THE ROLE OF SYKES MONKEYS (*Cercopithecus mitis albogularis*) IN NATURAL FOREST REGENERATION IN GEDE RUINS FOREST, KILIFI COUNTY, KENYA

LELEY C. NEREOH

COLLEGE OF PHYSICAL AND BIOLOGICAL SCIENCES

MSC. BIOLOGY OF CONSERVATION

REG NO. I56/80877/2012

A THESIS SUBMITTED IN PARTIAL FULFILMENT FOR THE DEGREE OF MASTER OF SCIENCE IN BIOLOGY OF CONSERVATION, SCHOOL OF BIOLOGICAL SCIENCES, UNIVERSITY OF NAIROBI.

November 2016

DECLARATION

I, Leley C. Nereoh, hereby declare that; this thesis is my own original work and has not been submitted in any other university for an award of a degree either in part or in its entirety and has not been published earlier in its present form to the best of my knowledge.

Sign…………………………………… Date……………………………………….

Leley C. Nereoh

Reg No. I56/80877/2012

SUPERVISORS' APPROVAL

This thesis has been submitted for examination with our approval as University supervisors.

Sign………………………………. Date…………………………………………

Dr. Robert Chira

Sign……………………………….. Date………………………………………..

Prof. Geoffrey Wahungu

DEDICATION

To all primate conservationists who work tirelessly to ensure existence and maintenance of primates population in their natural habitats so that they can continue to play the critical role of natural regeneration of degraded and fragmented forests through seed dispersal.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENT

First, I thank the Almighty God for the strength, wisdom, grace and knowledge that He bestowed me throughout the course. I wish to express my sincere gratitude to my supervisors Dr. R. Chira and Prof. G. Wahungu for their unwavering support, expertise, guidance and encouragement that made completion of the study possible.

I thank everyone at the National Museum of Kenya-Gede, for being friendly, open and willing to help in any way they could, particularly, the Curator, Mr. Mwarora, Education Officer, Mr. Kassim and Mr. Mathias, the plant taxonomist.

I extend my appreciation to Lucy Mureu for assisting with logistics throughout the study; I owe her a great debt of gratitude. I am grateful to Mr. Kalama and Ms. Colwell for their support during data collection. They made my data collection work easier and enjoyable and the study would not be complete if it were not for their encouragement.

I extend my appreciation to Mr. Mbuvi, Dr. Wekesa, Mr. Chemuku, Ms. Riziki and Ms. Carolyne of Kenya Forestry Research Institute (KEFRI) for their immense support. Special and sincere thanks go to my beloved parents, brothers and sisters for support and encouragement throughout the study. They are the best family one can ever ask for.

Last but not least, I am grateful to the University of Nairobi for the scholarship award to pursue my masters' degree.

God bless you all.

ABSTRACT

Primates are known in maintaining plant population and forest regeneration. They swallow and defecate, regurgitate or spit large quantities of viable seeds away from the parent plant. This study was conducted in Gede Ruins forest to establish the role of Sykes monkeys (*Cercopithecus mitis albogularis)* and dung beetles in maintenance of community structure and species composition through seed dispersal. The objectives were to determine: forest structure and species composition; seed dispersal by Sykes monkeys and complementary role of dung beetles; and to establish the viability of dispersed seeds by the monkeys. The forest was stratified into primary and secondary forest and data collected during rainy and dry periods for seasonal comparative studies. Two groups of habituated monkeys were studied; provisioned and free ranging groups.

Age classes in the forest exhibited a reversed exponential curve a characteristic of a regenerating forest. Lack of marked difference in vegetation structure and species composition between primary and secondary forest suggest that secondary forest had regained most of its diversity attributed to seed dispersal and successful regeneration and recruitment. The monkeys dispersed diverse seeds to at least 5 m from mother tree crucial for maintenance of plant population and diversity in the forest. Seasonality and provisioning were the key factors that significantly affected seed dispersal by Sykes monkeys and hence forest regeneration. Dung beetles played a complementary role through seed cleaning, rolling away dung with seeds to suitable microsites and burrowed dung balls in forest litter precluding seed predation. Ingestion significantly reduced latency period and enhanced germination success implying that endozoochory was critical for regeneration of Gede forest.

Sykes monkeys were, therefore, effective and efficient seed dispersers because they; moved large numbers of seeds, did not decrease seed viability and dispersed array of species. This suggests that enhancing population of the monkeys in Coastal forests of Kenya is critical for natural forest regeneration for conservation and management of fragmented and degraded forests.

Key words; *Forest regeneration; seed dispersal; Sykes monkeys; dung beetles; Gede ruins forest*

CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

Seed dispersal is an important ecological process known to maintain forest structure and species composition through natural regeneration and recruitment. However, frugivory, seed dispersal and forest regeneration interactions have remained under-studied. Plant-frugivore mutualistic interactions form the physical template for seed dispersal and thus forest regeneration (Bascompte and Jordano, 2007) and maintenance of genetic diversity and plant population viability (Howe and Miriti, 2000; Jordano *et al*., 2011). Most tree species in tropical forests have developed mutualistic relationship with vertebrate seed dispersers (Herrera, 2002). About 75–90% tree species produce fruits that are adapted to consumption and potential seed dispersal by animals (Howe, 1989). These fruits provide nutrients in exchange for potential dispersal of their seeds (Herrera, 2002).

Dispersed seeds escape from high density of competing siblings and species specific pathogens, fungi and herbivores which occur in high densities near parent trees (Howe and Smallwood, 1982). Moreover, seed dispersal enables the colonization of vacant recruitment sites and directed dispersal to non-random habitats suitable for establishment (Howe and Smallwood, 1982). Birds and mammals (mainly primates and bats) are the most important vertebrate frugivores, which swallow and defecate, regurgitate or spit seeds away from the parent plant (Jordano, 2000). Primates for instance, comprise averagely 24-40% of frugivore population in tropical forests (Chapman and Chapman, 1996). They consume large quantities and diverse fruits and defecate or spit large numbers of viable seeds (Lambert, 1997).

Seeds may be destroyed after primary dispersal by abiotic and biotic factors (Fenner and Thompson, 2005) hence can affect the distribution and survival of seeds and seedlings (Forget *et al*., 1998).

Coprophagous beetles (Scarabaeidae) feed on the microorganism-rich liquid component of mammalian dung and use the more fibrous material to brood their larvae (Halffter and Edmonds, 1982). While moving seeds both horizontally and vertically, they reduce seed clumping, make seeds less detectable to seed predators thus enhanced seed survival (Forget *et al.,* 2002).

Extensive anthropogenic activities due to the rapid global human population growth have resulted in the fragmentation of natural forests and subsequent decrease in the population sizes of forest animals owing to decline in their habitat size (Cordeiro and Howe, 2003). If animal seed dispersers decrease in abundance, fewer frugivores might visit fruiting trees, fewer seeds might be dispersed (Kirika *et al*., 2008; Holbrook and Loiselle, 2009) and dispersal distances of seeds might decrease (Wright *et al*., 2000). This consequently lead to increased post-dispersal seed predation (Galetti *et al*., 2006), lower seedling recruitment (Cordeiro and Howe, 2003) and local plant extirpation and subsequently decline in plant diversity (Terborgh *et al*., 2008). Attempts have been made to rehabilitate degraded forests with little success (Catterall *et al.,* 2008). Their failure has been attributed to inadequate understanding of suitable rehabilitation approaches to address the various constraints to natural forest regeneration (Smidt and Blinn, 1995; Turner *et al.,* 1998).

This research study aimed at exploring the potentiality of Sykes monkeys and complimentary role by the dung beetles in maintaining the structure and woody species composition of Gede forest, through seed dispersal and natural regeneration. To achieve this, the following were determined; woody species composition and forest structure characterization, amount of seeds dispersed through seed rain and ingestion, secondary seed dispersal by dung beetles and germination trials of monkey dispersed seeds. The findings are key for conservation and sustainable management of degraded terrestrial natural forests.

1.2 Literature Review

1.2.1 Global forest coverage, disturbance and loss

Forest degradation and loss are the greatest threats to terrestrial floral and faunal species (Baillie *et al*., 2004). World forests cover about 4 billion hectares, (31 %) of the earth's land surface hectares (FAO, 2010). This is down from the pre-industrial area of 5.9 billion hectares (FAO, 2010). Tropical forests covered as much as 12 % of the Earth's land surface, (6 million square miles) but presently, less than 5% of Earth's land is covered with these forests (FAO, 2011). Estimates of annual loss of tropical forest range from 8.7 – 12.5 Million ha (Mayaux *et al*., 2005). Over the past century tropical forests have been suffering from exceptional rates of change as they are degraded by human activities each year (Achard *et al*., 2002; Asner *et al*., 2005).

Forests in Africa cover an estimated area of 650 Million hectares accounting for 16.8 % of the global forest cover (FAO, 2011). These forests are being lost at a rate of more than 4 million hectares per year; twice the world's deforestation average. According to FAO (2011), losses totaled more than 10% of the continent's total forest cover between 1980 and 1995. Approximately 6.1% (3,467,000 ha) of Kenya is forested. Between 1990 and 2010, Kenya lost 6.5% of its forest cover, caused mainly by anthropogenic fragmentation and selective logging (FAO, 2011). The loss of tropical coastal forests in Kenya has been rampant. By the early 1990s, there were about 107 forest patches in the Coastal Forest Mosaic in Kenya covering an area of 660 km^2 (Burgess *et al*., 2000). Burgess *et al*. (2003) estimated that, the Coastal forests in Kenya have decreased in area from over 50,000 km^2 in the early 1900s to about 650 km^2.

1.2.2 Effects of anthropogenic disturbance on seed dispersal cycle

Human disturbance can affect animal-mediated seed dispersal and natural regeneration of plant populations by altering components of dispersal (escape, colonization or recruitment). Fragmentation of forest remnants (Cordeiro and Howe, 2003), hunting (Peres, 2000) and selective logging (Kirika *et al*., 2008) and subsequent forest loss, severely affect species and ecological processes such as seed dispersal in tropical forests (Morris, 2010).

Small forest fragments cannot support as many individuals as large continuous forests; consequently, fragmentation often leads to the local extirpation of frugivores (Valdivia and Simonetti, 2007). Hunting reduces frugivore abundance directly and can result in the local extirpation of game species especially those preferred by hunters, which often include large frugivores (Palacios and Peres, 2004). Increased intensities of selective logging can also reduce the abundance of frugivores through decreased fruit availability and loss of forest structure (Lambert, 2011). The effects of different types of direct human disturbance, such as hunting and selective logging, are impossible to separate because many intensively logged forests simultaneously experience high levels of hunting (Kirika *et al*., 2008; Babrainyeera and Brown, 2009).

If animal seed dispersers decrease in abundance or are extirpated, it may lead to breakdown in seed dispersal processes of concerned plants (Pizo, 1997). Seeds not dispersed by frugivores fall from the parent's canopy to the ground and have a low probability of surviving and establishment (Sork, 1985; Chapman and Chapman, 1996). Seedling mortality result from increased competition among seedlings and increased attacks by predators, herbivores and pathogens beneath the parent plant canopy (Bleher and Böhning -Gaese 2001; Cordeiro and Howe, 2003). Consequently, leading to local plant extirpation and decline in plant diversity (Terborgh *et al*., 2008).

1.2.3 The spatial distribution of seeds: seed rain, seed shadow and dispersal distances

Seed rain is the flux of seeds from reproductive plants without considering space explicitly (Nathan and Muller-Landau, 2000). Seed shadow on the other hand, is the spatial distribution of dispersed seeds in relation to their source and other con-specifics (Nathan and Muller-Landau, 2000; Jordano and Godoy, 2002). Seed shadows have two horizontal dimensions; the number (density) of dispersed seeds in relation to the distance from the source; and the directionality with regard to the seed source (Willson and Traveset, 2000).

Generally, only a few seeds are dispersed over very long distances as vast majority of seeds fall beneath the parent plant (Willson, 1993). Many frugivores create a highly heterogeneous and aggregated seed rain. As a consequence of aggregation, most sites in the landscape receive no or few seeds despite high fruit production, therefore, seed delivery is insufficient to saturate suitable microhabitats for plant establishment. This is referred to as 'dissemination limitation' or 'dispersal limitation' (Jordano and Godoy, 2002; Muller- Landau *et al.,* 2002).

Typically, long-distance dispersal capacity is higher in wind- or vertebrate-dispersed plant species than in species dispersed by ants or by ballistic mechanisms (Willson and Traveset, 2000). Willson and Traveset (2000) found that, seeds that reached distant islands were often carried by water, wind or inside bird guts or feathers. In contrast, Clark *et al.* (2005) found that animal dispersed species had longer mean dispersal distances than wind-dispersed species (but lower fecundity). Seed shadows, however, can vary widely even within species and dispersal vectors (Clark *et al.*, 2005). The ability of a species to reach distant habitats may be a critical feature in maintaining biodiversity, particularly with regards to an increasing habitat fragmentation (Ouborg *et al.*, 1999; Levin *et al.*, 2003).

1.2.4 Potential advantages of seed dispersal

Seed dispersal is the spatial distribution of viable seeds away from the parent plant (Nathan and Muller-Landau, 2000). It is the link in the demographic transition between the ripe fruit on the plant and the whole recruitment cycle (Jordano and Godoy, 2002). Dispersal of seeds takes place at the plant's final stage of each reproductive episode, and can thus potentially "screen off" previous selection effects in the reproductive cycle (e.g. effects of pollination and fruit growth).

Frugivorous vertebrates disperse the seeds of most rainforest plants (Howe and Smallwood, 1982). Therefore, decline in the abundance of frugivores following tropical forest clearing and fragmentation may alter the rates or patterns of seed dispersal and plant regeneration (Bleher and Böhning - gause, 2001, Cordeiro and Howe, 2003). In complete absence of dispersers for particular plant species would mean that recruitment could only occur beneath the crown of the parent plant and may result in reduced recruitment, restricted spatial distribution and be vulnerable to stochastic extinction (Bleher and Bohning- gause, 2001; Babrainyeera *et al*., 2007). Dispersal failure, therefore, prevents the plant species from recolonizing forest remnants from which it had once became extinct, and this would mean it is unable to colonize cleared land during secondary succession (Duncan and Chapman, 2002).

Regarding scale, two major types of dispersal can be distinguished; dispersal relevant to immigration at geographical scales and dispersal relevant to colonization of new sites in the same general area or community where the parent plant lives (Dirzo and Domínguez, 1986). In the escape hypothesis; it is assumed species specific pathogens, fungi and herbivores occur in high densities near parent trees, which increase seed and seedling mortality close to the parent tree (Howe and Smallwood, 1982). The colonization hypothesis; proposes that seed dispersal increases the probability that seeds reach new micro-sites where they can germinate and establish (Howe and Smallwood, 1982). The directed-dispersal hypothesis; suggests seed dispersal agents deposit seeds at sites that are particularly suitable for germination and recruitment (Howe and Smallwood, 1982). These hypotheses posit that animal-mediated seed dispersal enhances seedling recruitment and is thus important for maintaining genetic diversity and plant population viability (Jordano *et al*., 2011).

Seed dispersal is not only important for range expansion of species and the fitness of individual plants; it is also a key process for determining the spatial and genetic structure of plant populations (Jordano and Godoy, 2002; Levin *et al.,* 2003). The genetic consequence associated with seed dispersal is the prevention or reduction of the local genetic differentiation of plant populations (Herrera, 2002). Seed dispersal also sets the template for post-dispersal processes such as secondary seed dispersal and seed predation, and thus affects patterns and rates of early seed survival and seedling establishment (Jordano, 2000).

1.2.5 Coevolution between plants and their seed dispersers

Snow (1971) suggested that the production of abundant, conspicuous, easily accessible and nutritious fruit crops is designed to attract the greatest number and variety of disperser possible. This has led to the dichotomy view of specialist versus generalist fruit plant species and disperser with the implication of a close co-evolution between certain pairs or small sets of tree species and their seed dispersers. Large, single seeded fruits with pulp of high nutritive value would be associated with high-quality seed dispersal by specialized frugivores. The watery, carbohydrate-rich fruits with numerous seeds would be dispersed primarily by opportunistic frugivores (Jordano, 2000; Wenny, 2001). Many studies have failed to find clear adaptations of plants to their animal dispersers (Herrera, 1986). The paradigm of disperser-plant co-evolution has, therefore, changed to a diffuse, weak mutual, non-species-specific adaptation between large groups of plants and groups of dispersers (Lambert and Garber, 1998; Herrera, 2002).

1.2.6 Importance of primates in dispersing seeds in tropical forests

Seed dispersal is a complex process involving a number of different steps. To have the greatest ecological impact, primates have to; move large numbers of seeds and not decrease seed viability through their handling. They should defecate or spit those seeds in locations where they can avoid seed predation (or be suitably secondarily dispersed). The dispersed seeds should be able to germinate and grow (Eisenberg and Thorington, 1973).

