THE ROLE OF FRUIT BAT *EIDOLON HELVUM* AND AVIAN FRUGIVORES IN GUAVA SEED DISPERSAL AND TREE ESTABLISHMENT IN AGRICULTURAL LANDSCAPES IN VIHIGA, WESTERN KENYA

BY

ROGERS KATUA MAKAU, B. Sc. (Hons, University of Nairobi)

(REG. NO. I56/79604/2012)

Thesis submitted in partial fulfilment of the requirement for the award of the degree of Master of Science in Biology of Conservation, University of Nairobi.

SCHOOL OF BIOLOGICAL SCIENCES

COLLEGE OF BIOLOGICAL AND PHYSICAL SCIENCES

MSC. BIOLOGY OF CONSERVATION

UNIVERSITY OF NAIROBI

SEPTEMBER, 2016

DECLARATION

This thesis is my original work and has not been presented for award of a degree in any other university.

Makau Rogers Katua

Reg. No I56/79604/2012

Signature ...~~Makau~~... Date ...19\6\2017...

I confirm that this thesis has been submitted for examination with my approval as a supervisor.

Dr. Robert Chira

School of Biological Sciences

University of Nairobi

Signature ...~~Muthigi~~... Date 19|06|2017

DEDICATION

This thesis is dedicated to all conservation practitioners in the world.

AKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

ABBREVIATIONS AND ACRONYMS

BDG   Beginning day of Germination

DBH   Diameter at Breast Height

Gok   Government of Kenya

GP   Germination Percentage

MGT   Mean Germination Time

NEMA   National Environment and Management Authority

ABSTRACT

Seed dispersal by bats and avian frugivores is significant for plant regeneration in fragmented agricultural landscapes in tropical regions. This study was aimed at determining the role of the *Eidolon helvum* and other avian frugivores in guava seed dispersal and tree establishment in farmlands within Vihiga County. Its objectives were to: establish which frugivore assemblages are dispersing the seeds of *Psidium guajava* and their relative importance, determine the effects of gut treatment by *E. helvum* on germination of guava seeds and assess seed rain, seedling establishment, and tree density. Three study sites including two *E. helvum* roosting sites (Mbale and Ilwanda) and a non - roosting site (Chugi) were selected for study. In each site, 2 ha plots were defined where five transects measuring 100m long and 20m apart were established and 10 focal trees selected for sampling frugivores. Under, the crowns of the focal trees, data on seed rain was collected using $1m^2$ quadrats. Germination experiments were conducted to determine the effect of four treatments (manually extracted seeds, intact seeds, seeds from bat excreta and seeds obtained from spats) on the rate of germination of guava seeds. Data on seedling establishment were collected below the crowns of 20 selected trees in each study site by mapping seedlings in six randomly chosen $1m^2$ quadrats. In each site, one hectare plot was divided into 10 sampling plots measuring 10 m by 10m to collect data on tree density and diversity. Statistical analyses were performed using SPSS version 20.0 and STAT program software and were evaluated at $p < 0.05$ level of significance. A total of 4288 *E. helvum* fruit bats were recorded visiting guava trees in all the study sites. These were categorized as; Ilwanda (46%, n=1991), Mbale (34%, n=1446) and Chugi (20%, n=851). A total of 1,835 individual birds comprising of 61 species belonging to 21 families were observed visiting 30 *P. guajava* trees in all the three study sites. Visits by *E. helvum* fruit bats were significantly higher than avian frugivore visits in all the study sites ($Z = -4.78$, $p < 0.05$). Germination distributions of seeds among the four treatments were not significantly different (Kruskal-Wallis Test, $\chi2 = 4.32$, d.f. $= 2$, $p > 0.05$). The mean density of pellets (number of pellets/m^2) containing guava seeds deposited by *E. helvum* under the crowns of *P. guajava* trees were significantly different among sites ($F_{2, 27} = 10$, $p < 0.05$). The mean density of seedlings (number of seedlings/m^2) varied significantly among the ($F_{2, 57} = 29.5$, $p < 0.05$). The density of trees was highest in Ilwanda at 45.7 ± 1.3 trees/ha compared to Mbale at 38.1 ± 1.1trees/ha and Chugi at 30.9 ± 0.86 trees/ha. These findings clearly indicate that, the *E. helvum* is the most effective disperser of guava seeds and hence conservation of its roosting sites is critical to ensure plant regeneration in agricultural landscapes in Vihiga County.

CHAPTER ONE: INTRODUCTION

Seed dispersal ecology has recently gained rigorous scientific consideration focusing on the role it plays in various aspects of plant population and community dynamics (Nathan and Muller-Landau, 2000; Kunz *et al*., 2008; Uriante *et al*., 2011; Seltzer *et al*., 2013). Dispersal of seeds facilitates progenies to break away from competition with conspecifics, and closely related plant species so as to reduce dangers in spatiotemporally fluctuating environments and arrive at suitable areas that have suitable biotic or abiotic habitat requirements (Schupp and Fuentes, 1995; Wenny, 2000). In addition, dispersal affects abundance or steadfastness in meta-population dynamics (Premoli and Kitzberger, 2005), degrees of plant establishment and subjugation (Cain *et al*., 2000; Nielsen *et al*., 2005), genetic drift and population differentiation (Levin, 1974; Ennos, 1994), and species richness (Tilman, 1994; Snyder and Chesson, 2004).

Naturally, Seeds can be dispersed to a location though several means (Van der Pijl, 1982). For instance, in some plants species seeds are spread mechanically in which the ripe fruit open explosively or by the springing of a trip-lever. However, wind, water and animals are the main agents of seed dispersal. Animals are largely the main seed dispersers in the tropical ecosystems (Howe and Small wood, 1982, Levin *et al*., 2003; Dennis and Westcott, 2006). It is estimated that more than 95% of angiosperm species in tropical forests are dispersed by this method (Terborgh *et al*., 2002) where plants with fruits suited for vertebrate seed dispersal make 75-92 % of the vegetation (Jordano, 2000).

Guava (*Psidium guajava* L.) is an important tree cultivated in orchards or in home gardens in many tropical countries. It is widely cultivated in Africa, and incorporated into agroforestry systems in India (CABI, 2013). Guava is mainly grown for its edible fruits that are eaten raw or made into

purée (pulp), jam, jelly, paste, juice, syrup, chutney, etc. (Murray and Campbell, 1989; El Boushy and van der Poel, 2000). In Vihiga County, guava is mainly grown for its fruits. It is also used as natural fence, a source of firewood and provides shade in homesteads (Orwa and Campbell, 2009). Guava can grow under a wide range of environmental conditions and is considered invasive in some regions, which may be due to its allelopathic effects on native species (Smith, 1998). However, Guava has a positive environmental impact in some environments. For instance, in Gujarat (India), guava trees have been planted in association with *Leuceana leucocephala*, buffel grass (*Cenchrus ciliaris*) and African stylo (*Stylosanthes fruticosa*) in agro-silvo-pastoral systems to increase productivity and reclaim eroded, degraded and compacted soils with gullies and rocky parts (Raturi and Hiwale, 1993). A study by Berens *et al,* 2007 in western Kenya showed that guava trees did not suppress the establishment of indigenous species in Kakamega, and are gradually replaced during the course of succession.

Fruit bats are keystone species in the preservation and restoration of natural flora in the tropical regions (Fujita and Tuttle, 1991; Lobova *et al.*, 2009). Their function in dispersal of seeds and pollination is essentially crucial in succession and composition of plant communities in tropical rainforests (Henryi and Jouard, 2007; Muscarella and Fleming, 2007). Studies have shown that the 170 species of Pteropodidae bats in Africa, Southern Europe, Asia, Australia, and islands in Pacific and Indian oceans (Wilson and Reeder, 2005) are involved in seed dispersal of 145 plant genera (Marshall, 1985). One of the most important fruit bat species is the straw-coloured fruit bat *Eidolon helvum*. The species is characterized by occurrence in large colonies in tropical forests and farmlands such as the one in Kasanka National Park in Zambia, which seasonally hosts approximately ten million individuals (Richter and Cumming, 2006). Colonies in West Africa

range from a few thousand to one million bats (Thomas, 1983; Hayman *et al*., 2012a; Fahr *et al*., 2015). Its role as a seed disperser is significant for maintenance and establishment of plant species diversity and composition in forested habitats (Richter and Cumming, 2006). However, despite its importance in providing ecosystem services such as, seed dispersal and pollination the species is relatively understudied in Kenya.

Frugivorous birds play a key role in seed dispersal and establishment of a range of exotic plant species, such as the *Psidium guajava* (Berens *et al*., (2008) and Brazilian Pepper *Schinus terebinthifolius*, D'avila *et al*., (2010). Comprehensive studies of single plant-frugivores seed dispersal interactions have been undertaken in other tropical areas; Bas *et al*., (2005), D'avila *et al*., (2010), Nayara *et al*., (2017) but only a few studies have been made in Kenya (Berens *et al*., 2008 and Kirika *et al*. 2008). Moreover, few studies have compared the contribution made by both bats and birds to seed dispersal in degraded habitats in tropical regions (Rodrigo and Osiris, 1999), in Kenya there is paucity of knowledge in this field of study.

Fragmentation of landscapes is detrimental to biodiversity because it involves the removal, reduction, and isolation of native vegetation (Fahrig, 1999). Although native habitat loss is the leading cause of the loss of world's biodiversity (Myers *et al*., 2000), some agroecosystems can harbour a substantial portion of the biodiversity of the original land cover (Vandermeer and Perfecto, 1997) and can also buffer and complement protected areas (Curran *et al*., 2004; Schroth *et al*., 2004). Therefore, knowledge on the role of bat and avian frugivores in seed dispersal in degraded landscapes can be used to implement conservation strategies so as to restore native plant species in agricultural lands.

3

Vihiga County is among the highly populated counties in Kenya prompting an increased demand for arable land (GOK, 2005). This has led to severe land degradation exacerbated by encroachment of forested hilltops, wetlands and riverine ecosystems (NEMA, 2009). Eventually, the land cleared for agriculture losses its productiveness and is abandoned leading to slow recuperation of flora. According to Nepstad *et al*., (1991), Zimmerman *et al*., (2000), and Cubina and Aide (2001), the greatest impediments to vegetation regeneration are deficiency of seeds in the soil seed bank and extremely low levels of seed arrival at suitable sites through dispersers. The *E. helvum* and other avian frugivores can play a critical role in the regeneration of vegetation in degraded landscapes through dispersal of guava which are considered to be a foci of plant regeneration in Kenyan farm lands (Berens *et al*., 2008). However, the role of the frugivores in vegetation regeneration in agro-ecosystems is poorly known. This study was, therefore, aimed at determining the contribution made by the *E. helvum* and avian frugivores to guava seed dispersal and regeneration in degraded landscapes in Vihiga County, Western Kenya by using the *Psidium guajava* as a means to achieve the objectives. The objectives of the study were achieved through determination of the frugivore assemblages dispersing guava seeds, germination of guava seeds and seedling establishment. The results of the study will help to shed light on the effectiveness of the *E. helvum* and other avian frugivores as a seed dispersers in fragmented landscapes and hence raise the awareness on the importance of conserving the species to ensure plant regeneration in agroecosystems.

1.1 Problem statement and justification of the study

Vihiga County is one of the densely populated counties in Kenya prompting an increased demand for arable land. This has led to severe land degradation exacerbated by encroachment of forested hilltops, wetlands and riverine ecosystems. Anecdotal evidence shows that the land cleared for

agriculture eventually loses its fertility and vegetation recovery is slow. According to Nepstad *et al*., (1991), Zimmerman *et al*., (2000), and Cubina and Aide (2001), the greatest impediments to vegetation regeneration are deficiency of seeds in the soil seed bank and extremely low levels of seed arrival at suitable sites through dispersers. This problem is aggravated further by serious decline in the population of vertebrate dispersers such as primates owing to hunting pressure and changes in land use (von Hippel *et al*., 2000). Markedly, fruit bats are among the few remaining important groups of small to medium-sized vertebrate seed dispersers in western Kenya. They are highly mobile and potentially disperse seeds over long distances. As such, they play an important ecosystem service of maintaining floristic diversity in the region hence of conservation significance.

Degraded areas are recognized as appropriate sites for exotic species which foster native plants thus affecting plant regeneration positively (Neilan *et al*., 2006; Schlaepfer *et al*., 2012). For instance, exotic guavas are considered to be important foci of plant regeneration in farmlands in western Kenya (Berens *et al*., 2008). Since guavas are part of *E. helvum* and birds diet, they can largely contribute to vegetation reinforcement in degraded landscapes. However, our knowledge on the role of *E. helvum* and birds in seed dispersal and plant regeneration in farmlands is still scanty. This research study was therefore designed to evaluate the significance of *E. helvum* and birds in guava seed dispersal so as to demonstrate their functions in plant regeneration in degraded farmlands. The information obtained will be used as leverage for the protection and justification for the continued existence of the species and their current roosting sites.

1.2 General and Specific objectives

The general objective was to investigate the importance of the straw coloured fruit bat *Eidolon helvum* and avian frugivores in guava fruit seed dispersal, germination and tree establishment in fragmented landscapes of Vihiga County. The specific objectives were to:

1. To determine the frugivores that are responsible for dispersal of guava seeds in Vihiga farmlands.

2. To establish the effect of gut treatment by fruit bat *Eidolon helvum* on germination of guava seeds.

3. To determine the effect of *E. helvum* and avian frugivores seed dispersal on seed rain, seedling and tree establishment in bat roosting and non-roosting sites.

1.3 Research hypotheses

This research work was guided by two hypotheses which were:

1. The *E. helvum* fruit bat is the most effective disperser of *P. guajava* seeds in fragmented landscapes of Vihiga.

2. The passage of seeds through the gut of *E. helvum* influence the rate of guava seed germination.

CHAPTER TWO: LITERATURE REVIEW

2.1 The straw-coloured fruit bat *(Eidolon helvum)*

The *Eidolon helvum* also known as straw-coloured fruit bat is the second largest fruit bat in Africa and belongs to the family Pteropodidae. It is classified as Near-threatened under the IUCN Red Data List (IUCN, 2013) owing to habitat loss. Adult *E. helvum* weigh 250-310g, have mean wing span of 0.8m and show minor differences between sexes (DeFrees and Wilson, 1988; Bergmans, 1990; Kingdon *et al.*, 2013). Even though the main habitat for *E. helvum* is along the equator, its migratory range spreads out from sub-Saharan Africa to South Africa (Kingdon, 1984). Its body morphology is adapted to enable extensive movements while confining its foraging activities to the upper forest canopy due to its rather low maneuverability (Thomas, 1983; Kingdon *et al.*, 2013). However, colonies of *E. helvum* are rarely found in protected areas or deep in dense forests, but within human habitation especially roosting on trees in gardens, institutional houses (gorvernment offices) or in big towns (Racey, 2004).

The straw-coloured fruit bat, is a prime example of an animal disperser that could be particularly effective for seed dispersal and pollination of plants, especially in fragmented landscapes. This species congregates across tropical Africa in sometimes huge colonies such as the one in Kasanka National Park in Zambia, which seasonally hosts roughly ten million individuals (Richter and Cumming, 2006). Colonies in West Africa range from a few thousand to one million bats (Thomas, 1983; Hayman *et al.*, 2012; Fahr *et al.*, 2015). In Kenya, the largest colony of *E. helvum* occurs in Western Kenya with a population of approximately 25,000 bats (Webala *et al.*, 2014). *Eidolon helvum* seasonally migrates for more than 2000 km between forest and savanna biomes, likely in

response to seasonal fluctuations in food availability (Thomas, 1983; Richter and Cumming, 2008; Ossa *et al*., 2012). On a daily basis*, E. helvum* flies up to 88 km from its colony to foraging areas (Fahr *et al*., 2015) and in the process potentially disperses seeds and pollen over both short and long distances. Consequently, the *E. helvum* is significant in preserving and restoring vegetation in wooded habitats (Richter and Cumming, 2006). Studies by Thomas (1982) show that seed dispersal by the species facilitated the spread of the introduced neem tree (*Azadirachta indica*) across Ghana's Accra plains. Moreover, Taylor (2005) observed that the *E. helvum* was the main disperser of the *Milicia excelsa* and *M. regia* which are tropical hardwoods.

2.2 Frugivorous birds

Many frugivorous birds are persisting, at least in the short term, in human-dominated landscapes (Greenberg *et al*., 1997; Hughes *et al*., 2002). These birds serve important functions, such as seed dispersal and pollination (Sekercioglu, 2006). In their role as dispersers, birds are not only fundamental to the maintenance of diverse plant communities (Stiles, 1985), but may also have the capacity to restore them (Wunderle, 1997), thus potentially serving as important partners in tropical reforestation (Holl *et al*., 2000).

The relative importance of different frugivorous bird families varies with the stage of forest succession or restoration (Corlett and Hau, 2000). Frugivorous birds that can tolerate degraded landscapes are more important at the initial stage of forest succession or reforestation (Corlett, 1998). They include passerine birds belonging to the Corvidae (magpies, jays, orioles etc.), Muscicapidae-Turdinae (thrushes), Muscicapidae-Saxicolini (robins and chats), Sturnidae (starlings and mynas), Pycnonotidae (bulbuls), Zosteropidae (white-eyes) and Sylviidae-

Garrulacinae (laughing thrushes) (Corlett and Hau, 2000). However, none of these birds are strict frugivores and all depend on insects for a significant part of their diet. Other bird families, which are tolerant of fragmentation and disturbance and could make use of secondary and disturbed habitats. These will become increasingly important as forest succession or reforestation proceed, notably the highly frugivorous non-passerines Megalaimidae (barbets) and some Columbidae (fruit pigeons) (Corlett and Hau, 2000). The more tolerant species of Bucerotidae (hornbills) may also appear if there is primary forest nearby and no hunting (Corlett and Hau, 2000).

The fruit handling behaviour of frugivorous birds plays a key role in determining their contribution to the seed dispersal process (Jordano and Schupp, 2000). Frugivores that can swallow whole fruits, transport and defecate intact seeds in suitable habitats are often regarded as legitimate dispersers (Jordano and Schupp, 2000). Whether or not fruit consumption by birds translates into successful seed dispersal is still a subject of much debate. Successful seed dispersal involves not only the removal of fruit from a source plant and depositing the seed into suitable sites, but also the ability of the deposited seeds to germinate and establish seedlings after passage through digestive tracts of birds (Herrera and Jordano, 1981; Schupp, 1993). Frugivorous birds play a key role in seed dispersal and establishment of a range of tropical plant species, such as the *Accacia thonigii* Kirika *et al*., (2008), Brazilian Pepper *Schinus terebinthifolius*, D'avila *et al*., (2010). In addition to the role of avian frugivores in dispersing exotic plants, frugivores undertake a crucial importance in areas where endozoochory contributes toward regeneration of degraded areas or maintenance of forests (Silva and Tabarelli, 2000; Pizo, 2004; Hansen and Galetti, 2009). Comprehensive studies of single plant-frugivores seed dispersal interactions have been undertaken

9

in other tropical areas; D'avila *et al*., (2010), Nayara *et al*., (2017) but only a few studies have been made in Kenya (Berens *et al*., 2008 and Kirika *et al*. 2008).

