb et al. 1998). Recently, there have been some studies on other species in Ghana, using species-distribution modelling to investigate how climate and land-use changes affect species distribution and what it means for biodiversity (Yeboah 1998, Garshong 2013, Läderach et al. 2013, Amissah et al. 2014, van Andel et al. 2015, Ashiagbor and Danquah 2017, Penner et al. 2019).

This study employed bat species distribution and Species Distribution Modelling (SDM) to predict distribution of bat species in Ghana in relation to current scenarios of climate and land-use changes. It is essential to update bat-species distribution in Ghana. Ghana has nature reserves or forest reserves tasked with protecting areas with high animal diversity, however, added knowledge and understanding of the distribution patterns of bats in Ghana could help policymakers to focus their conservation efforts (Waldman et al. 2015). With the ecosystem services bats offer and the forest restoration plans Ghana has signed (African Forest Landscape

Restoration Initiative (AFR100) (WRI 2017), current knowledge information on the distribution of bats would assist the country accomplish this initiative. Furthermore, with the biological pest-control services bats provide, this information could assist farmers in using bats as pest control, rather than using insecticides that are harmful to wildlife (Stechert et al. 2014, Weier et al. 2018).

3.2. Methods and materials

3.2.1. Study area

The Republic of Ghana (5°5′39″N and 10°54′38″N latitudes, 0°05′04″E, and 3°14′12″W longitudes) is approximately 239000 km^2 (Gumma and Pavelic 2013). Ghana borders Côte d'Ivoire to the west, Burkina Faso to the north, the Atlantic Ocean to the south and Togo to the east (Figure 3.1). The country has three biotic zones (Savannah, Transitional Zone, and Forest) (Appiah et al. 2014). These zones were then sub-divided into six agro-ecological zones based on the climate, soil, and the natural vegetation in the country (National Biodiversity Strategy for Ghana 2002, Appiah et al., 2014). The six agro-ecological zones are the Savannah (Sudan, Guinea, and Coastal), Forest-Savannah Transitional Zone, the Semi-Deciduous Forest Zone, and the Rain Forest Zone (Figure 3.1). The Guinean and Sudanese Savannah are located along the Northern part of Ghana, with the Guinean region in a more north-easterly direction (Wongnaa and Awunyo-Vitor 2019). Both types of Savannah cover about 125430 km^2 with a tropical climate and wooded savannah vegetation (Asiedu et al. 2019, Wongnaa and Awunyo-Vitor 2019). The Guinean and Sudanese Savannah zone experience long periods of a dry climate, with the dry seasons occurring between October/November – April/May and the rainy season occurring between May and October (Wongnaa and Awunyo-Vitor 2019). Annual temperatures range from 27 – 35°C with a rainfall pattern that is unimodal and characterized by an average annual rainfall of 950 – 1300 mm during the rainy season (Addai and Owusu

2014, Asiedu et al. 2019, Atiah et al. 2019, Wongnaa and Awunyo-Vitor 2019). The Coastal Savannah agro-ecological zone is different from the other savannahs as it has two peaks of rainfall, namely, July as well as September-October (Wongnaa and Awunyo-Vitor 2019). The annual rainfall is bimodal and can range between 800 – 900 mm (Addai and Owusu 2014, Atiah et al. 2019). The Forest-Savannah transitional zone is located in the middle of Ghana and is a boundary between forest and savannah areas (Addai and Owusu 2014, Wongnaa and Awunyo-Vitor 2019). Due to its position, this zone experiences mixed weather patterns, with the climate being semi-equatorial and a savannah, woodland and forest belt vegetation (Addai and Owusu 2014, Atiah et al. 2019, Wongnaa and Awunyo-Vitor 2019). With the zone's bimodal rainfall, it can experience up to 1300 mm of rain annually and an annual temperature of approximately 26°C (Addai and Owusu 2014). Most of Ghana's forest is semi-deciduous covering about 66000 km^2 with a rainforest only covering about 633 km^2 (Addai and Owusu 2014, Wongnaa and Awunyo-Vitor 2019). The forest is situated at the southern part of Ghana; the rainforest is more southwest, it has a semi equatorial climate and is wet most of the year (Atiah et al. 2019). The forests have a bimodal rainfall pattern with rainfall of 1600 - 1800 mm annually and temperatures of up to 26.4°C (Addai and Owusu 2014, Atiah et al. 2019).

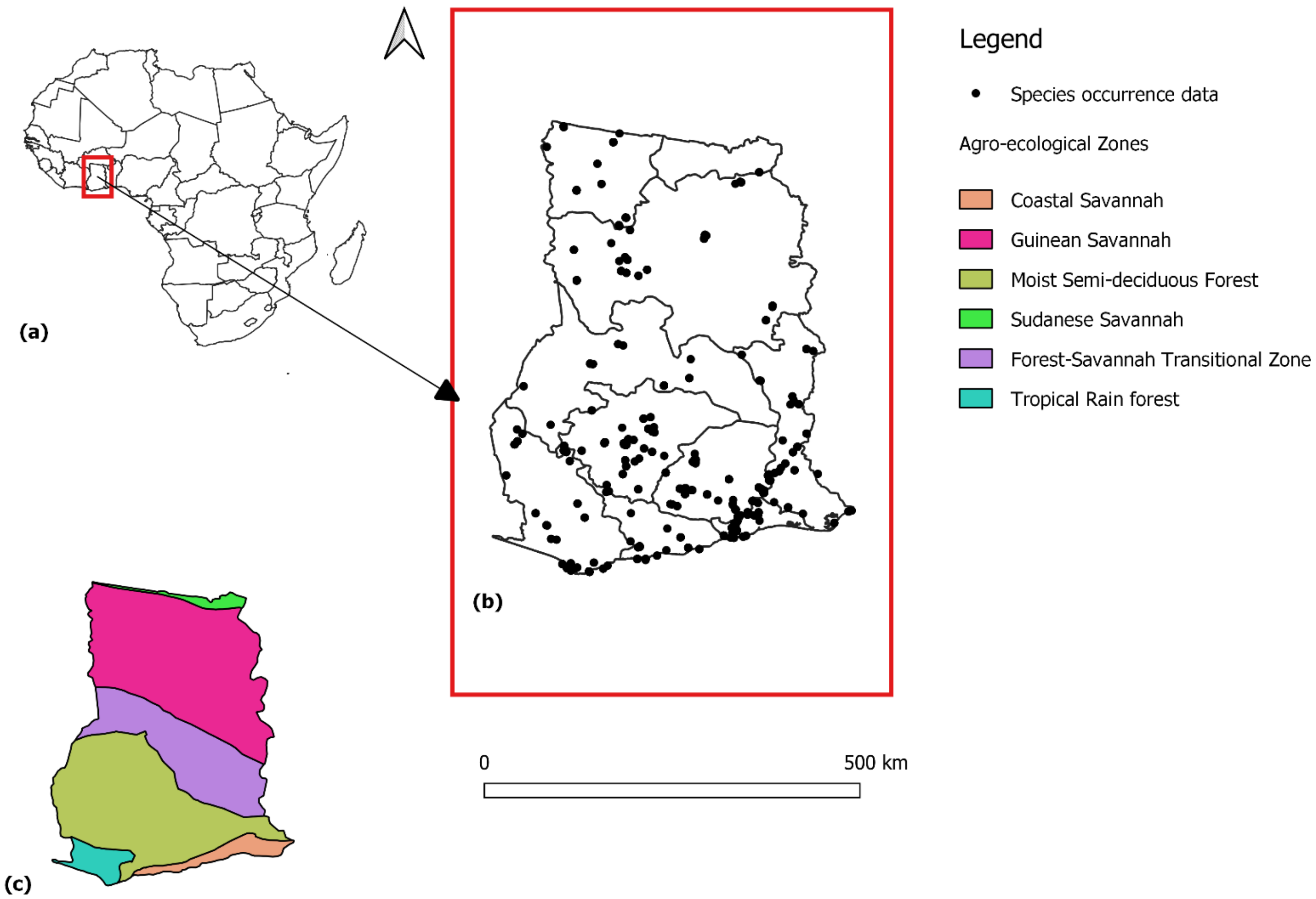

Figure 3.1: Study area, Ghana - (a) in relation to the African continent; (b) original species occurrence data for 95 bat species (see Table 1) in Ghana by the African Chiropteran Report (ACR) 2018, database https://africanbats.org/ (ACR 2018); (c) six agro-ecological zones of Ghana (Coastal Savannah, Guinean Savannah, Moist Semi-deciduous Forest, Sundanese Savannah, Forest-Savannah Transitional Zone, Tropical Rain Forest)

3.2.2. Locality records

Bat occurrence data were collected from the African Chiropteran Report (ACR) 2018 (ACR 2018). The ACR is a collection of information on bats in Africa complied by AfricanBats NPC (ACR 2015, 2018). ACR's database comprises of bat occurrence data collected from literature and museum databases, such as the American Museum of Natural History (AMNH), the British Museum of Natural History (BMNH), and the Field Museum of Natural History (FMNH), specifically, for the African continent (ACR 2018). In total, 5357 species-occurrence records were retrieved from the ACR database, 95 species across eight bat families (Appendix 1).

Emballonuridae (*n* = 6), Hipposideridae (*n* = *10*), Megadermatidae (*n* = *1*), Molossidae (*n* = *17*), Nycteridae (*n* = *8*), Pteropodidae (*n* = *17*), Rhinolophidae (*n* = *4*), Rhinopomatidae (*n* = *1*) and Vespertilionidae (*n* = *31*). ArcGIS version 10.2.2 (ESRI 2014) was used to filter the occurrence records of bats obtained from ACR distribution records. This was done to make sure there were no species records with no co-ordinates, records that had the family name rather than species name as well as any points that were located in water bodies. Furthermore, to avoid spatial bias, bat species with less than ten locality data points were not included in the final analysis (Stockwell and Peterson 2002, Blach-Overgaard et al. 2010, Smith et al. 2016). This reduced the bat species to 42 species across seven families with valid records (Table 3.1). Species count in each family were: Emballonuridae (*n* = 1), Hipposideridae (*n* = *8*), Molossidae (*n* = *7*), Nycteridae (*n* = *6*), Pteropodidae (*n* = *12*), Rhinolophidae (*n* = *1*) and Vespertilionidae (*n* = *7*).

3.2.3. Environmental variables

The environmental variables selected for this study were land-use cover, which was categorical and climate data that was continuous; Maximum Entropy (MaxEnt) was used for the SDM (Phillips 2017). 19 bioclimatic variables were downloaded from Worldclim 2.0 (Hijmans et al. 2005). The Worldclim 2.0 data were climate data collected for the years 1970 – 2000 (Hijmans et al. 2005). The highest resolution was used for all eco-geographical variables (EGV) (30 arc seconds, ~900 m^2, 0.0083° x 0.0083°) (Hijmans et al. 2005, Fick and Hijmans 2017). Pearsons' correlation test was performed to remove highly-correlate climatic variables influencing the model's performance; EGVs pairs with 0.75 or higher were removed using the SDM toolbox (Brown 2014). Based on the SDM toolbox, eight out of the 19 climatic variables were selected (Table 3.2). The land-use and land-cover data were sourced from West African Land Use

Dynamics Project (Cotillon 2017). The land-use data from 2013, with a resolution of 2 km^2 was selected for this modelling exercise (Table 3.2) (Cotillon 2017, Tappan et al. 2017).

Data on the agro-ecological zones of Ghana were sourced from the World Wide Fund for Nature's (WWF) Terrestrial Ecoregions of the World (Olson et al. 2001) (Table 3.2). All data layers were projected and formatted using ArcGIS version 10.2.2 (ESRI 2014) to have the same projection, spatial extent, grid cell size and alignment (Elith et al. 2006, Phillips et al. 2006). The projection used was the World Geodetic System Universal Transverse Mercator (WGS '84 UTM) zone 30 North (Gumma and Pavelic 2013). All projections and layers were extracted and clipped to the boundaries of Ghana (Aduah and Baffoe 2013).