Species that are extremely important seed dispersers are possibly ecosystem engineers, and some primates probably play this important ecological role (Andresen, 2000; Kaplin and Lambert, 2002). Primates constitute a large proportion of the frugivore biomass (25 to 40%) in tropical forests; they eat large quantities of fruit; are relatively large in size and they defecate and or spit out large numbers of viable seeds (Wrangham *et al*., 1994; Lambert, 1997; Stevenson, 2011). They may, therefore, disperse high numbers of seeds over wide areas (Wrangham *et al*., 1994; Link and Di-Fiore, 2006), thereby influencing the spatial and genetic structure of plant populations and contribute to plant community dynamics (Chapman and Onderdonk, 1998; Pacheco and Simonetti, 2000; Nuñez-Iturri and Howe, 2007).

Some primate species are considered particularly important for the dispersal of large seeded fruit that many other frugivores cannot swallow, without causing serious damage of the seeds (Peres and van Roosmalen, 2002; Nuñez- Iturri and Howe, 2007). Furthermore, unlike many other frugivores, primates are able to handle a wide variety of different fruit types and sizes, with their fingers and teeth; they can handle and open even large and indehiscent fruits with a hard pericarp (Julliot, 1996). Primate-dispersed seeds are capable of germination since the passage through the frugivores gut improves the rate of germination and reduces germination latency (Lieberman *et al*., 1979). Primates not only disperse many seeds but also are responsible for the dispersal of a large proportion of the seeds removed from parent trees of several tree species.

As much as primates disperse many seeds; there may be other taxonomic groups (e.g., birds) that disperse as many or more seeds (Chapman and Chapman, 1996; Lambert, 1997). However, through focal observations of individual trees, Chapman and Chapman (1996) quantified the percentage of forest trees removed by all diurnal frugivores and found that primates were responsible for 74.8% of the fruits removed from the 12 trees of the six species studied.

Balcomb and Chapman (2003) studied fruit and seed removal of *Monodora myristica*a, a low fecundity forest tree species in Uganda. The tree is characterized by thick and hard to break pericarp containing multiples seeds of approximately 18.5 cm and 2.0 cm length suggesting dispersal by only very large arboreal frugivores. The large bodied primates; chimpanzees *(Pan troglodytes)* and Grey-cheeked mangabey (*Laphocebus albigena)* played a critical role in primary seed dispersal of the tree species. They were the only frugivores that opened the hard- husked fruits and were estimated to disperse over 85% of mature seeds. In Kibale national park, Red tail monkeys (*Cercopithecus ascanius*); Blue monkeys (*Cercopithecus mitis*), mangabeys and chimpanzees spat or swallowed and dispersed approximately 35,000 fruits/km^2/day (Lambert, 1999).

1.2.9 Seed dispersal by monkeys in tropical lowland coastal forests

A study by Stevenson *et al,* (2002) on seed dispersal by Ateline monkey species in Tinigua National Park in Colombia, found that out of 14 species tested for germination, 6 had significantly higher germination rates for defecated seeds. In 3 other plant species dispersed by woolly and spider monkeys (*Simarouba amara, Inga edulis* and *Protium sagotianum*), there was higher germination in seeds defecated by them versus controls. For one of the species dispersed by howlers, *Guapira cuspidata,* endozoochory was necessary to induce germination, given that none of the control seeds germinated. The germination of dispersed seeds of *Ficus thunbergii, Eurya japonica* and *Vaccinium bracteatum*, was significantly enhanced by passage through the macaques' gut.

A study to determine seed dispersal by Vervet monkeys *(Chlorocebus pygerythrus)* in rehabilitating Coastal dune forests at Richards Bay, South Africa, Foord *et al.* (1994) revealed that the seeds of *Rhus nebulosa, Carissa maerocarpa, Scutia myrtina,* and *Chrysanthemoides monilifera* were not destroyed in the digestive tract. Mean germination success for seeds ingested by the monkeys was 47.6% and that of control seeds was 42.2%. Mureu (2009) found that ingestion of seeds by Sykes monkeys in Gede ruins forest, Kenyan Coast, enhanced seed germination of *Grewia plagiophylla*, *Grewia forbesii*, *Diospyros squarrosa*, *Tarrena supra-axilaris*, *Cissus integrifolia* and *Tamarindus indica*. All these studies posit that monkey dispersed seeds are viable, suggesting that primates play critical role in natural regeneration of forests through seed dispersal and subsequent maintenance of forest structure and diversity.

1.2.10 Post-dispersal seed fate

The effectiveness of a seed disperser cannot be accurately evaluated without considering the post dispersal fate of seeds (Garber and Lambert, 1998; Andresen and Levey, 2004). Seeds may be destroyed after primary dispersal by abiotic and biotic factors. They may land in habitats or microsites unsuitable for germination, they can be attacked by fungi and pathogens, and they may also be eaten by granivores and/or burrowed at depths too deep for seedling emergence (Fenner and Thompson, 2005). Processes like post-dispersal seed predation and secondary seed dispersal can alter the template set by primary dispersal (Nathan and Muller-Landau, 2000).

Secondary seed dispersal often moves the seeds to discrete microsites favorable for seedling establishment (Vander Wall and Longland, 2004). Seeds dispersed secondarily from feaces by rodents, dung beetles, or to ant nests often have a higher probability of seedling establishment than seeds remaining at the primary deposition (Vander Wall and Longland, 2004). Burying may decrease the risk of being eaten by seed predators (Andresen, 1999; Fenner and Thompson, 2005), prevent seeds from desiccation (Vander Wall and Longland, 2004) and this may facilitate seed germination (Estrada *et al.,* 1993; Feer, 1999; Fenner and Thompson, 2005).

1.2.11 Dung beetles as secondary seed dispersers

Seed dispersal in tropical ecosystems by vertebrates is often followed by secondary seed dispersal by rodents, ants or dung beetles (Shepherd and Chapman, 1998; Andresen, 1999; Jansen *et al.*, 2002). Whereas rodents and ants are simultaneously antagonistic and mutualistic towards seeds, dung beetles do not directly feed on seeds. They use the dung for feeding and to provision their larvae, and by removing small portions from the source they may accidentally disperse some seeds incorporated in the fecal material.

In many species, immature adults use the more nitrogen-rich omnivore dung but the more carbohydrate-rich herbivore dung is used for breeding (Cambefort and Hanski, 1991). The larvae use the microorganisms in herbivore dung as food source (Cambefort and Hanski, 1991). Dung beetles can be divided into four behavioral and functional groups or guilds: dwellers (endocoprids), tunnelers (paracoprids), rollers (telecoprids), and kleptoparasites. The species of rollers and tunnelers are mostly found in tropics (Cambefort and Hanski, 1991).

Colonization of a dung pat by dung beetles usually is within the first few minutes after defecation (Andresen, 1999; Feer, 1999). They locate the resource by odour and/or visual clues (Herrera, 2002). The interaction between dung beetles and seeds however is influenced by many factors (Andresen, 2002). These include the size of the dung pat which can affect the mean number of dung beetle individuals and/or species at the resource (Andresen, 2002) and the probability of seed removal by dung beetles (Andresen, 2002). Seed size can negatively affect both the rate of seed burial (Feer, 1999; Andresen and Levey, 2004) and burrowing depth (Shepherd and Chapman, 1998; Andresen, 2002; Andresen and Levey, 2004), as can dung beetle size (Feer, 1999). Probability of seed burrowing by dung beetles and burrowing depth, are positively related with the amount of dung around the seeds (Andresen, 2002; Andresen and Levey, 2004).

1.2.12 Seed dispersal and forest regeneration

Previous studies on seed dispersal by monkeys have been conducted in Kenya. In the heavily fragmented and disturbed Kakamega forest, Farwig *et al.* (2006) studied seed dispersal of *Prunus africana*. A total of 36 frugivores were recorded visiting the tree species. Of these, three monkey species visited the *P. africana* trees; Blue monkey (*Cercopithecus mitis*), Black-and-white Colobus monkey (*Colobus guereza*) and Red-tailed monkey (*Cercopithecus ascanius*). However, quantification of seed dispersed by the monkeys, viability of dispersed seeds and their contribution to forest regeneration was not undertaken. In Kenyan Coast, Mureu (2009) studied the effect of food provisioning by tourists and crop raiding on seed dispersal by Sykes monkeys. The results indicated that provisioning affects seed dispersal through reduced feeding time and spontaneous clump defecation prior to a provisioning bout in unsuitable germination sites; however, the contribution of the monkeys to regeneration of the forest was not intensively studied.

Kimuyu *et al*. (2012) studied fruit handling behavior and the post-dispersal fate of seeds ingested by the mangabeys in Tana River. The results indicated that free ranging group of Tana River mangabeys (*Cercocebus galeritus*) which had previously been regarded as seed predator, played an important role in seed dispersal and contributed to the regeneration of the highly fragmented gallery forest. The two main fruit handling behaviors observed; fruit swallowing and processing fruits in cheek pouches, positively contributed to seed dispersal. The role of the mangabeys in dispersing seeds and facilitating forest regeneration was enhanced by their movement across forest patches through non-forested matrix, which contributed to the deposition of seeds and regeneration in habitat gaps. The study also found that dung beetles buried 56% of the experimental fecal clumps within one day after deposition. The rest (44%) were probably rolled away and buried elsewhere or removed by other secondary disperser or predators. The study did not determine the distance this dung balls were rolled away from the point of deposition (directed dispersal) and depth they were burrowed (escape from seed predation).

1.2.13 Gede ruins forest status and restoration needs

Gede Ruins, a thirteenth-seventeenth century stone city, covers an approximate area of 44 hectares (Robertson *et al.,* 2002). In the 1980's, Gede village surrounding the ruins, was expanding, and the forest surrounding the ruins was cleared for cultivation, poles and firewood (Robertson *et al.,* 2002). The forest is threatened by fragmentation caused by anthropogenic activities including illegal logging, firewood collection and charcoal burning. Hunting of monkeys which are the main seed dispersal agents in the forest exacerbates forest degradation.

Despite the degradation, Gede ruins forest remains key conservation hotspot, because; it is one of the remaining fragment of tropical coastal indigenous forest, a home to Sykes monkeys and endemic birds species of the near Arabuko Sokoke forest especially the spotted ground thrush as well tourist attraction site. There is need to rehabilitate the forest patch to ensure it continues to play critical ecological functions. The easy and cost effective way is through natural regeneration. Sykes monkeys are the key dispersal agents in the forest and regeneration and maintenance of forest structure is dependent on them. This study focused on the contribution of Sykes monkeys in seed dispersal and ultimate natural regeneration of Gede ruins forest.

1.2.14 Study area background information

The study was undertaken in Gede ruins forest. The Forest is a fragment of Arabuko Sokoke Forest ecosystem, the largest and most intact coastal forest in East Africa, and by far the largest remnant of the forests that once dominated Kenya's coastal fringe (Burgess *et al.,* 2000). It is completely enclosed by a fence and is surrounded by farmland. The ruins is overgrown with indigenous forest trees and has a high plant diversity, particularly in the over storey. It is characterized by primary forest at the southern end with close proximity and easily accessible to the community; and secondary forest at the northern part of the forest which is less accessible. Aided regeneration was undertaken in a section of the secondary forest in 1992 (Robertson *et al.*, 2002) in order to accelerate regeneration of the forest. Nonetheless, the forest still holds diverse fauna and flora.

1.3 Conceptual Framework

This study posit that forest degradation through anthropogenic disturbance can have long-term consequences on species diversity, community structure and ecosystem processes such as seed dispersal. Degradation results in small forest fragments (reduced habitat for frugivores) and consequent extirpation of frugivores (Figure 1). Seed dispersal failure as a result of decline in frugivores encourage deposition of seeds beneath the canopy of mother trees resulting to high seed and seedling mortality associated with high population of species specific pathogens and fungi. Nonetheless, remnant frugivores population can enhance natural regeneration through seed dispersal of relic trees (Figure 1). Furthermore, the relic trees act as perching areas for seed dispersers further encouraging seed dispersal, recruitment and enhanced plant diversity.

Seed dispersed by frugivores escape high density mortalities near the parent tree and allows colonization of vacant microsites in degraded forest (habitat gaps) as well as directed dispersal to suitable sites where they can germinate and establish. The seed dispersal loop (escape, colonization and recruitment) enhance regeneration of degraded and fragmented forests and restores community structure, plant population and diversity (Figure 1). This could only be achieved provided the seed plants and dispersal agents are available; and drivers of degradation are terminated.

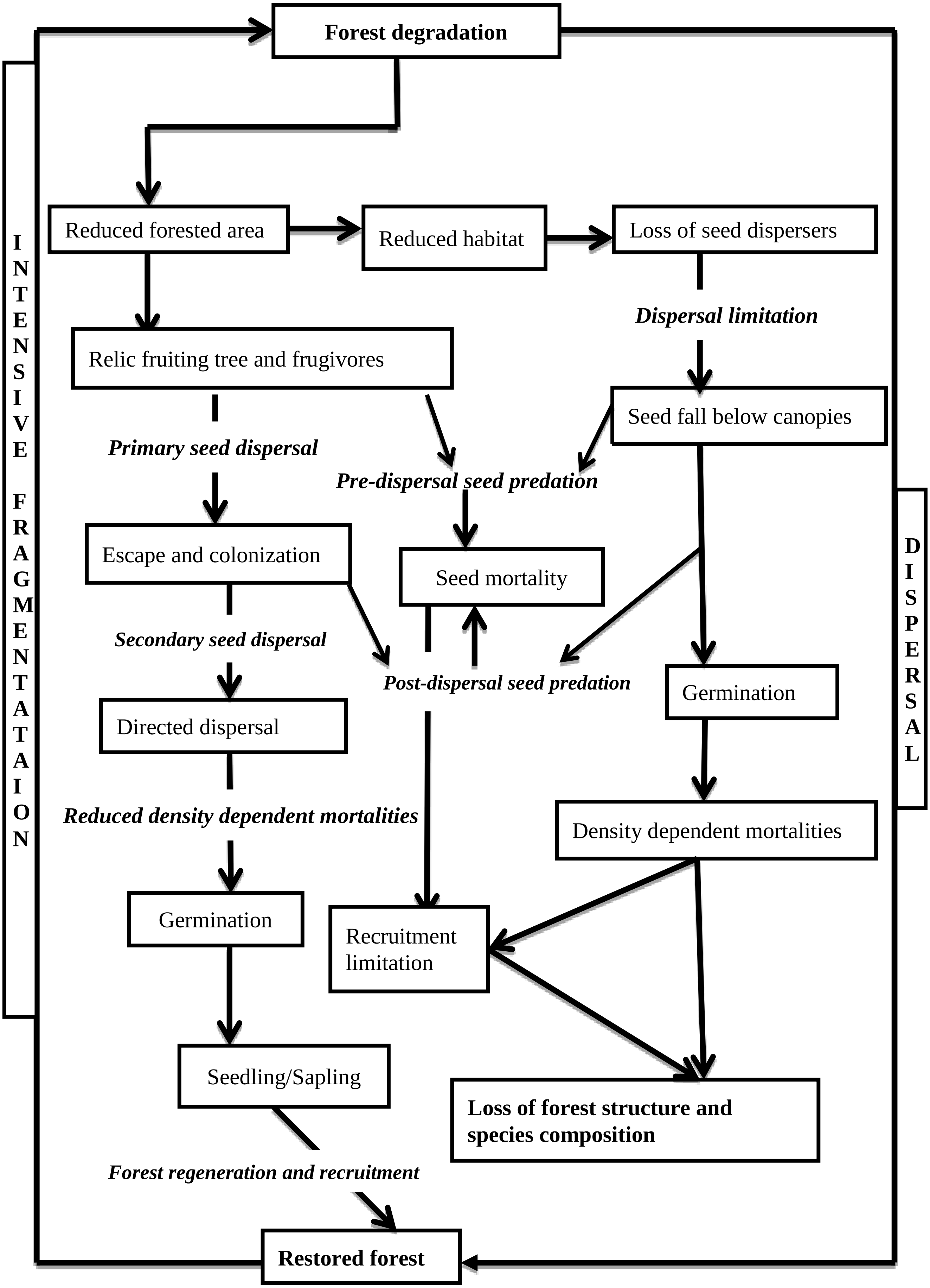

Figure 1: Conceptual framework

1.4 Justification

Gede Forest is a fragment of Arabuko Sokoke forest, but has been and continues to be degraded by anthropogenic activities through; firewood collection and illegal logging. This has created small gaps that encourage seedling recruitment. The forest is a home to several troops of Sykes monkeys which are the main seed dispersal agents in the forest.