Although less than 1 % of the world's bird species primarily prefer agricultural areas, nearly a third of all bird species occasionally use such habitats (Sekercioglu *et al*. 2007), often providing important ecosystem services, such as pest control, pollination, seed dispersal, and nutrient deposition (Sekercioglu, 2006). There is growing interest in avian functional diversity in tropical forests and agroecosytems, especially in tree-dominated agroforestry systems such as shade coffee and cacao plantations that harbor higher bird diversity than open agricultural systems with few or no trees (Marsden *et al*. 2006; Clough *et al*. 2009). However, recent research has focused disproportionately on Neotropical coffee plantations (Komar, 2006). More studies on other types of tropical agroforest systems are needed particularly in Africa where there has been less research on these issues than in Asia and the Neotropics (Naidoo, 2004; Waltert *et al*. 2005; Holbech, 2009). In this study the diversity of birds visiting guava fruiting trees was investigated.

One major aspect of the behaviour of fruit eating birds that affect their suitability as seed dispersers is the amount of time they spend in fruiting plants during foraging trips. The more time birds spend on a tree, the higher the chances of the seeds falling beneath the plant where the seeds and seedlings suffer mortality (Howe *et al*., 1985). If bird visits are short, they are more likely to carry seeds away from the parent plant, make more visits per day, and produce a less clumped distribution of seeds (Howe and Estabrook, 1977). In this study, the time spent by avian frugivores on selected focal guava trees was investigated.

10

2.3 Frugivory and seed dispersal

Animal seed dispersal is largely the main method of seed dispersal in the tropical ecosystems (Howe and Small wood, 1982, Levin *et al*., 2003; Dennis and Westcott, 2006). It is estimated that more than 95% of angiosperm species in tropical forests are dispersed by this method (Terborgh *et al*., 2002) where plants with fruits suited for vertebrate seed dispersal make 75-92 % of the vegetation (Jordano, 2000). Many of these plants have evolved traits for attracting fruit eating fauna. These include fruits that are often brightly coloured, have relatively high nutritional content (e.g. lipids and proteins), have characteristic odors, and are positioned on the parent plant to facilitate capture and consumption by frugivores (Howe, 1986). In highly degraded landscapes, throughout the world, the presence of frugivores is a major factor behind the dispersal and success of animal dispersed plants found establishing there (Maina and Howe, 2000; Martinez-Garza and Howe, 2003).

Among all vertebrates, three classes are particularly recognized as important seed dispersers in tropical ecosystems. These include; birds, reptiles and mammals (Stiles, 2000; Olesen and Valido, 2003). Even though avian and mammal species are significant in continents, reptiles perform a significant part on islands, mainly within those situated at tropical and subtropical latitudes (Olesen and Valido, 2003 and Kaiser-Bunbury *et al*., 2010). Lizards are regarded as fundamental dispersers of seeds belonging to gymnosperms and angiosperms (Tiffney, 1984; Olesen and Valido, 2003). Evidently, among the most developed reptiles, tortoises are the only animals recognized as essential seed dispersers since 25% of tortoises are herbivorous in nature (King, 1996).

Primates constitute 25 to 40% of frugivore biomass in tropical forests (Chapman, 1989) and are major seed dispersers (Gross-amp, 2009), for example, the Neotropical howler monkeys (*Alouatta seniculus*) and spider monkeys (*Ateles* spp.) (Andersen, 2002; Link and Di Fiore, 2006). The Tana River Mangabeys (*Cercocebus galeritus*) have been reported as effective dispersers of *Phoenix reclinata* seeds; one of their main dietary plants (Kimuyu *et al*., 2012). Other animals such as the African elephants (*Loxodonta africana*), Asian gibbons (*Hylobates spp*.), Moustached tamarin (*Saguinus mystax)* and Saddleback tamarins (*S. fuscicollis*) are known to disperse many plant species (McConkey, 2000; Culot *et al*., 2010). Large carnivorous mammals are also considered to be potential seed dispersers of fleshy- fruited plants in tropical ecosystems (Jordano *et al*., 2007). Scatter-hoarding rodents bury intact seeds in shallow caches, and those seeds that are not retrieved by the animals, are protected from invertebrate predation, and can germinate and establish (Briggs *et al*., 2009, Hirsch *et al*., 2012, Jansen *et al*., 2012). Thus, seed dispersal by scatter-hoarding rodents results from forgotten cached or re-cached intact seeds. Generally, however, rodents will not disperse intact or undamaged seeds; instead, they remove the seeds and either (1) eat them completely or (2) partially consume them, discarding uneaten seed fragments (e.g., Steele *et al*., 1993, Perea *et al*., 2011, Shiels and Drake, 2011).

Worldwide birds are the most studies group of vertebrates with regard to seed dispersal. This is because they are the main fruit consumers (Ingle, 2003; Pejchar *et al*., 2008; Böhning-Gaese, 2012). In their role as dispersers, birds such as the African hornbill (*Bycanistes* spp. and *Ceratogymna* spp.) are fundamental to the maintenance of diverse plant communities (Stiles, 1985; Holbrook and Loiselle, 2009; Kitamura, 2011). In addition, they have the capacity to restore them thus potentially serving as important partners in tropical reforestation. The interaction between

frugivorous birds and fruiting plants has been examined in a range of studies (Jordano, 1995). But the relationship between frugivorous birds and fruiting plants has often been asymmetrical (Mccann *et al*, 1998; Paine, 1992) and not all frugivores are effective dispersers to the plant species consumed (Bradford and Westcott, 2011). For example, for a given species of plant, not all the visiting birds but only one or two bird species have a mutualistic and compact relationship with it (Silveira *et al*, 2012).

Fruit bats are keystone species in the maintenance and re-establishment of natural vegetation in the Old World (Fujita and Tuttle, 1991; Mickleburgh *et al*., 1992; Lobova *et al*., 2009). Their role in seed dispersal and pollination is particularly important in tropical rain forest succession and community composition (Henryi and Jouard, 2007; Muscarella and Fleming, 2007). The Neotropical Phyllostomid fruit bats are exceptionally diverse of which about 142 species are recognized as being partially frugivorous, dispersing over 549 plant species in 191 genera belonging to 62 families (Lobova *et al*., 2009). The Pteropodidae bats comprised of over 170 species (Wilson and Reeder, 2005), are involved in dispersal of at least 145 distinct plant genera (Marshall, 1985). These bats disperse seeds over long-distances of about 1-20km for eaten seeds (Tsoar *et al*., 2010). In Tanzania, studies by Seltzer *et al.* (2013) show that at least 49 plant species are dispersed by bats. Out of this, 28 species are considered as new reports in Africa concerning dispersal of seeds by bats. This encompasses approximately 20% of the sub- montane trees found in East Usambara Mountains (Ruffo *et al*., 1989; Lovett *et al*., 2006). Notably, this is above the 6% of tree plant life dispersed by bats in central French Guiana where fruit bats are largely acknowledged as agents of seed dispersal (Lobova *et al*., 2009). Moreover, in other parts of Africa 20 genera and 16 plant species have been verified as being dispersed by bats. This clearly

underpins the extensive involvement of fruit bats in seed dispersal and plant re-establishment throughout Africa.

In Kenya, a study by Webala *et al* (2014) on the movements and roost occupancy of the *E. helvum* indicate that the species colonies are located in areas near human habitations. For instance, the roost site at Ilwanda Village is located on a 2.0-ha private agroforestry farm with more than 100 indigenous and exotic trees interspersed within crops such as coffee, bananas, and maize. According to Webala *et al.* (2014) direct observations of fruit fragments and fecal material at active roost sites showed that *E. helvum* consumed fruits from at least 31 plant species belonging to 15 families. These included fruits from locally-cultivated fruit trees (both indigenous and exotic) such as; *Psidium guajava, Carica papaya; Eriobotrya japonic* as well as water berries (*Syzygium cordatum* and *S. guineense*; *Myrtaceae*) (Webala *et al.*, 2014). No previous studies have examined in detail the role of *E. helvum* in dispersal of individual plant species.

2.4 Dietary analysis of fruit visiting bats and birds

Conventional methods of dietary analysis of fruit visiting bats have relied on visual identification of food items directly consumed by bats (Kunz, 1990). Fruit-eating bats may eat either whole fruits or parts of them, in case of whole fruits, seeds pass through their digestive tract and can be found in feaces (Fleming, 1981; Tang *et al.*, 2007). Fruit eating bats may only take a bite, ingest the fruit pulp, and reject masticated pellets. Fig eating bats, for example, masticate figs and spit out pellets with seeds (Morrison, 1978; Charles –Dominique, 1991). The timing of the appearance of seeds in the excreta depends on the time of fruit ingestion and the gut transit time. Transit time through the digestive tract ranges from 15 and 60 minutes in small fruit eating bats (Fleming and Heithaus,

1981) and seeds may vary in their retention characteristics according to their size and morphology. In large flying foxes, seeds may remain in the digestive tract for a prolonged time so that the animals may disperse the fruit more than 100km from the source tree (Shilton *et al*., 1999).

When bats ingest and digest a fruit close to the fruiting tree, fecal droppings can be found close to the fruiting tree. More often however, fruit eating bats remove fruits and transport them from the fruiting tree to a feeding roost, where they process the given food item (Fleming, 1988). Bats that commute between fruiting trees and feeding roosts often defecate on their way to and from fruiting trees, thus depositing seeds along their way (Charles –Dominique, 1986; Duncan and Chapman, 1999). The latter phenomenon is referred to as seed dispersal resulting in the production of 'seed rain.' Past studies have demonstrated the importance of fruit bat seed dispersal by investigating the germination rates, seed deposition and seed predation in forest ecosystems (Nyhagen *et al*., 2004; Taylor, 2005; Muscarella and Fleming, 2007; Tang *et al*., 2008; Selter *et al*., 2013). However, there is paucity in studies on the effect of gut treatment on germination of guava seeds.

Most fruit-eating birds feed on only a portion of the diversity of fleshy fruits produced in any habitat (Snow, 1976). Fruit selection presumably depends on the behavior, morphology, and nutritional requirements of birds, the abundance of alternative food resources, and fruit characteristics such as temporal availability, habitat, taste, color, abundance, and placement on a plant (Sorensen, 1983; Wheelwright and Janson, 1985). Fruit characteristics such as, fruit size, pulp-to-seed ratio and nutrient composition also partly determine the net value of a fruit. The quality of treatment these birds provide to the guava seeds they ingest (i.e., if they destroy or pass

15

seeds intact through the gut or even if they alter the germination pattern) requires further investigation.

2.5 Factors influencing dispersed seed germination

2.5.1 Seed dispersal effectiveness

The mechanisms of frugivore seed dispersal and the design in which seeds are positioned are known to influence several factors that affect plant regeneration including; seed viability and survival, germination, emergence, and development of novel plants (Izhaki *et al*., 1991; Traveset and Wilson, 1997; Alca' ntara *et al*., 2000). Therefore, the role of frugivores in plant survival is subject to the quantity and quality of seed dispersal (Schupp, 1993; Jordano and Schupp, 2000). The quantity of seed dispersal is governed mainly by the number of frugivores visiting the parent plant and the quantity of seeds eaten during every visit (Schupp, 1993). However, the quality of dispersal is centered on the action of digestion on the seeds and the suitability of the site where seeds are deposited and subsequent seedlings establishment (Howe and Smallwood, 1982). Both aspects of quantity and quality determine if a frugivore is a genuine disperser for a specific plant species (Alca ntara *et al*., 2000; Jordano and Schupp, 2000). Several studies have compared the relative importance of different frugivores in relation to seed dispersal of specific individual tree species. For example, Taylor (2005) observed that *E. helvum* bats flew constantly around focal trees, as well as back and forth to several feeding roosts, or among several fruit bearing (*Milicia*) trees while foraging. This behaviour, combined with their large foraging group and colony size, ability to excrete during flight, and fast digestion (Thomas, 1982) proves that *Eidolon* carry out an important ecological service by dispersing thousands of seeds throughout the forest.

16

Disturbed areas are commonly avoided by animal dispersers owing to low availability of resources and vulnerability to predation. Birds living in such habitats, are observed to drop seeds below the parent tree or transport fruit to a perch or roost preceding falling or excreting seeds (Charles-Dominique, 1986; McClanahan and Wolfe, 1993; Corlett, 1998). Therefore, avian frugivores are less likely to deposit seeds in forest glades or in exposed areas compared to bats (Medellin and Gaona, 1999; Ingle, 2003). Fruit bats drop several seeds while flying regardless of their inclination to deposit most of the seeds at roosting trees (Thomas *et al*., 1988; Banack *et al*., 2002; Hodgkison *et al*., 2003). As such, seeds dispersed by bats are predisposed to reach extensively degraded sites without settling and nesting sites required by avian frugivores. Due to this variation, bats are more significant dispersers of seeds than birds during the first phases of plant succession (Muscarella and Fleming, 2007).

Many studies indicate that worldwide habitat loss and fragmentation lead to a decline in bird species richness (Turner, 1996; Brooks *et al*., 1999). It is also known that dispersal mutualists such as birds are important for seed dispersal, for without them seedling recruitment is limited due to the high mortality in non-dispersed seeds that merely fall beneath parent trees (Janzen *et al*., 1976; Augspurger, 1983; Howe *et al*., 1985). However, understanding of the link between bird species diversity and its consequences in vegetation regeneration in agroecosystems is still meagre. Few studies have compared the consequences of disperser declines for plant populations, although some possible scenarios have been presented (Howe, 1984; Bond, 1995). Studies by Pizo, (1997) indicate that local bird species richness determined the frugivore assemblages of fruiting trees, with a higher number of more reliable and efficient bird species visiting trees and dispersing seeds in a large forest site than in a small forest fragment. Santos and Telleria (1994) also showed in a

comparison of large and small forest sites that a low number of dispersal agents at the small sites, both in species and abundance, led to a reduction in seed transfer and seedling establishment in *Juniper* trees. In this study, the avian species diversity visiting guava trees in both bat roosting sites and non-roosting sites will be investigated to determine the most effective guava seed disperser.

2.5.2 Gut conditioning

The greatest impact of seed dispersal by vertebrates is the transfer of propangules from parent plants to sites where conditions are suitable for establishment (Primack and Miao, 1992; Howe and Miriti, 2000; Herrera, 2002). Vertebrate seed dispersal also enhances the germination of seeds through passage of seeds through their digestive tract (McKey, 1975; Thomas, 1982). This is referred to as quality of treatment (Schupp, 1993) and has been evaluated by Traveset (1998) who established the enhancement of seed germination through gut passage. The rate of seed germination generally takes place through two ways. Primarily seeds undergo mechanical or chemical processes that change the seed coat thus influencing germination capacity (Agami and Waisel, 1988; Yomtov and Fried Man, 1990). Secondly, viability of seeds is influenced through separation of seeds from chemical inhibitors in the fruit pulp thereby enhancing germination by changing the seed's immediate environment (Lisci and Pacini, 1994; Cipollini and Levey, 1997). Passage of seeds through the gut of some frugivores particularly birds and mammals enhance seed germination rates (McKey, 1975; Thomas, 1982). Utzurrum and Heideman (1991) report germination rates of 91 percent for *Ficus chrysolepsis* seeds from the excreta of three different pteropidid fruit bats, compared to germination rates of 48% seeds from ejecta pellets, and 57%

18

from fruit fragments. Izhaki *et al*., (1995) fed ripe fruits from six different species of wild and cultivated fruits to captive Egyptian rousette bats, *Rousettus aegypticus*. They compared the temporal and total germination rates of seeds from bat excreta, ejecta pellets, and uneaten fruits (control). The results showed that germination rates were significantly higher for only one fruit species for seeds ejected in pellets. Studies by Lopez and Vaughan (2004) established that seeds of *Piper multiplinervium* and *Ficus insipida*, defecated *by Carollia brevicauda* and *Artibeus jamaicensis*, displayed higher germination rates than seeds not consumed by bats. However, Naranjo *et al* (2003) studied the germination of *Stenocereus griseus* and *Subpilocereus repandus* seeds after passing through the alimentary canal of the Miller's long tongued bat *Glossophaga longirostris* and report that gut treatment had no effect on germination rate and only facilitated seed dispersal by distribution of seeds. Similarly, Taylor (2005) found that gut treatment by *E. helvum* had no effect on germination of *Milicia* seeds. Furthermore, Tiang *et al*., (2008) established that the movement of seeds across the digestive system of bats did not enhance germination rate of *M. macroura* seeds. In this study, the effect of gut treatment on the germination of guava seeds will be investigated.

2.6 The importance of seed dispersal to plant regeneration

Seed dispersal is recognized as one of the several processes that determine the extent and patterns of plant regeneration (Wang and Smith, 2002). For, example, following seed dispersal, the process of plant regeneration may strongly be influenced by seed predation, which is in turn related to seed predator abundance (Murray and Garcia, 2002; Babweeteera *et al*., 2007). Nevertheless, seed dispersal establishes the critical template for plant regeneration (Nathan and Muller-Landau, 2002; Levin *et al*., 2003) and makes an important contribution to individual plant reproductive success,

plant dynamics and the ability of plant species to colonise new habitats (Howe and Smallwood, 1982). Seed dispersal increases the likelihood of successful reproduction by individual plant by

removing its seeds from the region of highest seedling mortality (Howe and Smallwood, 1982; Harms *et al*., 2000). However, the benefits of escape depend on how these agents of mortality vary in relation to the position of the parent tree and to seed and seedling density (Levin *et al*., 2003). For example, seedlings of certain plant species may suffer high mortality beneath parent plants (Chapman and Chapman, 1995), whereas those of other plant species may not (Baider and Florens, 2006). Seed dispersal may increase a plants reproductive success by delivering seeds to 'microsites' that contain combinations of abiotic conditions (e.g., soil fertility, moisture, light) and biotic factors (e.g., competitors, predators) that improve germination, survival and growth (Grubb, 1977; Hubbell, 1979).

Seed dispersers affect the demographic characteristics and dynamics of plant populations. For example, the size and rate of expansion of plant populations are products of reproductive success of individual plants which depends on the successful dispersal and establishment of propangules (Levin *et al*., 2003). Furthermore, seed dispersal to suitable 'microsites' is critical factor in the recovery of plant populations following localized extinctions, whether from stochastic environmental and demographic causes or from human activities (Cochrane *et al*., 1999). Seed dispersal is fundamental to plant colonization of new habitats. For example, in fragmented forest landscapes seed dispersal strongly influences patterns of plant regeneration on cleared land (Zimmerman *et al*., 2000; Hooper *et al*., 2004; Franklin and Rey, 2007). In this study, seedling establishment will be compared between the bat roosting sites and non-roosting site.