3.2.4. Modelling procedure and evaluation

As presence-only data were available, a program like MaxEnt (Phillips 2017) that uses a modelling algorithm to predict distributions using eco-geographical variables as restrictions was used for the SDMs (Elith et al. 2006, Phillips et al. 2006, Franklin and Miller 2010, Schoeman et al. 2013). Presence-only SDMs were generated using MaxEnt v3.4.1 (Franklin and Miller 2010, Merow et al. 2016, Phillips 2017). Eight climatic variables (continuous) and one land-use (categorical) parameter were used for bat species models to ensure that model comparisons would be possible (Table 3.2). The model calculations were made using the MaxEnt logistical output (Phillips 2017). Following standard procedure, 80% of the occurrence records were used to train the model, while 20% were used to test it (Phillips 2017). Model performance was assessed using the area under the curve (AUC) of the receiver-operator's characteristics (ROC) value (Phillips et al. 2004, Cooper-Bohannon et al. 2016, Phillips 2017). The AUC value was an indicator of the prediction accuracy of the model. The AUC values ranged from 0 to 1, with higher values indicating a better model fit (Lobo et al. 2008, Hijmans 2012, Yang et al. 2013). According to Young et al., (2011), values over 0.75 are categorized as ‘accurate models’, whereas AUC values of 0.5 indicate a prediction which is not different to a random value (Phillips and Dudík 2008). The Jack-knife analysis of gain was used, as it is popularly used to evaluate which environmental variables are most relevant or have contributed the most to the models (Pearson et al. 2007, Yang et al. 2013, Smith et al. 2016).

3.2.5. Prediction of species distribution

MaxEnt produces logistical output maps, showing the distinction between the modelled suitability of different areas (Elith et al. 2011). The non-binary maps that were generated by MaxEnt were reclassified to distinguish between partial absence (0) and presence (1), using the logistical threshold (Cooper-Bohannon et al. 2016); this was based on “Maximising the training for sensitivity and specificity” (Liu et al. 2016). Maps showing the probability of species presence and absence in Ghana, were created using ArcGIS version 10.2.2 (ESRI 2014); these maps were created for each species and each family to model the potential geographic distribution of the different species, across Ghana.

3.2.6. Species distribution within agro-ecological zones and land-use

Maps generated for each species of bats in Ghana were used to calculate the potential suitable area per agro-ecological zone as a percentage of the total, relative to the whole agro-ecological zone for each species (Table 3.3) (Cooper-Bohannon 2015, Cooper-Bohannon et al. 2016). The results helped determine which agro-ecological zone and land-use each species associated with, as this procedure was repeated for land-use (Franklin 2010, Merow et al. 2016). The maps also assisted with calculating the potentially suitable area (km^2) as well as determining the percentage cover (%) for each species, within the agro-ecological zone and land-use, in terms of the study area (Ghana) (Table 3.3) (Cooper-Bohannon et al. 2016).

Table 3.1: Number of bat species locality records obtained from the African Chiropteran Report (ACR 2018) used for MaxEnt modelling, showing 42 species across seven families with a total of 4724 locality records

Bat species	**Family**	**Initial points**
Chaerephon leucogaster	Molossidae	42
Chaerephon major	Molossidae	41
Chaerephon pumilus	Molossidae	134
Doryrhina cyclops	Hipposideridae	70
Eidolon helvum	Pteropodidae	70
Epomophorus gambianus	Pteropodidae	619
Epomops buettikoferi	Pteropodidae	88
Epomops franqueti	Pteropodidae	336
Glauconycteris poensis	Vespertilionidae	33
Hipposideros beatus	Hipposideridae	20
Hipposideros caffer	Hipposideridae	264
Hipposideros fuliginosus	Hipposideridae	70
Hipposideros jonesi	Hipposideridae	26
Hipposideros ruber	Hipposideridae	79
Hipposideros tephrus	Hipposideridae	120
Hypsignathus monstrosus	Pteropodidae	40
Macronycteris gigas	Hipposideridae	21
Megaloglossus azagnyi	Pteropodidae	69
Micropteropus pusillus	Pteropodidae	397
Mimetillus moloneyi	Vespertilionidae	10
Mops (Mops) condylurus	Molossidae	512
Mops (Xiphonycteris) brachypterus	Molossidae	98
Mops (Xiphonycteris) spurrelli	Molossidae	61
Mops (Xiphonycteris) thersites	Molossidae	336
Myonycteris angolensis	Pteropodidae	45
Myonycteris leptodon	Pteropodidae	101
Nanonycteris veldkampii	Pteropodidae	73
Afronycteris nana	Vespertilionidae	57

Pseudoromicia tenuipinnis	Vespertilionidae	23
Nycteris arge	Nycteridae	20
Nycteris gambiensis	Nycteridae	144
Nycteris grandis	Nycteridae	28
Nycteris hispida	Nycteridae	145
Nycteris macrotis	Nycteridae	297
Nycteris thebaica	Nycteridae	22
Rhinolophus landeri	Rhinolophidae	16
Rousettus aegyptiacus	Pteropodidae	15
Scotonycteris occidentalis	Pteropodidae	29
Scotophilus dinganii	Vespertilionidae	36
Scotophilus leucogaster	Vespertilionidae	28
Scotophilus viridis	Vespertilionidae	67
Taphozous perforatus perforatus	Emballonuridae	22

Table 3.2: Environmental variables used for MaxEnt modelling of species distributions of different bat species from occurrence records in Ghana.

Variable categories	Description	Source
Climate	BIO1 - Annual Mean Temperature **(°C)** BIO2 – Mean diurnal temperature range (mean of monthly (max temp – min temp)) **(°C)** BIO6 - Minimum temperature of coldest month **(°C)** BIO8 – Mean temperature of wettest quarter **(°C)** BIO12 - Annual Precipitation BIO16 – Precipitation of wettest quarter (mm)	WorldClim – Global Climate Data (1970-2000) (Hijmans et al. 2005) http://www.worldclim.org/
Land cover	West Africa Land cover (2013)	(CILSS 2016) https://eros.usgs.gov/westafrica/data-downloads

3.3. Results

3.3.1. Model performance

For Pteropodidae, model performance for both test and training AUC was above 0.70, except for *Megaloglossus azagnyi*, which had an AUC test value of 0.50. For Hipposideridae, AUC values ranged from 0.77 – 0.92 and for training 0.51 - 0.99. *Hipposideros ruber* had an AUC test data value of 0.50. One species represented both Emballonuridae and Rhinolophidae each; *Rhinolophus landeri* and *Taphozous perforates perforatus*; both had poor AUC test values (0.17 and 0.41, respectively), likely suggesting model overfitting. In Nycteridae, two species *Nycteris gambianis* and *N. thebiaca* had a poor model performance with AUC data values below 0.60, therefore, the accuracy of their occupancy predictions could be skewed. Molossidae had AUC test and training values ranging between 0.44 – 0.97 and 0.83 – 0.96, respectively, except for *Chaerephon pumilus*, which was the only species with an inferior model performance, with an AUC test value of 0.44. For Vespertilionidae, the AUC values ranged from 0.74 – 0.93 for training and 0.31 – 0.90 for test values.

3.3.2. Variable contribution and distribution

The modelled distributions of 31 species were influenced by land-use (Table 3.3). The mean diurnal range influenced the modelled distributions of six species. For three species (*Megaloglossus azagnyi*, *Micropteropus pusillus,* and *Afronycteris nana*), the modelled distributions were influenced by annual mean temperature. For two species (*Chaerephon major* and *Scotophilus viridis*), modelled distributions were influenced by annual mean precipitation. Results showed that coastal savanna had the highest number of species, at 37.65%, followed by moist semi-deciduous forest at 31.73%. The tropical rain forest showed the least number of species, at 6.82%. The species modelled were predicted to occupy the Moist semi-deciduous forest, followed by Guinea savannah, then the Coastal savannah (Table 3.4).

a. Pteropodidae

The land-use variable was the best predictor of species distribution for the species in Pteropodidae (Table 3.3). Annual mean temperature contributed to two of the species' modelled distribution - *Megaloglossus azagnyi* and *Micropteropus pusillus. Epomops buettikoferi's* distribution was influenced by the mean diurnal range, with a 50% contribution (Table 3.3). The species under this family were predicted to occupy the moist deciduous agro-ecological zone and agriculture areas (Table 3.5), however, *Epomophorus gambianus'* distribution favoured the Guinean savanna when it came to agro-ecological zones (Figure 3.2; Table 3.4). *Nanonycteris veldkampii* was predicted to occupy degraded forests and *Rousettus aegyptiacus* to occupy the forests when it came to land-use (Figure 3.2; Table 3.4).

b. Hipposideridae

Land-use variables were the best predictor of species distribution with Hipposideridae (Table 3.3), however, *Hipposideros tephrus* distribution was influenced by the mean diurnal range with 89.60% of the contribution. *Hipposideros beatus* was modelled to cover more of the study area than any other Hipposideridae species, 24.89% (Figure 3.3; Table 3.4). Hipposideridae were predicted to occupy moist deciduous forests and agricultural lands, however, *H. fuliginosus* was found to occupy the forests.

c. Emballonuridae & Rhinolophidae

Both species' distributions in these families were influenced by mean diurnal range, with 50.33% for *Taphozous perforates perforates* and 42.15% for *Rhinolophus landeri* (Table 3.3). They were predicted to occupy the agro-ecological zone of moist deciduous forest, however, when it came to land-use, *T. perforates perforates* occupied the savanna, whereas *Rhinolophus landeri* was modelled to occupy the agricultural lands (Figure 3.4; Table 3.4).

d. Nycteridae

Land-use was the most substantial contributor to the modelled distribution of all six species represented by Nycteridae, with an average of 66.14% contribution (Table 3.3). Nycteridae were predicted to occupy the moist deciduous forest agro-ecological zone and agricultural lands (Figure 3.5; Table 3.4). *Nycteris gambianis* was modelled in the Guinean savanna agro-ecological zone with a savannah land-use, whereas *N. thebiaca* was predicted to occupy the Guinean savanna agro-ecological zone (Figure 3.5; Table 3.4).

e. Molossidae

The distributions in Molossidae were influenced by land-use. *Chaerephon major,* had a 54.7% from the annual precipitation for this specific species distribution model, and *Mops spurrelli*'s species distribution was influenced by mean diurnal range (Table 3.3). Considering the distribution throughout Ghana, out of the seven species, six were predicted to occupy the moist deciduous forest agro-ecological zone and land with an agricultural land-use (Figure 3.6; Table 3.4). *Chaerephon. pumilus* was shown to occupy the coastal savanna biotic zone, and *C. major* also occupied areas with savanna land-use (Figure 3.6; Table 3.4).

f. Vespertilionidae

Land-use was the contributor to four of the species' distribution for Vespertilionidae (Table 3.3). However, *Glauconycteris poensis* had mean diurnal range contribute of 66.51% for its species distribution, *Afronycteris nana* with 58.22% of annual mean temperature contribution, and *Scotophilus viridus* with an annual precipitation contribution of 47.21% (Table 3.3). *Scotophilus dinganii, S. leucogaster,* and *S. viridis* were predicted to occupy areas of savanna land-use (Table 3.4). Those same species were also predicted to occupy the Guinean savanna agro-ecological zone (Figure 3.7; Table 3.4). The other four were predicted to occupy the moist deciduous forest agro-ecological zone and places of agricultural land-use (Figure 3.7; Table 3.4).