Aided regeneration to accelerate restoration of Gede ruins forest was attempted in the secondary forest in 1992 (Roberson *et al.*, 2002). However, aided regeneration apart from being time consuming, is expensive; costs are incurred in propagating, raising and planting seedlings. It allows the introduction of new species hence reduced ecological integrity of the forest. Besides, inaccessible sites like steep terrains may be difficult to rehabilitate. Furthermore, skills are required in planting as improper planting may cause death of seedlings hence more cost for replacement may be incurred. Natural regeneration via seed dispersal and succession on the other hand is cost effective, can be employed on sites with difficult accessibility and labor is not required. Natural regeneration result in a forest that is unevenly naturally spaced and heterogeneous of high ecological integrity. Based on tradeoffs between aided and natural regeneration process, it is economical and sustainable to allow natural regeneration in the forests if seed sources and seed dispersal agents are available; if the microsites are conducive for seed germination and regeneration and if the drivers of degradation are halted.

Past studies on Sykes monkeys have been undertaken in Gede ruins. Leslie (2009), studied human primate interaction with focus on provisioned monkeys; Kiio (2009) investigated the gastro-intestinal parasites commonly occurring in free-ranging Sykes monkeys. Mureu (2009) studied the effect of provisioning on seed dispersal. Adequate information is lacking on the contribution of

Sykes monkeys to natural forest regeneration and secondary seed dispersal by dung beetles in Kenya. This study therefore aimed to assess the contribution of primates and dung beetles in natural forest regeneration and maintenance of forest structure and species composition in fragmented terrestrial tropical coastal forests through seed dispersal.

1.5 Objectives

Main objective

To determine the critical role played by Sykes monkeys (*Cercopithecus mitis albogularis)* and complimentary dispersal role of coprophagous dung beetle (*Phanaeus vindex)* in seed dispersal in Gede forest and their contribution to the natural restoration of the forest fragment.

Specific objectives

1) To determine the structure and composition of woody tree species in Gede Ruins forest fragment.
2) To determine seed dispersal by Sykes monkeys and complimentary role of dung beetles.
3) To establish the viability of seeds dispersed by Sykes monkeys in the forest.

1.6 Research Hypothesis

Sykes monkeys and dung beetles can potentially contribute to regeneration and maintenance of forest structure in Gede ruins forest through seed dispersal.

CHAPTER TWO: STUDY AREA, MATERIALS AND METHODS

2.1 Study Area

2.1.1 Location and area

This study was undertaken in Gede ruins forest. The forest is located in Coast province, Kilifi County, Malindi sub-County. It lies approximately 90 km North East of Mombasa town, 16 km south of Malindi town and about 0.5 km from Gede Centre. The Global Positioning System (GPS) position of the forest is 613027 S, 9634715 E (Figure 2). Gede ruins forest is a fragment of the previously larger Arabuko Sokoke Forest ecosystem, the largest and most intact Coastal Forest in East Africa as well as the largest remnant of the forests that once dominated Kenya's coastal fringe (Burgess *et al.*, 2000). It covers an area of approximately 44 hectares (Robertson *et al.,* 2002); and is completely enclosed by a fence and surrounded by farmlands on all sides.

2.1.2 Topography and soil

The forest lies on a flat coastal plain at an altitude of about 45 m above the sea level. The land rises gradually from the coastline to inland. The forest is characterized by coral rag soil (Matiku *et al.*, 2011) and red earth (Kirkman, 1975). The red soil also referred to as Magarini soils, are well drained and relatively infertile. The coral rag soils which underlie the forest are shallow, stony and free drained, but hold sufficient moisture to allow plant growth.

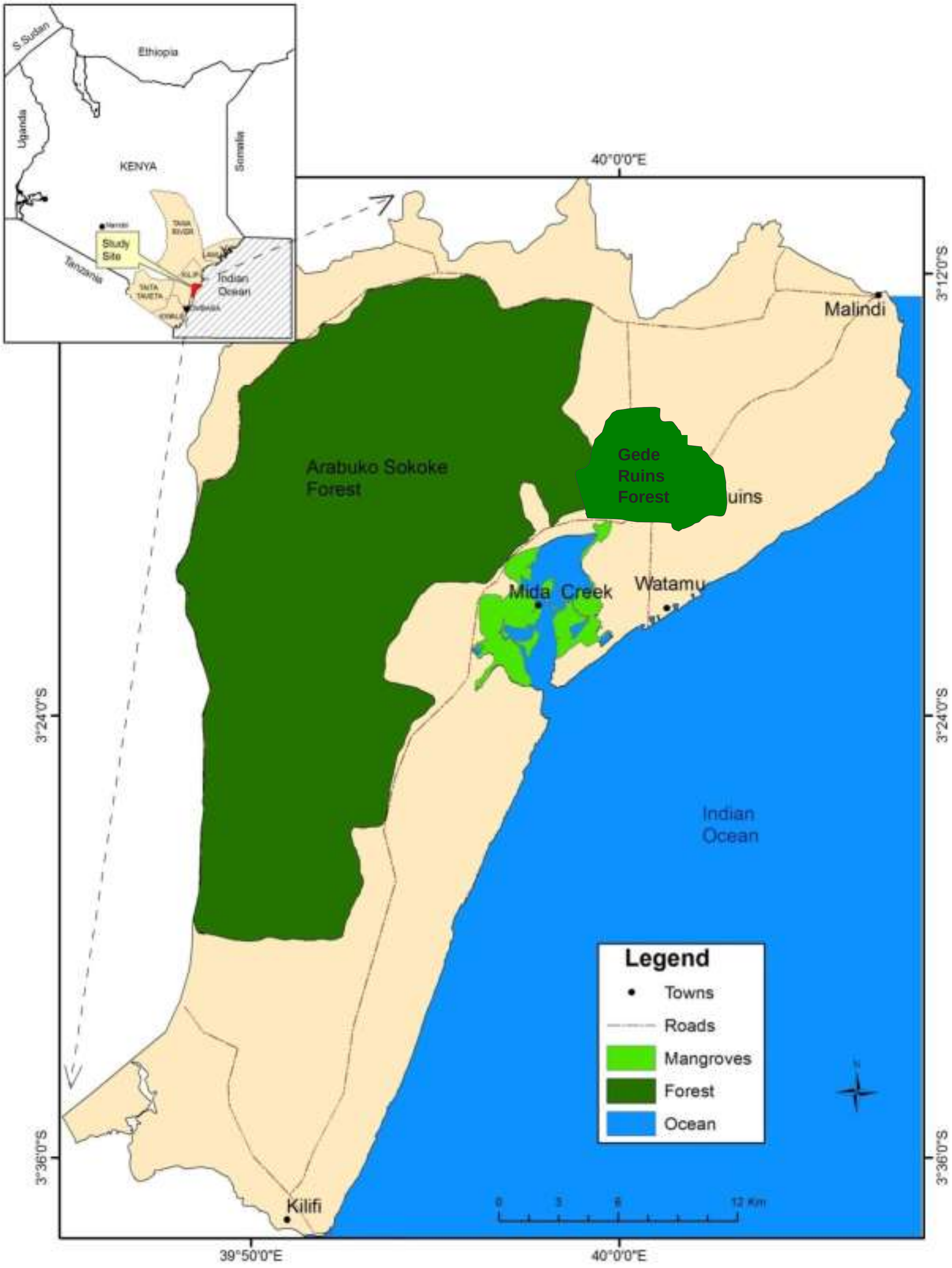

Figure 2: Location of the study site, Gede ruins forest along the Kenyan Coast

2.1.3 Rainfall pattern and temperature

The yearly rainfall cycle is bimodal with the long rains brought by south – east monsoon winds and falls in March to July. Light showers may be experienced in August and September. The short rains come in November and December during north- east monsoon winds although some showers may occur throughout the year. The remaining months from January to February are usually the hottest and driest. The Mean rainfall ranges from 600 - 1,000 Millimeter per year (mm/yr) (Matiku *et al.*, 2011). The region experiences extreme dry seasons and droughts. The mean daily temperature is 25°C. Mean evaporation can potentially be higher than rainfall which remain fairly constant throughout the year (Burgess *et al.*, 2000), consequently, there is lower rainfall with most areas being semi-arid.

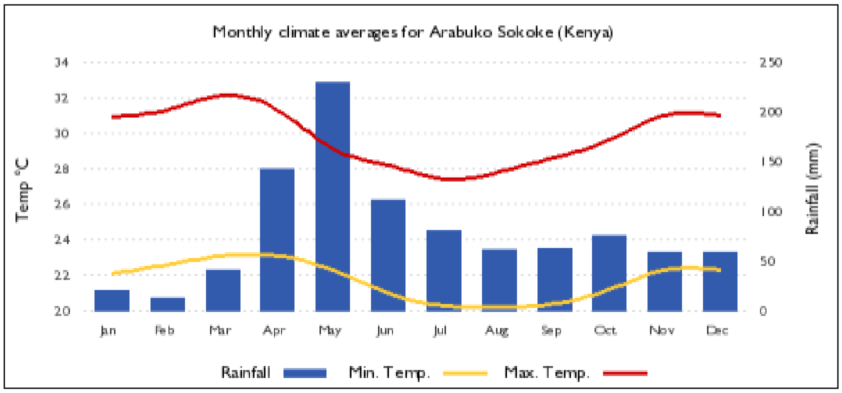

Figure 3: Mean monthly rainfall and temperature for Gede ruins forest (UNEP-World Conservation and Monitoring Center (WCMC) (2006)

2.1.4. Flora

The forest has diverse vegetation, with more than 50 indigenous tree species of commercial importance occurring. Unlike nearby Arabuko Sokoke forest with distinct vegetation types, Gede ruins is characterized by mixed tree species which is an extension of the previously mixed vegetation type of Arabuko sokoke forest. The key tree species of high economic value include

Afzelia quanzensis, Combretum schumannii, Gyrocarpus americanus and *Sterculia appendiculata*. The forest is also overgrown by *Tamarindus indica, Adansonia digitata* and *Azadirachta indica*. Generally, tree species composition resembles that of the nearby Arabuko Sokoke Forest.

2.1.5 Fauna

Gede Ruins forest harbors rich fauna. The birds assemblage is diverse, closely resembling the diversity in Arabuko Sokoke forest, and includes six globally threatened avian species: Clarke's weaver (*Ploceus golandi*), Sokoke scops owl (*Otus ireneae*), Amani sunbird (*Anthreptes pallidigaster),* Sokoke pipit (*Anthus sokokensis*), Spotted ground thrush (*Zoothera guttata)* and East Coast Akalat (*Sheppardia gunningi*) (Mureu, 2009).

The forest is also a habitat for small mammal species like Suni (*Neotragus moschatus*), bush buck (*Tragelaphus scriptus)*, endangered Golden-rumped Elephant-shrew (*Rhynchocyon chrysopygus*) (Gibbon and Rathbun, 2015) and tree squirrel (*Sciurus Carolinensis).*It is also a home for several troops of Sykes monkeys and a single ververt monkey (*Chlorocebus pygerythrus*) (Mureu, 2009).

Diverse populations of reptiles including the great plated lizard (*Gerrhosaurus major*), green mamba (*Dendroaspis angusticeps*), black mamba (*Dendroaspis polylepis*), forest cobra (*Naja melanoleuca),* and several harmless snake species inhabit the forest. Invertebrates are also present; comprising of more than 250 recorded species of butterfly (Burgess *et al.,* 2000).

2.1.6 Socio economic activities in Gede ruins forest

The forest is surrounded by arable land with main socio-economic activities being small scale farming. At the entrance of the forest is Kipepeo butterfly farm, which is a communal initiative aimed at enabling communities living adjacent to Arabuko Sokoke and Gede Ruins forests earn a living through the sale of butterfly pupae. The communities breed the unique butterflies of the Arabuko Sokoke and Gede ruins forests then export pupae abroad in exhibitions to live butterfly display museums in USA, Europe and Japan. The main aim of the project is to link conservation and socio-economic development through sustainable utilization of butterfly biodiversity in the forest for the benefit of local communities. The project further demonstrates that forests can provide alternative and additional income sources and would have greater value as intact forest than being cleared for agriculture. The project also help to diversify coastal tourism through the exhibit of live butterflies. Through this, the project provide employment and earn export revenues for Kenya. Additionally, the project support conservation education activities for protection and management of Arabuko-Sokoke Forest.

Gede ruins is also a tourist attraction site due to its historic scenic monuments of a thirteen –century stone city earning the government and local community income. Furthermore, the snake and tortoise park habiting rescued animals attract tourists.

2.2 Materials and Methods

Data collection was carried out for four months from 4thNovember 2013 to 28th February 2014 encompassing two sampling periods. The first sampling period (November – December 2014) was characterized by short rains, whereas the second sampling period (January – February 2014) was dry. The two periods were considered important for comparative seasonal studies. The rainy period coincided with peak tourism while low tourism was observed during the dry period.

2.2.1 Forest structure and woody species composition characterization

Stratified random plot sampling design was used. Forest was stratified into primary and secondary forest; the former had a relatively higher abundance of *Azadiracta indica* and *Tamarindus indica* compared to the latter. Transects were established at random locations purposively avoiding the excavated ruins (excavations were undertaken to get the artifacts for the museum). However, the distance between the transects were at least 100 m. A total of five replicate line transects were randomly established measuring 250 m long covering the whole study area, running from the edge of each forest type towards the interior (Figure 4). In secondary forest, two transects were established while three transects covered the primary forest; this is because the former covered a relatively smaller area (about 15 ha) compared to the primary forest (approximately 30 ha). Along each transect, six plots each measuring 10.0 x10.0 m were established systematically at 30 m interval. Sub-plots measuring 2.0 x 2.0 m and 1.0 x1.0 m were established nested inside the large plot for sampling of saplings and seedlings respectively.

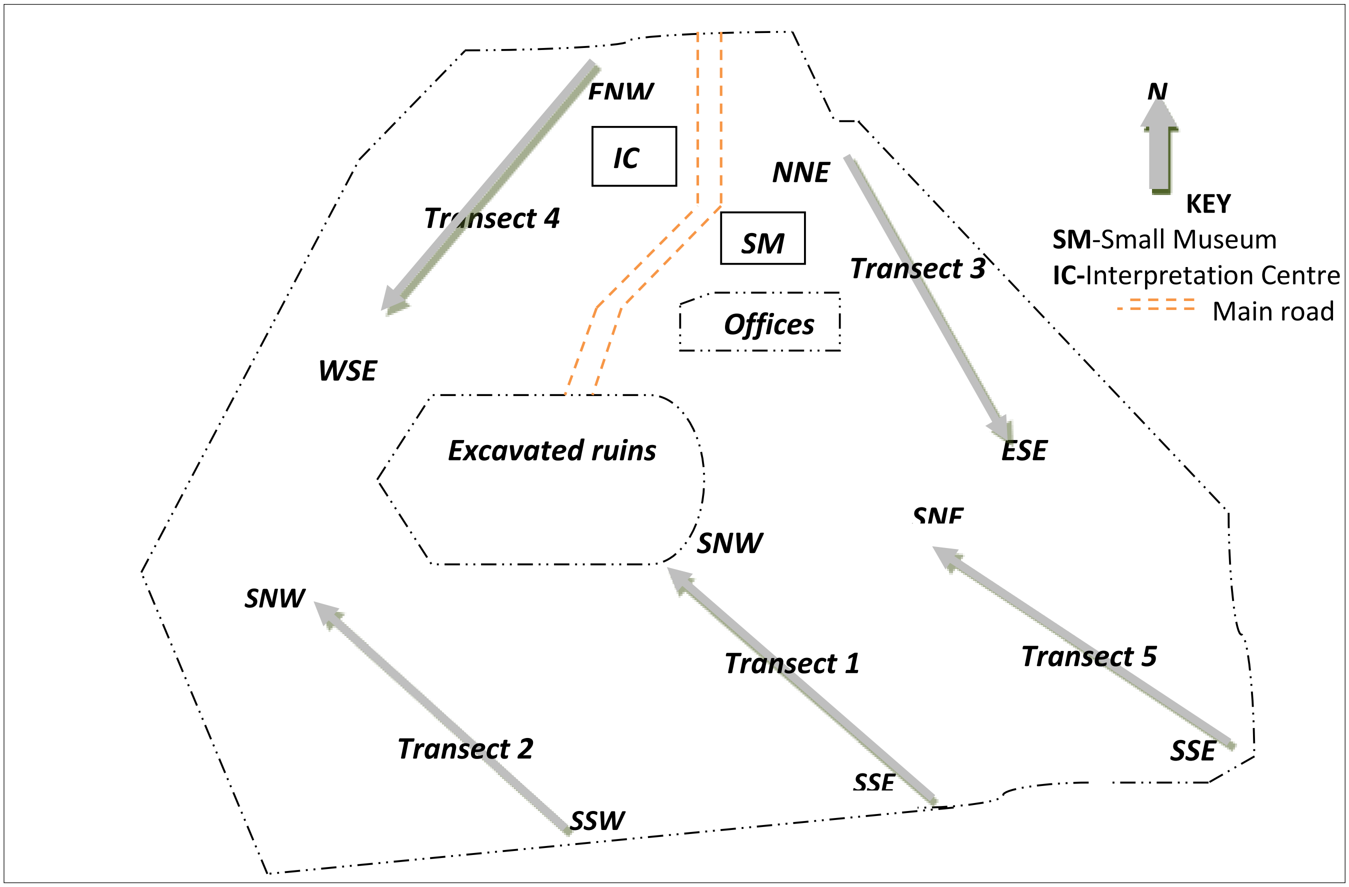

Figure 4: Sketch map showing the outlay of the transects in Gede ruins forest
Note: Transects 3 and 4 were established in secondary forest whereas 1, 2 and 5 covered primary forest

In the 1.0 x1.0 m subplot, all seedlings (first two true leaves) were enumerated by species and their height estimated using a meter rule. In the 2.0 x 2.0 m subplot, saplings (<1.5 m in height) were identified by species and height estimated using a calibrated pole. In the 10.0 x10.0 m plot, individual woody plant species; immature trees (1.5 – 3.0 m in height) and mature trees (> 3.0 m height) were identified by species and measured for height and canopy diameter. Diameter at breast height (Dbh) was measured for mature trees at 1.3 m above the ground using a diameter tape (Sykes and Lane, 1996). Height was estimated using a suunto clinometer, and to estimate canopy diameter, a tape measure was run from edge to edge of canopy with longest spread (D1); the tape measure was then again run perpendicular to the first cross-section through the central mass of the crown (D2).