CHAPTER THREE: STUDY AREA, MATERIALS AND METHODS

3.1 Study area

3.1.1 Location

This study was carried out in Vihiga County in western Kenya. It is approximately 355km from Nairobi and 25km from Kisumu. The county lies between longitudes 34° 30´ and 35° 0´ east of the Prime Meridian and 01° 5´ north and at an altitude range of between 1750 – 2000m above the sea level. It neighbours Kakamega County to the North, Kisumu County to the South, Nandi County to the East and Siaya County to the South-west. The total area covered by the county is approximately 530.9 km^2 (G.o.k, 2005) making it one of the smallest counties in the country (Fig.1). Three study sites, each measuring 20,000m^2 (2 hectares) were selected. These included two *E. helvum* roosting sites (Mbale and Ilwanda) and a non - roosting site (Chugi). The roost sites were located using records from previous studies in the area. Mbale site lies at coordinates 0° 05′ 35″ N, 34° 43′ 09″ E and is located near Mbale town a few meters from the Kakamega-Kisumu road. It is dotted by private farms of <0.5 ha with roost trees positioned along the hedge rows. Ilwanda lies at coordinates 0°05′ 47″ N, 34°44′21″ E and is 2km from Mbale town. It is the largest of the roosting sites with roost trees occurring within a private farm of approximately 20,000m^2 and along the hedge rows. Chugi study site lies at co-ordinates 0° 04' 32" N 34° 35' 69"E. It is non-roosting site and the control for this study. The site is located 5.36km Mbale town (Fig 1).
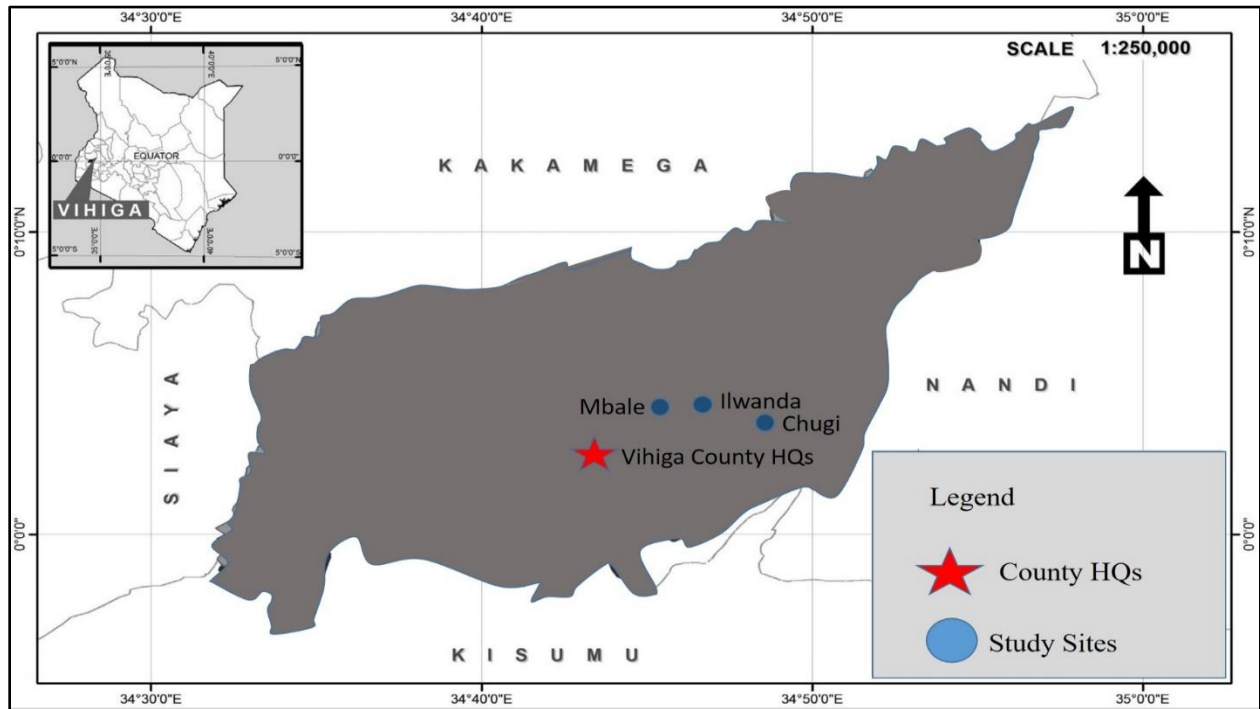
Figure 1: A map showing the study area and study sites

3.1.2 Climate

Annual rainfall average is 900mm spread over two seasons with the long rains and short rains occurring in April - May and October - November respectively. Other seasons within the area are a Cold - Dry season which occurs in June - August and a short dry season around December - February. The mean daily minimum temperature is approximately 14° C while maximum daily temperature is about 26 ^{o} C (NEMA, 2009).

3.1.3 Topography and soils

Vihiga County is situated on the eastern parts of the Rift Valley's Lake Basin. The altitude ranges between 1750-2000m above the sea level and slopes gently from east to west. It is characterized by undulating hills and valleys. The main rivers are Esalwa and Yala which drain in Lake Victoria.

The southern part is characterized by rugged granite hills of Maragoli, Bunyore and Nyangori. Major soils found in the area are acrisols which are deep, well drained and slightly acidic. Humic nitosols and ferrosols are also found but to a smaller extent especially on the southern parts of the county (GoK, 2009). These soils are very fertile and exhibit characteristics that favour most of the agricultural activities carried out by most of the residents.

3.1.4 Fauna

Historically, large animals were common in this region due to plenty of habitats. They included: lions, leopards, buffaloes, hippos and antelopes. As the population grew and more land for settlement was sought, most of these animals were displaced from their habitats. The major animals now common in the county are: colobus monkey, baboon, small antelopes, civet cats, bats, birds, snakes, fish, frogs and very few crocodiles in River Yala. The forested areas are also rich in many insect species of butterflies and bees (NEMA, 2009).

3.1.5 Vegetation

The vegetation in the area is natural moist forest comprising of riverine vegetation along rivers and thick bushes and woodland with dense undergrowth in the undulating plains. Like in most areas of Kenya where crop husbandry is the major land use system, natural vegetation in most parts of the county is disturbed and has been replaced with fast growing exotic species. This is due to increasing demand for arable land. Remnants of the original tree cover can still be found only in gazetted forest nature reserve, along river banks in some Tiriki cultural forests and rain making groves of the Bunyore tribe. Apart from the gazetted area, most of these natural forest remnants are under intense human pressure despite concerted efforts for their conservation. The main exotic species include: *Eucalyptus spp*. *Pinus patula*, *Cupressus lusitanica*, *Gravellea robusta*, *Persea*

americana and *Zyzigum cuminii*. Indigenous trees include: *Croton megalocarpus*, *Ficus thonningii, Ficus sycomorus, Croton machrostachyus*, *Teclea nobils*, *Antiaris toxicaria*, *Bridelia micrantha, Ficus sp* among others. Other indigenous trees are being domesticated such as, *Prunus africana*, *Maesopsis eminii*, *Markhamia lutea*, *Olea spp*. and *Cordia abbysinica* (NEMA, 2009).

3.1.6 Population and social-economic activities

Vihiga County has the highest human population in rural Kenya at more than 1000 persons per square kilometer and a population growth rate of 3.3 percent. The county has seen the average farm sizes steadily decline to 0.5 ha (GoK, 2005). Agriculture is the major economic activity carried in the area. Tea is the main cash crop, usually cultivated in plantations located on the highlands. Subsistence crops in the county include: millet, cassava, vegetables, beans, maize, potatoes and peas. These crops are mainly produce for domestic consumption but the surplus is sold locally. Dairy, beef, fish and poultry farming are also practiced. There exist a few industries in the county that are agricultural based. Other industrial activities in the county include the formal Jua Kali who specialises in making house hold furniture, metal and motor vehicle garages. These are found in major shopping and market centers all over the county. Currently, individuals carry out gold mining on a small scale along the river valleys (GoK, 2005).

3.2 Materials and Methods

3.2.1 Sampling design

This study was carried out over a period of 6 months with sampling every month starting from December 2013 to June 2014. Three study sites including two *E. helvum* roosting sites (Mbale and Ilwanda) and a non - roosting site (Chugi) were selected for study. In each site, 2 ha plots were

defined where five transects measuring 100m long and 20m apart were established and 10 focal trees selected for sampling frugivores. Under, the crowns of the focal trees, data on seed rain was collected using 1m^2 quadrats. Germination experiments were conducted to determine the effect of four treatments (manually extracted seeds, intact seeds, seeds from bat excreta and seeds obtained from spats) on the percentage germination of guava seeds. Data on seedling establishment were collected below the crowns of 20 selected trees in each study site by mapping seedlings in six randomly chosen 1m^2 quadrats. In each site, one hectare plot was divided into 10 sampling plots measuring 10 m by 10m to collect data on tree density and diversity.

3.2.2 Frugivore observations

3.2.2.1 Selection of focal trees

To select study trees for frugivore assemblages in each site 2-hactare plots were demarcated. In each one hectare plot five transects measuring 100m long and 20m apart were established (Kirika, 2005). Fruiting trees were sampled for fruit availability by walking along transects using a pair of binoculars (Nikon 10x50). All trees with ripe fruits occurring within 10m on either side of transect were identified and recorded (Bleher & Böhning-Gaese, 2001). In each site, 10 study trees were selected for sampling of frugivore assemblages. Focal trees were selected based on the occurrence of least 10 to15 ripened fruits, with ripeness assessed relative to the colour of fruit (Berens *et al*., 2007). A Global Positioning System (GPS) device (Garmin etrex 10) was used to take the geographical coordinates of each focal tree. In addition, the distance of the focal tree from the nearest roosting site was measured using GPS device.

3.2.2.2 Frugivores visits

This method involved observation of frugivores visiting guava fruiting trees selected for study. Observations were conducted for three months from May 2014 to July 2014 to determine which avian and bat assemblages were visiting fruiting guava trees. For avian frugivores a total of 300 hours of diurnal observations were conducted at 30 fruiting trees, 10 from each study site by two observers. Observations were done starting from 0600h to 1100h and conducted twice for every fruiting tree at a distance of 15 to 20 m (distance far enough that the behavior of birds was unaffected) with the aid of a 10 x 40 binoculars (Berens *et al*., 2008). Each bird entering a fruiting was recorded and identified using bird guide by Zimmerman *et al*. (1998) (Berens *et al*., 2008; Yilangai *et al*., 2014). Feeding guilds were classified using a list of main diet items of birds from sub-Saharan Africa. (Kissling *et al*. 2007). The feeding guilds included: frugivores (fruit eaters), granivores (seed eaters), insectivores (invertebrate eaters), nectivores (feeding on nectar) and omnivores (consuming both plant and animal materials).

To collect data on the number of *E. helvum* fruit bats visiting guava trees, a total of 300 hours of nocturnal observations were conducted at the 30 selected fruiting guava trees by two observers. Each focal tree was watched for two nights consecutively from 1900h to 2400h, a peak feeding time for bats using a NI-TEC night vision scope (Fleming and Williams, 1990). After recording the number frugivores, focal animal sampling was carried out in which a single frugivore was monitored. The arrival time, departure time, and activities (feeding, patching, moving) carried out by the targeted frugivore was recorded. The duration of the frugivore's visit was defined as the time of departure minus the time of entry. The same method was applied to both bats and birds.

The diversity of birds visiting guava trees in the three study sites was calculated using Shannon Diversity Index (H), (Zar, 1996); $H = \Sigma - (P_i * \ln P_i)$. Where H = Shannon diversity index, P_i = proportion of a species relative to the total number of species present, $\ln P_i$ = natural logarithm of P_i and Σ is the total sum.

3.2.3 Guava seed germination

3.2.3.1 Seed collection

Fruits selected by *E. helvum* are usually, sweet, juicy and pulpy (Taylor, 2005). As such, 60 ripe fruits were collected directly from the focal trees. This was carried out during their peak fruiting period in June 2014. They were then packed in sealed plastic bags and transported to the laboratory for seed extraction. Among the fruits collected 10 were left intact and placed in a drying tray in the open air to dry. The remaining 50 were used to obtain the manually extracted seeds for germination. To obtain seeds from ripe guava fruits, fruits were crushed by hand and washed with distilled water. The seeds were then dried for two consecutive days in the open air to minimize water content (Djossa *et al*., 2008). Dry intact fruits and fruit fragments from spats were crushed gently using pestle and mortar and seeds extracted by hand. The extracted seeds were then put in sealed paper envelopes and labeled for use in the germination experiment.

3.2.3.2 Seed germination

Germination experiments involving four treatments: manually extracted seeds, seeds from bat excreta (fecal), intact seeds and seeds from fruit fragments dropped by the bats (ejecta or spats) were carried out (Samuels and Levey, 2005; Nakamoto *et al*., 2007) for a period of two months.

Manually extracted seeds included seeds extracted from ripe guava fruits. Intact seeds were obtained from un-manipulated fruits. Gut passed seeds included those that were defecated by bats. Ejecta were seeds obtained from fruit fragments dropped by bats while feeding. Seeds were first tested for viability before germination. This was done by soaking them in 400 ml of distilled water in 500 ml-beakers. The seeds that floated were discarded as they were not viable (Mabundza *et al.*, 2010). From each treatment 10 samples containing 30 seeds were selected for germination (Nakamoto *et al.*, 2007). These were put in petri dishes (10 cm diameter) on moistened cotton wool and placed in an unheated glasshouse (Izhaki and Safriel, 1990). These were inspected and watered daily with distilled water (Pjil van der, 1972). Germination was ascertained through growth of seed radicle. Germinated seeds were counted and immediately removed to minimize their influence on the remnant seeds (Izhaki *et al*, 1995). The germination experiments were stopped one month after the last seed was observed to germinate.

Plate 1: Guava seeds germination

Three aspects of seed germination were examined. Beginning day of germination (BDG) referring to the first day when seeds were observed to germinate. Mean germination time (MGT), which was obtained by the following equation: MGT = $\Sigma n_i\, d_i\, /n$, where *n* is sum of seeds germinated in

the course of the experiment; *ni* is number of seed germinated on day *di; di* is day during germination period (Tang *et al*., 2008). Percentage germination (germination rate) was calculated from each treatment by the formula:

Percentage germination = <u>Number of germinated seeds</u> x 100
                                       Total number of seeds

3.2.4 Seed rain, seedling establishment and tree density sampling

3.2.4.1 Seed rain and spats sampling

Seed rain refers to the pattern of seed fall to the ground (Wang and Smith, 2002). Spats refer to fruit fragments dropped by bats while feeding. Data on seed rain were collected below the crowns of *P. guajava* trees for a period of one month to collect seed rain generated by bats through fecal droppings and spats. This was done by placing seed traps in six randomly chosen $1m^2$ quadrats (Bleher and Böhning-Gaese, 2001; Kirika, 2005). The quadrats were placed randomly within the radius of the crown of the selected tree (Duncan and Chapman, 1999). Thus, a total area of $6m^2$ per tree was covered. Seed traps were wooden frames covered with a nylon paper and had a size of 1m by 1m ($1m^2$ per trap).

Plate 2: Seed trap used for seed rain sampling

The seed rain traps were placed at 1800h and the fecal material removed at 0600h to ensure that only seeds generated by bats were collected. The seeds of *P.guajava* in each fecal pellet were counted and the number of pellets containing guava seeds in each quadrat was recorded and used to calculate the density of pellets containing guava seeds. All seeds belonging to tree species other than *P. guajava* were collected, identified to genus level and where possible to a species level and counted at the end of each monitoring day (Kirika, 2005). From each seed trap faecal samples were collected to extract guava seeds for germination experiment. The seeds were then dried for two consecutive days in the open air to minimize water content (Djossa *et al*., 2008). Guava seeds were later separated from other seeds in the laboratory for germination. Fruit fragments dropped by bats (spats) on the seed traps were also recorded. Samples of spats were collected for germination experiments in the green house. They were then dried using the same procedure as the faecal samples. All the samples were later packed in sealed paper envelopes and labelled for germination.

3.2.4.2 Seedling and tree density sampling

In each site, 20 trees were randomly selected for studying tree seedling establishment. This was done by selecting 50 roosting trees within the study sites based on the presence bat scats at the tree base or DBH ≥ 20 cm in the case of non-roosting site. These have the likelihood of being used as roost trees by *E. helvum* according to Webala *et al*. (2014). The DBH was used as an indicator of tree size (Caughlin, *et al*., 2012). Markers made of white cotton cloth were numbered 1-50 with a mark pen and pinned on the selected tree trunks with a small nail (0.25 inch) to identify them. Then numbers 1-50 were written on small pieces of paper and placed in a box after which 20 pieces of paper were handpicked through blind grabs. The numbers written on the chosen pieces of paper were then used to select the sampling trees. Data on seedling establishment were collected below

the crowns of selected trees for a period of one month. This was done by mapping seedlings in six randomly chosen 1m^2 quadrats (Bleher and Böhning-Gaese, 2001; Kirika, 2005). Thus, a total area of 6m^2 per tree was covered. The quadrats were placed randomly within the radius of the crown of the selected tree (Duncan and Chapman, 1999). All the seedlings belonging to tree species occurring within each quadrat were identified and counted. The seedlings considered were those having cotyledons and first or second set of true leaves. Seedling species recorded were classified according to their succession status as either pioneer or climax species and by their mode of dispersal as either wind, animal or ballistically dispersed.

Plate 3: Quadrat sampling for seedling establishment

Guava tree densities in each of the study sites were obtained to determine to ascertain if they correlate to patterns of guava seed dispersal by both bat and bats. In each study site, 2 one-hectare plots were established for vegetation sampling. Each one hectare plot was then divided into 10 sampling plots measuring 10 m by 10m. Overall, 60 plots were sampled in all the study sites for a period of two months. Trees with diameter at breast height DBH > 20 cm were identified and counted, a common standard for the tree data collection (Gentry, 1982). Tree species were identified according to Beentje (1994). The diameter at breast height (DBH) of each guava tree

was measured using a tape measure. The DBH was measured at 1.3 m above the ground (Kennard, 2002) using a tape measure. For trees that forked just below 1.3M, diameter was measured just below the point of branching (Lwanga, 2003). For trees splitting into several stems, DBH was obtained by calculated as the square root of the sum of all squared stem DBHs (Lwanga, 2003). For trees growing vertically on the slope the DBH of the trunk on the upper side of the slope was measured (Lwanga, 2003). Basal area for the guava trees was calculated using the formula; Basal area $(BA) = \pi \, (DBH/2)^2$. Shannon-Wiener diversity index (H′) was used to determine the diversity of tree species in all the study sites.

3.3 Data analysis

All data collected were entered into an excel spread sheet. Statistical analyses were performed using SPSS version 20.0 and STAT program software. Prior to analysis necessary data sets were subjected to Sharpiro-Wilk test for normality, non-normal data was log transformed and analyzed using parametric statistics. However, non-parametric tests were used if variables did not conform to conditions of normality and homoscedasticity after transformation. All statistical analyses were evaluated at $p < 0.05$ level of significance. Contingency Chi square test was performed to compare; avian feeding guilds, frugivore visits; time spent by avian frugivores and *E. helvum* visits between the study sites. Wilcoxon test was used to compare the number of individual frugivores observed in all the study sites.

Independent t test was used to compare bird diversity between the sites. Wilcoxon test was performed to examine significant differences between the activities and time of visits by frugivores. Correlation was calculated to determine the relation between *E. helvum* visits and the

distance between focal trees and the nearest roosting site. Non-parametric Kruskal–Wallis test was carried out to determine whether the mean germination time (MGT) and seed germination proportions were different among all treatments. One way ANOVA was used to compare densities of pellets of *E. helvum* with guava seeds, fruit fragments and seedlings among the study sites. Where significance differences occurred a *post hoc* test (Tukey honestly significance difference test) was applied to identify homogenous subsets of means that were not different from each other. Independent t test was used to; compare the densities of pioneer and climax seedling species, compare tree species diversity indices and to compare tree densities and basal area among the study sites.