Table 3.3: Predictor bioclimatic variables for bat species and the percentage contribution (%) from Species Distribution Modelling (SDM) based on MaxEnt using African Chiropteran Report (ACR) species occurrence records for Ghana. The figures in bold text indicate the bioclimatic variables that had the highest contribution to the SDMs. (AMT – annual mean temperature, AP – annual mean precipitation, MDR – mean diurnal range, MTC – minimum temperature of the coldest month, TCQ – temperature of the coldest quarter, TWQ – temperature of the wettest quarter)

Species	AP	MDR	MTC	TCQ	TWQ	AMT	LU
			Pteropodidae				
Eidolon helvum	0.00	0.00	0.00	0.00	0.00	**20.47**	**79.53**
Epomophorus gambianus	**35.02**	0.00	0.00	3.61	0.00	3.30	**58.06**
Epomops buettikoferi	14.25	**49.95**	0.45	0.00	0.00	0.00	**35.35**
Epomops franqueti	0.16	3.33	0.00	0.00	2.11	**22.41**	**72.00**
Hypsignathus monstrosus	2.55	**20.55**	0.00	0.00	0.02	16.88	**60.01**
Megaloglossus azagnyi	14.42	21.79	0.00	0.14	3.38	**33.59**	**26.69**
Micropteropus pusillus	**32.15**	2.53	0.00	0.88	2.74	**36.20**	25.51
Myonycteris angolensis	0.00	0.40	0.00	0.00	0.00	**40.47**	**59.13**
Myonycteris leptodon	20.84	18.99	0.00	0.00	0.00	**22.64**	**37.54**
Nanonycteris veldkampii	0.00	0.00	0.00	**0.02**	0.00	0.00	**99.98**
Rousettus aegyptiacus	0.00	0.00	0.00	0.00	0.00	**2.00**	**98.00**
Scotonycteris occidentalis	**48.29**	0.00	0.00	0.00	0.00	1.27	**50.44**
			Hipposideridae				
Doryrhina cyclops	0.00	7.06	0.00	**7.44**	0.00	0.82	**84.68**
Hipposideros beatus	0.00	**11.54**	0.00	0.00	4.19	7.64	**76.62**
Hipposideros caffer	9.45	17.81	3.78	**19.36**	0.00	7.51	**42.08**
Hipposideros fuliginosus	0.00	**22.47**	0.00	0.00	0.00	3.27	**74.26**
Hipposideros jonesi	7.65	**13.50**	0.00	1.40	0.00	1.77	**75.69**
Hipposideros ruber	0.33	0.74	1.43	**19.75**	0.36	0.27	**77.12**

Hipposideros tephrus	0.00	**89.60**	0.00	0.00	0.00	0.00	**10.40**
Macronycteris gigas	**17.76**	0.00	0.74	0.00	0.35	0.00	**81.15**
Rhinolophidae							
Rhinolophus landeri	0.00	**42.15**	**34.42**	0.00	0.00	0.00	23.43
Emballonuridae							
Taphozous perforatus perforatus	**27.64**	**50.33**	0.00	0.00	0.00	2.15	19.89
Nycteridae							
Nycteris arge	**26.88**	0.00	0.00	0.00	0.00	0.18	**72.94**
Nycteris gambiensis	9.04	8.59	**39.07**	0.00	3.03	0.00	**40.27**
Nycteris grandis	1.19	0.00	0.00	0.00	0.19	**26.15**	**72.47**
Nycteris hispida	8.43	0.63	**13.38**	0.45	0.45	3.19	**73.46**
Nycteris macrotis	**19.68**	7.79	1.58	1.56	1.41	16.87	**51.11**
Nycteris thebaica	0.00	**9.92**	3.40	0.00	0.00	0.00	**86.67**
Molossidae							
Chaerephon leucogaster	**14.10**	13.55	0.00	0.06	0.00	0.00	**72.29**
Chaerephon major	**54.72**	**40.80**	0.00	0.00	0.00	4.41	0.07
Chaerephon pumilus	**40.10**	1.41	0.00	2.25	0.00	0.00	**56.25**
Mops (Mops) condylurus	11.37	**36.38**	0.15	0.00	0.14	0.00	**51.96**
Mops (Xiphonycteris) brachypterus	0.00	**27.03**	0.00	0.00	0.00	0.00	**72.97**
Mops (Xiphonycteris) spurrelli	0.00	**55.68**	0.00	0.00	0.00	0.72	**43.61**
Mops (Xiphonycteris) thersites	**44.95**	0.00	0.00	0.00	0.00	0.09	**54.96**
Vespertilionidae							
Glauconycteris poensis	3.30	**66.51**	0.00	0.00	0.00	3.27	**26.92**
Mimetillus moloneyi	0.01	0.00	0.00	**0.12**	0.00	0.00	**99.87**
Afronycteris nana	3.99	1.51	0.00	0.00	0.00	**58.22**	**36.29**
Pseudoromicia tenuipinnis	1.82	0.00	0.00	0.00	0.00	**20.08**	**78.11**
Scotophilus dinganii	**15.56**	0.00	0.00	0.14	0.00	0.00	**84.30**
Scotophilus leucogaster	0.00	0.00	**4.76**	0.00	0.00	0.00	**95.24**
Scotophilus viridis	**47.21**	0.00	0.00	0.86	14.23	0.00	**37.71**

Table 3.4: Prediction of Species distribution within Agro-ecological zones and land-use from Species Distribution Modelling (SDM) in MaxEnt (Phillips 2008) using the logistic threshold value that "Maximizing the training for sensitivity and specificity" (Liu et al. 2016). The values in bold text indicate the agro-ecological zones and land-use variables that had the highest percentage cover to the SDMs.

Species	Agro-ecological zones						Land-use				
	Tropical Rain forest	**Coastal Savannah**	**Transitional Zone**	**Moist deciduous**	**Guinea Savannah**	**Savannah**	**Forest**	**Savannah**	**Agriculture**	**Settlements**	**Degraded Forests**
					Pteropodidae						
Eidolon helvum	3.33	3.13	11.40	**32.92**	6.63	0.00	5.18	14.93	**20.19**	1.46	11.43
Epomophorus gambianus	0.00	3.00	0.95	7.59	**12.42**	1.03	0.06	8.43	**12.40**	0.93	1.84
Epomops buettikoferi	3.33	1.18	0.64	**10.26**	0.03	0.00	2.09	0.10	**6.67**	0.87	4.67
Epomops franqueti	1.52	1.77	0.98	**16.92**	1.20	0.00	0.79	1.36	**12.49**	1.17	6.06
Hypsignathus monstrosus	2.58	1.83	2.21	**21.28**	1.64	0.00	1.34	1.97	**15.60**	1.30	8.67
Megaloglossus azagnyi	1.92	0.50	0.58	**12.02**	0.23	0.00	1.09	0.23	**8.06**	0.69	4.88
Micropteropus pusillus	0.00	2.54	2.93	**14.87**	8.10	0.00	0.72	9.32	**11.97**	1.10	4.23
Myonycteris angolensis	1.01	0.31	0.85	**14.71**	0.50	0.00	0.64	1.07	**9.95**	0.48	4.97
Myonycteris leptodon	2.55	0.40	0.15	**4.63**	0.05	0.00	1.23	0.17	**3.01**	0.70	2.32
Nanonycteris veldkampii	0.09	0.41	0.28	**3.08**	0.26	0.00	0.20	0.13	1.03	0.64	**2.00**
Rousettus aegyptiacus	0.61	0.40	0.10	**4.48**	0.22	0.00	**2.83**	0.16	1.07	0.63	1.09

Scotonycteris occidentalis	1.91	0.03	0.48	**9.94**	0.01	0.00	0.64	0.14	**6.66**	0.62	4.02
Hipposideridae											
Doryrhina cyclops	1.36	1.91	0.99	**18.28**	0.20	0.00	0.92	1.20	**12.10**	1.17	6.16
Hipposideros beatus	1.52	1.83	2.35	**19.08**	0.03	0.00	1.79	2.23	**13.01**	1.19	6.05
Hipposideros caffer	0.41	1.54	0.16	**12.41**	0.19	0.00	1.61	0.97	**7.14**	0.86	3.67
Hipposideros fuliginosus	2.59	1.31	0.08	**7.32**	0.25	0.00	**4.48**	0.22	3.20	0.68	2.59
Hipposideros jonesi	1.29	0.49	0.27	**10.60**	0.03	0.00	0.42	0.23	**6.95**	0.95	3.94
Hipposideros ruber	0.87	0.10	1.06	**11.20**	1.27	0.00	1.37	0.75	**5.94**	0.33	5.81
Hipposideros tephrus	3.33	3.16	0.02	**14.61**	0.01	0.00	3.06	1.20	**9.00**	0.93	5.98
Macronycteris gigas	3.31	0.40	0.17	**13.21**	0.18	0.00	4.68	0.07	**5.97**	0.82	5.31
Rhinolophidae											
Rhinolophus landeri	3.24	3.21	0.05	**7.53**	0.03	0.00	1.75	1.74	**5.48**	0.77	3.39
Emballonuridae											
Taphozous perforatus perforatus	0.37	3.30	4.06	**7.75**	5.90	0.00	0.45	**12.19**	5.72	0.55	1.27
Nycteridae											
Nycteris arge	2.42	0.97	2.30	**16.76**	3.09	0.00	0.99	2.27	**14.39**	1.17	6.09
Nycteris gambiensis	0.04	1.09	3.76	14.58	**31.28**	1.42	0.76	21.57	**21.72**	0.68	4.62
Nycteris grandis	3.17	0.58	0.74	**19.61**	0.47	0.00	3.78	1.21	**9.83**	1.08	8.14
Nycteris hispida	0.00	1.19	0.07	**1.38**	1.06	0.03	0.16	0.54	**1.66**	0.65	0.53
Nycteris macrotis	0.06	3.11	1.99	**8.44**	1.98	0.00	0.06	5.25	**7.07**	0.66	1.66

Nycteris thebaica	0.00	0.02	0.51	2.43	**14.52**	1.40	0.36	7.27	**8.89**	0.18	1.04
Molossidae											
Chaerephon leucogaster	0.21	3.30	0.77	**9.30**	0.03	0.05	0.73	3.31	**5.69**	0.83	2.37
Chaerephon major	0.30	3.30	2.95	**17.02**	8.97	0.52	1.81	**12.72**	11.73	0.84	4.37
Chaerephon pumilus	0.00	**2.45**	0.01	0.90	0.18	0.31	0.01	1.15	**1.53**	0.44	0.20
Mops (Mops) condylurus	0.55	3.04	0.02	**3.19**	0.00	0.00	0.33	0.93	**3.14**	0.68	1.13
Mops (Xiphonycteris) brachypterus	1.29	1.43	0.14	**16.46**	0.00	0.00	0.47	0.97	**11.47**	0.55	5.52
Mops (Xiphonycteris) spurrelli	3.33	2.95	1.79	**21.88**	0.18	0.00	3.13	2.09	**14.66**	1.25	7.85
Mops (Xiphonycteris) thersites	2.13	0.12	1.10	**12.04**	0.05	0.00	0.78	0.41	**8.68**	0.44	4.83
Vespertilionidae											
Glauconycteris poensis	3.26	1.89	0.04	**13.30**	0.00	0.00	2.00	0.42	**9.34**	1.02	5.29
Mimetillus moloneyi	1.29	0.13	1.95	**11.76**	1.99	0.00	0.43	1.19	**10.13**	0.43	4.54
Afronycteris nana	1.93	2.68	3.00	**28.24**	3.35	0.00	3.96	6.28	**17.00**	1.36	9.56
Pseudoromicia tenuipinnis	1.29	0.53	0.42	**12.89**	0.05	0.00	0.62	0.55	**8.25**	1.01	4.53
Scotophilus dinganii	0.00	2.47	0.04	0.82	**16.35**	1.42	0.01	**12.89**	6.02	0.72	0.09
Scotophilus leucogaster	0.00	0.40	4.73	9.81	**32.72**	1.42	1.21	**24.34**	16.13	1.00	3.25

Scotophilus viridis	0.00	1.57	1.00	1.41	**16.40**	1.42	0.29	**12.73**	6.50	0.56	0.49