The data was used to calculate the following parameters according to Cox (1990)

$$\text{Density} = \frac{\text{Total number of individuals of a species in all quadrats}}{\text{Total area of quadrats sampled}}$$

$$\text{Relative density (\%)} = \frac{\text{Density of individual of the species}}{\text{Total density of all the species}} \text{ X } 100$$

$$\text{Frequency} = \frac{\text{Number of quadrats in which the species occurred}}{\text{Total number of quadrats sampled}}$$

$$\text{Relative frequency (\%)} = \frac{\text{Frequency of the species}}{\text{Total frequencies of all the species}} \text{ X } 100$$

$$\text{Dominance} = \frac{\text{Total basal area of the species}}{\text{Total area sampled}}$$

$$\text{Relative dominance (\%)} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all the species}} \text{ X } 100$$

Importance value index (IVI) = Relative Density + Relative Frequency + Relative Dominance

The canopy diameter was used to determine canopy dominance using the formula πr^2.

Where; r = the mean radii of two distances measured from the edge to edge of the crown.

Structural Complexity of the forest was determined using complexity Index (CI) recommended for dry forest (Murphy and Lugo, 1986), calculated as the product of number of species, basal area ($m^2ha^{0.1}$), maximum tree height (m), and number of stems in 0.l ha, times 10^{-3}.

Shannon–Weiner index of diversity was calculated using the formula below (Shannon and Weaver, 1963);

$$H' = -\Sigma\, p_i \ln p_i$$

Where;

H'= Shannon index of diversity

P_i= the proportion of the i^{th} species ($p_i = n_i / N$, n_i is the total number of i^{th} species sampled

N = the total number of all the tree species sampled.

The vegetation data was also used to calculate Morisita's index of dispersion using the following formula (Morista, 1959);

$$Id = n\,(\sum X^2 - N)/\, N\,(N - 1)$$

Where;

n = total number of plots

X = number of individuals of one species in a single plot

$\sum X^2$= sum of all values of X^2

N = total number of individuals in all plots.

The data collected on seedlings and saplings was used to determine the regeneration of the forest in terms of density and diversity of the regenerates.

2.2.2 Estimation of seed dispersal by Sykes monkeys and dung beetles

2.2.2 (a) Selection of Sykes monkey groups for study

Diurnal seed dispersal by Sykes monkeys inhabiting the Gede ruins forest was studied. Two troops of previously habituated monkeys were chosen for the study. One group was provisioned with food by tourists while the other was free ranging. The free ranging group comprised of 32 individuals; 15 adult females, 16 juveniles and 1 adult male. The provisioned group, on the other hand, consisted of 47 individuals; 14 adult females, 32 juveniles and an adult male.

2.2.3 Seed rain estimation

Seed rain was sampled below the canopies of tree species that were predominantly dispersed by Sykes monkeys using seed traps (Chapman and Chapman, 1996; Goodman and Ganzhorn, 1997). Focal trees were randomly selected for placement of the seed traps. The traps used consisted of rectangular mosquito nets measuring 80.0 ×130.0 cm; the trap area was, therefore, approximately 1.04 m^2.

2.2.3 (a) Selection of study trees and placement of seed traps

The criterion of selecting the focal trees was based on: phenology where fruiting trees were selected. The selected tree was at least 100 m radius from the nearest fruiting conspecific to decrease the effect of overlapping seed shadows. It was important that the selected focal tree was within the ranging areas of the study monkey troops. Further, the selected fruiting tree was forming a major diet of the Sykes monkeys as observed during feeding and from the seeds extracted from fecal samples. The following trees were selected for the placement of seed traps; *Tamarindus indica, Diospiros squarrosa, Combretum schumannii, Azadiracta indica, Mimusops obtusifolia* and *Lecaniodiscus fraxinifolius.*

The traps were set just before fruits were mature and were left in place until all the fruits had been removed from the tree. Two seed traps were set per each selected focal tree. One seed trap was placed below the crown of the focal tree, while another was set 5.0 m away from the edge of the canopy; this was replicated for the six selected trees. The traps were raised approximately 0.8 m above the ground to prevent predation of seeds and fruits collected on the seed traps.

2.2.3 (b) Collection of seed trap contents

Seed trap contents (fecal clumps, dropped fruits and spat seeds) were removed daily to prevent loss of trap contents by external factors. Dropped fruits hereby implied fruits that escaped mainly from the monkeys while feeding or dropped due to shaking of branches by the Sykes monkeys when they came to feed and not as a result of natural see fall. Spat seeds on the other hand referred to seeds spat by monkeys after removing the pulp (cheek pouching). Fecal clumps referred to dung defecated on the seed traps by the Sykes monkeys while foraging or resting on tree branches.

Fecal clumps collected were washed through running tap water and their seed contents identified by species and counted. Similarly, spat seeds were identified by species and counted. Seeds were mechanically extracted from the dropped fruits and counted. The extracted seeds from the seed trap contents were recorded as either being whole (undamaged to the human eye or had shallow scratches) or destroyed (contain visible evidence of deep bites or occur in species identifiable pieces).

The data collected was used to determine the density of tree seeds dispersed via seed rain. The data was also used to determine seed handling (destroyed vs. whole) by Sykes monkeys during feeding.

2.2.4 Estimation of seed dispersal via egestion

2.2.4 (a) Fecal sample collection

Two study groups of previously habituated monkeys (provisioned and free ranging) were followed separately on different days. A monkey was chosen and observed for thirty minutes; after which another was chosen; a stop watch was used in timing. The aim was to enhance chances of collecting fecal samples as well as diversify fecal clumps from the entire troop members. Each time the focal animal defecated, the fecal clump was collected. The dung dropped by a monkey which was not being followed but was observed as it defecated was also collected. Moreover, intact fecal samples from other individuals ranging in the same group as the focal animal were collected opportunistically to add-on to the fecal samples collected during observations. Each independent fecal sample was put in a separate plastic bag, differently labelled and kept for seed extraction.

2.2.4 (b) Fecal seeds extraction

At the end of each sampling day, each fecal sample was thoroughly mixed with water and rinsed exhaustively through running tap water using a 1.0 mm sieve (Julliot and Sabatier, 1993; Stevenson, 2000). All seeds remaining in the sieve were collected, counted and identified by species. The presence of very small seeds such as *Ficus spp* was noted as they could not be counted since they occurred in very large uncountable numbers.

Extracted seeds were visually examined for damage and coded as either whole (undamaged to the human eye or had shallow scratches) or destroyed (contain visible evidence of deep bites or occur in species identifiable pieces). The seeds were then dried between filter papers and later in the sun and stored for germination trials.

The data collected on seed dispersal via egestion was used to determine the mean number of fecal samples containing seeds and average number of seeds per fecal sample for comparison between the provisioned and the free ranging group as well as between the two sampling periods (rainy and dry periods).

2.2.5 Seed processing by dung beetles

Each time the focal monkey defecated, a stop watch was started. The dropping was observed and the time taken for the first dung beetle to attack the dung pat was recorded. The dung beetles were observed as they rolled the dung pat and individuals were followed until they abandoned the dung ball on the surface or burrowed it. The distance the dung beetle(s) moved the dung ball away from the point of deposition was measured using a meter rule. For those dung balls which were buried, depth of burial was measured using a 30.0 cm ruler. Some dung balls left on the surface and those burrowed were marked and monitored weekly for nine weeks for seed germination. Other dung balls were collected and put in polythene bags, clearly labeled and later washed through running water to obtain the seeds.

The data collected was used to determine the mean time taken by the dung beetles to attack the dung, the mean distance the dung balls were rolled away, the mean depth dung balls were burrowed, the tree species secondarily dispersed by the dung beetles as well as the germinability of seeds dispersed by dung beetles.

2.2.6 Viability of Sykes monkey dispersed seeds

Seeds dispersed by Sykes Monkeys were categorized as ingested, spat and dropped fruit seeds which had their seeds tested for viability. Ingested seeds were obtained from fecal samples, whereas spat seeds were obtained from seed traps. Dropped fruits seeds from the seed traps which acted as control for the experiment were obtained by mechanically removing the fruit pulp to reduce/eliminate potential inhibition effects of fruit pulp on seed germination. Dropped fruit seeds were used instead of mature seeds picked directly from the tree canopies; because primates preferentially select healthy fruits with viable seeds in the forest canopy. Fruits gathered from the forest floor or tree canopy for germination tests may have been less fit than fruits eaten by primates and less likely to germinate (Poulsen *et al.*, 2001).

Germination trials were conducted using forest top soil after removal of humus. The soil was sterilized through solarization (*worldagroforestry.org/NurseryManuals/Research/Hygiene, September 2015)* to kill any pathogenic microorganisms in the soil that would otherwise attack the seeds and or seedlings. The soil was then sieved using 3.0 mm sieve to ensure seeds that might be present in the soil were eliminated. The soil was then filled in the nursery potting tubes.

A total of 16 tree species had their seeds tested for germination. Five seeds of the same species were used per treatment (i.e. 5 ingested seeds, 5 spat seeds, 5 dropped fruit seeds per species). Seeds of the same species per treatment were planted in each nursery potting tube. Seeds were planted at approximately 1.0 cm depth on the same day in order to standardize procedures to allow for comparison of seedling emergence. The seeds were watered regularly and monitored daily for nine weeks for penetration of the seed coat by the radicle. Germination of a seed was defined as the moment the radicle appeared (Knogge and Heyman, 2003). The data from the experiment was used to determine germination success (germinated seeds/total seeds planted) and latency period (time taken between sowing and germination) of the seeds across the treatments.

2.3 Data analysis

Prior to analysis, necessary data sets were subjected to Sharpiro-Wilk test for normality, non-normal data was transformed and analyzed using appropriate parametric statistics. All statistical analyses were evaluated at $p < 0.05$ level of significance. Statistical analyses were performed using GENSTAT and PAST program soft wares.

Difference in density, basal area, canopy area and diversity between primary and secondary forest was determined using t-test. To compare density of seeds dispersed via seed rain below the crowns and 5 metres away from the edge of the canopy, t test was used. Analysis of Variance (ANOVA) was done to determine differences in seed dispersal mechanisms (egestion, spat and dropped seeds) via seed rain. Analysis of variance was also used to determine variation in density of seeds dispersed below the canopies of focal trees and five metres away from the edge of the canopies by conspecific and non-conspecific trees. Tukey multiple comparison test was adopted to separate means with significant effects.

Chi-square tests were performed to determine the mean number of fecal samples containing seeds between the two groups of study monkeys as well as between the two sampling periods. To test the difference in average number of seeds per fecal sample between the free ranging and provisioned group across the two sampling periods (dry and rainy), ANOVA was conducted after logarimithic transformation of data; $x' = \text{Log}(x+1)$ and Tukeys multiple comparison performed to delineate the means with significant difference. Chi-square test was done to determine mean number of seeds destroyed or whole (seed handling).

Variation in time taken to attack the dung, depth the dung ball was burrowed and distance dung ball was moved between the two sampling periods was tested using t- test. To test germination success and latency periods across the treatments (ingested, spat and dropped seeds) chi square test and ANOVA were undertaken.

CHAPTER THREE: RESULTS

3.1 Woody species composition and structure characterization

3.1.1 Woody species composition

Species richness

Within the study area, a total of 1029 trees belonging to 63 tree species were sampled and identified. Species richness in primary forest was 48 (Appendix 1) while in the secondary forest, it was 41 (Appendix 2). For the regenerates, 156 seedlings were encountered belonging to 13 tree species. In primary forest, seedlings species richness was 8 (Appendix 3) compared to 6 seedling species encountered in secondary forest (Appendix 4). On other hand, the total number of saplings was 717 representing 36 different tree species. Saplings richness was 27 in primary forest (Appendix 5), whereas in secondary forest, 18 species were identified (Appendix 6).

Dominant tree species in the forest

The tree species dominating primary forest which also formed a key diet of the Sykes monkeys were *Lecaniodiscus fraxinifolius, Diospyros squarrosa, Tarrena supra-axilaris* and *Combretum schumannii* as exhibited by their respective relative frequencies (Appendix 1). Although *Ficus bussei* and *Mimusops obtusifolia* were the least common species in primary forest (Appendix 1), they formed a major dietary source for the Sykes monkeys. *Trichilia emetica*, *Lecaniodiscus fraxinifolius*, *Azadiracta indica* and *Grewia plagiophylla* had the highest relative frequencies in secondary forest (Appendix 2). Some of the major tree species that Sykes monkeys depended on for food but were least dominant in secondary forest included *M. obtusifolia* and *C. schumannii* (Appendix 2).The most common seedlings and saplings species in primary forest were *C. schumannii* and *L. fraxinifolius* as shown by their relative frequencies (Appendices 3 and 5). Secondary forest was mostly dominated by seedlings and saplings of *A. indica* and *L. fraxinifolius* (Appendices 4 and 6).

Lecaniodiscus fraxinifolius, *Adansonia digitata*, *Ficus bussei* and *Combretum schumannii* which were the main food tree species for the Sykes monkeys showed high importance value index in primary forest (Appendix 1). On the other hand, *Azadiracta indica*, *Tamarindus indica*, *Trichilia emetica* and *Lecaniodiscus fraxinifolius* had the highest important value index in secondary forest (Appendix 2).

Species Diversity

Tree diversity in the forest was generally high (H`=3.9) indicating a forest in stable state. The diversity difference between the two forest types was negligible (Primary forest H′=3.5; Secondary forest H′=3.2). Similarly, the diversity of seedlings did not vary in the forest; Secondary forest H′= 1.3; Primary forest H′= 1.2. However, sapling diversity was higher in secondary forest (Primary forest H′= 1.8, Secondary forest H′ = 2.2).

3.1.2 Key tree species that formed Sykes Monkeys' diet

The key tree species which formed a major diet of the Sykes monkeys in Gede ruins forest were *Ficus bussei*, *Combretum schumannii*, *Lecanodiscus fraxinifolius*, *Azadiracta indica*, *Tamarindus indica* and *Diospyros squarrosa* as per the tree seed species extracted from fecal samples (Appendix 8) and field observations made where the monkeys were observed foraging on their fruits. *Lecanodiscus fraxinifolius* (6.6 ± 1.1 seedlings m^{-2}), *A. indica* (4.7 ± 1.3 seedlings m^{-2}), *C. schumannii* (5.1 ± 0.7 seedlings m^{-2}) and *D. squarrosa* (2.0 ± 0.3 seedlings m^{-2}) showed a stable population structure in the forest with high densities of regenerates and relatively few mature trees, indicating that these species have good regeneration capability (Figure 5). *Ficus bussei* and *T. indica* showed lack of regeneration in the forest with saplings and seedlings totally being absent. Additionally, immature trees were also lacking for *F. bussei* (Figure 5).