CHAPTER FOUR: RESULTS

4.1 Frugivore observations

4.1.1 *Eidolon helvum* visits

During the 240 hours of nocturnal observations, a total of 4288 individual of *E. helvum* fruit bats were recorded visiting guava trees in all the study sites (see appendix 1). Those encountered in Ilwanda were 1991 representing 46% of the total. In Ilwanda Mbale 1446 were observed representing 34% of the total while in Chugi 851 bats were observed representing 20% of the total. The number of individual bats recorded per night on *P. guajava* trees were significantly higher in Ilwanda than in Mbale ($Z = -2.8$, $p < 0.05$) and Chugi ($Z = 3.74$, $p < 0.05$). Similarly, the number of individual *E. helvum* bats recorded per night per guava tree in Mbale were significantly higher than in Chugi ($Z = 3.74$, $p < 0.05$).

4.1.2 Time of visits by *E. helvum* fruit bats on guava trees

E. helvum fruit bats visited the focal trees throughout the night with peak visits made early in the night between 7pm to 9pm (Figure 2). The number of visits was significantly higher between 7 pm to 9pm than between 9pm to 11pm ($Z = 1.8$, $p < 0.05$). This indicates that bat activity was high during the early hours of the night and decrease towards late night hours. The time spent by *E. helvum* on fruiting guava trees in Ilwanda and Mbale was not significantly different ($Z = -0.26$, $p > 0.05$). However, the time spend by bats in Ilwanda was significantly lower than Chugi ($Z = -1.83$, $p < 0.05$). Time spent by *E. helvum* on focal trees in Mbale and Chugi were not significantly different ($Z = -1.31$, $p > 0.05$).

34
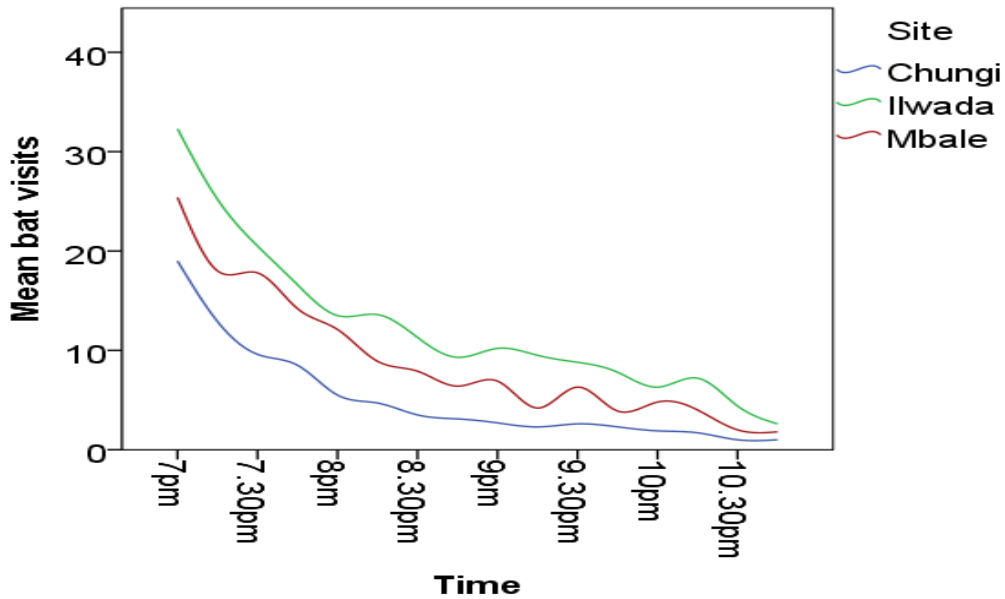
Figure 2: Nocturnal trends in *E. helvum* visits to *P. guajava* trees in all study sites.

4.1.3 Distance between focal trees and *E. helvum* visits

Correlations between *E. helvum* visits and the distance between the focal trees and the nearest roosting site was explored to show the relationship between distance from the roost site and visitation rate. There was a significant weak negative correlation between the two variables in Ilwanda (Pearsons correlation, r = -0.1, d.f. = 8, $p < 0.05$), Mbale (Pearsons correlation, r = -0.36, d.f. = 8, $p < 0.05$) and Chugi (Pearsons correlation, r = -0.1, d.f. = 8, $p < 0.05$). Overall, there was a strong significant negative correlation between the distance from the roost site and number of visits in all the study sites (Pearsons correlation, r = - 0.82, d.f. = 28, $p < 0.05$), Figure 3.
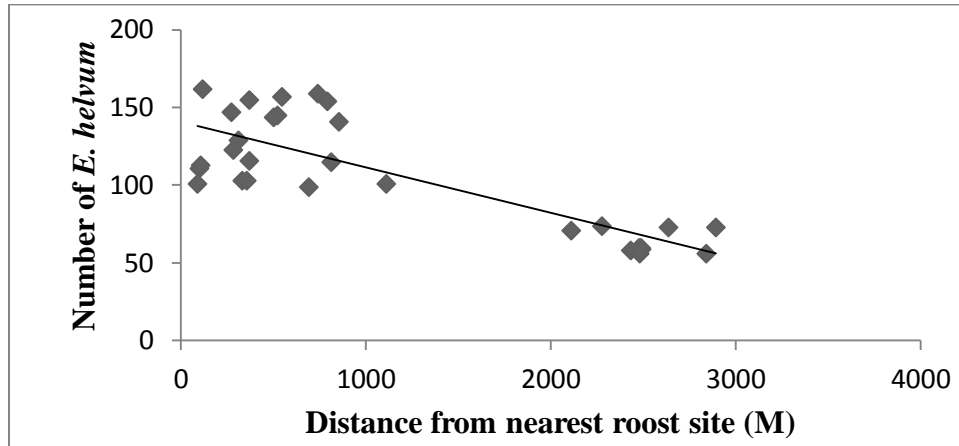
Figure 3: A graph showing correlation between the numbers of *E. helvum* fruit bats recorded on guava trees and the distance in meters from the nearest roosting site.

4.1.4 Activities carried out by frugivores on guava trees

Activities carried out by *E. helvum* fruit bats included feeding and moving across the branches. Out of 4288 individuals of *E. helvum* fruit bats recorded on guava trees, 75 % (n= 3216) were seen feeding on guava fruits. The remaining 25 % (n = 1072) individuals were observed moving across the tree branches. Among all the sites the number of bats recorded feeding on guava fruits were significantly higher than those moving along the branches ($\chi^2 = 4.3$, d.f. = 2, $p < 0.05$). The number of bats observed feeding on guava fruits was significantly higher in Ilwanda than in Mbale (Z= -3.4, $p < 0.05$) and significantly higher in Ilwanda than in Chugi (Z = -2.8, $p < 0.05$). Similarly, bats recorded consuming guavas in Mbale was significantly higher than those in Chugi (Z= -2.6, $p < 0.05$).

Activities carried out by avian visitors included feeding and perching. Out of 1313 frugivore birds observed on guava trees, 67 % (n= 884) were seen feeding on guava fruits. The remaining 33 % (n = 429) individuals perched on the trees (Table 1). Among all the study sites the number of birds observed feeding and perching on the guava trees were significantly different (χ^2 = 3.7, d.f. = 2, p < 0.05). The number of birds recorded feeding on guava fruits Mbale were significantly higher than those recorded in Ilwanda (Z = -2.31, p < 0.05). Similarly, the number of birds observed feeding on guava fruits in Chugi were significantly higher than those observed in Ilwanda (Z = -2.68, p < 0.05). However, the number of birds observed feeding on guavas in Mbale and Chugi were not significantly different (Z = -0.42, p > 0.05).

Table 1: Contingency table showing the observed and expected values (in parenthesis) of avian frugivores observed feeding or perching on guava trees in the study sites.

ACTIVITIES	STUDY SITES			
	Ilwanda	**Mbale**	**Chugi**	**Total**
Feeding	250 (237.66)	307 (320.48)	327 (325.86)	884
Perching	103 (115.34)	169 (155.52)	157 (158..14)	429
Total	353	476	484	1313

4.1.5 Comparison between *E. helvum* and avian frugivores visits

A Chi square test show that the mean number of *E. helvum* fruit bats observed visiting guava trees in all the study sites were significantly higher than avian frugivores in all the study sites (χ^2 = 215.7, d.f. = 2, p < 0.05), Table 2. The mean number of bats and avian frugivores observed visiting

guava fruiting trees was not significantly different between Mbale and Ilwanda ($Z = 6.4$, $p > 0.05$).

However, the mean number of bats and avian frugivores observed in Chugi were significantly

lower than in Ilwanda ($Z = 18.9$, $p < 0.05$) and Mbale ($Z = 10.8$, $p < 0.05$). In Chugi, a significant

weak negative correlation was observed between the mean number of *E. helvum* bats and avian

frugivores visiting guava trees (Pearsons correlation, $r = -0.38$, d.f. $= 8$, $p < 0.05$). However, there

was a significant weak positive correlation between the mean number of *E. helvum* and avian

frugivores recorded on guava tree in Ilwanda (Pearsons correlation, $r = 0.04$, d.f. $= 8$, $p < 0.05$)

and Mbale (Pearsons correlation, $r = 0.42$, d.f. $= 8$, $p < 0.05$). Overall, there was a significant

negative correlation between the mean number of *E. helvum* and avian frugivores observed visiting

guava trees in all the study sites ($r = -0.65$, d.f. $= 28$, $p < 0.05$), Figure 4.

Table 2: A Chi square contingency table showing the observed and expected values (in parenthesis) of *E. helvum* fruit bats and avian frugivores in all the study sites.

Frugivore	Study Site			Total
	Ilwanda	Mbale	Chugi	
E. helvum	1991 (1794.51)	1446 (1471.44)	851 (1022.05)	4288
Birds	353 (549.49)	476 (450.56)	484 (312.95)	1313
Total	2344	1922	1335	5601
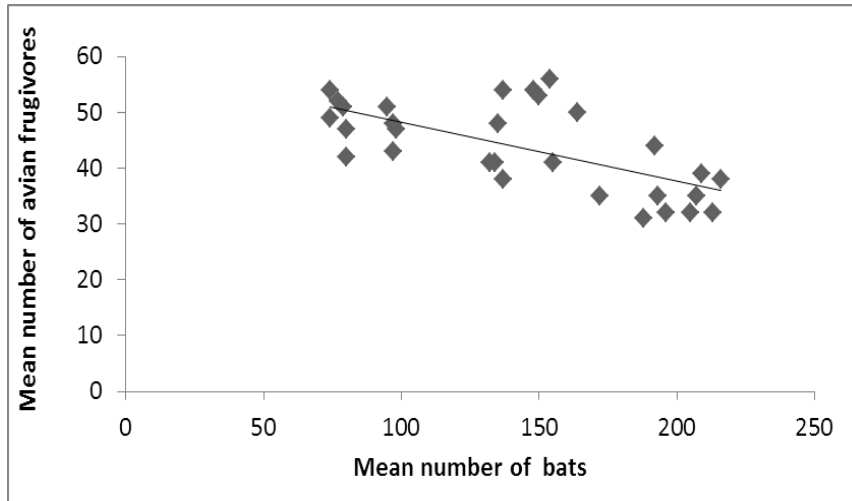
Figure 4: A graph showing correlation between the mean number of avian frugivores and bats recorded on guava trees.

4.1.6 Avian observations within sites

During the 420 hours of observations, a total of 1,835 individual birds comprising of 61 species belonging to 21 families were observed visiting 30 *P. guajava* trees in all the three study sites (see appendix 3). Bird species observed included: Frugivores (72 %, n = 1313), Granivores (15%, n = 278), Insectivores (8 %, n = 148), Nectivores (3 %, n = 62) and Omnivores (2 %, n =33), Table 3. The number of individuals in each feeding guild were not significantly different among the study sites (χ^2 = 8.8 d.f. = 8, p > 0.05). A total of 12 frugivore species were recorded on *P. guajava* trees (see appendix 2). The most common frugivore visitors were the Speckled Mouse bird (*Colius striatus kikuyuensis*), Common Bulbul (*Pycnonotus barbatus*) and the Yellow White-eye (*Zosterops senegalensis*) accounting for 27.8%, 19.8% and 7.6% respectively of the visits made by avian frugivore . The mean number of avian frugivore individuals recorded per day on *P. guajava* trees were highest in Chugi (66.3 ± 3.1) followed by Mbale (64.6 ± 3.5) and Ilwanda (53.0

39

± 1.8) respectively. The mean number of avian frugivores recorded in Mbale and Ilwanda were significantly different (Z = -3.33, *p* < 0.05). Similarly, the mean number of avian frugivores observed in Ilwanda and Chugi were significantly different (Z = -3.69, *p* < 0.05). However, the mean number of avian frugivores recorded on focal guava trees in Mbale and Chugi were not significantly different (Z = -0.08, *p* < 0.05). Shannon- Wiener diversity index (H') for avian frugivores among the sites were; Ilwanda (H' = 2.02), Mbale (H' = 2.26) and Chugi (H' = 2.25). Diversity indices between Ilwanda and Mbale were significantly different (t $_{(16)}$ = 2.1, d.f = 18, *p* < 0.05). Similarly avian frugivores diversity indices were significantly different between Ilwanda and Chugi (t $_{(16)}$ = 2.12, d.f = 18, p < 0.05). However, the diversity indices were not significantly different between Mbale and Chugi study sites (t $_{(16)}$ = 0.42, d.f. = 18, p > 0.05).

Table 3: Contingency table showing the observed and expected values of feeding guilds among the study sites.

SITE	FEEDING GUILDS					
	Frugivores	**Granivores**	**Insectivores**	**Nectivores**	**Omnivores**	**Total**
Ilwanda	353	76	38	24	13	504
	(360.63)	*(76.63)*	*(40.65)*	*(17.03)*	*(9.06)*	
Mbale	476	109	56	22	9	672
	(480.84)	*(102.17)*	*(54.2)*	*(22.71)*	*(12.09)*	
Chugi	484	94	54	16	11	659
	(471.54)	*(100.2)*	*(53.15)*	*(22.27)*	*(11.85)*	
Total	1313	279	148	62	33	1835

4.1.7 Time of visits by avian frugivores on *P. guajava* trees

Frugivores visited the focal trees throughout the day with peak visits made early in the morning hours (Figure 5). Visits made by avian frugivores between 0700-0900h were significantly higher than visits were made between 0900-1100h ($Z = 1.6$, $p < 0.05$). Avian frugivores spent approximately equal amounts of time in *P. guajava* trees in Ilwanda and Mbale ($Z = 1.6$, $p > 0.05$). However, avian frugivores spent a significantly longer time in Ilwanda compared to Chugi ($Z = -3.4$, $p < 0.05$) and in Mbale compared to Chugi ($Z = 4.3$, $p < 0.05$).
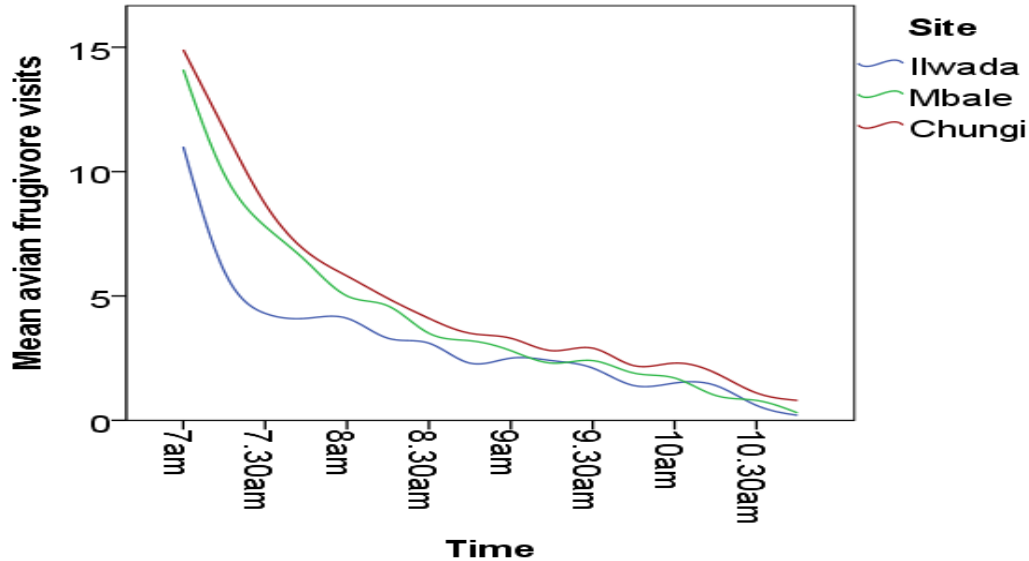
Figure 5: Diurnal trends in the mean number of avian frugivores visiting *P. guajava* in different study sites.

4.2 Seed germination

Seeds obtained from dried fruits (intact) started to germinate after 14 days, while seeds from the other treatments (Ejecta, Fecal and manually extracted) began to germinate after 15 days. Among

the four treatments seeds from fecal treatment had the highest Mean Germination Time (MGT) of 22 days followed by seeds obtained from ejecta which had a MGT of 21 days. Both intact and manually extracted seeds had the same MGT of 20 days. A Kruskal Wallis test showed that the distributions of MGT was not the same among the four treatments (Kruskal Wallis Test, $X^2 = 25.7$, d.f. = 3, $p < 0.05$). Overall, seeds from fecal materials had the highest germination percentage (86.6%) followed by intact (82.2%), manually extracted (76.5%) and ejecta (73.3%) respectively. The seeds were observed to germinate exponentially; slowly at beginning, increased rapidly and then leveled off (Figure 6). In all the treatments the numbers of germinated seeds were significantly higher than the non-germinated seeds ($\chi^2 = 16.8$, d.f. = 1, p < 0.05). Although seed from fecal samples were observed to have a higher germination percentage, germination distributions of seeds among the four treatments (ejecta, fecal, intact and manually extracted) was not significantly different (Kruskal-Wallis Test, $X^2 = 4.32$, d.f. = 3, $p > 0.05$).
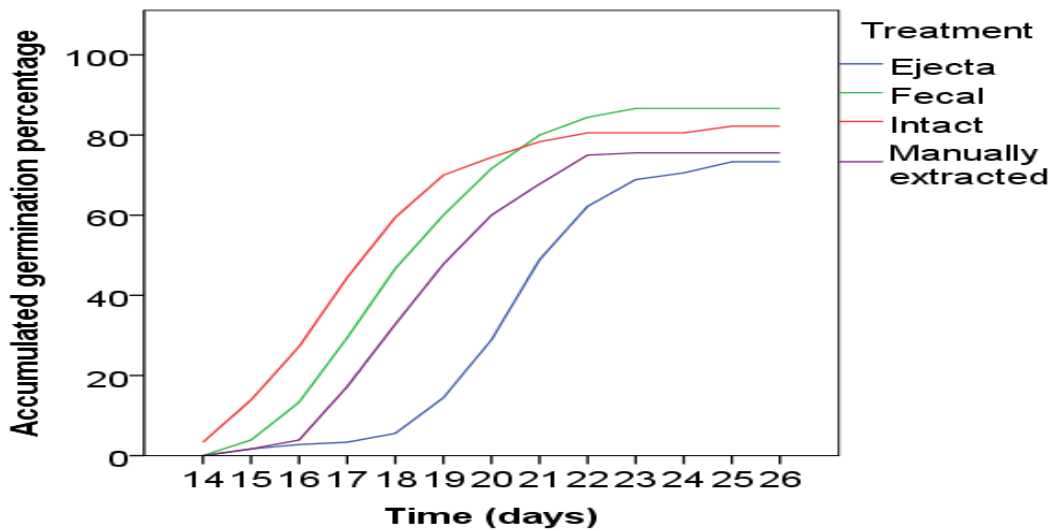
Figure 6: Seed germination rate of four treatments.