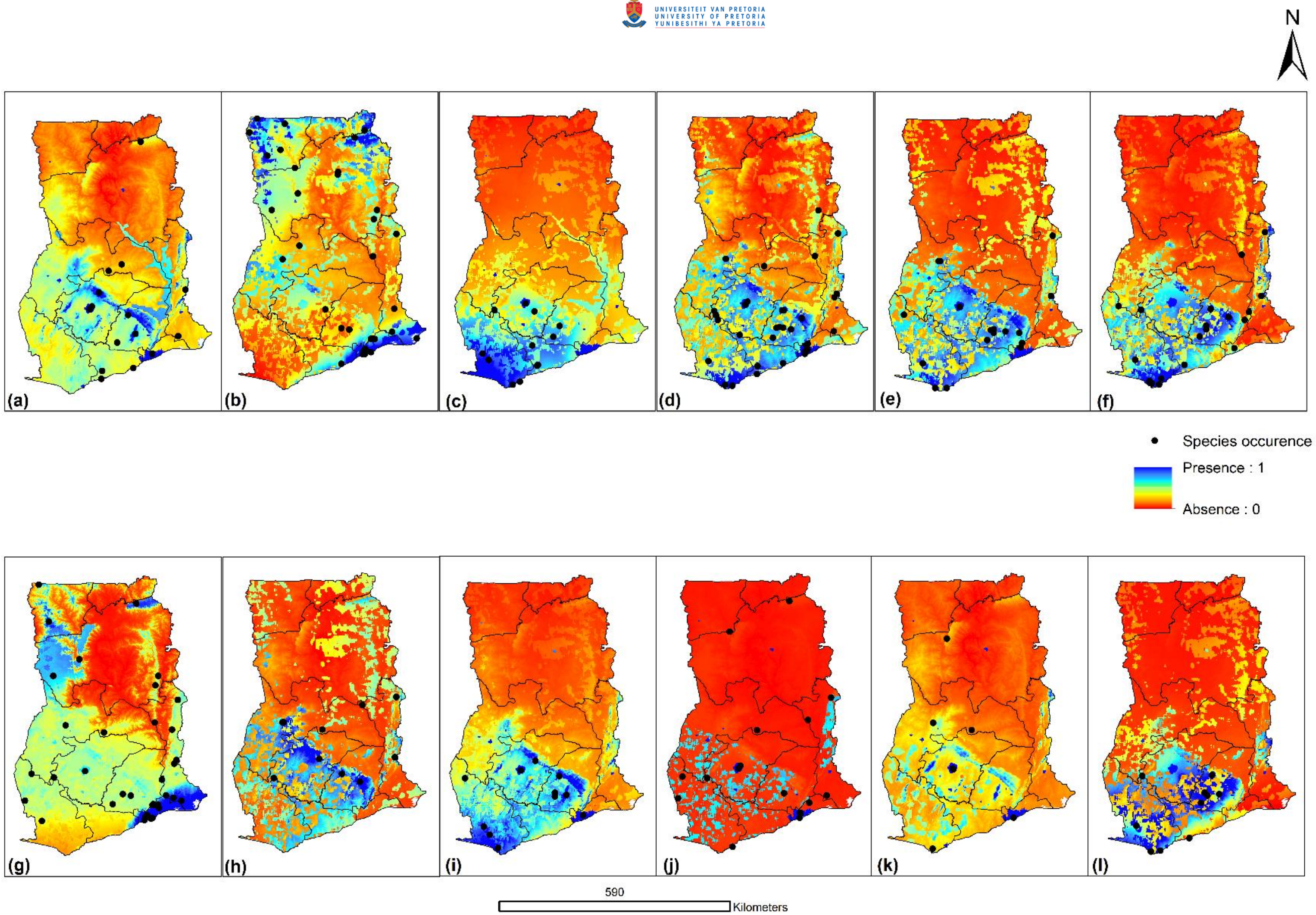

Figure 3.2: Presence-absence maps generated for the current predicted distribution of Pteropodidae where (a) is *Eidolon helvum*, (b)*Epomophorus gambianus*, (c) *Epomops buettikoferi*, (d) *Epomops franqueti*, (e) *Hypsignathus monstrosus*, (f) *Megaloglossus azagnyi*, (g) *Micropteropus pusillus*, (h) *Myonycteris angolensis*, (i) *Myonycteris leptodon*, (j) *Nanonycteris veldkampii*, (k) *Rousettus aegyptiacus, and* (l) *Scotonycteris occidentalis*. Known occurrence records are illustrated in black. Shades closer to blue predict suitable areas (presence) whereas the shades closer to red predict unsuitable areas (absence).

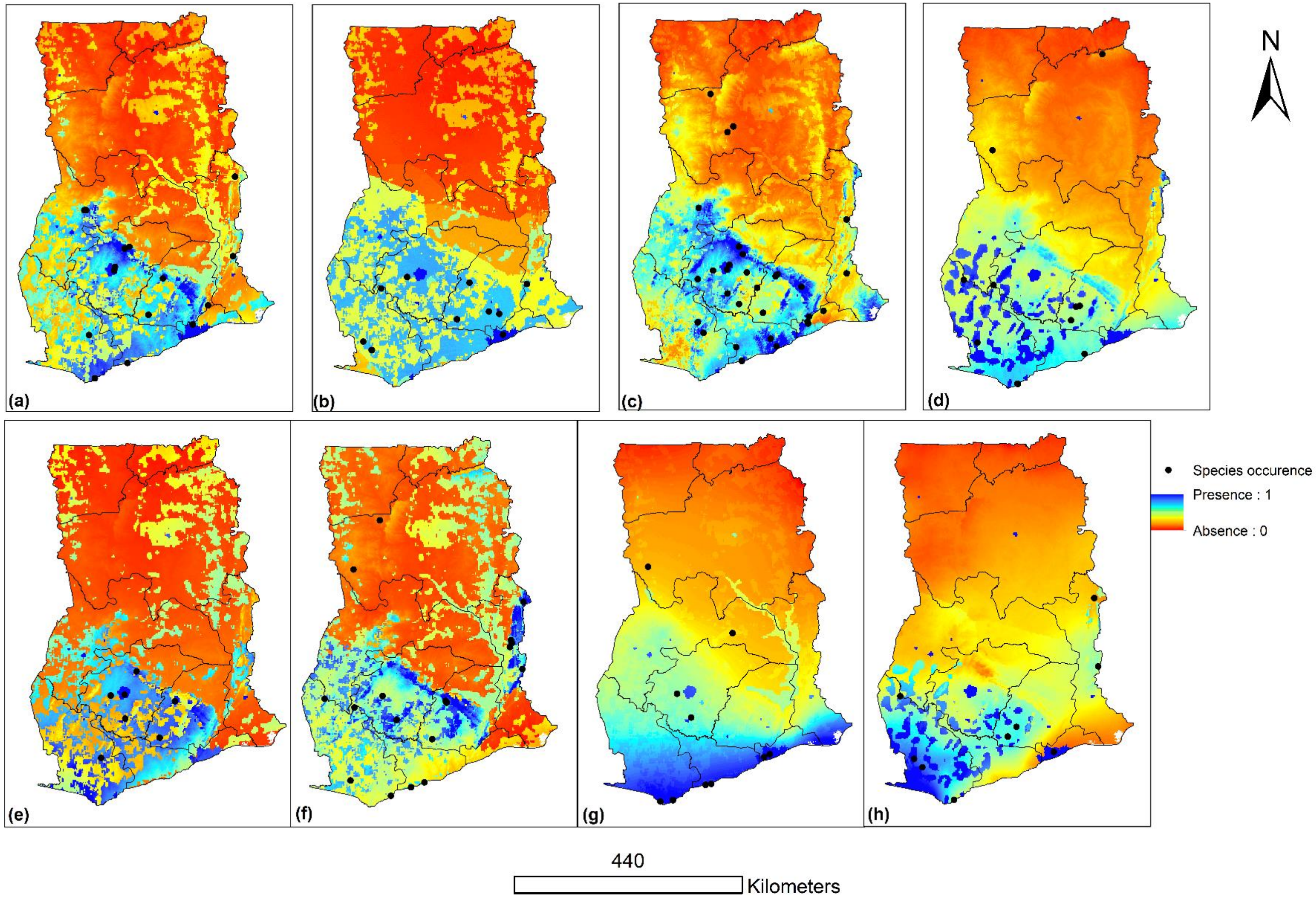

Figure 3.3: Presence-absence maps generated for the current predicted distribution of Hipposideridae where (a) is *Doryrhina cyclops*, (b) *Hipposideros beatus*, (c) *Hipposideros caffer*, (d) *Hipposideros fuliginosus*, (e) *Hipposideros jonesi*, (f) *Hipposideros ruber*, (g) *Hipposideros tephrus*, and (h) *Macronycteris gigas*. Known occurrence records are illustrated in black. Shades closer to blue predict suitable areas (presence) whereas the shades closer to red predict unsuitable areas (absence).

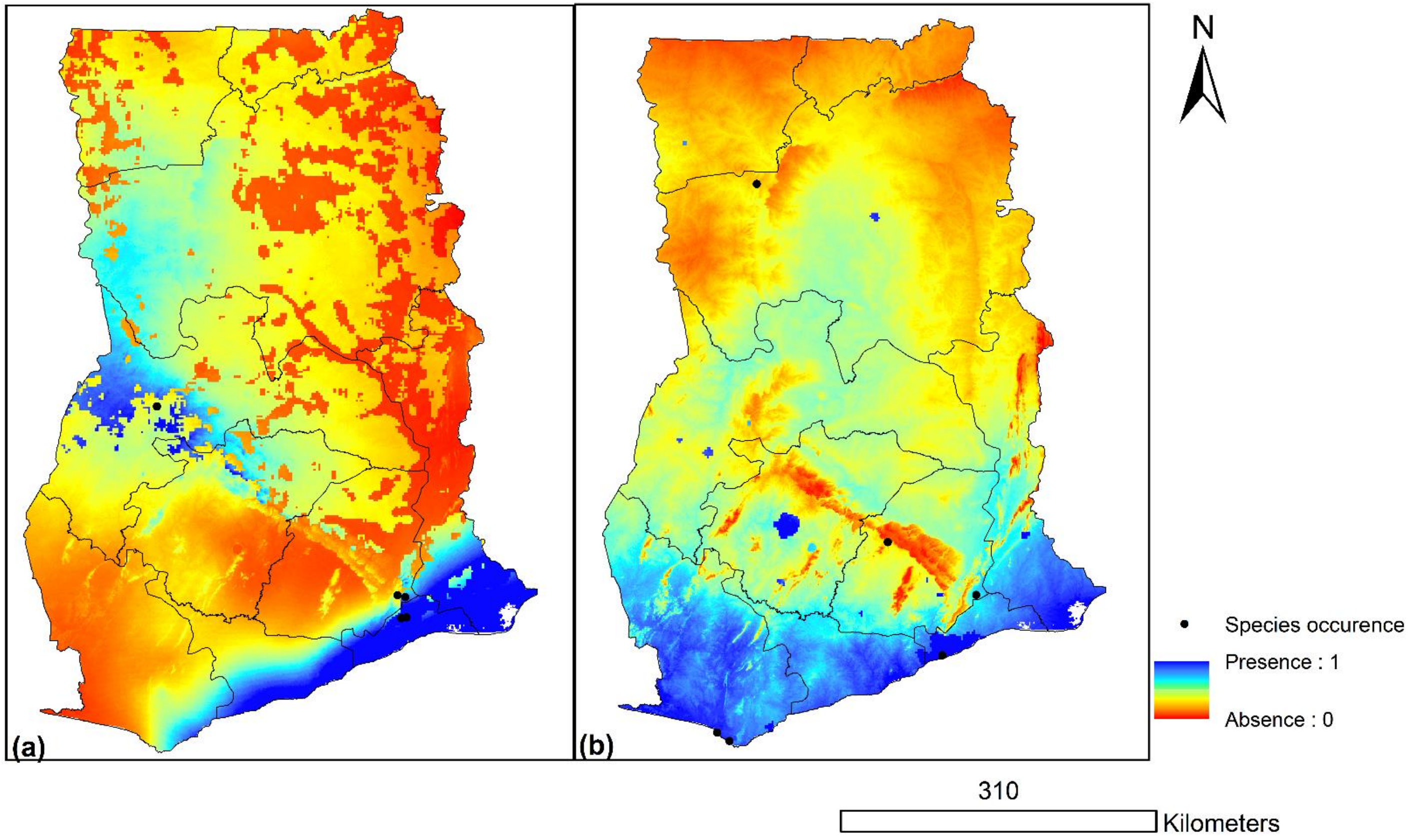

Figure 3.4: Presence-absence maps generated for the current predicted distribution of Rhinolophidae and Emballonuridae where (a) is *Rhinolophus landeri*, and (b) *Taphozous perforatus perforates*. Known occurrence records are illustrated in black. Shades closer to blue predict suitable areas (presence) whereas the shades closer to red predict unsuitable areas (absence).