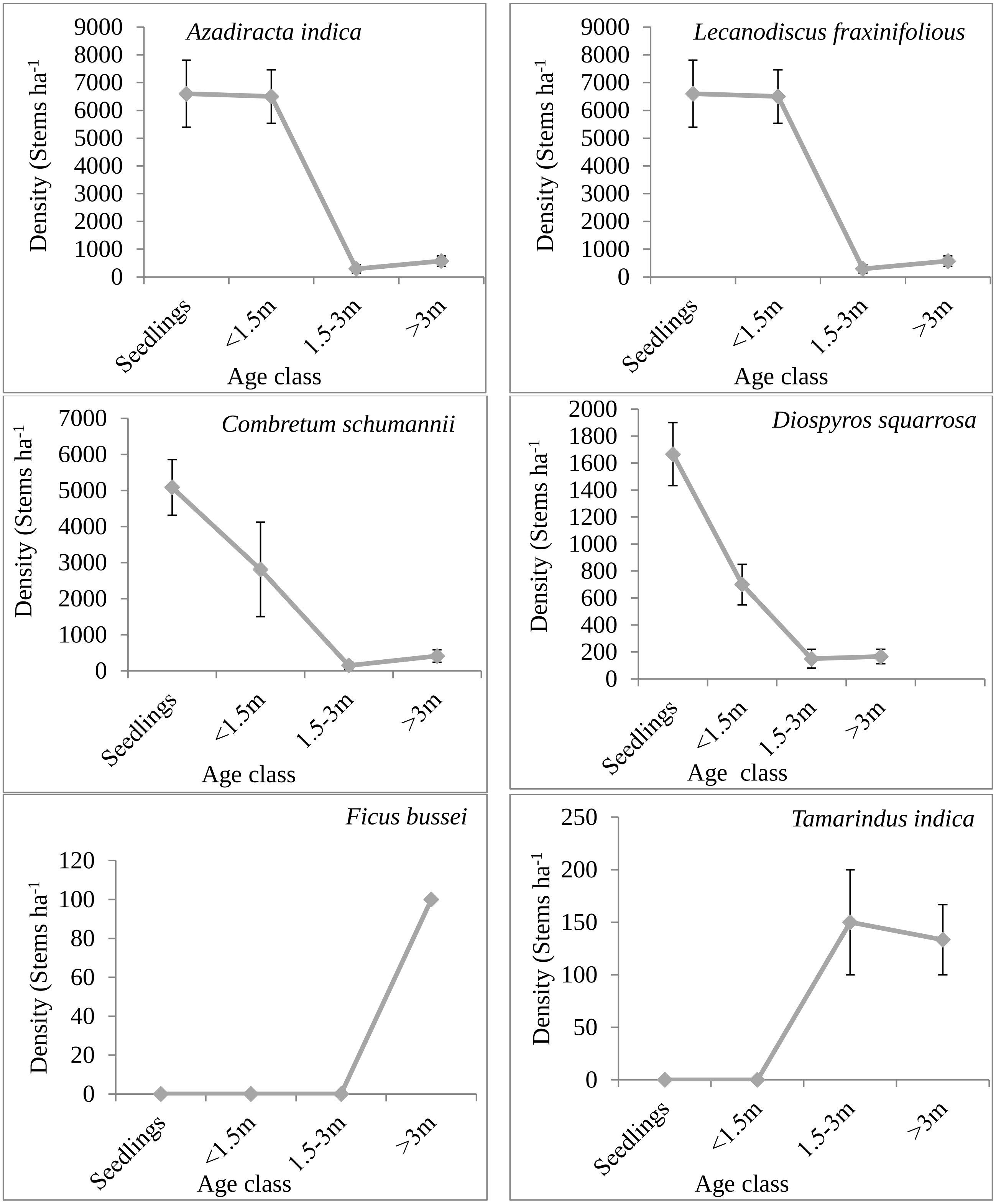

Figure 5: Mean density (±SE) per age class of key tree species dispersed by Sykes monkeys in Gede ruins forest

3. 1.3 Forest structure characterization

Density, Age class structure, Canopy structure, basal area and spatial distribution

Density

Tree density was generally high in both forest types with over 3000 stems ha^{-1}. Although not significantly different, secondary forest had slightly high tree density of 3967 stems ha^{-1} compared to 3072 stems ha^{-1} in primary forest; ($t = 0.57$, $df = 88$, $p > 0.05$). In primary forest, mature trees (>3 m height) significantly existed in higher densities (2000.0 ± 215.3 stems ha^{-1}) than immature trees (1.5-3 m height) (1055.6 ± 128.1 stems ha^{-1} ; $t = 3.342$, $df = 17$, $p < 0.05$). In secondary forest, although not significant, immature trees existed in higher densities (1054.2 ± 304.3 stems ha$^{-1)}$ than mature trees (787.4 ± 227.3 stems ha^{-1}); $t = 0.577$, $df = 11$, $p > 0.05$).

Significant difference was not observed in mean density of seedlings between the two forest types (primary forest density = 6.8 ± 1.7 seedlings m^{-2}, secondary forest density = 4.02 ± 0.8 seedlings m^{-2}; ($t = 1.63$, $df = 18$, $p > 0.05$). The results indicate that regeneration was occuring equally in the forest. Equally, significant variation was not observed in sapling density in the forest (primary forest 2521.4 ± 173.3 saplings ha^{-1}; secondary forest 2434.2 ± 161.1 saplings ha^{-1}).

The tree density of tree species the monkeys relied for food and subsequent seed dispersal varied in the forest. Some of the key species which formed a diet of the Sykes monkeys that exhibited high density were; *Lecanodiscus fraxinifolius* (696.1 ± 93.9 stems ha^{-1}), *Combretum schumanii* (400.0 ± 88.2 stems ha^{-1}), *Azadirachta indica* (360.0 ± 79.2 stems ha^{-1}), and *Diospyros squarrosa* (171.4 ± 36.0 stems ha^{-1}). While *T. indica* (166.7 ± 33.3 stems ha^{-1}) and *F. bussei* (*1*00.0 ± 0.0 stems ha^{-1}) equally formed key diet of the monkeys, they existed in relatively low densities in the forest. In the regenerating class, *L. fraxinifolius* (6.6 ± 1.1 m^{-2} seedlings), *C. schumanii (*5.1 ± 0.7

m^{-2} seedlings and *A. indica* (4.7 ± 1.3 m^{-2} seedlings) existed in high densities. Similarly for the saplings, *L. fraxinifolius* (6500.1 ± 962.8 saplings ha^{-1}), *A.indica* (2812.5 ± 309.1 saplings ha^{-1}) and *C. schumanii (*928.6 ± 129.6 saplings ha^{-1}) occurred in high densities in the forest.

Age class structure

In general, both forest types were characterized by uneven aged classess and showed reversed J-shaped population curve with a large density of young individuals (seedlings and saplings) and relatively few old trees a characteristic of a regenerating forest (Figure 6).

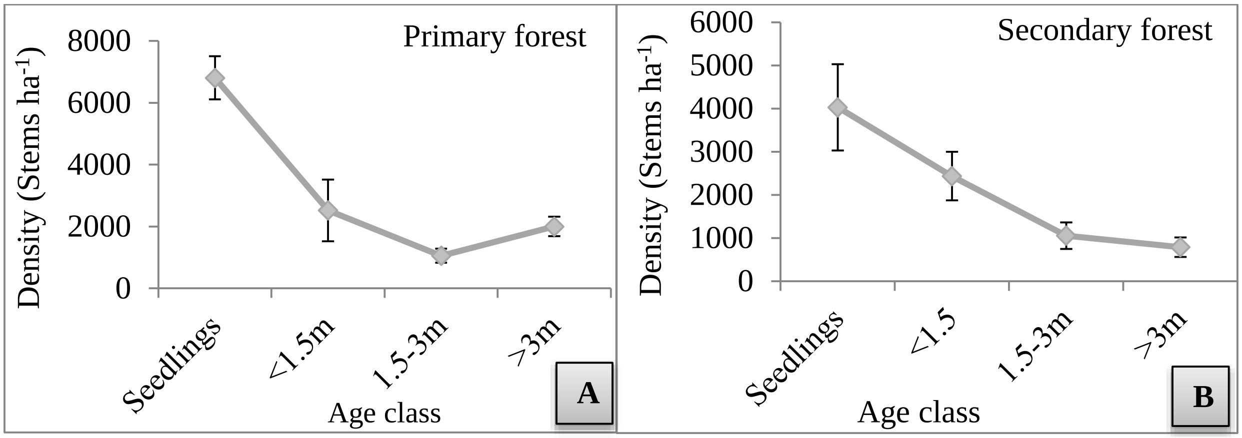

Figure 6: Mean tree density (±SE) per age class for primary (A) and secondary (B) forest

Canopy structure

Primary forest exhibited significantly high mean canopy cover of 64.5 ± 3.2 $m^2\ ha^{-1}$ than secondary forest which had a mean canopy cover of 39.3 ± 2.1 $m^2\ ha^{-1}$ ($t = 3.329$ $df = 475$, $p<0.05$). Although different tree species have different growth forms in terms of canopy spread, the key species that monkeys depended on for food in primary forest were *F. bussei* and *C. schumannii*; had mean canopy cover of 79.3 ± 0 $m^2\ ha^{-1}$ and 56.1± 4.1 $m^2\ ha^{-1}$ respectively. On the other hand, canopy cover in secondary forest was largely contributed by *A. indica* (41.3 ± 10.9 $m^{-2}\ ha^{-1}$) and *T. indica*

(68.6 ±16.9 m^{-2} ha^{-1}). Although *F. bussei* and *T. indica* had the lowest densities in the forest, they exhibited the highest canopy cover (Figure 7).

The percentage canopy cover in primary forest was 140.4% while in secondary forest had a canopy cover of 70.1 %. This shows that primary forest is characterized by wide spread inter locking dense canopies suggesting high food resources compared to secondary forest which had medium dense canopy. Generally, the key tree species which were a diet to Sykes monkeys that contributed significantly to total canopy cover included; *T. indica* (13.0%), L. *fraxinifolious* (12.9%), *A. indica* (11.7%), *C. schumannii* (6.2%), F. *bussei (*3.4%), and *D. squarrosa* (1.0%).

Basal area

Trees in primary forest exhibited significantly high mean basal area of 23.5 ± 9.5 m^2ha^{-1} compared to10.8 ± 3.7 m^2ha^{-1}in secondary forest (t =3.188, df = 33, p<0.05). Despite *D. squarrosa* and *L. fraxinifolius* having high densities in the forest, they had slightly lower basal and canopy dominance (Figure 7).

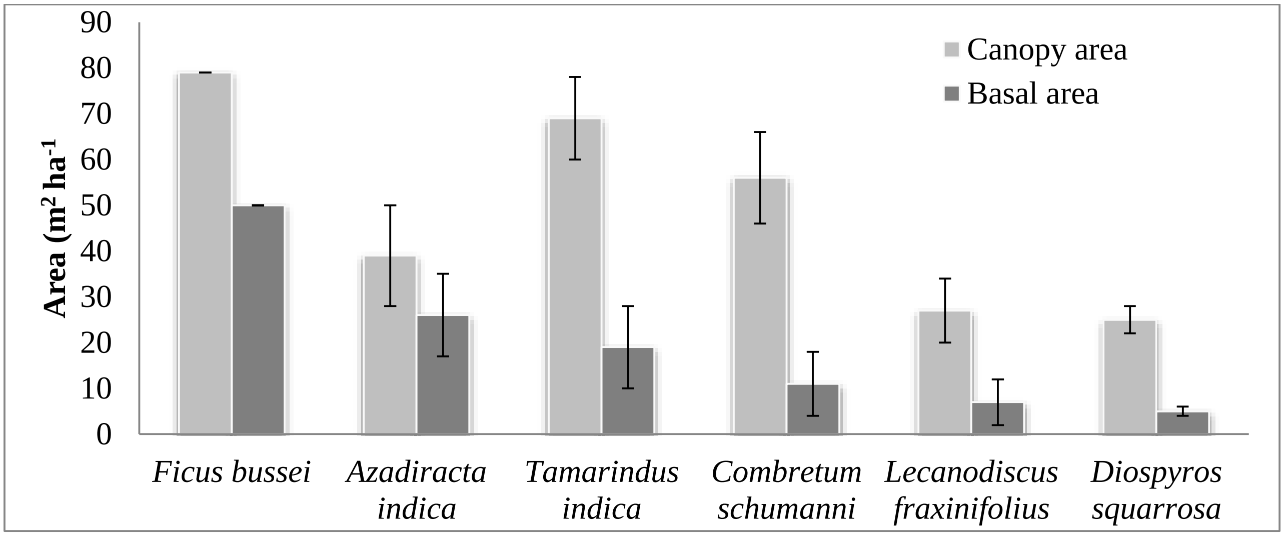

Figure 7: Mean basal area (±SE) and canopy cover (±SE) of key tree species dispersed by Sykes monkeys for both primary and secondary forest

Spatial distribution

The dispersion index is a measure of trees' distribution in the forest which can either be clumped, random or uniform. The Primary forest had a dispersion index of 1.8 compared to 1.3 in secondary forest. Generally, the forest(s) exhibited a clumped dispersion, since dispersion index was greater than one. This implies that aggregated seed dispersal could be occurring in the forest. To examine whether the dispersion index values were significantly different from one in order to reach correct conclusion, chi square test revealed that the values did not deviate significantly from one suggesting a random dispersion; therefore seed dispersal by Sykes monkeys was more random than clumped (primary forest $\chi^2 = 39.92$, df = 47, $p>0.05$, secondary forest $\chi^2 = 33.391$, df = 40, $p>0.05$). Complexity index in primary forest was higher (26.8) compared to a moderate complexity index of 10.7 for the secondary forest as described by Murphy and Lugo (1986).

A summary of forest structure and species characterization in Gede ruins forest is presented in table 1.

Table 1: Summary of primary and secondary forests structure characterization in Gede ruins forest

Indicators	**Primary forest**	**Secondary forest**	**P**
Tree density (stems ha^{-1})	3072	3967	>0.05
Seedling density(seedlings m^{-2})	6.8± 1.7	4.02± 0.8	>0.05
Sapling density(saplings ha^{-1})	2521.4 ± 173.3	2434.2 ± 161.1	>0.05
Basal area (m^{2}ha^{-1})	23.5± 9.5	10.8 ± 3.7	<0.05
Tree Diversity (H′)	3.5±0.1	3.2±0.1	>0.05
Seedling diversity	1.2±0.06	1.3±0.3	>0.05
Sapling diversity	1. 8±0.4	2.0±0.2	<0.05
Canopy diameter(m^{2}ha^{-1})	64.5 ± 3.2	39.2± 2.1	<0.05
Percent canopy coverage	140.4	70.1	
Dispersion index	1.8	2.0	<0.05
Complexity index	26.8	10.7	

3.2 Sykes monkey and dung beetle seed dispersal

3.2.1 Seed rain estimation

Sykes monkeys dispersed seeds of 14 tree species via seed rain. Beneath the canopies of focal trees, 11 different tree species were dispersed whereas away from the canopies, 12 tree species had their seeds dispersed (Appendix 7). This denotes that Sykes monkeys consume and disperse array of fruit trees.

The mean density of seeds dispersed through seed rain during the four months of study was 17.7 ± 2.4 seeds m^{-2}. Analysis of Variance test showed that significant variation existed among dispersal mechanisms (egested, spat and dropped fruits) via seed rain ($F_{2,174}$, = 7.231, $p<0.05$). The seeds dispersed through dropped fruits significantly contributed to seed rain followed by spat seeds. Seed dispersal through egestion contributed minimally to seed dispersal via seed rain as shown in Table 2.

Table 2: Seed dispersal mechanisms through seed rain in Gede ruins forest

Seed dispersal mechanism	**Mean density of seeds (seeds m^{-2})**	**N**
Egestion	1.2 ± 0.4^{a}	59
Spat	$30. \pm13.3^{b}$	59
Dropped	78.60 ± 33.2^{c}	59

Note: Means denoted by the same superscript letter show no significant difference according to Tukeys post hoc test

Significant mean number of seeds were dispersed beneath the canopies of focal trees than 5 metres from the edge of the canopies; (beneath; 20.7 ± 3.2 seeds m^{-2}; 5 metres away; 2.9 ± 0.8 seeds m^{-2}, t = 2.7, df = 44, $p<0.05$). Majority of the seeds collected from the seed traps were significantly contributed by conspecific trees via the high deposition of seeds beneath their canopies (37.3 ± 4.03 seeds m^{-2}, $F_{3, 232}$ = 5. 522, $p<0.05$, Table 3). Seed dispersal through seed rain was contributed minimally by non-conspecific tree species (Table 3). However, variation did not exist in amount of seed rain contributed by non-conspecific trees below and away from the canopies and by conspecific tree species away from the crown edges (Table 3).