42

4.3 Seed rain, seedling and tree densities

4.3.1 Seed rain density

Accumulative total of 1656 fecal pellets were recorded in all the study sites, out of this 63.1% were observed to contain guava seeds. The mean density of pellets (number of pellets/m^2) containing guava seeds deposited by *E. helvum* under the crowns of *P. guajava* trees were significantly different among sites ($F_{2, 27} = 10$, $p < 0.05$). This suggests that the presence of roosting sites in Ilwanda and Mbale had an effect on the number of *E. helvum* visiting guava trees and hence the densities of pellets. Significantly lower densities of pellets with guava seeds (Figure 7) were recorded in Chugi compared to Ilwanda and Mbale (Tukey HSD, $p < 0.05$). The mean density of guava fruit fragments (number of fruit fragments/ m^2) dropped by *E. helvum* under the crowns of guava trees were significantly different among the sites ($F_{2, 27} = 17.6$, $p < 0.05$). Overall, the mean density of fruit fragments dropped by the *E. helvum* were significantly higher than the mean density pellets with guava seeds (t = 21.6, d.f. = 29, $p < 0.05$) in all study sites.
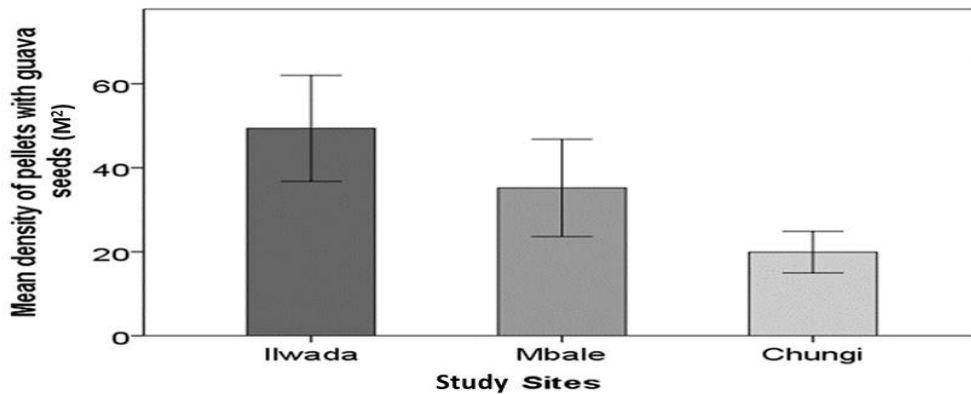
Figure 7: Mean (± SE) density (number of pellets/m^2) of pellets with guava seeds deposited by *E. helvum* under the crowns of guava trees in different sites.

4.4.2 Seedling density

Pioneer plant species are hardy species which are the first to colonize previously disrupted or damaged ecosystems, beginning a chain of ecological succession that ultimately leads to a more biodiverse steady-state ecosystem. Climax species, also called late seral, late-successional, K-selected or equilibrium species, are plant species that will remain essentially unchanged in terms of species composition for as long as a site remains undisturbed. A total of 3,651 seedlings belonging to 18 tree species were recorded in all the sites (see appendix 4). Out of this, 2,456 individuals (67.3%) belonged to the pioneer species whereas 1,195 individuals (32.7%) were of climax species. *P. guajava* had the highest density of 30.3 seedlings/m^2 followed by *Makhamia lutea* (4 seedlings/m^2) and *Bridelia micrantha* (2.1 seedlings/m^2). The mean density of seedlings (number of seedlings/m^2) varied significantly among the sites ($F_{2, 57} = 29.5$, $p < 0.05$) with Ilwanda having the highest density followed by Mbale and Chugi respectively (Figure 8). Overall, the densities of pioneer species were significantly higher than the climax species in all study sites (t = 23.6, d.f. = 29, $p < 0.05$).
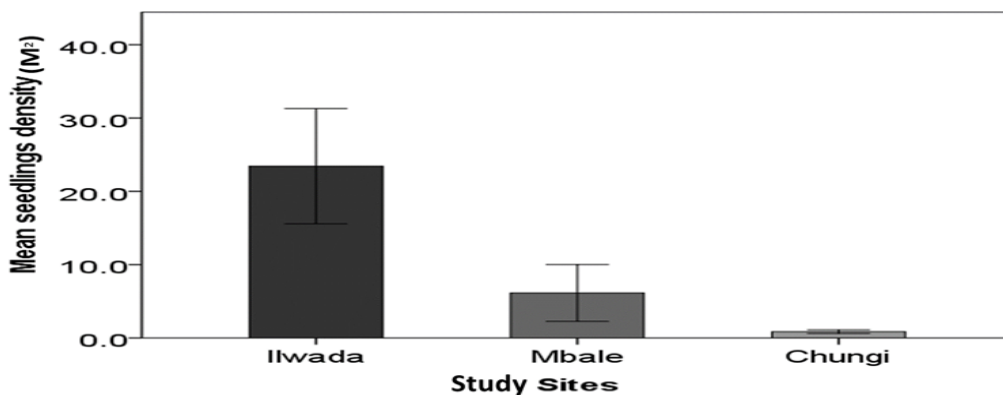
Figure 8: Mean (± SE) seedling densities (seedlings/m^2) among different sites.

4.4.3 Tree density and diversity

A total of 476 trees (DBH > 20 cm) comprising of 49 species belonging to 21 families were recorded in all the study sites (see appendix 5). Out of this 76% (n = 354) were of exotic species while 24% (n = 122) belonged to indigenous species. The highest number of tree species were recorded in Ilwanda (48) followed by Mbale (46) and Chugi (41). The *Eucalyptus spp* had the highest density (16.34 ± 1.7 trees ha^{-1}) followed by *Compressus lusitanica* (8.16 ± 2.3 trees ha^{-1}) and *Croton macrostachyus* (6.71 ± 2.2 trees ha^{-1}) respectively. Tree density was significantly higher in Mbale at 41.9 ± 1. 04 trees/ha compared to Chugi at 30.9 ± 0.86 trees/ha (t = 7.02, d.f. = 38, $p < 0.05$). Similarly, the density of trees was significantly higher in Ilwanda at 45.7 ± 1.3 trees/ha compared to Mbale at 38.1 ± 1.1trees/ha (t = 5, d.f. = 38, $p < 0.05$). Moreover, the density of trees was significantly higher in Ilwanda than in Chugi (t = 6.4, d.f. = 38, $p < 0.05$). A One Way Anova test showed that the density of guava trees (DBH > 10 cm) was significantly higher in Ilwanda at 27.8 ± 1. 5 trees/ha followed by Mbale 22.2 ± 0.6 trees/ha and Chugi at 11 ± 0.7 trees/ha respectively ($F_{2,57} = 8.6$, $p < 0.05$), Figure 9. Shannon-Wiener diversity index (H') for tree species was higher in Ilwanda (H´=3.1) than in Mbale (H´ = 2.98) however, the two indices were not significantly different (t = 0.24, d.f. = 58, $p > 0.05$). Chugi (H´ = 1.54) had a lower tree species diversity compared to Ilwanda (t = 1.72, d.f = 38, $p < 0.05$) and Mbale (t = 1.81, d.f = 38, $p < 0.05$).
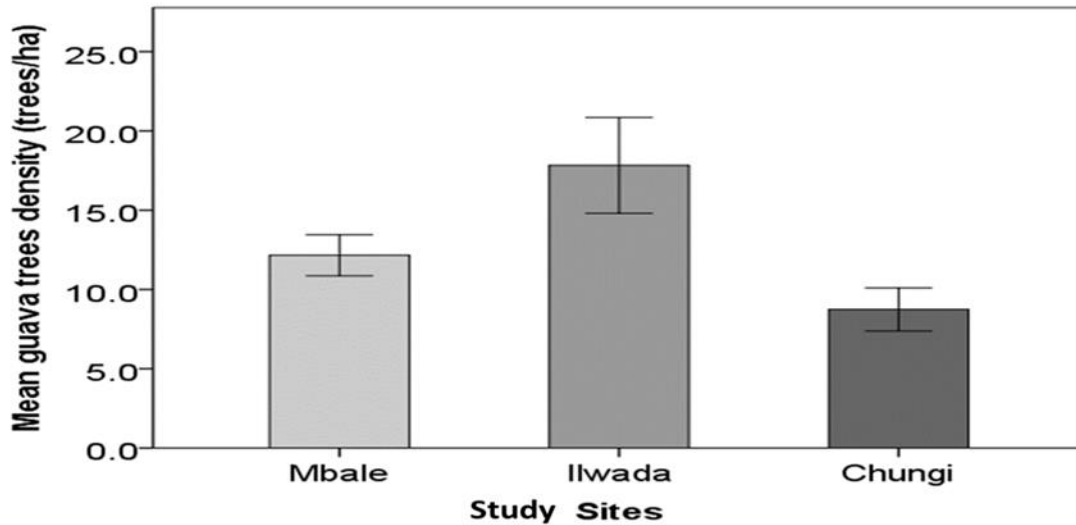
Figure 9: Mean density (± SE) of guava trees (trees/ha) recorded at the study sites.

There were no significant differences between sampled focal trees basal area among the study sites (One Way Anova, $F_{2, 27} = 0.8$, $p > 0.05$), Figure 10. This indicates that the selected focal trees in all the study sites had similar characteristics and could be compared against each other. A linear correlation was performed to determine the relationship between basal area as a measure of tree size and mean number of frugivore species recorded on the focal trees. There was a significant positive correlation between mean number of avian frugvore species and the basal area (Pearson's correlation, $r = 0.39$, d.f $= 28$ $p < 0.05$). Similarly, there was a significant positive correlation between visits by *E. helvum* fruit bats and focal tree basal area (Pearsons correlation, $r = 0.55$, d.f. $= 28$, $p < 0.05$).
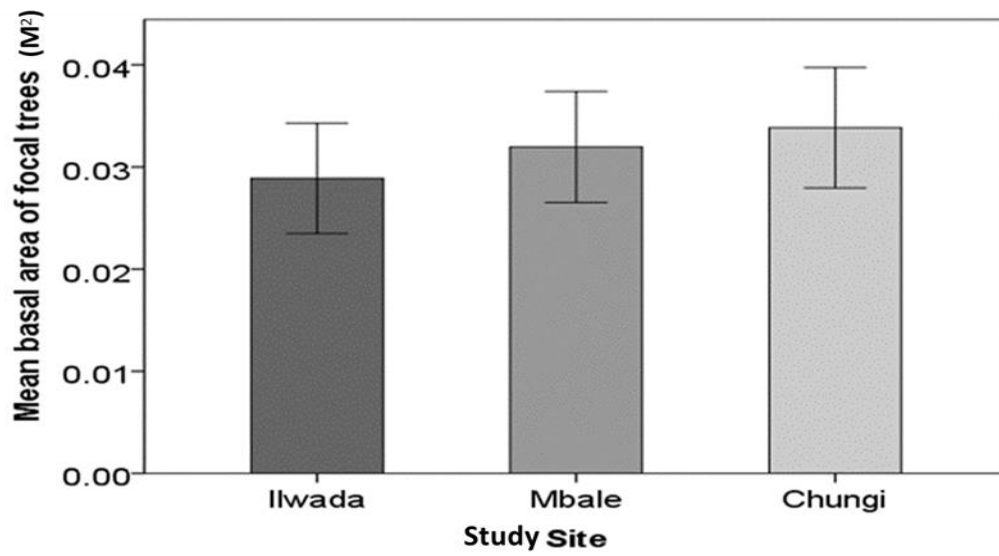
Figure 10: Mean (±) basal area (m^2) of focal trees in study sites.

CHAPTER FIVE: DISCUSSION, CONCLUSION AND RECOMMENDATIONS

5.1 Discussion

5.1.1 Frugivore observations

Even though frugivore bats are commonly acknowledged as vital seed dispersers, limited studies have revealed the relative significance of bats and avian frugivores compared concurrently (Medellin and Gaona (1993). The magnitude of seed dispersal is determined mainly by the quantity of visits by frugivores to the plant. In this study, a higher number of *E. helvum* fruit bats was observed visiting *P. guajava* fruiting trees compared to other studies. For instance, a study by Ritcher and Cumming, 2006, sighted a total of 42 *E. helvum* on *Uapaca sansibarica* fruiting trees in Kasanka National Park, Central Zambia. Similarly, Daïnou *et al*, 2010, recorded a low number of *E. helvum* visiting *Milicia excelsa* in western Africa forests. This study clearly indicate a higher foraging activity of the species on guava trees in agricultural landscapes in which fruits can be considered to be higher than in protected areas. However, this requires further investigation. The higher number of *E. helvum* can also be attributed to the decrease in the number of other fruiting trees foraged by the species owing to increased deforestation. This is supported by the high density of guava trees in the roosting sites. The presence of roosting sites appeared to influence the number of visits by the *E. helvum* to the guava fruiting trees. This is evidenced by highest number of visits in Ilwanda where bats were roosting during the study period and lowest number of visits recorded in the non-roosting site. As such, increased visits can be attributed to the proximity of the fruiting guava trees to the roosting sites which reduced the distance covered in flight in search for food by the *E. helvum*. This concurs with energy maximization idea in the theory of optimal foraging (Pyke

et al., 1977). This theory suggests that animals will optimize their total energy intake while searching and consuming food. Therefore, the *E. helvum* selectively forage to minimize travel time and maximize energy gain by feeding closer to the roosting site hence the high number of sightings. Certainly, fruits close to the roost site should be depleted before the bats travel farther to feed. This is supported by the low number of *E. helvum* recorded in guava tree in Chugi about 3 km from the nearest roosting site. The loss of roosting sites for the *E. helvum* could lead to diminished seed flow of plant species throughout the landscape, limited seedling establishment and hence extirpation of certain plant species as observed by Da Silva and Tabarelli (2000).

In this study, the number of *E. helvum* visits to guava trees was higher than that of avian frugivores. This is in line with other studies that showed a high frequency of frugivorous bat visits to fruiting trees (Korine *et al*, 2000, Godnez-Alvarez *et al*., 2002, Meng *et al*., 2012). Elsewhere, avian frugivores have generally been shown as being the main dispersers of seeds and architects of successional activities in farmland occurring in tropical ecosystems (Galindo-Gonzalez, 2000; Böhning-Gaese, 2012). However, the latter studies did not investigate the contribution made by fruit bats to seed dispersal in such areas. Avian frugivores had higher visitation rates and species diversity in non-roosting than in roosting site. This could be attributed to high removal rates of guava fruits by *E. helvum* in the roosting sites owing to the high number of visits and requires further investigation. Low diversity of avian frugivores is evident in disturbed areas such as agricultural fields in which trees are few and hence nesting and perching sites become a major limiting factor for the dispersal role of birds (Gorchov *et al*., 1993). The *E. helvum* can therefore play a critical role in dispersing seeds in Vihiga as it is considered to be the most abundant frugivore.

In this study, avian frugivores spent more time on guava fruiting trees than *E. helvum*. These results have also been reported elsewhere by (Bronstein and Hoffmann, 1987; Kalko *et al*., 1996). The avian frugivores spent more time in non-roosting site than in roosting site. This may be explained by resource partitioning between the *E. helvum* and the avian frugivores to minimize interspecific competition. However, this subject needs further investigation. Larger avian frugivores such as the hornbills spent much longer time in the trees than most of the other avian frugivores. This observation is in agreement with Green (1993) and Kirika *et al*., (2008) that birds reduce the danger of predation by decreasing their ability to be seen at the foraging site and by choosing suitable places in adjacent foliage were they can be hidden them when processing food. When birds spend more time on a tree most of the seeds fall beneath the plant where the seeds and seedlings suffer mortality (Howe and Schupp, 1985). Since bat visits are short they are more likely to carry seeds away from the parent plant, make more visits per day, and produce a less clumped distribution of seeds (Howe and Estabrook, 1977). Birds mainly deposit seeds beneath the focal tree or transport fruits to a perch or roost prior to passing out the seeds (Charles-Dominique, 1986; McClanahan and Wolfe, 1993; Corlett, 1998). In western Kenya the *E. helvum* bats were observed to drop some seeds during flight and deposited the majority at roosting trees and also under feeding and focal trees. These observations were also noted by Banack *et al*., (2002), Hodgkison *et al*., (2003) and Webala *et al*., (2014). Guava seeds dispersed by the *E. helvum* are more probable to reach greatly disturbed areas deficient in perching and nesting sites than seeds dispersed by birds. Therefore, the *E. helvum* can be considered to be the main disperser of *P.guajava* seed in fragmented landscapes of Vihiga county contributing largely to vegetation regeneration and hence of conservation importance.

5.1.2 Seed germination

The influence of digestion process on germination rate is an important property of foraging behaviour that determines the efficacy of animals as dispersers of seeds (McKey, 1975; Howe, 1986). In this study, the passage of guava seeds through the gut of *E. helvum* had not effect on the rate of germination. A similar, study by Taylor, (2005) indicated that gut treatment by *E. helvum* had no effect on the germination of *Milicia excelsa*. Other studies by Naranjo *et al*. (2003), Hodgkison *et al*., (2003) and Tiang *et al*., (2008) established that the passage of seeds across the gut of bats did not enhance germination of seeds from single fruit species. Owing to the little period by which food materials pass through the bat digestive tract (Abedi-Lartey, 2016), it is possible that ingestion has insignificant scarifying influence on the seed testa. However, other studies have reported that passage of seeds through the gut of bats enhance germination (Izhaki *et al*., 1995; Lopez and Vaughan, 2004). Evidently, many guava seeds capable of germinating were spread out by *E. helvum* through defecation. Since the *E. helvum* fruit bats are known to repeatedly alter their roosting locations and regularly excrete while flying, the guava seeds from excreta can be dispersed widely and help to foster plant regeneration in degraded landscapes.

Results indicate that the germination rates of seeds obtained from intact fruits and those manually extracted from fresh fruits did not differ significantly. This is contrary to other studies which indicate that seeds from intact fruits have a much lower germination percentage (Samuels and Levey, 2005; Robertson *et al*., 2006). However, the results concur with Ferreira *et al*., (2016) that the germination rates of intact and extracted seeds of Babasu seeds were not different. Germination rates of seeds obtained from spats were significantly lower than all the other treatments. This could

have been as a result of chemical substances in the pulp that hinder germination if allowed to remain in contact with the seeds (Yagihashi *et al*., 1998; Samuels and Levey, 2005). In addition, seeds that are dispersed through spats have high chances of being destroyed by fungal contaminations than those that are excreted (Utzurrum, 1995). The results indicate then that ingestion of guava seeds by *E. helvum* is not necessary for germination. Irrespective of whether the passage of guava seeds through the gut of *E. helvum* directly affects germination of guava seeds, the *E. helvum* may nevertheless contribute significantly through positioning of seeds in microsites that differ in suitability for germination (Schupp, 1993).