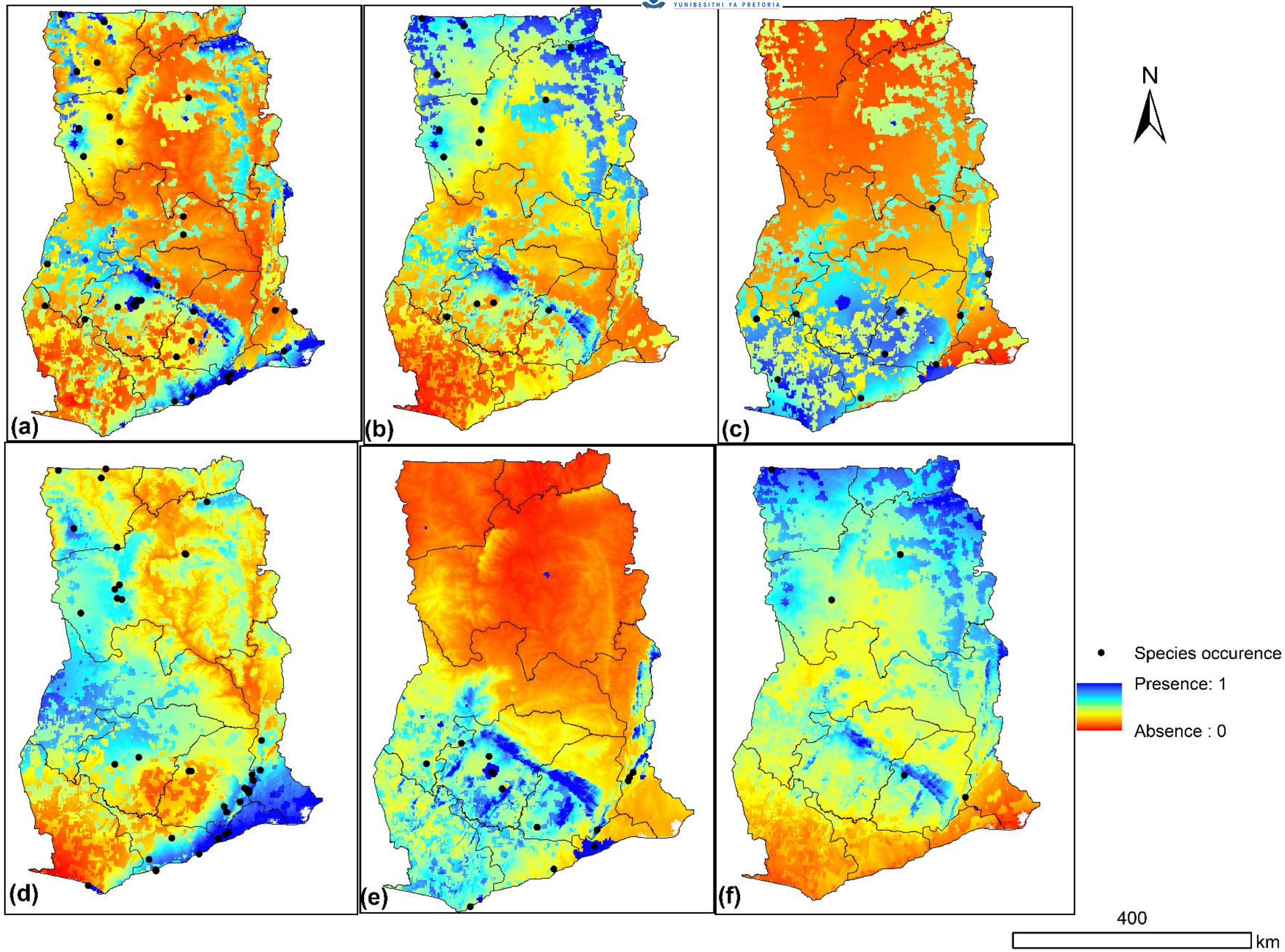

Figure 3.5: Presence-absence maps generated for the current predicted distribution of Nycteridae where (a) is *Nycteris arge*, (b) *Nycteris gambiensis*, (c) *Nycteris grandis*, (d) *Nycteris hispida*, (e) *Nycteris macrotis*, and (f) *Nycteris thebaica*. Known occurrence records are illustrated in black. Shades closer to blue predict suitable areas (presence) whereas the shades closer to red predict unsuitable areas (absence).

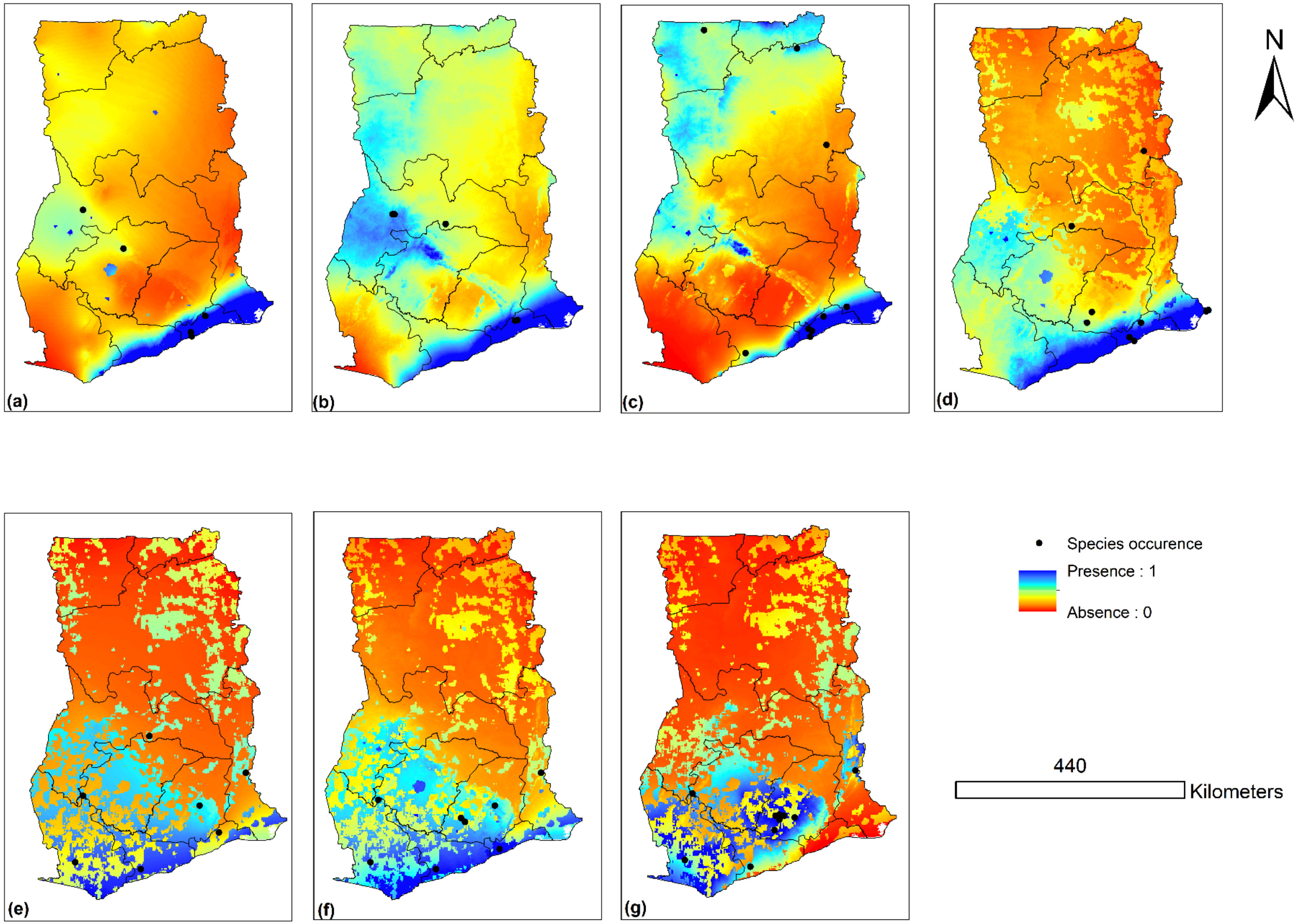

Figure 3.6: Presence-absence maps generated for the current predicted distribution of Molossidae where (a) is *Chaerephon leucogaster*, (b) *Chaerephon major*, (c) *Chaerephon pumilus*, (d) *Mops (Mops) condylurus*, (e) *Mops (Xiphonycteris) brachypterus*, (f) *Mops (Xiphonycteris) spurrelli*, and (g) *Mops (Xiphonycteris) thersites* Known occurrence records are illustrated in black. Shades closer to blue predict suitable areas (presence) whereas the shades closer to red predict unsuitable areas (absence).

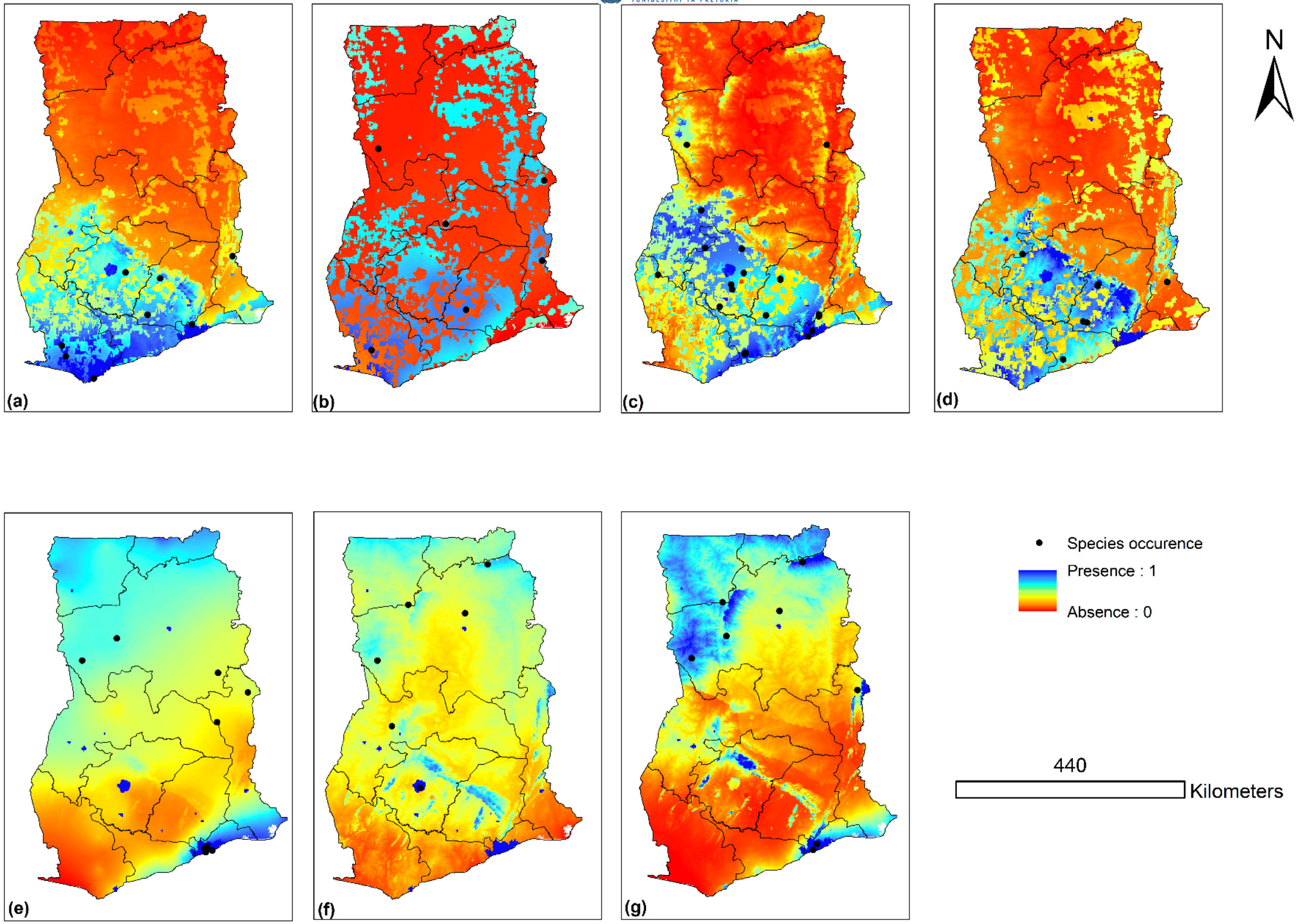

Figure 3.7: Presence-absence maps generated for the current predicted distribution of Vespertilionidae where (a) is *Glauconycteris poensis*, (b) *Mimetillus moloneyi*, (c) *Afronycteris nana*, (d) *Pseudoromicia tenuipinnis*, (e) *Scotophilus dinganii*, (f) *Scotophilus leucogaster*, and (g) *Scotophilus viridis*. Known occurrence records are illustrated in black. Shades closer to blue predict suitable areas (presence) whereas the shades closer to red predict unsuitable areas (absence).