Table 3 : Summary of mean density seeds dispersed below the canopies and five metres away from the canopies of focal trees by conspecific and non-conspecific tree species

Seed dispersal	**Mean density (seeds m^{-2})**	**N**
Below the canopies by conspecific	37.3^{b} ±4.03	59
Away from the canopies by conspecific	2.9^{a} ±0.2	59
Below the canopies by non-conspecific	2.0^{a} ±0.5	59
Away from the canopies by non-conspecific	0.8^{a} ±0.6	59

Note: Means denoted with the same superscript letter along the column are not significantly different according to Tukeys test

3.2.2 Analysis of quantity and quality of seeds dispersed by Sykes monkeys

During the study, a total of 701 fecal clumps samples were collected; (free ranging, N = 317; provisioned group, N = 384). Seeds were present in 60.5% of the total fecal samples collected. Generally, fecal clumps containing seeds was significantly higher in free ranging monkeys; 65.7% compared to the provisioned group 46.4% ($\chi^2 = 36.864$, df = 23, $p<0.05$). When presence of seeds in fecal samples were compared between the two sampling periods (rainy and dry periods), fecal clumps collected during rainy period had significantly higher percentage containing seeds (rainy period; 65.8%, dry period; 32.9%, $\chi^2 = 43.933$, df = 23, $p<0.05$).

The percentage of fecal samples containing seeds showed no significant difference between the two groups during the dry period (free ranging dry period; 35.9%, provisioned dry period: 30.7% ($\chi^2 =17.4911$, df = 23, $p>0.05$). However, significant variation in fecal samples containing seeds between the study groups was observed during the rainy period (Free ranging rainy period: 88.3%, Provisioned rainy period: 40.1 %, ($\chi^2 = 23.25$, df = 23, $p<0.05$).

The number of seeds in a fecal sample ranged from (0-67 seeds for free ranging group and 0-26 seeds for provisioned group). The number of seeds extracted from the free ranging group was higher (1,095) belonging to 28 tree species compared to 817 seeds collected from the provisioned group belonging to 20 tree species (Appendix 8). Significant difference existed in the number of seeds per fecal sample between the two study groups (Free ranging 3.5 ± 0.4, Provisioned, 2.1 ± 0.2 $\chi^2 = 38.341$, df = 23, $p<0.05$). Generally, rainy period showed significantly higher number of seeds per fecal sample of 4.1 ± 0.6 seeds, compared to 1.6 ± 0.2 seeds per fecal sample exhibited during dry period ($\chi^2= 42.581$, df = 23, $P<0.05$).

Average number of seeds per fecal sample was log transformed and Analysis of variance undertaken to determine the difference in average number of seeds per fecal sample between the two groups across the two sampling periods. The average number of seeds per fecal sample in the free ranging group during the rainy season was significantly higher compared to the other treatments (free ranging dry period, provisioned both rainy and dry periods, $F_{3,44} = 6.59$, $p<0.05$, Table 4). During dry period, mean number of seeds per fecal sample was not significantly different between the two groups of monkeys $F_{3, 44} = 6.59$, $p<0.05$, Table 4).

Table 4: Mean number of seeds per fecal sample between the two groups during the dry and rainy season

Troop	**Transformed mean number of seeds per fecal sample**	**N**
Free ranging	Rainy period; $0.7^{b}\pm0.09$	12
	Dry period; $0.5^{a}\pm0.04$	12
Provisioned	Rainy period; $0.5^{a}\pm0.03$	12
	Dry period; $0.4^{a}\pm 0.06$	12

Note: Means denoted with the same superscript letter are not significantly different according to Tukeys post hoc test following logarimithic transformation x'=Log (x+1)

3.2.3 Complimentary role of dung beetles to regeneration of forest

The dung beetles rolled away the dung ball, singly or as a pair or sometimes even more than two individuals. The percentage of the dung balls abandoned on the surface was 4.7% while 95.4% was burrowed. The seeds were observed being buried in litter material rather than being buried deep in the soil. Of the burrowed dung balls that were collected for extraction of seeds, 8.7% contained seeds mainly from *Ficus spp*.

The mean distance dung balls were rolled away was 92.5 ± 5.1 cm from the point of deposition. Although the mean distance dung balls were rolled away was slightly higher during the rainy period, differences were not significant, (rainy period mean distance; 96.6 ± 7.4 cm, Dry period mean distance; 88.4 ± 7.2 cm, $t = 0.484$, $df = 62$, $p > 0.05$).

The dung beetles burrowed the dung balls at a mean depth of 1.5 ± 0.1cm below the forest litter. Similarly, the depth dung balls were burrowed showed insignificant variation between the rainy and dry period; rainy mean depth = 1.5 ± 0.1cm and dry periods mean depth= 1.5 ± 0.2cm, $t = -0.16$, $df = 62$, $p > 0.05$). This suggests that seasonality does not affect the activity of dung beetles in terms of distance dung ball is rolled away as well as the depth it is burrowed.

The mean time taken by the beetles to attack a dung pat from the time of dung deposition was 65.4 ± 2.3 seconds. They took significantly less time to attack during rainy period; 56.6 ± 1.8 seconds; compared to dry period; 74.4 ± 4.0 seconds, $t = -4.429$, $df = 62$, $p < 0.05$), an indication that dung beetles are more active during the rainy seasons. Of the 30 dung balls which presumably contained seeds of *Ficus spp* that were monitored weekly for a period of ten weeks showed no germination of seeds.

3.2.4 Seed handling by Sykes Monkeys

Seed handling herein refer to the seeds that were either destroyed or were whole. During feeding, the monkeys did not cause significant damage to the seeds (mean number of spat seeds destroyed 3.1± 0.4, mean number of whole spat seeds 12.4± 1.9 $\chi^2 = 39.2761$, df = 25, $p < 0.05$). Of the seeds extracted from the fecal samples, 98.5% had no observable damage. The results showed that Sykes monkeys cause insignificant damage to the seeds they dispersed.

3.3 Germination trials

Two aspects of germination were determined; germination success and latency period. Germination success and latency periods were contrasted among the seeds dispersed by monkeys via different mechanisms (ingested seeds, spat seeds and seeds from dropped fruits, hereafter referred as treatments).

3.3.1 Germination success

Generally, 38% of the total seeds tested for viability germinated. Germination success of ingested seeds averaged 52.5% (42 of 80); 35% for spat seeds (28 of 80), and 27.5% for dropped seeds (22 of 80) germinated (Figure 8). For ingested and dropped seeds, germination of new seedlings halted on the 7th week of monitoring, whereas for spat seeds plateau was attained on the 8th week (Figure 8).

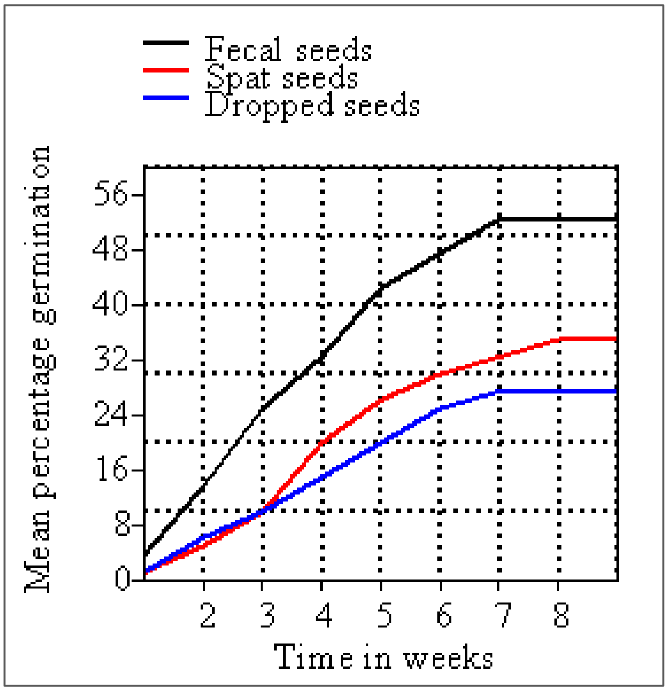

Figure 8: Cumulative germination success across the treatments in weeks

Germination experiments generally revealed that germinated seeds was significantly lower than non- germinated seeds that were tested for viability (germinates 38%, non germinates62%, χ^2 = 46.753, df = 33, $p<0.05$). However, apart from ingested seeds where there was no variation, variation between germinated and non-germinated seeds existed for spat and dropped seeds with the seeds that germinated being significantly lower compared to non-germinated $F_{5,90}$ =12.3246, $p<0.05$, Table 5). Comparison of germinated seeds only across the three treatments, showed variation in germination success ($F_{5, 90}$ =12.3246, $p<0.05$, Table 5). The ingested and spat seeds showing significantly high germination success compared to dropped seeds (Table 5). However, significant variation did not exist in germination success between ingested and spat seeds (Table 5).

Table 5: Variation in germination success between germinates and non germinates across the treatments

Treatment	**Germination**	**Mean percentage germination**	**N**
Fecal seeds	Germinates	$45.7+5.9^{bcd}$	16
	Non germinates	$44.3+2.9^{bc}$	16
Spat seeds	Germinates	$31.4+6.2^{ab}$	16
	Non germinates	$58.6+6.3^{cde}$	16
Dropped seeds	Germinates	$24.9+6.5^{a}$	16
	Non germinates	$65.1+7.3^{ef}$	16

Note: means denoted by the same superscript letter indicates no significant variation as per Tukey test following arcsine transformation

Generally there was significant variation in mean number of seeds that germinated across the treatments; ingested seed 2.6 ± 0.4, spat 1.0 + 0.4 and dropped seeds 0.6+ 0.2, ($\chi^2 = 41.305$, df = 26, $p < 0.05$). Ingested seeds germinated significantly higher than dropped seeds ($\chi^2 = 24.843$ $P < 0.05$) and spat seeds (whereas significant variation was not observed in mean number of seeds that germinated between the spat ($\chi^2 = 14.802$, df = 13, $p > 0.05$) and dropped seeds ($\chi^2 = 14.179$, df = 10, $p > 0.05$). This was an indication that ingestion of seeds by Sykes monkeys improved mean seed germination.

Of the 16 tree species whose seeds are dispersed by Sykes monkey, seeds of 13 species (81.3%) successfully germinated from fecal seeds, seeds of 11 tree species (68.8%) from spat seeds germinated, while seeds of 8 tree species (50%) for the dropped seeds germinated (Appendix 9). This suggests that all seeds dispersed by Sykes monkey via ingestion, spitting or dropped fruits are viable and capable of germinating thus contributing to forest regeneration. Out of the 16 tree species whose seeds were tested for germination, it was observed that seven had higher germination success if the seeds were defecated while two species showed indistinguishable germination success across the three treatments. None of the ingested species exhibited lower germination success than non ingested control seeds (Appendix 9).

3.3.2 Germination latency period

Majority of the species dispersed by Sykes monkeys through ingestion (7 of 16) had low latency periods compared to dropped seeds (non –ingested control). Two species had similar latency periods across the treatments with none of the tree species showed earlier tendency to germinate than ingested seeds. Mean latency period (in days) was significantly different across the treatments; Ingested; 11.8 ± 2.3, Spat =13.6±3.2, Dropped 13.2 ± 3.6 df = 24, (χ^2 = 70.873, $p<0.05$). Significant variation was not observed in mean latency period between spat and dropped seeds (χ^2 =17.291, df = 10, $p>0.05$), however, significant variation was observed in mean latency period between ingested and spat (χ^2 = 21.103, df = 12, $p<0.05$) as well as between ingested and dropped seeds (χ^2 = 46.956, df = 10, $p<0.05$). These findings suggest that passage through the monkeys gut improved mean germination and shortened latency period.

CHAPTER FOUR: DISCUSSION

4.1 Contribution of Sykes monkeys to vegetation composition and structure dynamics

Understanding forest tree species composition and structure dynamics is important in assessing the sustainability of the forest (regeneration potential) and species diversity status for conservation and management of forest ecosystems. The forest generally showed a species rich ecosystem as a result of regeneration of the forest attributed to seed dispersal by Sykes monkeys which were the main seed dispersal guild. The findings were did not deviate from those of a recent study in the Gede ruins forest (Macfarlane *et al.*, 2015). Additionally, the species richness was within the range typical for tropical dry forest (35–90 species as described by Murphy and Lugo (1986) suggesting a forest in stable condition. The slightly higher species richness recorded in primary forest than in secondary forest conformed that secondary forest was still undergoing succession towards climax vegetation as described by Turner *et al*, (1997) and Parthasarathy (1999). Nonetheless, secondary forest had regained most of the species attributed to successful seed dispersal and recruitment.

Species diversity index did not deviate from the values obtained by a recent study at the site (Macfarlane *et al.*, 2015). Contrary to (Chazdon, 2008), lack of variation in species diversity between the two forest types as found in the study is an indication that seed dispersal and natural regeneration was occurring heterogeneously in the forest and consequent maintenance of ecological integrity of the forest. It was observed that ranging behavior of Sykes monkeys changed during dry period when there was scarcity of fruits. Members of the groups sometimes occupied different areas outside group's home ranges with provisioned group ranging in primary forest and at times the free ranging group crossed to secondary forest a ranging area for the provisioned group. This have significantly contributed to high species diversity and heterogeneity in the forest. Furthermore, the fact that group members do not all range together may have generated a more scattered and uniform distribution of defecated seeds across the habitat thus decreasing seed or seedling mortality due to density-dependent factors acting at the site of defecations and enhanced diversity across the landscape.

Generally, both forest types were characterized by uneven aged classess and showed reversed exponential curve with a large density of young individuals (seedlings and saplings) and relatively few old trees. This is an indication of a forest in regenerating status which conformed to the required population demography. This was as a result of successful natural regeneration and succession via seed dispersal consequently maintenance of forest regeneration and structure.

Despite successful seed dispersal and seed germination, a general decline was observed in recruitment of the seedlings to saplings in the forest in terms of density as expected. The low recruitment was attributed to non-conducive rocky habitat microsites in the forest. The observed low recruitment was attributed to density independent factors mainly unsuitable habitat and prolonged dry periods as opposed to potential for density dependent effects on mortality, growth and recruitment as suggested by Uriarte *et al. (*2004).

The dispersion index as a measure of trees' distribution in the forest (clumped, random or uniform); Gede ruins forest demonstrated a random dispersion. This was an indication that seed dispersal by Sykes monkeys was more random creating an unevenly spaced stable heterogeneous forest. The complexity index of both forest types was typically within the range described for dry tropical forest of 5-45 as described by Murphy and Lugo (1986). The results suggest that, the forest was generally ecologically complex due to well-maintained forest structure as a result of seed dispersal exhibited by diverse tree species and with mature trees of wider basal area.

Mature trees are a key source of food for seed dispersers and consequent natural regeneration of the forest. Although the primary forest had mature trees in high densities compared to immature trees which was contrary to secondary forest, seedling density was not different in both forest types. This indicated that regeneration was occurring heterogeneously in the entire forest. Although there were inadequate seed source in secondary forest, the high regeneration was also contributed by the free ranging monkeys. They were observed to extend their ranging area to the secondary forest thus dispersed seeds thus enhancing seedling density and plant diversity in diversity in secondary forest.

However, significantly higher sapling regeneration was observed in primary forest compared to secondary forest which was attributed to; (i) high tree density in secondary forest thus competition for sunlight and other resources that affect plant growth, establishment and distribution (Brearley *et al.*, 2004), (ii) provisioning of the monkeys by tourists may have limited seed dispersal effectiveness for the provisioned monkeys which inhabited secondary forest. This is because of high chances of defecation near parent trees or near con-specific tree species resulting to high sapling mortality as a result of high species specific pathogens which occur in high densities near parent trees.

Sykes monkeys greatly contributed to seed dispersal and natural regeneration of *Azadiracta indica*, *Combretum schumannii*, *Diospyros squarrosa* and *Lecanodiscus fraxinofolius* as indicated by high density of the regenerates of the tree species. However despite *Ficus bussei* and *Tamarindus indica* being a major dietary source for the monkeys, regeneration for the species was not occurring in the forest. This is an indication that species are likely to decline in population and disappear gradually indicating a possible change in forest composition and structure in the near future whereby *C. schumannii, L fraxinifolious, A. indica* and *D. squarrosa* are likely to gain dominance. The lack of regeneration of *F. bussei* despite dispersal by monkeys was attributed to the fact that propagation of the species is more successful vegetatively than through seeds (www.treesagrofostree, July 2015). Further lack of germination and regeneration could also be due to thick litter in the forest which could be an impediment to emergence of germinated seeds given the small size of Ficus seeds. Previous study by Parvez *et al.* (2004) found biologically active growth regulators present in roots, leaves, bark and seeds of *Tamarinds indica* which had inhibiting effects on weeds. A study by Blumenfeld *et al.* (2006) found that 97% of tamarind seedlings did not grow in sites dominated by large mature tamarinds, suggesting that lack of regeneration of tamarinds was due to other factors than competition or decreased light.

Similarly to MacFarlane *et al.* (2015), secondary forest appeared to be recovering much of its original structure and diversity, despite the heavy and successful invasion of *A. indica.* The recovery was largely attributed to seed dispersal by Sykes monkey which are the main dispersal guilds in the forest and successful natural regeneration and recruitment of dispersed seeds.