5.1.3 Seed rain

The quantity of seeds that reach at a site and death of seeds and seedlings in the site restrict plant regeneration (Schupp *et al.* 1989; Tilman, 1997; Svenning and Wright 2005). As such, a large number of seeds of pioneer species are necessary to guarantee seedling establishment. The difference in the number of visits by the most effective dispersers has implications for the successful dispersal of zoochorous seeds (Jordano, 1994). Seed rain deposition under remnant trees in degraded habitats by bats is significant vegetation regeneration as the offer food or perch sites (Ragusa-Nettoa, 2015). In this study, high seed deposition was observed under the crowns of *P. guajava* in the roosting sites compared to the non-roosting site. The difference in the densities of *E. helvum* fecal pellets among the three study areas suggest the importance of the roosting sites in seed dispersal. Therefore, the conservation of the current roosting site is critical for effective plant regeneration in Vihiga County farmlands. The *Eidolon helvum* continuously moved within the study sites while feeding a phenomenon observed as well by Taylor (2005). Owing to this foraging behavior, their inclination to excrete while flying, and their fast digestion time (Thomas, 1982),

the *E. helvum* conduct out a first-class dispersal service spreading thousands of guava seeds throughout the farmlands every night. Although agricultural fruits may be less nutritionally beneficial than wild fruits for bats (Nelson *et al.*, 2000), the presence of large amounts of such fruits could allow a higher density to be supported than by primary forest (Dallimer *et al.*, 2006). Large numbers of *E. helvum* were observed during the peak fruiting season of the guava trees (June, July and August) thus helping to disperse enormous quantities of guava seeds during this time. Richter and Cumming (2006) reported a similar pattern for *E. helvum* in Kasanka National Park, Zambia, where the relative abundance of this species also increased during the peak fruiting period of key resources. *Eidolon helvum* has the ability to forage as far as 59 km or more from the roost site in a single night (Richter and Cumming, 2008), suggesting that the species is a long-distance seed disperser. Thus because of their high mobility, the *E. helvum* can transport guava seeds to sites with suitable light and water conditions for germination, especially in areas of lower land-use intensity such as farm edges and abandoned lands. The *E. helvum* fruit bats are effective seed dispersers of guava trees as they were observed to drop seeds beneath the guava fruiting trees either as excreta or spats. They also carried the fruits to roosting sites where large number of seeds were deposited as excreta under the canopies of the roosting trees. However, there were no feeding roosts observed. Since guavas are important pioneer plants that act as ''recruitment foci'' for other early successional species in Kenyan farmlands (Berens *et al.*, 2008). When they eat guava fruits the *E. helvum* contribute immensely to plant succession and vegetation regeneration in degraded farmlands.

5.1.4 Seedling and tree establishment

In this study, seedling establishment was significantly different among the sites with Ilwanda having the highest seedling density. This could be attributed to the presence of the roosting sites, thus the movement of bats between the roosting sites and the focal trees could be responsible for high seed deposition and hence increased seedling establishment. It could also be as a result of facilitation by guava seedlings which are important pioneer species in farmlands (Berens *et al*., 2008). Frugivores are responsible for the seed rain that enables the parent plant to place seeds in locations that are appropriate for germination. With a high visitation rate by highly mobile *E. helvum*, guava trees are likely to achieve a higher success rate in the recruitment of seedlings (Tellería *et al*. 2005). Many bat dispersed plants are from pioneer species which are the first to grow in degraded landscapes (Muscarella and Fleming, 2007). In this study, pioneer species had the highest density in all the three sites being higher in the roosting sites. This has conservation implications as to enhancement of plant biodiversity in degraded landscape. A decrease in the number animal seed dispersers or their extinction can contribute to less frugivores visiting fruit bearing trees and therefore smaller amount of seeds may be dispersed (Kirika *et al*. 2008; Holbrook and Loiselle 2009). These reductions in dispersal of seeds by animals can eventually culminate to a decrease in recruitment of seedlings (Cordeiro and Howe 2003, Uriarte *et al*., 2010), and local plant extinction and hence diminishing plant species richness.

In this study, the diversity of tree species was low in non-roosting sites where avian frugivore diversity was also observed to be low. This concurs with other studies in which tree species is positively correlated to species richness (Harvey, *et al*., 2006, Ana *et al*., 2017). Markedly, the density of *P. guajava* trees was also found to be high in roosting sites than in non-roosting sites.

54

However, a higher seedling establishment does not necessarily lead to higher tree densities as shown by Kirika, (2005) and Berens *et al*., (2008). In these studies carried out in Kakamega forest and the surrounding farmlands, the survival of seedlings to maturity was observed to be curtailed in the forest fragments. As such, the low densities of adult trees were attributed to other factors such as logging or pole wood collection rather than low seedling establishment. In this study the low density of trees could be attributed to similar anthropogenic factors.

5.2 Conclusion

When they eat guava fruits, the *E. helvum* and avian frugivores perform important ecological role in vegetation regeneration in Vihiga farmlands. With a high visitation rate and low duration of visits the *E. helvum* can be described as the most important disperser of *P. guajava* seeds within Vihiga agricultural farmlands. Due to habitat degradation in agro ecosystems the abundance and diversity of avian frugivores is declining in tropical regions. This will in turn contribute to decline in seeds arrival at suitable sites leading low vegetation regeneration. In Vihiga County, the *E. helvum* occur in fairly large numbers at specific roosting sites. These sites are located in homesteads where the bats are constantly being persecuted by farmers mainly through cutting down of the roosting trees and use of pesticides. Decline in the abundance of *E. helvum* in these farmlands could have serious implications on plant regeneration. The results of the study show clearly that the *E. helvum* is imperative to vegetation regeneration in these fragmented landscapes. As such, concerted efforts are required by all conservation stake holders including the county government and the public to conserve the species and their roosting sites. This is imperative so as to safeguard the role that *Eidolon helvum* fulfills not only in seed dispersal but also in pollination of numerous plant species. More conservation education projects are therefore recommended to

ensure that the local people recognize the value of bats and do not cause damage through the careless destruction of vital habitats.

The passage of guava seeds through the gut of *E. helvum* was found to be unimportant to guava seed germinations. However, the effect produced by ingestion of seeds by the same bat species may vary according to the plant species. In this study only the guava tree was considered. Since the *E. helvum* fruits are known to defecate while in flight they are significant ensuring plant regeneration in Vihiga farmlands.The results show that presence of roosting sites is closely linked to dispersal seedling establishment. As such, there is need for concerted efforts to conserve the existing roosting sites to ensure seed dispersal of other important keystone species such as the *F. thonningii*. However, there other factors which influence seed dispersal and seedling establishment such as light availability, predation of seeds, scatter hoarding and secondary seed dispersal which are beyond the scope of this study. As only one tree species was studied, these results apply to the *P. guajava* and to make generalizations, further studies on other species are required. Despite the fact that guava trees are exotic species, they are significant pioneer species and hence act as a baseline for the growth and establishment of other late successional plants.

5.3 Recommendations

5.3.1 Further research

- A comparative study on the effects on human disturbance on dispersal of seeds by avian and bat frugivores in farmlands.
- A study on the role of *E. helvum* movements on seed dispersal in agro ecosystems through closer monitoring of individual bats by the use of either radio–telemetry equipment or satellite transmitters could provide invaluable data.

56

- The effect produced by ingestion of seeds by the same bat species may vary according to the plant species therefore, the same concept can be tested to determine the effects of gut conditioning by *E. helvum* on other tree species.

- Additional studies on the effects of *P. guajava* on local ecological communities are needed regarding, for instance, relations with indigenous plant species and its influence on soil, water and nutrient cycling.

REFERENCES

Abedi-Lartey, M., Dechmann, D. K. N., Wikelski, M., Scharf, A. K. & Fahr, J. (2016). Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. *Global Ecology and Conservation* **7**: 12-24.

Agami, M., & Waisel, Y. (1988). The role of fish in distribution and germination of seeds of the submerged Macrophytes. *Oecologia* **76**:83-88.

Alcántara, J. M., Rey, P. J., Valera, F. & Sanchez-Lafuente, A. M. (2000). Factors shaping the seed fall pattern of a bird-dispersed plant. *Ecology* **81**:1937-1950.

Ana, C.M., Martins., Willig, M. R., Presley, S. J. & Marinho-Filho, J. M. (2017). Effects of forest height and vertical complexity on abundance and biodiversity of bats in Amazonia Forest. *Ecology and Management* **391**: 427–435.

Andresen, E. (2002). Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica* **34**: 261–272.

Augspurger, C. K. (1983). Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* **72**:759–771.

Ayensu, E. S. (1974). Plant and bat interactions in West Africa. *Annals of the Missouri Botanical Gardens* **61**:702-727.

Babweteera, F., Savill, P. & Brown, N. (2007). *Balanites wilsoniana*: regeneration with and without elephants. *Biological Conservation* **134**:40–47.

Baider, C. & Florens, F. B. V. (2006). Current decline of the 'Dodotree': a case of broken-down interactions with extinct species or the result of new interactions with alien invaders? In: Laurance WF, Peres CA (eds) Emerging threats to tropical forests. University of Chicago Press, Chicago, pp 199–214.

Banack, S. A., Horn, M. H. & Gawlicka, A. (2002). Disperser- vs. establishment-limited distribution of a riparian fig tree (*Ficus insipida*) in a Costa Rican tropical rain forest. *Biotropica* **34**: 232–243.

Bas, J.M., Pons, P. & Gómez, C. (2006). Exclusive frugivory and seed dispersal of *Rhamnus alaternus* in the bird breeding season. *Plant Ecology* **183**:77.

Beentje, H. (1994). Kenya's trees, shrubs and lianas. National Museums of Kenya. Nairobi Kenya.

Berens, D. G., Farwig, N., Schaab, G. & Bohning-Gaese, K. (2008). Exotic Guavas are Foci of Forest Regeneration in Kenyan Farmland. *Biotropica* **40** (1): 104–112.

Bergmans, W. (1990). Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 3. The genera Scotonycteris Matschie, 1894, Casinycteris Thomas, 1910, Pteropus Brisson, 1762, and Eidolon Rafinesque, 1815. *Beaufortia* **40** (7): 111-177.

Bleher, B. & Bohning-Gaese, K. (2001). Consequences of frugivore diversity for seed dispersal, seedling establishment, and the spatial pattern of seedling and trees. *Oecologia* **129**: 385-394.

Böhning-Gaese, K. (2012). BOU Proceedings – Ecosystem services: do we need birds? http://www.bou.org.uk/bouproc-net/ecosystem-services/bohning-gaese.

Bond, W. J. (1995). Assessing the risk of plant extinction due to pollinator and disperser failure. In: Lawton JH, May RM ed. Extinction Rates. London: Oxford University Press, 131–146.

Bradford, M. G. & Westcott, D. A. (2011). Predation of cassowary dispersed seeds: is the cassowary an effective disperser? *Integrative Zoology* **6** (3): 168-177.

Bronstein, J. L. & Hoffmann, K. (1987). Spatial and temporal variation in frugivory at a neotropical fig, Ficus pertusa. *Oikos* **49**: 61–68.

Brooks, T. M., Pimm, S. L. & Oyugi, J. O. (1999). Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* **13**: 1140–1150.

Cain, M. L., Milligan, B. G. & Strand, A. E. (2000). Long distance seed dispersal in plant populations. *American Journal of Botany* **87**: 1217-1227.

Caughlin, T.T., Ganesh, T. & Lowman, M.D. (2012). Sacred fig trees promote frugivore visitation and tree seedling abundance in South India. Current Science **102** (6): 918-922

Centre for Agriculture and Bioscience International (CABI). (2013). Invasive Species Compendium. Wallingford, UK: CAB International.

Chapman, C. A. & Chapman, L. J. (1995). Survival without dispersers: seedling recruitment under parents. *Conservation Biology* **9**: 675-678.

Chapman, C.A. (1989) Primate seed-dispersal: the fate of dispersed seeds. *Biotropica* **21**:148-154.

Charles-Dominique, P. (1986). Inter-relations between frugivorous vertebrates and pioneer plants: Cecropia, birds, and bats in French Guyana. In Frugivores and Seed Dispersal (eds. A. Estrada and T. H. Fleming), pp. 119–135. Dr. W. Junk, Dordrecht, Netherlands.

Cipollini, M. L. & Levey, D. J. (1997). Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *American Naturalist* **150**: 346–372.

Clough, Y., Putra, D. D., Pitopang, R. & Tscharntke, T. (2009). Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biology of Conservation* **142**:1032–1041.

Cochrane, M. A., Alencar, A., Schulze, M.D., Souza, C.M., Nepstad, D.C., Lefebvre, P. & Davidson, E. A. (1999). Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* **284**: 1832–1835.

Cordeiro, N. J. & Howe, H. F. (2003). Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *National Academy of Sciences* **100**:14052-14056.

Corlett, R. T. (1998). Frugivory and seed dispersal by vertebrates in the oriental (Indomalayan) region. *Biological Review* **73**:413-448.

Corlett, R. & Hau, B. C. (2000). Seed dispersal and forest restoration. In: Forest Restoration for Wildlife Conservation (eds. Elliott, S., J., Kerby, D. Blakesley, K. Hardwick, K. Woods and V. Anusarnsunthorn). International Tropical Timber Organization and The Forest Restoration Research, Chiang Mai University, Thailand. pp. 317-325.

Cubina, A. & Aide, T. M. (2001). The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* **33**: 260–267.

Culot, L., Lazo, F., Huynen, M.C., Poncin, P. & Hey-mann, E.W. (2010). Seasonal variation in seed dispersal by tamarins alters seed rain in a secondary rain forest. *International Journal of Primatology* **31**: 553-569.

Curran, L.M., Trigg, S.N., McDonald, A.K., Astiani, D., Hardiono, Y.M., Siregar, P., Caniago, I. & Kasischke, E. (2004). Lowland forest loss in protected areas of Indonesian Borneo. *Science*, **303**, 1000–1003.

Daïnou, K., Bizoux, J. P., Doucet, J. L., Mahy, G., Hardy, O. J. & Heuertz, M. (2010). Forest refugia revisited: nSSRs and cpDNA sequences support historical isolation in a widespread African tree with high colonization capacity, *Milicia excelsa* (Moraceae). *Molecular Ecology* **19** (20): 4462 - 4477.

D'Antonio, C. & Meyerson, L. A. (2002). Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecol*ogy **10**: 703–713.

D'avila, G., Gomes-Jr., A., Canary, A.C. & Bugoni, L. (2010). The role of avian frugivores on germination and potential seed dispersal of the Brazilian Pepper Schinus terebinthifolius. *Biota Neotropica* **10** (3).

Da Silva, J. M. C. & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northern Brazil. *Nature* **404**: 72-74.

Dallimer, M., King, T., Cope, D. & Jiana, B. M. (2006). Estimation of population density of Eidolon helvum on the island of Príncipe, Gulf of Guinea. *Mammalia* **70**: 48–51.

Defrees, S. L. & Wilson, E. D. (1988). Eidolon helvum. Mammalian Species. *The American Society of Mammalogists* **312**: 1-5.

Dennis, A. J. & Westcott, D. A. (2006). Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia* **149**: 620–634.

Duncan, R. S. & Chapman, C. A. (1999). Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecology Appllied.* **9**: 998–1008.

El Boushy, A. R. Y. & van der Poel, A. F. B. (2000). Handbook of poultry feed from waste: processing and use. Springer-Verlag New York, 428 p.

Ennos, R. A. (1994). Estimating the relative rates of pollen and seed migration among plant populations. *Heredity* **72**: 250–259.

Evenari, M. (1949). Germination inhibitors. *Botanical Review* **15**: 153-194.

Fahr, J., Abedi-Lartey, M., Esch, T., Machwitz, M., Suu-Ire, R., Wikelski, M. & Dechmann, D.K.N. (2015). Pronounced seasonal changes in the movement ecology of a highly gregarious central-place forager, the African straw-coloured fruit bat (*Eidolon helvum*). *PLoS ONE* **10** (10): e0138985.

Fahrig, L. (1999). Forest loss and fragmentation: which has the greater effect on persistence of forest-dwelling animals? Pages 87–95 in J. A. Rochelle, L. A. Lehmann, & J. Wisniewski, editors. Forest wildlife and fragmentation: management and implications. Brill, Leiden, The Netherlands.

Ferreira, P. H. G., Nunes, Y.R.F., Faria., M. L., Brandão., M.M., Costa, C. S. R., Valério, H.M., Melo, G.A. & Pimenta, M.A.S. (2016). Do fruit morphology and scarification affect germination and predation rates of Babassu seeds? *Acta Botanica Brasilica* **30**(4): 658-666.

Fleming, T. H. (1981). Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. *Oecologia* **51**: 42–46.

Fleming, T. H. (1988). The Short-tailed Fruit Bat: a Study in Plantanimal Interactions. University of Chicago Press, Chicago, Illinois.

Fleming, T. H. & Williams, C. F. (1990). Phenology, seed dispersal and recruitment in Cercropia peltata (Moraceae) in Costa Rican dry forest. Journal of Tropical Biology : 163-179.

Fujita, M. S. & Tuttle, M. D. (1991). Flying foxes (Chiroptera: Pteropopidae): threatened animals of key ecological and economic importance. *Conservation Biology* **5**: 455-463.

Franklin, J. & Rey, S. J. (2007). Spatial patterns of tropical forest trees in Western Polynesia suggest recruitment limitations during secondary succession. *Journal of Tropical Ecology* **23**: 1-12.

Galindo-Gonzalez, J., Guevara, S. & Sosa, V. J. (2000). Bat- and bird-generated seed rains at isolated trees in pastures in a tropical forest. *Conservation Biology* **14**: 1693–1703.

Gentry, A. H. (1982). Patterns of Neotropical plant species diversity. *Evolutionary Biology* **15**:1-84.

Godínez-Alvarez, H., Valiente-Banuet, A., & Rojas-Martínez, A. (2002). The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology* **83**(9): 2617-2629.

Gorchov, A. D., Cornejo, F., Ascorra, C., & Jaramillo, M. (1993). The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio **107/108**: 339-349.

Government of Kenya (GOK), (2005). *Vihiga District Strategic Plan 2005-2010 for implementation of the National Policy for Sustainable Development.* National Coordination Agency for Population and Development.

Green, R. (1993). Avian seed dispersal in and near subtropical rain forests. *Wildlife Restoration* **20**: 535-547.

Greenberg, R., Bichier, P., Sterling, J. (1997). Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, Mexico. *Biotropica* **29**: 501–514.

Gross-Camp, N., Mulindahabi, F. & B. Kaplin, B. (2009). Comparing the dispersal of large-seeded tree species by frugivore assemblages in tropical montane forest in Africa. *Biotropica* **41**: 442–451.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review.* **52**: 107-145.

Haggar, J., Wightman, K. & Fisher, R. (1997). The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. *Forest Ecology Management* **99**: 55-64.

Hansen, D. M. & Galetti, M. (2009). The Forgotten Megafauna. *Science* **324**: 42-43

Harms, K. E., Wright, S. J., Calderon, O., Hernandez, A. & Herre, E. A. (2000). Pervasive density–dependent recruitment enhances seedling diversity in tropical forest. *Nature* **404**:493-5.

Harvey, C. A., Medina, A., Sa´nchez, D., Vi´lchez, S., Herna´ndez, B., Saenz, J. C., Maes, J. M., Casanoves, F. & Sinclair, F.L. (2006). Patterns of animal diversity in different forms of tree cover in agricultural landscapes *Ecological Applications* **16**(5): 1986–1999.

Hayman, D.T.S., McCrea, R., Restif, O., Suu-Ire, R., Fooks, A.R., Wood, J.L.N., Cunningham, A.A. & Rowcliffe, J.M. (2012). Demography of straw-colored fruit bats in Ghana. *Journal of Mammals* **93**: 1393–1404.

Henry, M., & Jouard, S. (2007). Effect of bat exclusion on patterns of seed rain in tropical rain forest in French Guiana. *Biotropica* **39**: 510-518.