3.4. Discussion

Biotic and abiotic factors influence bat species' distribution (Arumoogum et al. 2019, Cruz et al. 2019). This study focused on the abiotic factors, land-use, and climate change. Which revealed that land-use types contributed to the modelled distribution of 31 of the 42 species. The SDM also identified that 36 out of the 42 species were predicted to be in the Moist Semi-deciduous forest, and 34 species were predicted to occupy the agriculture land-use type.

Species-distribution models have been useful in conservation measures to analyse bat species ranges and expansions under climate and land-use change scenarios (Rodríguez et al. 2007, Franklin 2013). Studies have suggested that species that use climatic cues (temperature and rainfall) are the most affected by climate change (Brook 2008, Sherwin et al. 2013). Bats are no exception, with variations in climate reducing bat reproduction rates, distributional ranges and diversity (Sherwin et al. 2013, Pretorius et al. 2020*b*). In Africa, high rainfall and a stable temperature equate to an abundance of food for all bats, due mainly to an increase in insect and fruit availability (Thomas and Marshall 1984, Andrews and O'Brien 2000, Wickramasinghe et al. 2004). However, in this study climatic variables did not contribute as much as the land-use variable did. Less than 20% of the bat species' modelled distribution were either determined by annual mean temperature or annual mean precipitation. The annual mean temperature variable is based on basic climatic parameters, whereas, the annual mean precipitation is based on the long term quality of water availability (Venturi et al. 2004). Fluctuating temperatures and precipitation have been reported across temperate areas and have been linked with decline in bat populations in Europe (Wickramasinghe et al. 2003, 2004). Elsewhere and in an extreme scenario, the bushfires in Australia, fuelled by climate change, have killed thousands of Australia's endangered flying foxes (*Pteropus* species) (Dickman and Fleming 2002, Baranowski et al. 2020). With one particular species, the Grey-headed flying foxes (*Pteropus* *poliocephalus*), the population declining by 30% was due to habitat loss and anthropogenic disturbances (Dickman and Fleming 2002).

In tropical areas (neotropics and tropical rainforests), climate change, however, has had a different effect (Maas et al. 2016). Bats are known to migrate, usually following food resources, and maternal roosts for the females (Popa-Lisseanu and Voigt 2009). A few studies about the migration of bats, have suggested that with climate change, the migration of bats has been threatened (Popa-Lisseanu and Voigt 2009, Altringham 2011, Nkrumah et al. 2017*a*). For example, Adams (2010), predicted that there will be a decline in bat population in response to climate change, hence, due to rising temperatures and low precipitation, as a consequences of climate change, access to water during bat migration periods will be limited (Altringham 2011, Reardon and Schoeman 2017).

Limited access to water, puts added stress onto lactating females, who need water for milk production (Popa-Lisseanu and Voigt 2009). Lack of water can cause them to lose their offspring thus, reducing the population of bats (Popa-Lisseanu and Voigt 2009, Adams 2010). Apart from reproductive problems for bats, small sized insectivores bats are more sensitive to climate change as they use up a lot of metabolic energy to maintain their body temperature (Adams 2010, Pretorius et al. 2020*a*). Fluctuations in temperature throughout the year can impact insectivorous bats by a reduction in insect availability for food (Boyles et al. 2011, Reardon and Schoeman 2017). The neo-tropics and tropical rainforests pride themselves in their high canopy trees and ambient temperature under these canopies; this provides a stable temperature for bats to survive (Muscarella and Fleming 2007, Maas et al. 2016). In their study, Russo and Jones (2015) concluded that a high canopy density reduces light availability, thereby, reducing the visibility of bats to predators. Similarly, Cruz et al.(2019) assert that there was higher activity on sites with more significant canopy cover throughout the year, therefore, presenting better feeding opportunities for insectivores bats as this attracts more insects to the area (Cruz et al. 2019).

In tropical areas such as Ghana, land-use change, however, has a greater effect on the distribution and population of bats as they are regulated by the availability of food (Rice and Greenberg 2000, Seto et al. 2012). From the current study, this theory was supported, with land-use contributing to the distribution of 73% of the bat species modelled. Fuentes-Montemayor (2013) suggested that woodlands have widely been affected by anthropogenic impact. Woodlands offer a wide range of roosting and feeding sites to bats (Fuentes-Montemayor et al. 2013, Kirkpatrick et al. 2017). However, bats are now at a disadvantage with increase in land-use changes due to the growing human population in many African countries (Hayman et al. 2012). According to other studies, a few frugivorous and insectivorous bats have become adapted to habitat fragmentation and more agricultural land-use types (Meyer et al. 2004, Kunz et al. 2011, Ripperger et al. 2015). But not all bat species can succeed in fragmented forests, as a result, rare and specialised species are lost (Sampaio et al. 2003). Ripperger et al. (2015), maintained that frugivorous bats succeed in fragmented areas and degraded habitat. Other species like *Nanonycteris veldkampii*, rather migrate to savanna regions during rainy season in search of food (Cosson et al. 1999, Popa-Lisseanu and Voigt 2009).

Bats and birds complement each other in dispersing seeds and pollinating plants, especially in the tropics (Costa et al. 2018). Frugivores are known to pollinate plants and disperse seeds, especially fruit bats (Pteropodidae) (Fujita and Tuttle 1991). According to Kunz et al. (2011), fruit bats pollinate the flowers of about 168 plant species. This study demonstrated that the Pteropodidae occupied the moist deciduous-forest agro-ecological zone and within areas of agricultural land-use. In Ghana, *Eidolon helvum* spread seeds by defecating as they fly to reduce their weight (Abedi-Lartey et al. 2016). Fruit bats like *Eidolon helvum*, for example, have promoted the regeneration of the fig tree (*Ficus sp.*) and the African corkwood tree (*Musanga cecropioides*); these are examples of forest tree species (Fahr et al. 2015, Abedi-Lartey et al. 2016). Bats further promote the dispersal of seeds from the Papaya (*Carica papaya*) and Neem tree (*Azadirachta indica*), which are essential buffer food sources for bats during food scarcity (Abedi-Lartey et al. 2016). Some fruit bats are specialist feeders, while others are generalists or opportunistic feeders (Nkrumah et al. 2017*b*). *Epomophorus gambianus* is a known generalist and opportunistic fruit feeder that thrives in a variety of human-modified habitats (Amponsah-Mensah et al. 2019). In this study, this species was predicted to occur in places of agriculture land-use. The diet of *E. gambianus* in Ghana can consist of about 30 plant species, from 16 families, linked to the seasonal availability of these species (Amponsah-Mensah et al. 2019). In the study by Amponsah-Mensah et al., (2019), 58% of the faecal matter collected from *E. gambianus* showed seeds of plant species of the forest and savanna transition agro-ecological zone of Ghana. *Bombax buonopozense, Ficus spp.*and *Milicia excelsa* are being threatened by overexploitation in Ghana (Hawthorne and Abu-Juam 1995, Hawthorne 2014). As specialist feeders, *E. gambianus* are more sensitive to change and therefore have a higher chance of becoming extinct (Schulze et al. 2004); this is evident in both habitat and resource specialists. Essentially, about 24% of all known bat species are threatened by habitat loss and other anthropogenic destruction (Kunz et al. 2011). Bat species, such as *Epomops buettikoferi* and *Epomops franqueti,* are known as strict forest dwellers; they also feed mainly on *Ficus spp.* (Nkrumah et al. 2017*b*). With more forest being fragmented and degraded, these species have found roosting places in cocoa (*Theobroma cacao*) farms and travel long distances to find food (Cosson et al. 1999).

Frugivorous bats provide seed dispersal and pollination services, whilst, insectivorous bats play an essential role as bioindicators and biological pest controllers (Boyles et al. 2011, Kalda et al. 2015). There have been reports of how bats have played an essential role in controlling the pests that could lead to losses in cocoa (*Theobroma cacao*), coffee (*Coffea*), and corn (*Zea mays*) agricultural productions (Maas et al. 2013, 2016). Bats have saved the farming industry $1 billion per year in pesticides (Maas et al. 2016, Costa et al. 2018). Therefore, with this study showing a large number of insectivorous species predicted to occupy agricultural lands, this could assist in the mitigation of pests in the croplands and plantations (Cleveland et al. 2006);

Humans have directly used, approximately, 40% of the terrestrial biosphere for agriculture and settlements (Cisneros et al. 2015*b*). This has been the same for Ghana, where there have been constant anthropogenic influences on the forests and biodiversity (Hill and Curran 2003, Holbech 2005). The country is the second highest producer of cocoa (*Theobroma cacao*), and other cash crops which contribute to the economy. Forest land had to be sacrificed, both for the growing population and to sustain the economy (Läderach et al. 2013, Deikumah et al. 2014). Ghana's forests are mostly semi-deciduous forests, with only a small portion being rain forest (Addo-danso 2016). Most of Ghana's land is either mines or agricultural lands and plantations (Quagraine et al. 2017, Asiedu et al. 2019, Wongnaa and Awunyo-Vitor 2019).

In this study, it was evident that a significant number of bat species could persist in the moist semi-deciduous forest biotic zone. With most of Ghana’s forest being within forest reserves, it could be that most bat species are within these forest reserves (Davis and Philips 2005, Vordzogbe et al. 2009). Nevertheless, this does not equate to the bat species being protected or conserved, therefore, using SDMs helps to identify variables (climate and land-use changes) affecting the bat species distribution and conservation priority areas (Cooper-Bohannon et al. 2016, Smith et al. 2016). This study concludes that a wide diversity of bats is predicted to occupy agricultural lands. Plantations or agricultural woodlands have been presumed to have little value for wildlife, however, understanding how bats use agricultural sites to their advantage could also be necessary for their conservation (Razgour et al. 2016, Kirkpatrick et al. 2017). Most countries in Africa are developing nations; their environmental regulations are not as strictly enforced as those of other continents (Strassburg et al. 2009, Deikumah et al. 2014). Ghana has a rich biodiversity to protect but with it being a developing nation with limited resources, predicting potentially suitable areas within agro-ecological zones and land-use, could help the country focus its conservation efforts. Knowing the importance of bats, in both restoring fragmented forests and providing ecosystem services such as biological pest control, means that more effort must be made to inform the Ghanaian community of this (Jones et al. 2009). This study concludes that fruit bats need to be protected as they are responsible for restoring species of forest trees that are their roost sites and food sources (Fahr et al. 2015). Putting in place conservation strategies within forest reserves and national parks can assist in the country's forest restoration mandate for 2030 (AFR100) (WRI 2017). Furthermore, the biological pest control ecosystem service that bats provide, could save farmers (commercial and subsistence) millions in harvest and the use of insecticides (Linden et al. 2019). This protects the economy of the country and extends the protection of other wildlife affected by harmful chemicals used in the agriculture industry (Stechert et al. 2014, Weier et al. 2018).

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Chapter 4: General Conclusion

Shelter, food and water are crucial elements needed for the survival of animals (Krebs 1972). The increase in human population and the resultant increased need for land has threatened the survival of animals (Laurance et al. 2014). Habitat degradation is a major threat to biodiversity (Bellard et al. 2014); this impact is especially pronounced in biodiversity hotspots. Biodiversity hotspots and pristine habitats are under severe pressure and risk the loss of many endemic and threatened species in the area (Malcolm et al. 2006, Bellard et al. 2014, Lisón and Sánchez-Fernández 2017).

Ghana forms part of the Guinean Forest biodiversity hotspot (Myers 2003, Küper et al. 2004). These forests were known for a diversity of indigenous and endemic species (Deikumah and Kudom 2011, Pimm et al. 2014). Due to the growing population of the country, a deforestation rate of 1.68% was recorded between 1990-2010 (Quacou 2016), as forests within the country are converted to agricultural lands and settlements (Attuquayefio and Fobil 2005, Kayode et al. 2012, Ofori et al. 2013). The loss of the indigenous forest led the country to create forest reserves (McCullough et al. 2007). However, these forest reserves and the species within them are still being threatened by large agricultural lands surrounding or being within the forest reserves (Ofori et al. 2012). Apart from land-use change, climate change has also been a cause for concern all over the world, also in Africa (Bomhard et al. 2005). Climate change has caused shifts in seasons and has affected temperature and precipitation (Hogg and Wall 2011). There has been a shift in temperature (too hot or too cold) and precipitation (floods or drought); these shifts can be extreme and/or unpredictable (Svenning and Skov 2007, Brown and Yoder 2015). Climate change has also been a threat to species endemic to Africa (Reardon and Schoeman 2017);. Climate and land-use change have both played a big role in the distribution of species, hence, these disturbances have caused species to either leave their known distributional range or become extinct (Brooks et al. 2002, Cooper-Bohannon et al. 2016).