4.2 Contribution of Sykes monkeys and dung beetles to forest regeneration

Generally, primary seed dispersal took place via seed swallowing and defecation some distance away from the parent tree (fecal analysis) and also through cheek-pouching fruit and spitting of unwanted seeds some distance away from where fruits were removed (seed rain). Seed dispersal was also achieved through shaking of the branches as the monkeys moved or during feeding (seed rain). Secondary seed dispersal was accomplished by dung beetles via seed cleaning, rolling away of seeds to some distance and burial of dung balls with seeds.

Sykes monkeys dispersed a mean density of 17.1 seed m^{-2} during the four month study which was high compared to a similar study where monkeys were found to disseminate 7.8 seeds $m^{-2}yr^{-1}$ in Dja Reserve, south–central Cameroon (Clark *et al.*,2001). Additionally, dissemination of large numbers of seeds of different species in this study is critical in the maintenance of plant species richness and diversity. Although insignificant, the results suggested that monkeys were able to disperse seeds to random sites, some distance away from the mother plant as evidenced by presence of many different species other than the conspecific seeds on the seed traps 5 m away from the crown. This was important because such seeds are able to escape the density dependent mortalities below the crown hence an important nuclei for regeneration for forest especially the habitat gaps.

Sykes monkeys were effective and efficient seed dispersers. The mean number of seeds per fecal clump in this study was higher than 0.37 recorded by Wrangham *et al.* (1994) in frugivorous monkey dung in the Kibale forest, Uganda. The large number of seeds dispersed translated to high regeneration that was observed in the forest hence rapid recovery of the forest.

Two important factors affecting seed dispersal and regeneration of the forest was observed in the study: (i) seasonality and (ii) provisioning of monkeys by tourists. Availability of food resources for seed dispersers is critical for regeneration of degraded forests. Presence of seeds and average number of seeds per fecal sample was higher during the rainy season. From the phenological observations, majority of the tree species dispersed by the Sykes monkeys were fruiting during the rainy period translating to high food availability and subsequent high seed dispersal and regeneration (high moisture content in soil). However, the presence of seeds as well as average number of seeds per fecal sample was significantly lower in the provisioned group compared to free ranging groups during the rainy period. The rainy period was characterized by peak tourism hence high provisioning thus the monkeys foraged less on the fruits hence subsequent low dispersal. From these findings, provisioning reduced the average number of seeds dispersed by the Sykes monkeys. However, average number of seeds did not vary between the two groups during the dry period an indication that when provisioning is minimal provisioned monkeys dispersed seeds effectively as free ranging monkeys.

It was further observed that the provisioned group defecated mostly by the road where provisioning occurred. The site conditions by the road were unsuitable micro sites for seed germination and establishment as most seeds are stumbled over and destroyed, and if the seeds managed to germinate, the seedlings were stepped on or swept away during cleaning hence hindering regeneration. This suggests that provisioning did not only reduce the number of seeds dispersed, but also that the provisioned monkeys deposited seeds on unsuitable sites for establishment.

Dung beetles played an important complementary role as secondary seed dispersers towards regeneration of the forest. Attack of dung pat by dung beetles occurred with the first few minutes of deposition, competition for dung was intense and dung ball rolling occurred rapidly and typically ‘cleaning’ the seed from a dung and abandoning it on the soil surface. For small seeds such as Ficus, they were rolled together with the dung. The combined impact of this post dispersal process enhances seed/seedling survival (and therefore plant recruitment) by ; (i) burying of dung ball with seeds reduces seed predation and mortality due to seed predators and pathogens (Andresen, 1999; Andresen and Levey, 2004; Shepherd and Chapman, 1998);(ii) rolling of dung balls from the site of deposition directs dispersal to favorable microclimates for germination and emergence (Andresen and Levey, 2004); (iii) seed cleaning decreases residual post-dispersal seed clumping (Andresen, 2001), with potential effects on density dependent seed mortality, seedling competition, predation risk with the consequent natural regeneration of the forest. While deeper seed burial depths decreases rodent detection and predation, buried seeds must also be shallow enough to permit germination and emergence (Dalling *et al.*, 1998). While the emergence success of most seeds is greatly reduced at depths below 3 cm (Pearson *et al.*, 2002), this study found that dung beetles buried most seeds at depths of 1.5 cm hence reducing susceptibility of the seeds to predation as well as encouraged seedling emergence.

4.3 Germination of Sykes monkey dispersed seeds

The findings of the study showed that ingestion of seeds and gut passage significantly enhanced germination success and reduced latency period compared no non ingested control. Several studies concur to the findings of this study. Steveson *et al*,(2002), in studying seed dispersal by Ateline monkey species in Tinigua National Park in Colombia, found that endozoochory was necessary to induce germination given that seeds passed through monkeys gut sprouted more than non passed fruits. Further, a study to determine seed dispersal by Vervet monkeys (*Chlorocebus pygerythrus*) in rehabilitating Coastal dune forests at Richards Bay, South Africa, (Foord *et al.*, 1994) revealed that the seeds passed by the monkeys were not destroyed in the digestive tract and mean germination success for seeds ingested by the monkeys was 47.6% and that of control seeds was 42.2%. Similarly, a study in the Kibale National Park, Uganda (Wrangham *et al.*, 1994) also revealed that passage through the chimpanzee gut improved the rate of germination and reduced latency period in all the ten fruiting tree species tested. The findings were however contrary to a study by (Lieberman and Lieberman 1986) who found that monkeys did not consistently affect germination of seed they dispersed.

Further, ingested seeds are more likely to be dispersed farthest from the parent tree where they are ingested, escape potential competition and distance/density mortality and contribute best to colonization of suitable microsites (Russo and Augspurger, 2004). Gut passage of seeds is, therefore, critical for regeneration and maintenance of forest structure and species composition in Gede ruins forest.

4.4 Conclusion and recommendations

4.4.1 Conclusion

Sykes monkeys can be considered effective and efficient seed dispersers; they dispersed large number of seeds via different mechanisms (spat, dropped and defecated), they dispersed seeds of wide array of tree species; they caused minimal damage to the seeds during feeding as well as to ingested seeds, the seeds they dispersed were viable and randomly dispersed to suitable microsites for germination, and they dispersed seeds far from where they fed. Further, gut passage of seeds significantly enhanced germination success and reduced latency period. However, provisioning was found to considerably reduce seed dispersal effectiveness of the Sykes monkeys; reduced presence of seeds in a fecal clump, reduced average number of seeds per fecal sample compared to the free ranging group, and deposition of seeds on unsuitable micro site.

The dung beetles played a complimentary role through; seed cleaning which reduces clumping hence enhancing seed germination and establishment, they moved dung balls with seeds (*Ficus spp)* on averagely 93 cm enhancing the probability of seeds to reach suitable microsites, and they buried the dung balls at favorable depth which protect seeds from predation while allowing germination of seeds.

The forest demonstrated uneven aged classess with large density of young individuals (seedlings and saplings) and relatively few old trees indicating a demographically stable forest. The monkeys contributed to high regeneration through egestion, spitting and dropping of viable seeds. Dispersal occurred randomly creating a random dispersion of stable unevely spaced heterogenous vegetation.

Sykes monkeys contributed to about 38% of natural regeneration through ingestion, cheek pouching and spitting and by dropping fruits. It is therefore cost effective to allow natural regeneration of Gede ruins forest through seed dispersal by Sykes monkeys. Results of this study suggest that maintaining populations of monkeys in fragmented coastal forests of Kenya is important for forest regeneration through seed dispersal.

4.4.2 Recommendations for further studies and management

- Cercopithecus monkeys inhabiting degraded coastal forests of Kenya need to be protected for continued seed dispersal and regeneration of the forest since they can contribute up to 38% of the natural forest regeneration.
- It is recommendable to introduce and or re-introduce Cercopithecus monkeys in fragmented coastal forests of Kenya to enhance natural regeneration of the forests.
- In cases where aided regeneration of disturbed forest is needed, ingested seeds could be used in raising seedling as they have high germination success and reduced latency period.
- There is need for studies on conservation approaches of forest fragments along the Coast.
- Provisioning of monkeys should be completely eliminated; the study found that it negatively affects behavior and ability of the monkeys to contribute to forest regeneration.
- Sykes monkeys are the main tourist attraction at the site, but they are facing a great threat (hunting) due to direct conflict with humans due crop raiding at agricultural lands in the nearby farms. It is recommended that the effective methods should be structured such as use of boundaries and other strategies such as involvement of the local communities in conservation and management (Community Based Conservation) of the forest.

REFERENCES

Achard, F., Eva, H.D., Stibig, H.J. P., Mayaux, J., Gallego, T., Richards and Malingreau, J.P. 2002. “Determination of Deforestation Rates of the World’s Humid Tropical Forests”. Science 297: 999–1002.

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. Biotropica 31: 145-158.

Andresen, E. 2000. Ecological roles of mammals: the case of seed dispersal. In A. Entwistle and N. Dunstone (Eds.), Priorities for the conservation of mammalian diversity (pp. 2–26). Cambridge: Cambridge University Press.

Andresen, E. 2001. Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. Journal of Tropical Ecology 17: 61-78.

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.

Andresen, E. and Levey, D. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139: 45-54.

Asner, G. P., Knap,p D. E., Broadbent, E. N., Oliveira, P. J. C., Keller, M. and Silva, J. N. 2005 Selective logging in the Brazilian Amazon. Science 310, 480–482. (doi:10.1126/science.1118051).

Babrainyeera, F. and Brown, N. 2009. Can remnant frugivore species effectively disperse tree seeds in secondary tropical rain forests? Biodiversity and Conservation 18:1611-1627.

Babrainyeera, F., Savill, P. and Brown, N., 2007. *Balanites wilsoniana*: Regeneration with and without elephants. Biological Conservation 134, 40–47.

Baillie, J.E.M., C. Hilton- Chapman and Peres Taylor, and Stuart S.N. 2004: 2004 IUCN Red List of Threatened Species. A Global Species Assessment. IUCN, Gland, Switzerland.

Balcomb, S.R. and Chapman, C.A. 2003. Bridging the gap: Influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecological Monographs 73:625-642.

Bascompte, J. and Jordano, P. 2007. The structure of plant-animal mutualistic networks: the architecture of biodiversity. Annual Review of Ecology, Evolution, and Systematics, 38: 567-593.

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

Blumenfeld-Jones, K., Randriamboavonjy, T. M., Williams, G., Mertl-Millhollen, A. S., Pinkus, S. and Rasamimanana, H. 2006. Tamarind recruitment and long-term stability in the gallery forest at Berenty, Madagascar. In *Ring tailed Lemur Biology* (pp. 69-85). Springer US.

Brearley, F. Q., Prajadinata, S., Kidd, P. S., Proctor, J. and Suriantata, 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. Forest Ecology and Management, 195(3): 385-397.

Burgess, N.D., Clarke, G.P., Madgewick, J., Robertson, S.A. and Dickinsen, A. 2000. Distribution and Status in the Coastal Forests of Eastern Africa. N.D. Burgess and G.P. Clarke, eds. IUCN: Cambridge and Gland. Pp. 71–81.

Burgess, N.D., Doggart, N., Doody, K., Negussie, G., Sumbi, P. and Perkin, A. 2003. New information on the lowland coastal forests of Eastern Africa. Oryx 37: 280-281.

Cambefort, Y. 1991. Dung beetles in tropical savannas. Pp. 156-178 In Hanski, I. and Cambefort, Y. (eds.). Dung beetle ecology. Princeton University Press, Princeton.

Catterall, C. P., Kanowski, J. and Wardell-Johnson, J. 2008. Biodiversity and new forests: interacting processes, prospects and pitfalls of rainforest restoration. In: N. Stork and S. Turton (Eds), Living in a dynamic tropical forest landscape (pp. 510-525). Wiley-Blackwell, Oxford.

Chapman, C. A. and Chapman, L. J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. Journal of Tropical Ecology 12: 491-504.

Chapman, C. A. and Onderdonk, D. A. 1998. Forests without primates: primate/plant codependency. American Journal of Primatology 45: 127-141.

Chazdon, R. L. 2008. Chance and determinism in tropical forest succession. In Tropical forest community ecology (eds Carson W. P., Schnitzer S. A.). Oxford, UK: Wiley-Blackwell.

Clark, C. J., Poulsen, J. R. and Parker, V. T. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. Biotropica, 33: 606–620.

Clark, C. J., Poulsen, J. R., Bolker, B. M., Connor, E. F. and Parker, V. T. 2005. Comparative seed shadow of bird, monkey, and wind dispersed trees. Ecology 86: 2684–2694.

Cordeiro, N. J. and Howe, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences of the United States of America 100: 14052-14056.

Cox, G.1990. Laboratory manual of general ecology 6th Ed. Dubuque, Iowa: WIlliam C. Brown.
Dalling, J.W., Swaine, M.D. and Garwood, N.C. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. In: Ecology, vol. 79: 564-578.

Dirzo, R. and Domínguez, C. A. 1986. Seed shadows, seed predation and the advantages of dispersal. Pp. 237-249 in Estrada, A. and Fleming, T. H. (eds.). Frugivores and seed dispersal.

Duncan, R. S., and Chapman, C. A. 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. Seed dispersal and frugivory: Ecology, evolution and conservation. 2nd edition. CAB International, Wallingford.

Eisenberg, J.F. and Thorington, R.W. 1973. A preliminary analysis of a neotropical mammal fauna. Biotropica 5:150–161.

Estrada, A., Halffter, G., Coates-Estrada, R. and Meritt jr., D. A. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical forest of Los Tuxtlas, Mexico. Journal of Tropical Ecology 9: 45-54.

Farwig, N., Bohning-Gaese, K. and Bleher, B. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests? Oecologia 147:238–252.

Feer, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest.Journal of Tropical Ecology 15: 129-142.

Fenner, M. and Thompson, K. 2005. The ecology of seeds. Cambridge University Press.

Food and agriculture organization of the United Nations, Rome, 2011. The state of food and Agriculture 2010-2011.

Food and Agriculture Organization, 2010. Global Forest Resources Assessment, FAO forestry Paper 163 main report.

Foord, S.H., Van Aarde, R.J. and Ferreira, S.M. 1994. Seed dispersal by vervet Monkeys in Rehabilitating coastal dune forests at Richards Bay. South African Journal of Wildlife Research 24:56-59.

Forget, P. M., Hammond, D.S., Milleron, T. and Thomas, R. 2002. Seasonality of fruiting and food hoarding by rodents: consequences for seed dispersal and seedling recruitment. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. Wallington, Cab International.

Forget, P.M., Milleron, T. and Feer, F. 1998. Patterns in post-dispersal seed removal by neotropical rodents and seed fate in relation with seed size. Dynamics of tropical communities. 37th Symposium of the British Ecological Society, Blackwell Science, Oxford, U.K.

Galetti, M., Donatti, C.I., Pires, A.S., Guimaraes, P.R. and Jordano, P. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. Botanical Journal of the Linnean Society151: 141-149.

Garber, P. A. and Lambert, J. E. 1998. Primates as seed dispersers: ecological processes and directions for future research. American Journal of Primatology 45: 3-8.

Gibbon and Rathbun, 2015. The IUCN Red List of Threatened Species 2015.

Goodman, S.M. and Ganzhorn, J.U. 1997. Rarity of figs (Ficus) on Madagascar and its relationship to a depauperate frugivore community. Terre Vie-Rev Ecol 52:321-329.

Halffter, G. and Edmonds,W. D. 1982. The nesting behavior of dung beetles (Scarabaeinae):An ecological and evolutive approach. México D.F., Man and the Biosphere Program UNESCO,177p.

Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. Pp.5-18 in Estrada, A. and Flemming, T. H. (eds.). Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht.

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

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

Howe, H. 1989. Scatter-and clump-dispersal and seedling demography: hypothesis and implications. Oecologia, 79(3), 417-426.

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

Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

Jansen, P. A., Bartholomeus, M., Bongers, F., Elzinga, J. A., den Ouden, J. and van Wien, S. E. 2002. The role of seed size in dispersal by a scatter-hoarding rodent. Pp. 209-225 in Levey, D.
Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American naturalist 104: 501-528.

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

Jordano, P. and Godoy, J. A. 2002. Frugivore-mediated seed shadows: a landscape view of demographic and genetic effects. Pp. 305-321 in Levey, D. J., Silva, W. R. and Galetti, M. (eds.). Seeds dispersal and frugivory. CABI, Wallingford.

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

Julliot, C. 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. American Journal of Primatology 40: 261-282.

Julliot, C. and Sabatier, D. 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. International Journal of Primatology 14:527±550.