Herrera, C. M. (2002). Seed dispersal by vertebrates. Plant-animal interactions. Pp. 185-208 In Herrera, C. M. & Pellmyr, O. (eds.). An evolutionary approach. Blackwell, Oxford.

Herrera, C. M. & Jordano, P. (1981). *Prunus mahaleb* and Birds: The High-Efficiency Seed Dispersal System of a Temperate Fruiting Tree. *Ecological Monographs* **51** (2): 203-218.

Hodgkinson, R. Balding, T. S. Zubaid, A. & Kunz, H.T. (2003). Fruit Bats (Chiroptera: Pteropopidae) as Seed Dispersers and Pollinators in a Lowland Malaysian Rain Forest. *Biotropica* **35 (4)**: 491-502.

Holbech, L. H. (2009). The conservation importance of luxuriant tree plantations for lower storey forest birds in south-west Ghana. *Bird Conservation International* **19**: 287–308.

Holbrook, K. M. & Loiselle, B. A. (2009). Dispersal in a Neotropical tree, *Virola flexuosa* (Myristicaceae): Does hunting of large vertebrates limit seed removal? *Ecology* **90**:1449-1455.

Holl, K.D., Loik, M.E., Lin, E.H.V. & Samuels, I.A. (2000). Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* **8**: 339–349.

Hooper, E.R., Legendre, P., & Condit, R. (2004). Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology* **85**: 3313–3326.

Howe, H. F. (1984). Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation* **30**: 261–281.

Howe, H. F. & Estabrook, G. F. (1977). On intraspecific competition for dispersal agents in tropical trees. *American Naturalist* **111**: 817-832.

Howe, H. F. & Miriti, M. N. (2000). No question: seed dispersal matters. *Trends in Ecology & Evolution* **15**: 434-436.

Howe, H. F., Schupp, E. W. & Westley, L. C. (1985). Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* **66**:781-791.

Howe, H. F. & Smallwood, J. (1982). Ecology of seed dispersal. *Anuual Review of Ecology and Systematics* **13***:* 201-228.

Howe, H. F. (1986). Seed dispersal by fruit-eating birds and mammals. In Seed Dispersal (ed. D. R. Murray), pp. 123–189. Academic Press, Sydney.

Hubbell, S. P. (1979). Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest. *Science* **203**: 1299-1309.

Hughes, R. F., Kauffman J.B. & Jaramillo, V. J. (1999). Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* **80**:1892-1907.

Ingle, R. N. (2003). Seed dispersl by wind, birds, and bats between philippine montane rain forest and successional vegetation. *Ocecologia* **134**: 251-261.

IUCN. (2013). IUCN Red List of Threatened Species. Version 2013.1.

Izhaki, I., Korine, C. & Arad, Z. (1995). The effect of bat (*Rousettus aegypticus*) dispersal on seed germination in eastern Mediterranean habitats. *Oecologia*: **101**: 335-342.

Izhaki, I., Walton, P. B. & Safriel, U. N. (1991). Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology* **79**: 575-590.

Janzen, D. H., Miller, G. A., Hackforth-Jones, J., Pond, C. M., Hooper, K. & Janos, D. P. (1976). Two Costa Rican bat generated seed shadows of *Andira inermis* (Leguminoseae). *Ecology* **57**:1068–1075.

Jenkins, C. N. & Pimm, S. L. (2003). How big is the global weed patch? *Annals of the Missouri Botanical Garden* **90**: 172–178.

Jens, M., Olessen., Alfredo. & Valido. (2007). Lizards as pollinators and seed dispersers: an island phenomena. *Trends in Ecology and Evolution* **4**: 177-181.

Jordano, P. (1994). Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos* **71**: 479-491.

Jordano, P. (1995). Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant animal interactions. *American Naturalist* **145**: 163-191.

Jordano, P. (2000). Fruits and frugivory. Pp. 125-165 In Fenner, M. (ed.). The ecology of regeneration in plant communities. CABI, Wallingford.

Jordano, P. & Schupp, E. W. (2000). Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* **70**: 591–615.

Jordano, P. & Godoy, J. A. (2002). Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. Pp 305-321 in: Levey, D.J., Silva, W.R. and M. Galetti (eds). Seed dispersal and frugivory: Ecology, evolution and conservation. CAB International, Wallingford, UK.

Jordano, P., Garcia, C., Godoy, J. A. & Garcia-Castano, J. L. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *National Academy of Sciences* **104**: 3278–3282.

Jordano, P. (2010). Pollen, seeds, and genes: the movement ecology of plants. *Heredity* **105**: 329-330.

Jordano, P., Forget, P. M., Lambert, J. E., Bohning-Gaese, K., Traveset, A. &Wright, S. (2011). Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters* **7**:321–323.

Jorge, E. L. & Vaughan, C. (2004). Observations on the role of frugivorous bats as seed dispersers in Costa Rican secondary humid forests. *Acta Chiropterologica* **6**: 111-119.

Kaiser-Bunbury, C. N., Traveset, A. & Hansen, D. M. (2010). Conservation and restoration of plant-animal mutualisms on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics* **12**: 131–143.

Kennard, D. K. (2002). Secondary forest succession in a tropical dry forest: patterns of development across a 50 year chronosequence in lowland Bolivia. *Journal of Tropical Ecology*. 18:53-66.

Kalko, E. K. V., Herre, E. A. & Handley, Jr, C. O. (1996). The relation of fig fruit syndromes to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography* **23**: 565–576.

Kimuyu, D. M., Geoffrey, M., Wahungu, G. M. & Otieno, D. O. (2012). Seed dispersal by Tana River mangabeys in fragmented gallery forests. *Open Journal of Ecology* **2**: 12-20.

King, G. (1996) Reptiles and Herbivory. Chapman & Hall. London.

Kingdon, J. (1984). East African Mammals: An atlas of evolution in africa.Volume 2A. London: Academic press.

Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M. & Kalina, J. (eds). (2013). *Mammals of Africa* (6 vols). Bloomsbury Publishing, London.

Kirika, J. M., Farwig, N. & Böhning-Gaese, K. (2008). Effects of local disturbance of tropical forests on frugivores and seed removal of a small-seeded Afrotropical tree. *Conservation Biology* **22**:318-328.

Kissling, W. D., Rahbek, C. & K. Böhning-gaese. (2007). Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society of London. Series B* **274**: 799–808.

Kitamura, S. (2011). Frugivory and seed dispersal by hornbills (Bucerotidae) in tropical forests. *Acta Oecologia*. **37**: 531–541.

Komar, O. (2006). Ecology and conservation of birds in coffee plantations: a critical review. *Bird Conservation International* 1**6**:1–23.

Korine, C., Elisabeth, K., Kalko, V. & Herre, E. (2000). Fruit Characteristics and Factors Affecting Fruit Removal in a Panamanian Community of Strangler Figs. *Oecologia* **123(4)**: 560-568.

Kunz, K. B., Hovestadt, T. & Linsenmair, E. K. (2008). Variations of dispersal agents? Frugivore assemblages and fruit handling in a typical bird dispersed tree (*Lannea acida*, Anacardiaceae). *Ecotropica* **14**: 101-112.

Kunz, T. H. (1990). Ecological and Behavioral Methods for the Study of Bats. (ed.). Smithsonian Institution Press, Washington, D. C.

Levin, D. A. & Kerster, H. W. (1974). Gene flow in seed in seed plants. *Evolution Biology* **7**: 139-220.

Levin, S. A., Muller-Landau, H. C., Nathan, R. & Chave, J. (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology Evolution and Systematics* **34**: 575-604.

Link, A. & Di Fiore, A. (2006). Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain forest. *Journal of tropical ecology* **22**: 235-246.

Lisci, M. & Pacini, E. (1994). Germination ecology of drupelets of the fig (Ficus carica L.). *Evolution and Systematics* **34**: 133-146.

Lobova, T. A., Geiselman, C. K. & Mori S. A. (2009). Seed dispersal by bats in the neotropics. New York Botanical Garden, Bronx, New York.

Lopez, J. E. & Vaughan, C. (2004). Observations on the role of frugivorous bats as seed dispersers in Costa Rican secondary humid forests. *Acta Chiropterologica* **6**: 111-119.

Lovett, J. C., Ruffo, C. K., Gereau, R. E. & Taplin, J. R. D. (2006). Field guide to the moist forest trees of Tanzania. Society for Environmental Exploration, London, UK.

Lwanga, J.S. (2003). Forest Succession in Kibale National Park, Uganda. Implications for forest restoration and management. *African Journal of Ecology* **41**: 9-22.

Mccann, K., Hastings, A. & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature* **395** (6704): 794-798.

Maina, G. & Howe, H. F. (2000). Inherent rarity in community restoration. *Conservation Biology* **14**: 1335-1340.

Marsden, S. J., Symes, C. T. & Mack, A. L. (2006).The response of a New Guinean avifauna to conversion of forest to small-scale agriculture. *Ibis* **148**: 629–640.

Marshal, A. (1985). Old World phytophagus bats (Megachiroptera) and their food plants. *A* Survey. *Zoology Journal* **83**: 351-369.

Marshall, A. G. (1983). Bats, flowers and fruit: evolutionary relationships in the old world. *Biological Journal of the Linnean Society* **20**: 115-135.

Martinez-Garza, C. & Howe, H. F. (2003). Restoring tropical diversity: beating the time tax on species loss. *Journal of Applied Ecology* **40**: 423-429.

Mati'as, L., Zamora, R., Mendoza, I. & Jose, H. A. (2009). Seed Dispersal Patterns by Large Frugivorous Mammals in Degraded Mosaic Landscape. *Restoration Ecology* **100**: 475-526.

Mayer, A. M. & Poljakoff-Mayber, A. (1989). The Germination of Seeds, 4th edn. Oxford: Pergamon Press.

MCkey, D. (1975). The ecology of coevolved seed dispersal systems. In Coevolution of Animals and Plants (eds. L. E. Gilbert and P. H. Raven), pp. 159–191. University of Texas Press, Austin, Texas.

McClanahan, T. R. & Wolfe, R. W. (1993). Accelerating forest succession in a fragmented landscape. *Conservation Biology* **7**: 279-288.

McConkey, K. (2000). Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, Central Borneo. *American Journal of Primatol*ogy **52**: 13–19.

Mendellin, A. R. & Gaona, O. (1999). Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica* **31**: 478-485.

Meng, L., Gao, X., Chen, J. & Martin, K. (2012). Spatial and temporal effects on seed dispersal and seed predation of *Musa acuminata* in southern Yunnan, China. *Intergrative zoology* **7**: 30-40.

Mickleburgh, S. P., Hutson, A. M. & Racey, P. A., editors. (1992). *Old World Fruit Bats, an Action Plan for Their Conservation*. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Mickleburgh, S., Hutson, A.M., Bergmans, W., Fahr, J. & Racey, P.A. (2008). Eidolon helvum. The IUCN Red List of Threatened Species 2008.

Morrison, D. W. (1978). Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* **59**: 716–723.

Mulwa, R. K., Bo¨hning-Gaese. & Schleuning, K. (2012). High Bird Species Diversity in Structurally Heterogeneous Farmland in Western Kenya. *Biotropica* **0** (0): 1–9.

Murray, M. J. & Campbell, C. A. (1989). Guava and passion fruit as commercial crops in Florida. *Proceedings of the Florida State Horticultural Society* **102**: 212-21.

Murray, K. G., & Garcia-C, J. M. (2002). Contributions of seed dispersal and demography to recruitment limitation in Costa Rican cloud forest. Pp 323-338, in: Levey, D. J., Silva, W. R. & Galetti, M. (eds). Seed dispersal and frugivory: Ecology, evolution, and conservation. CABI Publishing, Wallingford, Uk.

Muscarella, R. & Fleming, T. H. (2007). The role of frugivorous bats in tropical forest succession. *Biological Rev*iew **82**: 573–590.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

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

Naranjo, M.E., Rengifo, C. & P. J. Soriano. (2003). Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae). *Journal of Tropical Ecology* **19**: 19–25.

Nathan, R. & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**: 278-285.

Nayara, C., Raizer. J. & Fischer, E. (2017). Passage Through *Artibeus lituratus* (Olfers, 1818) Increases Germination of *Cecropia pachystachya* (Urticaceae) Seeds. *Tropical Conservation Science* **10**: 1–7.

Neilan, W., Catterall, C. P., Kanowski, J. & MCkenna, S. (2006). Do frugivorous birds assist rainforest succession in weed dominated old field regrowth of subtropical Australia? *Biological Conservation* **129**: 393–407.

Nelson, S. L., Miller, A.M., Haeske, J. E. & Fahey, C. G. (2000). Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. *Ecography* 23: 393-401.

National Environmental Management Authority (NEMA), (2009). Vihiga District Environmental Management Plant 2009-2013. Ministry of Environmnet and Natural Resources. Nairobi.

Nepstad, D. C., Uhl, C. & Serrao, E. A. (1991). Recurperation of a degraded amazonian landscape: Forest recovery and agricutural restoration. *Ambio* **20**: 248-255.

Nielsen, Ch., Ravn, H.P., Netwig, W. & Wade, M. (eds). (2005). The Giant Hogweed Best Practice Manual. Guidelines for the Management and Control of Invasive Weeds in Europe. Forest and Landscape, Hørsholm, Denmark.

Nowak, R. M. (1994). *Walkers bats of the world.* Baltimore: The Johns Hopkins University Press.

Nyhagen, F. D., Turnbull, D. S., Olesen, M. J. & Jones, G. C. (2005). An investigation into the role of the Mauritian flying fox, *Pterops niger* in forest regeneration. *Biological Conservation* **122**: 491-497.

Olesen, M. J. & Valido, A. (2003). Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution* **18**: 177-181.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R. & Anthony, S. (2009). Agro-forest tree Database: a tree reference and selection guide version 4.0. World Agroforestry Centre, Kenya.

Ossa, G., Kramer-Schadt, S., Peel, A.J., Scharf, A.K. & Voigt, C.C. (2012). The movement ecology of the straw-colored fruit bat, *Eidolon helvum*, in Sub-Saharan Africa assessed by stable isotope ratios. *PLoS One* **7**: e45729.

Paine, R. T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature* **355**(6355): 73-75.

Parotta, J. A. (1992). The role of plantation forests in rehabilitating degraded tropical ecosysytems. *Agriculture Ecosystems and Environment Journal* **41**: 115-133.

Pejchar, L., Pringle, R. M., Ranganathan, J., Zookb, J. R., Duranc, G., Oviedoc, F. & Dailya, G. C. (2008). Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica. *Biological Conservation* **141**: 536-544.

Pizo, M. A (1997). Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic forest of southeastern Brazil. *Journal of Tropical Ecology* **13**: 559–578.

Pizo, M.A. (2004). Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeastern Brazil. *Ornitologia Neotropical* **15**:117-126.

Pjil van der, L. (1972). Principles of dispersal in higher palnts. Second Edition. Berlin: Springer-Verlag.

Premoli, A. C. & Kitzberger, T. (2005). Regeneration mode affects spatial genetic structure of Nothofagus dombeyi forests. *Molecular Ecology* **14**: 2319–2329.

Primack, R. B. & Miao, S. L. (1992). Dispersal can limit local plant distribution. *Conservation Biology* **6**: 513-519.

Pyke, H. G., Pulliam, R. H. & E. L. Charnov, L. E. (1977). Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* **52** (2): 137–154.

Racey, P. (2004). 8,000,000 Fruit Bats, Africa's best kept Wildlife Secret. *Bats* **22**: 1-5.

Raturi, G. B. & Hiwale, S. S. (1993). Horti-silvi-pastoral system for increased productivity of marginal and degraded lands under rain fed conditions. *Advances in Horticulture and Forestry* **3**: 179-186.

Richter, H. V. & Cumming, G. S. (2006). Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology* **268**: 35–44.

Richter, H.V. & Cumming, G.S. (2008). First application of satellite telemetry to track African straw-coloured fruit bat migration. *Journal of Zoology* **275**: 172–176.

Robertson, A. W., Trass, A., Ladley, J. J. & Kelly, D. (2006). Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology* **20**(1): 58-66.

Rodrigo, A., Medellin. & Gaona, O. (1999). Seed Dispersal by Bats and Birds in Forest and Disturbed Habitats of Chiapas, Mexico. *Biotropica* **31**: 478-485.

Rosevear, D. R. (1965). *The bats of West Africa*. London: British Museum (Natural History).

Ruffo, C. K., Mmari, C., Kibuwa, S. P., Lovett, J., Iversen, S. & Hamilton, A. C. (1989). A preliminary list of plant species recorded from the East Usambara Forests. In A. C. Hamilton and R. Bensted-Smith (Eds.). Forest conservation in the East Usambara Mountains, Tanzania. pp. 157–180. IUCN, Gland, Switzerland.

Santos, T. & Telleria, J. L, (1994). Influence of forest fragmentation on seed consumption and dispersal of Spanish Juniper. *Biological Conservation* **70**: 129–134.

Samuels, A. I. & Levey, D. J. (2005). Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology* **19**: 365-368.

Schlaepfer, M. A., Sax, D. F. & Olden, J. D. (2012). The Potential Conservation Value of Non-Native Species. *Conservation Biology* **26**: 428-443.

Schoener, W. T. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**: 369–404.

Schroth, G., Da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Lasconcelos, H.L. & Izac, A.-M.N. (2004). *Agroforestry and biodiversity conservation in tropical landscapes*. Island Press, Washington, D.C.

Schupp, E.W., Howe, H.F., Augspurger, C.K. & Levey, D.J. (1989). Arrival and survival in tropical tree fall gaps. *Ecology* **70**: 562-564.

Schupp, E.W. (1993). Quantity, quality, and the effectiveness of seed dispersal by animals. *Vegetatio* **107/108**: 15–29.

Schupp, E. W. & Fuentes, M. (1995). Spatial pattern of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**: 267-275.

Sekercioglu, C.H. (2006). Increasing awareness of avian ecologicl function. *Trends in Ecology and Evolution* **21**: 464–471.

Sekercioglu, C.H., Loarie, S., Oviedo-Brenes, F., Ehrlich, P.R. & Daily, G.C. (2007). Persistence of forest birds in tropical countryside. *Conservation Biology* **21**: 482–494.

Seltzer, C.E., Ndangalasi, H.J. & Cordeiro, N. J. (2013). Seed Dispersal in the Dark: Shedding Light on the Role of Fruit Bats in Africa. *Biotropica* **45** (4): 450–456.

Silva, J. M. C. & M. Tabarelli. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* **404**: 72– 73.

Silveira, F. A. O., Mafia, P. O., Lemos-Filho, J. P. & Fernandes, G. W. (2012). Species-specific outcomes of avian gut passage on germination of Melastomataceae seeds. *Plant Ecology and Evolution* **145** (3): 350-355.

Silveira, M., Trevelin, L., Port-Carvalho, M., Godoi, S., Mandetta, E. N. & Cruz-Neto, A. (2011). Frugivory by phyllostomid bats (Mammalia: Chiroptera) in a restored area in Southeast Brazil. *Acta Oecologica* **37:** 31-36.

Shilton, L. A., Altringham, J. D., Compton, S.G. & Whittaker, R. J. (1999). Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266**: 219–223.

Smith, C. W. (1998). Pest plants of Hawaiian native ecosystems. University of Hawaii, USA: Department of Botany.

Sorensen, A. E. (1983). Taste aversion and frugivore preference. *Oecologia* **56**: 117-120.