Bats are part of a diverse group of mammals making up more than 20% of mammal species (Simmons 2005, Jones et al. 2009, Fenton and Simmons 2015). Bats offer ecosystem services, such as pollination and assist in the dispersal of seeds (Roscioni et al. 2014, Russo and Jones 2015). They also consume a wide range of insects that are pests in agricultural lands, therefore, bats are known as 'biological pest controllers' (Monadjem and Fahr 2007*b*, Boyles et al. 2011). There is a high diversity of bats in Africa and there have been various studies conducted on the ecology of bats in the continent, especially, in the tropical areas of the continent (Decher et al. 2015, Abedi-Lartey et al. 2016, Nkrumah et al. 2017*b*, Shapiro et al. 2020). Bats in Ghana have been studied in the past, but the last known complete survey conducted on the distribution of bats in Ghana was by Grubb et al.,(1998). Studies in Ghana, have focused on either protected areas or in areas historically known for bat occurrences (Decher and Fahr 2005, Weber and Fahr 2007). Studies like these show a biased view of the distribution, diversity and richness of bat species in Ghana.

This study explored the richness and distribution of bats in Ghana. The thesis focused on bat species distribution models and the impact of climate and land-use change. I used diversity indices to quantify which agro-ecological zones reflected high species richness and species distribution modelling (SDM) to predict the distribution of bats in the country. Grubb et al.,(1998) report on the distribution of bats in Ghana using museum records gave an overview of what bat species had been collected in the country over the years. Their work also showed possible areas of interest for further studies.

The Moist Semi-deciduous forest was highlighted as the most diverse in species richness; with Shannon diversity Index of 3.26 and a Chao1of 110 (Chapter two). The distribution of bat records in Ghana was more affected by land-use than climate with land-use variables contributed to variables in the final model outputs for 31 of the 42 bat species (Chapter three).

With bats depending on viable roost sites, food resources and proximity to water, land-use change, and transformation had a more pronounced affect than climate variables in the final model outputs. It was predicted that more bat species would occupy the Moist Semi-deciduous forests of Ghana and the area would, therefore, have a higher species richness and diversity than other agro-ecological zones. However, this study showed modelled distribution predictions using specific scenarios, climate and land-use change. Showing predicted distribution of bat species in Ghana, has highlighted the importance of protecting bats in specific habitats but has also broadened the opportunity for further research to be conducted.

A species response to sensitivity is different, and sensitivity is often measured in abundance or density (Jones et al. 2009). Abundance has been shown to not be the most suitable form of measuring a species sensitivity to disturbance. Therefore, studies must collect critical information such as population numbers, sex ratios, dissimilarity of habitats use and physiological measures (Jones et al. 2009, Kunz et al. 2011). In chapter two, results showed that the Moist Semi-deciduous zone was the most diverse and the most dissimilar among the other agro-ecological zones. Moist Semi-deciduous forests are the most prominent vegetation type , the most degraded and the area with the most agricultural plantation and croplands in Ghana (Vordzogbe et al. 2009, Ofori-Boateng et al. 2013). This forest vegetation type is highly fragmented, yet it is an area that has a rich species diversity and richness (Vordzogbe et al. 2009). Specialist foragers, bat species that have a strict diet, and need specialized habitat requirements (Hutson et al. 2001, Lewanzik and Voigt 2014). These bat species would not be able to survive in a disturbed fragmented landscapes, such as the Moist Semi-deciduous forest (Wechuli et al. 2017, Costa et al. 2018). It was, therefore, concluded that the species that were abundant in the Moist Semi-deciduous forest were indeed generalist feeders.

Biodiversity hotspots are prevalent in southeast Asia and other tropical areas (Edwards et al. 2011, Hughes 2017). Unfortunately, many of these hotspots, especially the rainforests, are being fragmented and degraded (Edwards et al. 2011). There are many palm oil plantations and logging occurring in these rainforests, timber exports have also increased (Edwards et al. 2011, Lee-Cruz et al. 2013). In areas facing increased habitat disturbance, bat species that are specialist could potentially disappear from the area whereas, generalist feeders are more resilient to these disturbances (Blay et al. 2008, Edwards et al. 2011, Costa et al. 2018). An example of a bat species that is threatened by habitat loss globally, is *Mops petersoni* (Peterson's free-tailed bat) which, according to the IUCN Red List, is listed as near extinct (Mickleburgh et al. 2010).

Interestingly, the species diversity indices calculated in chapter two, show the Moist Semi-deciduous forest to be the most diverse. This was similar to the SDM results in chapter three showing that various bat species in this study show a high probability to be found in the Moist Semi-deciduous forest. The Moist Semi-deciduous forest was the most rich (Shannon diversity Index = 3.26; Chao1 = 110) as reported in (Chapter two). Thirty six out of the 42 bats species that were modelled, showed a high probability to be found in the Moist Semi-deciduous forest. Furthermore, 11 of the bat species that showed a high probability to be found in the Moist Semi-deciduous forest were Pteropodidae. The only bat species within Pteropodidae that did not occur in the Moist Semi-deciduous forest, was *Epomophorus gambianus* which was shown to be in the Guinean Savanna. which, according to Happold and Happold (2013) is its preferred habitat. Most Pteropodidae are strict and only partial forest dwellers, namely, *Epomops buettikoferi*, *Hypsignathus monstrous, Scotonycteris ophiodon and Scotonycteris zenkeri* (Henry et al. 2004). Others such as, *Eidolon helvum*, *Myonycteris torquata and Nanonycteris veldkampii*, usually move to the Savannah areas during the wet season (Henry et al. 2004).

All members of the Pteropodidae bats are known pollinators, either frugivores or nectarivores (Cosson et al. 1999, Muscarella and Fleming 2007, Sritongchuay et al. 2019), hence, bats are known pollinators of several tree species. Lack (1978) reported on the pollination of *Maranthes polyandra* and *Protea elliottii* trees by the nectivorous bat *Nanonycteris veldkampii* in the Guinean Savannah zone of West Africa. In Ghana, the vital role of bats to disperse seeds has been attributed to the thriving population of neem trees (*Azadirachta indica*) around the Ghanaian capital, Accra (Waldman et al. 2015, Nkrumah et al. 2017*b*). Neem trees assist the livelihoods of Ghanaians by providing firewood and building materials (Waldman et al. 2015).

Studies report a reduction in bats around the country, particularly, in the capital Accra; this coincided with a reduction in fruit production (Waldman et al. 2015, Ayivor et al. 2017, Ohemeng et al. 2017). In west Africa, the *Ficus* tree species is common among those present in the rain forests (Amponsah-Mensah et al. 2019). This tree species is an important food source for fruit bats in the west African tropics (Danquah et al. 2011). Bats disperse the *Ficus* fruit seeds, thereby, helping restore the *Ficus* tree component (Muscarella and Fleming 2007, Amponsah-Mensah et al. 2019, Asare et al. 2019). This highlights the importance to retain and conserver frugivorous animals in tropical forests areas, as they facilitate the regeneration of these forests.

In chapter three, the SDM showed that 34 out of the 42 bat species were predicted to occupy agriculture land-use types. Apart from bats being known as pollinators and seed dispersers, they serve as biological pest controllers (Jones et al. 2009). Some bat species prefer agricultural landscapes, where they assist in the consumption of agricultural pest insects (Taylor et al. 2013, Weier et al. 2018, 2020). In Shapiro et al., (2020) stated that tropical savanna fragments may provide habitat for not only bats but other species. This not only conserves bat species but conserve broader biodiversity. In an agricultural land-use type, the significance of bats is high

(Boyles et al. 2011). For example, in South Africa, bats and birds feed on macadamia (*Macadamia intergrifolia*) pest insects (macadamia nut borer) (*Cryptophlebia batracopha*) and the green vegetable bug (*Nezara viridula*)), whereas Vervet monkeys (*Chlorocebus pygerthrus*) are a threat to the premature macadamia nuts (Linden et al. 2019). Farmers would rather invest in the effects of biocontrol offered by bats and birds, amounting to USD5000 ha/year, than to lose crops caused by the predation of nuts by monkeys amounting to only USD1600 ha/year (Taylor et al. 2013, Kemp et al. 2019, Linden et al. 2019). The value of bat predation in agro-ecological zones is up to 47% of the value of the annual production (Weier et al. 2018, Linden et al. 2019). However, there is evidence that intense agricultural activities can affect bats negatively by reducing roosting and foraging sites (Weier et al. 2018). Agricultural intensification leads to more natural habitats being lost, and more pesticide usage (Jones et al. 2009).

Ghana's human population increased from 2.2 to 4.1 million from 1921-1948 (Codjoe 2007); in 2010 this increased to 24.6 million (Kayode et al. 2012). In 2016 the loss of forests in Ghana were approximately 190000 km^2 (Quacou 2016). With Ghana's commitment to African Forest Landscape Restoration Initiative in 2015, the increase in human population will affect wildlife. More lands will be converted into agriculture, and more mines will be created to sustain the livelihoods of the population (Deikumah et al. 2014, Owusu et al. 2018). The future of bats in Ghana will remain to be threatened as the disturbance and destruction of natural and potential habitat continues. An example of the potential effect habitat loss can cause to the bat population, Aguiar et al., (2016) in their results revealed that bat species in the Brazilian Cerrado could become locally extinct if habitat disturbances continue. It is possible that the continued presence of bats sensitive to land-use change and transformation in Ghana can be determined by what the country can do to protect these species.

This study has shown that, even with the increase in human population and its anthropogenic effects to bat distribution in Ghana, that some bat species can still be maintained in this environment (Starik et al. 2018, Mullin et al. 2020). The Moist Semi-deciduous forest is where the Ghanaian wildlife services should focus their conservation efforts (Vordzogbe et al. 2009, Ofori et al. 2013, Yahaya et al. 2013). Even within the agricultural lands, natural lands should surround it. Bats are everywhere in the world, especially, in the tropical areas therefore, the conservation of bats is imperative. There is increasing evidence on how important bats are to the ecosystem (Shapiro et al. 2020). They maintain ecosystem services such as seed dispersion and biological pest controlling (Kunz et al. 2011) Therefore, understanding what drives their distribution, which agro-ecological zone they prefer, and which land-use type they are successful in is important. It can inform us on where to concentrate conservation efforts and which landscapes are important to maintain or increase bat activity. For Ghana, an increasing and continued awareness of the benefits of bats is imperative. This continued awareness of the usefulness of bats in the ecosystem would encourage the population of Ghana to embrace, rather than fear bats. It will also reduce the consumption of bats as 'bushmeat', further increasing the conservation of bat species in the country (Kamins et al. 2011, Frick et al. 2019). Awareness programs and workshops in the rural parts of Ghana, especially the farming community, would allow the farming community to appreciate the ecosystem services bats provide and their importance. In doing so, more bats species can be conserved, and more studies can be conducted to understand, even better, the distribution and ecology of bats in Ghana.

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Supplementary tables: Chapter 3

Table 1: Number of records of each bat species and which family they belong to from the ACR database. There are 95 species across eight bat families with a total of 5357 locality records.

Bat species	**Bat family**	**No. of records**
Casinycteris ophiodon	Pteropodidae	1
Chaerephon aloysiisabaudiae	Molossidae	8
Chaerephon chapini	Molossidae	2
Chaerephon leucogaster	Molossidae	42
Chaerephon major	Molossidae	48
Chaerephon nigeriae nigeriae	Molossidae	1
Chaerephon pumilus	Molossidae	138
Chaerephon russatus	Molossidae	1
Coleura afra	Emballonuridae	9
Eidolon helvum	Pteropodidae	56
Eidolon helvum helvum	Pteropodidae	18
Epomophorus gambianus	Pteropodidae	578
Epomophorus gambianus gambianus	Pteropodidae	46
Epomophorus labiatus	Pteropodidae	2
Epomophorus wahlbergi	Pteropodidae	1
Epomops buettikoferi	Pteropodidae	91
Epomops franqueti	Pteropodidae	340
Glauconycteris beatrix	Vespertilionidae	1
Glauconycteris poensis	Vespertilionidae	36
Glauconycteris superba	Vespertilionidae	1
Glauconycteris variegate	Vespertilionidae	4
Hipposideros abae	Hipposideridae	14
Hipposideros beatus	Hipposideridae	23
Hipposideros caffer	Hipposideridae	348
Hipposideros cyclops	Hipposideridae	77
Hipposideros fuliginosus	Hipposideridae	72
Hipposideros jonesi	Hipposideridae	51
Hipposideros ruber	Hipposideridae	98
Hipposideros tephrus	Hipposideridae	122
Hypsignathus monstrosus	Pteropodidae	43
Hypsugo musciculus	Vespertilionidae	1
Kerivoula lanosa	Vespertilionidae	4
Kerivoula phalaena	Vespertilionidae	2
Lavia frons	Megadermatidae	18
Macronycteris gigas	Hipposideridae	35
Macronycteris vittatus	Hipposideridae	5

Megaloglossus azagnyi	Pteropodidae	90
Micropteropus pusillus	Pteropodidae	414
Mimetillus moloneyi	Vespertilionidae	10
Mops (Mops) condylurus	Molossidae	515
Mops (Mops) demonstrator	Molossidae	2
Mops (Mops) trevori	Molossidae	1
Mops (Xiphonycteris) brachypterus	Molossidae	105
Mops (Xiphonycteris) nanulus	Molossidae	21
Mops (Xiphonycteris) petersoni	Molossidae	7
Mops (Xiphonycteris) spurrelli	Molossidae	61
Mops (Xiphonycteris) thersites	Molossidae	339
Myonycteris angolensis	Pteropodidae	61
Myonycteris leptodon	Pteropodidae	121
Myopterus whitleyi	Molossidae	2
Myotis bocagii	Vespertilionidae	6
Nanonycteris veldkampii	Pteropodidae	99
Pseudoromicia brunnea	Vespertilionidae	2
Laephotis capensis	Vespertilionidae	46
Neoromicia guineensis	Vespertilionidae	2
Neoromicia helios	Vespertilionidae	1
Afronycteris nana	Vespertilionidae	69
Pseudoromicia rendalli	Vespertilionidae	8
Neoromicia somalica	Vespertilionidae	9
Pseudoromicia tenuipinnis	Vespertilionidae	23
Nycteris arge	Nycteridae	23
Nycteris gambiensis	Nycteridae	144
Nycteris grandis	Nycteridae	28
Nycteris hispida	Nycteridae	147
Nycteris intermedia	Nycteridae	4
Nycteris macrotis	Nycteridae	307
Nycteris nana	Nycteridae	3
Nycteris thebaica	Nycteridae	22
Nycticeinops schlieffenii	Vespertilionidae	2
Otomops martiensseni	Molossidae	1
Pipistrellus inexspectatus	Vespertilionidae	1
Pipistrellus hesperidus	Vespertilionidae	1
Pipistrellus kuhlii	Vespertilionidae	1
Pipistrellus nanulus	Vespertilionidae	9
Pipistrellus rusticus	Vespertilionidae	3
Rhinolophus alcyone	Rhinolophidae	22
Rhinolophus denti	Rhinolophidae	1
Rhinolophus fumigatus	Rhinolophidae	1
Rhinolophus landeri	Rhinolophidae	21

Rhinopoma microphyllum	Rhinopomatidae	1
Rousettus aegyptiacus	Pteropodidae	15
Saccolaimus peli	Emballonuridae	8
Scotoecus albofuscus	Vespertilionidae	2
Scotoecus hirundo	Vespertilionidae	16
Scotonycteris occidentalis	Pteropodidae	30
Scotophilus dinganii	Vespertilionidae	44
Scotophilus leucogaster	Vespertilionidae	29
Scotophilus nigrita	Vespertilionidae	5
Scotophilus nucella	Vespertilionidae	6
Scotophilus nux	Vespertilionidae	6
Scotophilus viridis	Vespertilionidae	76
Taphozous mauritianus	Emballonuridae	2
Taphozous nudiventris	Emballonuridae	2
Taphozous perforatus	Emballonuridae	4
Taphozous perforatus perforatus	Emballonuridae	19

Table 2: Species Distribution Model results table, for species modelled. A breakdown of each of the species modelled was grouped into families showing the AUC value (training and test), the area in km^2 and percentage of the study area each species covered, the percentage of the dominant agro-ecological zone and land-use they are predicted to cover and two eco-geographical variables that influenced the models. (CS – coastal savanna, MDF – moist deciduous forest, GS – Guinean savannah, LU – land-use, AMT – annual mean temperature, AP – annual mean precipitation, MDR – mean diurnal range, MTC – minimum temperature of the coldest month, TCQ – temperature of the coldest quarter, TWQ – temperature of the wettest quarter)

Species	**No. of Data points initial**	**AUC training**	**AUC test**	**Predicted area of occupancy km^2 | %**		**Dominant agro-ecological zones within predicted area of occupancy (% cover)**			**Dominant Land-use within predicted area of occupancy (% cover)**				**Potential influential EGVs**	
						CS	**MDF**	**GS**	**Forest**	**Savannah**	**Agriculture**	**Degraded**	**Var 1**	**Var 2**
Pteropodidae														
Eidolon helvum	70	0.6787	0.996	136997	57.48	3.13	32.92	6.63	5.18	14.93	20.19	11.43	LU	AMT
Epomophorus gambianus	619	0.8442	0.7259	59378.4	24.92	3.00	7.59	12.42	0.06	8.43	12.40	1.84	LU	AP
Epomops buettikoferi	88	0.9143	0.9197	36853.7	15.46	1.18	10.26	0.03	2.09	0.10	6.67	4.67	MDR	LU
Epomops franqueti	336	0.8451	0.8567	53294.4	22.36	1.77	16.92	1.20	0.79	1.36	12.49	6.06	LU	AMT

Hypsignathus monstrosus	40	0.8695	0.9372	70443.7	29.56	1.83	21.28	1.64	1.34	1.97	15.60	8.67	LU	MDR
Megaloglossus azagnyi	69	0.9093	0.5213	36276.9	15.22	0.50	12.02	0.23	1.09	0.23	8.06	4.88	AMT	LU
Micropteropus pusillus	397	0.8695	0.7503	68097.5	28.57	2.54	14.87	8.10	0.72	9.32	11.97	4.23	AMT	AP
Myonycteris angolensis	45	0.8898	0.7835	41090.1	17.24	0.31	14.71	0.50	0.64	1.07	9.95	4.97	LU	AMT
Myonycteris leptodon	101	0.95	0.7869	18387.3	7.72	0.40	4.63	0.05	1.23	0.17	3.01	2.32	LU	AMT
Nanonycteris veldkampii	73	0.7339	0.7012	9820.86	4.12	0.41	3.08	0.26	0.20	0.13	1.03	2.00	LU	TCQ
Rousettus aegyptiacus	15	0.8687	0.7992	13959.2	5.86	0.40	4.48	0.22	2.83	0.16	1.07	1.09	LU	AMT
Scotonycteris occidentalis	29	0.9499	0.9891	29321.8	12.30	0.03	9.94	0.01	0.64	0.14	6.66	4.02	LU	AMP
Hipposideridae														
Doryrhina cyclops	70	0.8887	0.7538	53967.5	22.65	1.91	18.28	0.20	0.92	1.20	12.10	6.16	LU	AMT
Hipposideros beatus	20	0.8508	0.8686	59319.4	24.89	1.83	19.08	0.03	1.79	2.23	13.01	6.05	LU	MDR
Hipposideros caffer	264	0.8343	0.7057	35255.9	14.79	1.54	12.41	0.19	1.61	0.97	7.14	3.67	LU	TCQ
Hipposideros fuliginosus	70	0.7748	0.7195	27529.7	11.55	1.31	7.32	0.25	4.48	0.22	3.20	2.59	LU	MDR
Hipposideros jonesi	26	0.9243	0.9652	30156.6	12.65	0.49	10.60	0.03	0.42	0.23	6.95	3.94	LU	MDR
Hipposideros ruber	79	0.8295	0.5122	34414.8	14.44	0.10	11.20	1.27	1.37	0.75	5.94	5.81	LU	TCQ
Hipposideros tephrus	120	0.7976	0.998	50283.3	21.10	3.16	14.61	0.01	3.06	1.20	9.00	5.98	MDR	LU
Macronycteris gigas	21	0.8602	0.7887	41163.7	17.27	0.40	13.21	0.18	4.68	0.07	5.97	5.31	LU	AP
Rhinolophidae														
Rhinolophus landeri	16	0.8134	0.1731	33421.1	14.02	3.21	7.53	0.03	1.75	1.74	5.48	3.39	MDR	MTC
Emballonuridae														
Taphozous perforatus perforatus	22	0.9333	0.4124	50977.3	21.39	3.30	7.75	5.90	0.45	12.19	5.72	1.27	MDR	AP

Nycteridae														
Nycteris arge	20	0.8109	0.8687	60918.1	25.56	0.97	16.76	3.09	0.99	2.27	14.39	6.09	LU	AP
Nycteris gambiensis	144	0.7928	0.5385	124135	52.09	1.09	14.58	31.28	0.76	21.57	21.72	4.62	LU	MTC
Nycteris grandis	28	0.8402	0.7755	58338.4	24.48	0.58	19.61	0.47	3.78	1.21	9.83	8.14	LU	AMT
Nycteris hispida	145	0.8208	0.6882	8960.67	3.76	1.19	1.38	1.06	0.16	0.54	1.66	0.53	LU	MTC
Nycteris macrotis	297	0.8278	0.7092	37335.1	15.67	3.11	8.44	1.98	0.06	5.25	7.07	1.66	LU	AP
Nycteris thebaica	22	0.899	0.1071	44599	18.71	0.02	2.43	14.52	0.36	7.27	8.89	1.04	LU	MDR
Molossidae														
Chaerephon leucogaster	42	0.9612	0.9243	32869.7	13.79	3.30	9.30	0.03	0.73	3.31	5.69	2.37	LU	AP
Chaerephon major	41	0.884	0.9462	78803.1	33.07	3.30	17.02	8.97	1.81	12.72	11.73	4.37	AP	MDR
Chaerephon pumilus	134	0.9204	0.4375	9205.92	3.86	2.45	0.90	0.18	0.01	1.15	1.53	0.20	LU	AP
Mops (Mops) condylurus	512	0.8309	0.6815	16314.5	6.85	3.04	3.19	0.00	0.33	0.93	3.14	1.13	LU	MDR
Mops (Xiphonycteris) brachypterus	98	0.8357	0.7838	45986.9	19.30	1.43	16.46	0.00	0.47	0.97	11.47	5.52	LU	MDR
Mops (Xiphonycteris) spurrelli	61	0.8679	0.9027	71670.9	30.07	2.95	21.88	0.18	3.13	2.09	14.66	7.85	MDR	LU
Mops (Xiphonycteris) thersites	336	0.8901	0.9683	36774.6	15.43	0.12	12.04	0.05	0.78	0.41	8.68	4.83	LU	AP
Vespertilionidae														
Glauconycteris poensis	33	0.9063	0.6792	44187.5	18.54	1.89	13.30	0.00	2.00	0.42	9.34	5.29	MDR	LU
Mimetillus moloneyi	10	0.9034	0.0935	40747.7	17.10	0.13	11.76	1.99	0.43	1.19	10.13	4.54	LU	TCQ
Afronycteris nana	57	0.8703	0.8623	93422.6	39.20	2.68	28.24	3.35	3.96	6.28	17.00	9.56	AMT	LU
Pseudoromicia tenuipinnis	23	0.9294	0.6213	36026.2	15.12	0.53	12.89	0.05	0.62	0.55	8.25	4.53	LU	AMT
Scotophilus dinganii	36	0.7887	0.3133	50292.4	21.10	2.47	0.82	16.35	0.01	12.89	6.02	0.09	LU	AP

Scotophilus leucogaster	28	0.7421	0.9035	116898	49.05	0.40	9.81	32.72	1.21	24.34	16.13	3.25	LU	MTC
Scotophilus viridis	67	0.9036	0.7321	51914.7	21.78	1.57	1.41	16.40	0.29	12.73	6.50	0.49	AP	LU