Stiles, F.G. (1985). On the role of birds in the dynamics of Neotropical forests. In: Diamond, A.W., Lovejoy, T.E. (Eds.), Conservation of Tropical Forest Birds. International Council for Bird Preservation, Cambridge, pp. 49–59.

Stiles, E. W. (2000). Animals as seed dispersers. Pp. 111-124 In Fenner, M. (ed.). Seeds: The Ecology of regeneration in plant communities. CABI, Wallingford.

Snow, D.W. (1976). The web of interactions. Collins. London.

Snyder, E. R. & Peter, C. P. (2004). How the Spatial Scales of Dispersal, Competition, and Environmental Heterogeneity interact to affect coexistence? *The American Naturalist* **164**: 633-650.

Svenning, J. C. & Wright, S. J. (2005). Seed limitation in a Panamanian forest. *Journal of Ecology* **93**:853–862.

Tang, Z., Sheng, L., Ma, X., Cao, M. Parsona, A., Ma, Jie. & Zang, S. (2007). Temporal and spatial patterns of seed dispersal of *Musa acuminata* by *Cynopterus sphinx*. *Acta Chiro repterologica* **9**: 229-235.

Tang, Z., Cao, M., Sheng, L., Ma, X., Walsh, A. & Zang, S. (2008). Seed dispersal of *Morus macroura* (Moraceae) by two frugivorous bats in Xishuangbanna, S W China. *Biotropica* **40**: 229- 235.

Taylor, D. A. R. (2005). The straw-colored fruit bat, *Eidolon helvum*, and *Milicia excelsa* seed dispersal, survival, and germination. M.Sci. Thesis, Northern Arizona University, Flagstaff, 102 pp.

Tellería, J.L., Ramírez, J. & Pérez-Tris, A. (2005). Conservation of seed-dispersing migrant birds in Mediterranean habitats: Shedding light on patterns to preserve processes. *Biological Conservation* **124**: 493–502.

Terborgh, J., Pitman, N., Silman, M., Schichter, H. & Nunez, V. P. (2002). Maintenance of tree diversity in tropical forests. In Levey, J. D., W. R. Silva, R. W., & Galetti, M. (Eds). Seed Dispersal and Frugivory: Ecology, Evolution and Conservation, pp. 1–17. CABI publis.

Thomas, D. W. (1982). The ecology of an African savanna fruit bat community: resources partitioning and role in seed dispersal. PhD thesis. Scotland: University of Aberdeen.

Thomas, D. W. (1983). The annual migrations of three species of West-African fruit bats (Chiroptera, Pteropodidae). *Canadian Journal of Zoology* **61**: 2266–2272.

Thomas, D. W., Cloutier, D., Provencher, M. & Houle, C. (1988).The shape of bird- and bat-generated seed shadows around a tropical fruiting tree. *Biotropica* **20**: 347–348.

Tilman, D. (1994). Competition and biodiversity in spatiallystructured habitats. *Ecology* **75**: 2–16.

Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**: 81–92.

Tiffney, B. H. (1984). Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. *Annal of the Missouri Botanical Gard*en **71**: 551–576.

Traveset, A. (1998). Effects of seed passage through vertebrate frugivores' gut on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* **1/2**: 151-190.

Traveset, A., & Wilson, M. F. (1997). Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. *Oikos* **80**: 89-95.

Traveset, A., Riera, N. & Mas, R. E. (2001). Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology* **15**: 669–675.

Tsoar, A., D. Shohami. & Nathan, R. (2010). A movement ecology approach to study seed dispersal and plant invasion: An overview and application of seed dispersal by fruit bats. In D. M. Richardson (Ed.). Fifty years of invasion ecology: The legacy of Charles Elton. pp. 103‑119. Blackwell Publishing, Oxford, UK.

Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'omo, G. & Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *National Academic Sciences*. **108**: 718–724.

Turner, I. M. (1996). Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* **33**: 200–209.

Uriante, A. M., Anciaes, M., Da Silva, T. B., Rubim, P., Johnson, E. & Bruna, E. M. (2011). Disentagling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. *Ecological Society of America* **92 (4)**: 924-937.

Uriarte, M., Bruna, E. M., Rubim, P., Anci̇̃ae, S. M. & Inge, J. I. (2010). Effects of forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site limitation. *Ecology* **91** (5): 1317–1328.

Utzurrum, R. C. B. (1995). Feeding ecology of Phillipine fruit bats: patterns of resource use and seed dispersal. In Ecology, Evolution, and Understorey of Bats (eds. P. A. Racey, P. A & Swift, S.), pp. 63–77. Clarendon Press, Oxford.

Utzurrum, R. C. B. & P. D. Heideman, P. D. (1991). Differential ingestion of viable vs. nonviable Ficus seeds by fruit bats. *Biotropica* **23** (3): 311-321.

Van der Pijl, L. (1982). *Principals of dispersal in higher plants, 3rd edn*. Berlin: Springer-Verlang.

Vandermeer, J. & Perfecto, I. (1997). The agroecosystem: a need for the conservation biologist's lens. *Conservation Biology* **11**: 591–592.

Wang, C. W. & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology and Evolution* **17(8)**: 379-385.

Waltert, M., Bobo, K. S., Sainge, N. M., Fermon, H. & Muhlenberg, M. (2005) From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecology Appllied* **15**:1351–1366.

Webala, P. W., Musila, S., & Makau, R. (2014). Roost occupancy, roost site selection and diet of straw-coloured fruit bats (Pteropodidae: *Eidolon helvum*) in western Kenya: the need for continued public education. *Acta Chiropterologica* **16** (1): 1508-1109.

Wenny, D. G. (2000). Seed dispersal, seed predation and seedling recruitment of Ocotea endresia (Lauraceae) in Costa Rica. *Ecological Monographs*. **70**: 331-351.

Wheelwright, N. T. & Janson, C. H. (1985). in press. Colon of fruit displays of bird-dispersed plants in two tropical forests. *American Naturalist* **126** (6).

Wilson, D. E. & Reeder, M. A. (2005). Mammal species of the world: A taxonomic and geographic reference. Baltimore: Johns Hopkins University Press.

Wunderle, Jr. & J.M. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* **99** (1-2):223-235

Yagihashi, T., Hayashida, M. & Miyamoto, T. (1998). Effects of bird ingestion on seed germination of *Sorbus commixta*. *Oecologia* **114**: 209–212.

Yilangai, M. R. Chaskda, A.A. & Georgina S. Mwansat, S. G. (2014). Avian Utilization of the Fruits of *Carissa Edulis* Vahl and *Jasminum Dichotomum* Vahl in A Central Nigerian Reserve. *Journal of Natural Sciences Research* **4**: 1-7.

Yom-Tov, Y., & J. Friedman, J. (1990). Differential germination of two closely related species of Solanum in response to bird ingestion. *Oikos* **57**:222-228.

Zimmerman, D. A., Turner, D. A. & Pearson, D. J. (1998). Birds of Kenya and northern Tanzania.

Zimmerman, J. K., Pascarella. & Aide, T. M. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* **8**: 350-360.

APPENDICES

Appendix 1: A list of the 30 *P. guajava* focal trees, their location, habitats, basal area and the number of frugivores recorded.

Focal Tree	Site	Basal area (m²)	Avian frugivore visits	*E. helvum* visits
1	Ilwanda	0.018	31	188
2	Ilwanda	0.035	32	205
3	Ilwanda	0.025	32	213
4	Ilwanda	0.038	39	209
5	Ilwanda	0.023	35	193
6	Ilwanda	0.031	35	207
7	Ilwanda	0.045	38	216
8	Ilwanda	0.028	32	196
9	Ilwanda	0.02	35	172
10	Ilwanda	0.025	44	192
11	Mbale	0.045	50	164
12	Mbale	0.035	54	137
13	Mbale	0.042	41	155
14	Mbale	0.028	54	148
15	Mbale	0.031	53	150
16	Mbale	0.035	41	134
17	Mbale	0.025	38	137
18	Mbale	0.018	41	132
19	Mbale	0.038	56	154
20	Mbale	0.023	48	135
21	Chugi	0.031	51	95
22	Chugi	0.045	47	98
23	Chugi	0.035	42	80
24	Chugi	0.028	52	77
25	Chugi	0.025	51	79
26	Chugi	0.028	47	80
27	Chugi	0.038	48	97
28	Chugi	0.031	54	74
29	Chugi	0.023	49	74
30	Chugi	0.053	43	97

Appendix 2: A list of the 12 avian frugivores observed visiting P. *guajava* trees.

Common name	Species name	Percentage visits
African Thrush	*Turdus pelios*	3
Black and white casqued Hornbill	*Bycanistes subcylindricus*	0.4
Common Bulbul	*Pyconatus barbatus*	24.7
Speckled Mousebird	*Colius striatus kikuyensis*	43.1
Veiollet's Black Weaver	*Ploceous nigerrimus*	2.1
Violet backed starling	*Cinnyricinclus leucogaster*	0.6
Yellow White-eye	*Zosterops senegalenses*	16
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	1.1
Yellow-throated Leaf love	*Chlorocinchila flavicollis*	5.8
African green pigeon	*Treron calva*	0.4
Black cap	*Sylvia atricapila*	0.4
Double-toothed Barbet	*Lybius bidentatus aequatorialis*	0.4

Appendix 3: A checklist of bird species observed visiting *P. guajava* trees in all the study sites. Given are their mean visits and feeding guild (Nomenclature by Bennun *et al.*, 1996)

Family	Species	Scientific name	Mean visits	Feeding Guild
Alcedinidae	African Pygmy Kingfisher	*Ispidina p. picta*	0.38	I
Bucconidae	Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	0.31	F
Bucerotidae	Black-and-white-casqued Hornbill	*Bycanistes subcylindricus subquadratus*	0.07	F
	Red-faced Cisticola	*Cisticola erythrops Sylvia*	0.03	I
	Red-faced Cisticola	*Cisticola erythrops Sylvia*	0.03	I
	Tawny-flanked Prinia	*Prinia subflava melanorhyncha*	0.38	I
Cisticolidae	White-chinned Prinia	*Prinia leucopogon reichenowi*	0.03	I
Coliidae	Speckled Mousebird	*Colius striatus kikuyensis*	19.79	F
	African Green Pigeon	*Treron calva gibberifrons*	0.07	F
	Red-eyed Dove	*Streptopelia semitorquata*	0.03	G
	Blue-spotted Wood Dove	*Turtur afer*	0.17	O
	Laughing Dove	*Streptopelia s. Senegalensis*	0.03	O
Columbidae	Ring-necked Dove	*Streptopelia capicola somalica*	0.03	O
Cuculidae	Diederik Cuckoo	*Chrysococcyx caprius*	0.03	I
	African Firefinch	*Lagonosticta rubricata hildebrandti*	0.1	G
	Black-crowned Waxbill	*Estrilda n. nonnula*	0.07	G
	Bronze Mannikin	*Lonchura cucullata scutata*	0.83	G
	Red-billed Firefinch	*Lagonosticta senegala ruberrima*	0.69	G
Estrildidae	Red-cheeked Cordon-bleu	*Uraeginthus b. bengalus*	0.24	G
	African Citril	*Serinus citrinelloides*	0.21	G
Fringillidae	Yellow-fronted Canary	*Serinus mozambicus*	1.9	G
Lybiidae	Double-toothed Barbet	*Lybius bidentatus aequatorialis*	0.07	F
	Brown-crowned Tchagra	*Tchagra australis eminii*	0.03	O
Malaconotidae	Tropical Boubou	*Laniarius aethiopicus*	0.07	O
Motacillidae	Yellow Wagtail	*Motacilla flava*	0.14	I
	African Blue Flycatcher	*Elminia longicauda teresita*	1.28	I
	African Dusky Flycatcher	*Muscicapa adusta interposita*	0.17	I
	African Grey Flycatcher	*Bradornis m. microrhynchus*	0.17	I
	African Paradise Flycatcher	*Terpsiphone viridis*	0.24	I
	Brown-backed Srub Robin	*Cercotrichas hartlaubi*	0.03	I
	Equatorial Akalat	*Sheppardia a. aequatorialis*	0.03	I
Muscicapidae	Northern Black Flycatcher	*Melaenornis pammelaina*	0.45	I

	Pale Flycatcher	*Bradornis pallidus murinus*	0.21	I
	Spotted Flycatcher	*Muscicapa striata neumanni*	0.48	I
	White-browed Robin-chat	*Cossypha h. heuglini*	0.1	I
	White-eyed Slaty Flycatcher	*Melaenornis f. fischeri*	0.03	I
	Eastern Grey Plantain-Eater	*Crinifer zonurus*	0.48	F
	Bronze Sunbird	*Nectarinia k. kilimensis*	2.07	N
	Variable Sunbird	*Nectarinia venusta*	1.57	N
	Copper Sunbird	*Nectarinia cuprea*	0.03	N
	Green-headed Sunbird	*Nectarinia verticalis viridisplendens*	0.03	N
Nectariiniidae	Marico Sunbird	*Nectairinia mariquensis suahelica*	0.07	N
	Baglafecht Weaver	*Ploceus baglafecht*	2.55	G
	Black-headed Weaver	*Ploceus cucullatus*	1.83	G
	Grey-headed Sparrow	*Passer griseus*	1.97	G
	Lesser-masked Weaver	*Ploceus i. intermedius*	0.14	G
	Yellow-mantled Widowbird	*Euplectes macrourus*	0.1	G
	Spectacled Weaver	*Ploceus ocularis suahelicus*	0.21	I
Ploceidae	Vieillot´s Black Weaver	*Ploceus nigerrimus*	0.34	O
	Common Bulbul	*Pycnonotus barbatus*	14.83	F
	Yellow White-eye	*Zosterops senegalensis*	5.52	F
Pycnonotidae	Yellow-throated Leaf-love	*Chlorocichla flavicollis pallidigula*	2.07	F
	Violet backed starling	*Cinnyricinclus leucogaster*	0.43	F
Sturnidae	Superb Starling	*Lamprotornis superbus*	0.03	O
	Blackcap	*Sylvia atricapilla dammholzi*	0.07	F
	Garden Warbler	*Sylvia borin*	0.21	O
Sylviidae	Olivaceous Warbler	*Hippolais pallida elaeica*	0.14	O
	African Thrush	*Turdus pelios centralis*	1.03	F
Turdidae	Common Stonechat	*Saxicola torquata axillaris*	0.1	O
	Olive Thrush	*Turdus olivaceus abyssinicus*	0.07	O
Viduidae	Pin-tailed whydah	*Streptopelia semitorquata*	0.03	G

Feeding guild: I = Insectivore, F = Frugivore, G = Granivore, N = Nectivore, and O = Omnivore

Appendix 4: Seedling species found established below the crowns of trees. Included are the study sites, density of seedlings (seedlings/m^2), mode of dispersal, ecological succession and succession stage of each species. Nomenclature is according to Beentje, 1994.

Scientific name	Ilwanda	Mbale	Chugi	Mode of dispersal	Ecological succession	Succession stage
Allophylus rubifolius	0	0	0.74	Animal	Climax	Late
Antiaris toxicaria	1.14	0	0	Animal	Climax	Early
Bridelia micrantha	2.3	2.16	1.67	Animal	Pioneer	Early
Clausena anisata	0.5	0.53	1.02	Animal	Climax	Late
Craterispermum schweinfurthii	0	1.07	0.75	Animal	Climax	Early
Croton macrostachyus	0.42	2.68	0.63	Wind	Climax	Early
Croton megalocarpus	0	0	0.2	Animal	Pioneer	Early
Cupressus lusitanica	3	7	0	Wind	?	?
Ficus sycomorus	0.43	0	0	Animal	Climax	Late
Harungana madagascariensis	0	0.2	0.95	Animal	Climax	Early
Maesa lanceolata	0	0	0.25	Animal	Climax	Early
Makhamia lutea	8.54	3.15	0.35	Wind	Climax	Late
Morus mesozygia	0	0	0.9	Animal	Pioneer	Early
Persea americana	0	1.26	0	Animal	Climax	Late
Psidium guajava	70.5	18.9	1.48	Animal	Pioneer	Early
Sapium ellipticum	0	0	1.27	Animal	Pioneer	Early
Teclea nobilis	0.61	1.07	1.08	Animal	Climax	Early
Zanthoxylum gillettii	0.2	0	0.86	Wind	Climax	Late

Appendix 5: Plant species recorded in the study sites. Plant nomenclature follows the International Plant Names Index (2005).

FAMILY	SCIENTIFIC NAME	Exotic/Indigenous
Bignoniaceae	*Makhamia lutea*	Exotic
Lauraceae	*Persea americana*	Exotic
Anacardiaceae	*Mangifera indica*	Exotic
Cyatheacea	*Cyathea manniana*	Indigenous
Cupressaceae	*Cupressus lusitanica*	Exotic
Cupressaceae	*Juniperus procera*	Exotic
Podocarpacea	*Podocarpus latifolius*	Indigenous
Piperaceae	*Piper capense*	Indigenous
Capparaceae	*Capparis tomentosa*	Indigenous
Capparaceae	*Maerua decumbens*	Indigenous
Phytolaccaceae	*Phytolacca dodecandra*	Indigenous
Balsaminaceae	*Impatiens sodenii*	Indigenous
Proteaceae	*Faurea saligna*	Indigenous
Proteaceae	*Protea gaugedi*	Indigenous
Flacourtiaceae	*Oncoba routledgei*	Indigenous
Flacourtiaceae	*Trimeria grandifolia*	Indigenous
Canellaceae	*Warburgia ugandensis*	Indigenous
Ochnaceae	*Ochna holstii*	Indigenous
Myrtaceae	*Syzygium cordatum*	Indigenous
Myrtaceae	*Eucalyptus spp**	Exotic
Myrtaceae	*Psidium guajava*	Exotic
Combretaceae	*Combretum molle*	Indigenous
Rhizophoraceae	*Cassipourea malosana*	Indigenous
Tiliaceae	*Grewia bicolor*	Indigenous
Tiliaceae	*Grewia similis*	Indigenous
Tiliaceae	*Grewia tembensis*	Indigenous
Tiliaceae	*Triumfetta tomentosa*	Indigenous
Sterculiceae	*Dombeya burgessiae*	Indigenous
Malvaceae	*Abutilon maurintianum*	Indigenous
Malvaceae	*Hibiscus calyphyllus*	Indigenous
Malvaceae	*Pavonia urens*	Indigenous
Euphorbiaceae	*Bridelia micrantha*	Indigenous
Euphorbiaceae	*Croton dichogamus*	Indigenous
Euphorbiaceae	*Croton macrostachys*	Indigenous
Euphorbiaceae	*Croton megalocarpus*	Indigenous
Euphorbiaceae	*Euphorbia candelabrum*	Indigenous

Euphorbiaceae	*Ricinus communis*	Indigenous
Rosaceae	*Prunus africana*	Indigenous
Mimosaceae	*Acacia abyssinica*	Indigenous
Mimosaceae	*Acacia nilotica*	Indigenous
Mimosaceae	*Acacia xanthophloea*	Indigenous
Mimosaceae	*Albizia gummifera*	Indigenous
Moraceae	*Ficus ovata*	Indigenous
Moraceae	*Ficus sur*	Indigenous
Moraceae	*Ficus sycomorus*	Indigenous
Moraceae	*Ficus thonningii*	Indigenous
Rutaceae	*Clausena anisata*	Indigenous
Rutaceae	*Zanthoxylum gilleti*	Indigenous
Rutaceae	*Teclea nobilis*	Indigenous