Kaplin, B.A. and Lambert, J.E. 2002. A review of seed dispersal effectiveness by Cercopithecus monkeys: Implications for seed input into degraded areas. In: Frugivory and Seed dispersal: ecology, evolution and conservation. Levey, D. J., Silva W. R. and Galetti M. (Eds). CABI Publishing, Wallingford, Oxfordshire.

Kiio Kithome, 2009. A case study for survey of gastro-intestinal parasites of Sykes monkeys (*Cercopithecus mitis albogularis*) at Gede ruins national monument forest, Coast province, Kenya. Master's thesis.

Kimuyu, D., Wahungu, G. and Otieno, D. 2012. Seed dispersal by Tana River mangabeys in fragmented gallery forests. Open Journal of Ecology, 2, 12-20. doi: 10.4236/oje.2012.21002.

Kirika, J. M., Bleher, B. Bohning-Gaese, K. Chira, R. and Farwig, N. 2008. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. Basic and Applied Ecology 9:663-672.

Kirkman James. 1975. Gedi Historical monument. Museum Trustees of Kenya, Nairobi.

Knogge, C. and Heymann, E. W. 2003. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis:* diversity and characteristics of plant species. Folia Primatologica 74: 33-47.

Lambert, J. E. 1999. Seed handling in chimpanzees (Pan troglodytes) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. American Journal of Physical Anthropology, 109(3), 365-386.

Lambert, J. E. 2011. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. American Journal of Primatology 73:9–24.

Lambert, J. E. and Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. American Journal of Primatology 45: 9-28.

Lambert, J.E. 1997. Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. African Journal of Ecology 36 (3): 234-240.

Leslie Kadane. 2009. Examining monkey tourist interaction at Gede National Monument, Masters thesis.

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

Lieberman, D., Hall, J. B., Swaine, M. D. and Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. Ecology 60: 65-75.

Lieberman, M., and Lieberman, D. 1986. Study of seed ingestion and germination in a plant–animal assemblage in Ghana. J. Trop. Ecol.2: 113–126.

Link, A. and Di-Fiore, A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. Journal of Tropical Ecology 22: 235-246.

MacFarlane, D. W., Andrew, T. K., John, E. B. 2015. Coupled human-natural regeneration of indigenous coastal dry forest in Kenya. Forest Ecology and Management Journal.

Matiku, P. Ogol, C. and Mireri, C. 2011. The impact of participatory forest management (PFM) on forest integrity and biodiversity in Arabuko -Sokoke forest, Kenya. Afr. J. Ecol., Doi: 10.1111/j.1365-2028.2011.01311.x.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H. and Branthomme, A. 2005. Tropical forest cover change in the 1990s and options for future monitoring. Phil. Trans. R. Soc. B 360, 373–384. (doi:10.1098/rstb.2004.1590).

Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. *Mem. Fac. Sci. Kyushu Univ. Ser. E* 2, 215–235.

Morris, R. J. 2010. Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3709–3718.

Muller-Landau, H. C., Wright, S. J., Calderón, O., Hubbell, S. P. and Foster, R. B. 2002.Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. Pp. 35-53 In Levey, D J., Silva, W. R. and Galetti, M. (eds.). Seed dispersal and frugivory: ecology, evolution and conservation. CABI, Wallingford.

Mureu L.K. 2009. Frugivory in Sykes monkeys (*Cercopithecus mitis albogularis*) at Gede forest, Kenya: Implications for forest regeneration. Master's thesis.

Murphy, P.G. and Lugo, A.E. 1986. Ecology of tropical dry forest. Ann. Rev. Ecol. Syst. 17.

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

Nuñez-Iturri, G. and Howe, H. F. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. Biotropica39: 348-354.

Ouborg, N. J., Piquot, Y. and Van Groenendael, J. M. 1999. Population genetics, molecular markers and the study of dispersal in plants. Journal of Ecology 87: 551-568.

Pacheco, L. F. and Simonetti, J. A. 2000. Genetic structure of a mimosoid tree deprived of its seed dispersers, the spider monkey. Conservation Biology 14: 1766-1775.

Palacios, E. and Peres, C.A. 2004. Primate population densities in three nutrient-poor Amazonian terra firme forests of South-Eastern Colombia. Folia Primatologica 76, 135-145.

Parthasarathy, N. 1999. Tree diversity and distribution in undisturbed and human-impacted sites of tropical rainy evergreen forest in Southern Western Ghats, India. Biodiversity and Conservation 8:1365-1381.

Parvez, S.S., Parvez, M.M., Fujii, Y. and Gemma, H. 2004. Differential allelopathic expression of bark and seed of *Tamarindus indica*.

Pearson, T.R.H., Burslem, D., Mullins, C.E., Dalling, J.W. 2002. Germination ecology of neotropical pioneers: Interacting effects of environmental conditions and seed size. Ecology 83, 2798–2807.

Peres C.A. and van Roosmalen, M.M. 2002. Primate frugivory in two species rich Neotropical forests: Implication for the demography of large seeded plants in overhunted areas in Levey DJ. Silva WR Galleti M(eds) ; seed dispersal and frugivory ecology; evaluation and conservation CABI publishing, Wallingford .

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian.
Pizo, M. A. 1997. Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic Forest of southeast Brazil. Journal of Tropical Ecology 13:559–578.

Poulsen, J. R., Clark, C. J. and Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. Journal of Tropical Ecology 17: 787-808.
Robertson, A., Hankamer, C. and Ngonyo, M. 2002. “Restoration of a Small Tropical Coastal Forest in Kenya: Gede National Monument Forest Restoration Project.” in: Plant Conservation in the Tropics: perspectives and practice. The Royal Botanical Gardens.

Russo, S. E. and C. K. Augspurger. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7:1058– 1067.

Shannon, C.E. and W. Weaver. 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana.

Shepherd, V. E. and Chapman, C. A. 1998. Dung beetles as secondary seed dispersers: impact on seed predation and germination. Journal of Tropical Ecology 14: 199-215.

Smidt, M. and Blinn, C. R.1995. Logging for the 21st century: Forest ecology and regeneration. Minnesota Extension Service, the College of Natural Resources, University of Minnesota.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis113: 194-202.

Sork, V. L. 1985. Germination response in a large seeded Neotropical tree species, *Gustavia superba* (Lecythidaceae). Biotropica 17:130–136.

Stevenson, P. R. 2011. The abundance of large Ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. Biotropica, 42, 512–519.

Stevenson, P. R., Castellanos, M. C., Pizarro, J. C. and Garavito, M. 2002. Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. Int. J. Primatoly. 23:1187–1204.

Stevenson, P.R. 2000. Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. In: American Journal of Primatology vol. 50: 275-289.

Sykes, J. M. and Lane, A. M. J. 1996. The United Kingdom Environmental Change Network: Protocols for Standard Measurements at Terrestrial Sites. (The Stationery Office, 1996).

Terborgh, J. G., Nunez-Iturri, N. C. A., Pitman, F. H. C. ,Valverde, P., Alvarez, V. , Swamy, E. G., Pringle, and Paine, C. E. T. 2008. Tree recruitment in an empty forest. Ecology 89:1757–1768.

Turner, I. M., Y. K. Wong,P.T.Chew,Anda.B.Ibrahim. 1997. Tree species richness in primary and old secondary tropical forest in Singapore.Biodiversity Conserv., 6: 537543.

Turner, M. G., Baker, W. L., Peterson, C. J. and Peet, R. K. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems, 1, 511-523.

Uriarte, M., Canham, C. D., Thompson, J. and Zimmerman, J. K. 2004. A maximum-likelihood, neighborhood analysis of tree growth and survival in a tropical forest. Ecological Monographs 71:591–614.

Valdivia, C. E., and Simonetti, J. A. 2007. Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of *Aristotelia chilensis* in a fragmented forest. Biodiversity and Conservation 16:1593–1602.

Vander Wall, S. B. and Longland, W. S. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution 19: 155-161.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research 3: 51-74.

Willson, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetation107: 261- 280.

Willson, M. F. and Traveset, A. 2000. The ecology of seed dispersal. Pp. 85-110 in Fenner, M. (ed.). The ecology of regeneration in plant communities. CABI, Wallingford.

worldagroforestry.org/NurseryManuals/Research/Hygiene, September 2015.

Wrangham, R. W., Chapman, C. A. and Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. Journal of Tropical Ecology 10: 355-3.

Wright, S. J., Zeballos, H., Dominguez, I., Gallardo, M. M., Moreno, M. C. and Ibanez, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. Conservation Biology14:227-239.

www.treesagrofostree, July 2015

APPENDICES

Appendix 1: Tree species sampled and their respective importance value index in Primary forest

Given are species basal area, relative dominance, density, relative density, frequency, relative frequency and importance value index for each of the sampled tree species

Species	Basal area (m^2/ha)	Density (Stems/ha)	Frequency	Relative density	Relative dominance	Relative frequency	IVI
Lecaniodiscus fraxinifolius	4.90	722.22	0.94	23.51	1.11	8.59	33.20
Tarrena supra-axilaris	0.54	394.44	0.89	12.84	0.12	8.08	21.04
Drypetes reticulata	0.78	277.78	0.67	9.04	0.18	6.06	15.28
Feretia apodanthera	0.24	205.56	0.67	6.69	0.06	6.06	12.81
Combretum schumannii	10.71	216.67	0.50	7.05	2.42	4.55	14.02
Techlea trichocarpa	0.08	111.11	0.56	3.62	0.02	5.05	8.69
Asteranthe asterias	0.14	138.89	0.44	4.52	0.03	4.04	8.59
Drypetes natalensis	0.58	88.89	0.39	2.89	0.13	3.54	6.56
Carpolobia goetzei	0.53	72.22	0.39	2.35	0.12	3.54	6.01
Erythroxylum emarginatum	0.15	88.89	0.28	2.89	0.03	2.53	5.45
Haplocoelum inoploeum	0.24	72.22	0.33	2.35	0.05	3.03	5.43
Canthium glaucum	1.34	38.89	0.39	1.27	0.30	3.54	5.10
Uvariodendron kirkii	0.45	72.22	0.17	2.35	0.10	1.52	3.97
Cassipourea euyroides	0.06	38.89	0.28	1.27	0.01	2.53	3.80
Zanthoxylem chalybeum	2.26	44.44	0.22	1.45	0.51	2.02	3.98
Diospyros squarrosa	1.29	27.78	0.28	0.90	0.29	2.53	3.72
Gyrocarpus americanus	39.15	27.78	0.22	0.90	8.84	2.02	11.76
Lannea schweinfurthii	19.21	27.78	0.22	0.90	4.34	2.02	7.26
Suregada zanzibariensis	0.01	27.78	0.22	0.90	0.00	2.02	2.93
Grewia plagiophylla	1.08	38.89	0.17	1.27	0.24	1.52	3.03
Tamarindus indica	28.79	22.22	0.22	0.72	6.50	2.02	9.24
Lonchocarpus bussei	3.29	22.22	0.22	0.72	0.74	2.02	3.49
Grewia truncata	0.41	22.22	0.17	0.72	0.09	1.52	2.33
Trichilia emetica	9.14	16.67	0.17	0.54	2.06	1.52	4.12
Diospyros abyssinica	0.31	16.67	0.17	0.54	0.07	1.52	2.13
Ludia Mauritania	0.06	16.67	0.11	0.54	0.01	1.01	1.57
Carpodiptera africana	2.34	27.78	0.06	0.90	0.53	0.51	1.94
Adansonia digitata	133.25	11.11	0.11	0.36	30.08	1.01	31.45
Cussonia zimmermannii	42.41	11.11	0.11	0.36	9.57	1.01	10.94
Terminalia spinosa	12.78	11.11	0.11	0.36	2.88	1.01	4.26
Bourreria petiolaris	6.44	11.11	0.11	0.36	1.45	1.01	2.83
Cassia afrofistula	3.96	11.11	0.11	0.36	0.89	1.01	2.27
Turraea floribunda	0.60	11.11	0.11	0.36	0.14	1.01	1.51
Deinbollia borbonica	0.04	11.11	0.11	0.36	0.01	1.01	1.38
Canthium pseudoverticillatum	0.01	11.11	0.11	0.36	0.00	1.01	1.37
Sideroxylon inerme	7.29	22.22	0.06	0.72	1.65	0.51	2.87
euclea natalensis	1.15	11.11	0.06	0.36	0.26	0.51	1.13
Ochna thomasiana	0.03	11.11	0.06	0.36	0.01	0.51	0.87
Ficus bussei	94.99	5.56	0.06	0.18	21.44	0.51	22.13

Mimusops obtusifolia	9.07	5.56	0.06	0.18	2.05	0.51	2.73
Terminalia boivinii	0.64	5.56	0.06	0.18	0.14	0.51	0.83
Ziziphus mucronata	0.64	5.56	0.06	0.18	0.14	0.51	0.83
Canthium mombazense	0.13	5.56	0.06	0.18	0.03	0.51	0.71
Salacia madagascariensis	0.07	5.56	0.06	0.18	0.02	0.51	0.70
Tarrena nigrescens	0.07	5.56	0.06	0.18	0.02	0.51	0.70
Maytenus undata	0.05	5.56	0.06	0.18	0.01	0.51	0.70
pleurostylia africana	0.03	5.56	0.06	0.18	0.01	0.51	0.69
Psydrax faulknerae	0.03	5.56	0.06	0.18	0.01	0.51	0.69
Oxyanthus Zanguebaricus	0.03	5.56	0.06	0.18	0.00	0.51	0.69
Total	**441.79**	**3072.2**	**11**	**100**	**99.7**	**100**	**300**

Appendix 2: Tree species sampled and their respective importance value index in Secondary forest

Given are species basal area, relative dominance, density, relative density, frequency, relative frequency and importance value index for each of the sampled tree species

Species	**Basal area (m^2/ha)**	**Density (Stems/ha)**	**Frequency**	**Relative density**	**Relative dominance**	**Relative frequency**	**IVI**
Trichilia emetica	0.83	1000.00	0.92	25.21	1.36	7.10	33.67
Suregada zanzibariensis	0.20	575.00	0.92	14.50	0.33	7.10	21.93
Lecaniodiscus fraxinifolius	0.45	366.67	0.83	9.24	0.73	6.45	16.42
Azadiracta indica	31.78	300.00	0.83	7.56	52.08	6.45	66.10
Grewia plagiophylla	1.12	183.33	0.75	4.62	1.84	5.81	12.27
Cussonia zimmermannii	0.85	158.33	0.50	3.99	1.39	3.87	9.25
Techlea trichocarpa	0.03	108.33	0.50	2.73	0.06	3.87	6.66
Lonchocarpus bussei	3.27	100.00	0.50	2.52	5.36	3.87	11.75
Feretia apodanthera	0.09	100.00	0.50	2.52	0.14	3.87	6.53
Turraea floribunda	0.05	75.00	0.50	1.89	0.07	3.87	5.84
Allophyllus rubifolius	0.20	75.00	0.42	1.89	0.33	3.23	5.45
Zanthoxylem chalybeum	5.46	66.67	0.42	1.68	8.96	3.23	13.86
Carpolobia goetzei	0.62	91.67	0.33	2.31	1.02	2.58	5.91
Diospyros squarrosa	1.33	58.33	0.42	1.47	2.18	3.23	6.88
euclea natalensis	2.62	75.00	0.33	1.89	4.29	2.58	8.76
Sorindeia madagascariensis	0.14	58.33	0.33	1.47	0.22	2.58	4.28
Dalbergia melanoxylon	1.18	50.00	0.33	1.26	1.93	2.58	5.77
Antiaris toxicaria	0.19	75.00	0.25	1.89	0.31	1.94	4.14
Sideroxylon inerme	1.43	41.67	0.33	1.05	2.34	2.58	5.97
Grewia truncate	0.98	50.00	0.25	1.26	1.61	1.94	4.80
Vismia orientalis	0.03	41.67	0.25	1.05	0.05	1.94	3.04
Lannea schweinfurthii	2.02	33.33	0.25	0.84	3.31	1.94	6.08
Diospyros abyssinica	0.11	33.33	0.25	0.84	0.18	1.94	2.95
Xylopia parviflora	0.04	33.33	0.25	0.84	0.06	1.94	2.84

Canthium mombazense	0.33	25.00	0.17	0.63	0.54	1.29	2.46
Grewia vaughanii	0.10	16.67	0.17	0.42	0.17	1.29	1.88
Lepisanthes senegalensis	0.04	16.67	0.17	0.42	0.07	1.29	1.78
Terminalia boivinii	0.02	16.67	0.17	0.42	0.03	1.29	1.74
Haplocoelum inoploeum	0.25	33.33	0.08	0.84	0.41	0.65	1.90
Cassipourea euyroides	0.07	16.67	0.08	0.42	0.11	0.65	1.17
Afzelia quansensis	2.27	8.33	0.08	0.21	3.72	0.65	4.57
Lannea welwitschii	2.27	8.33	0.08	0.21	3.72	0.65	4.57
Mystroxylon aethiopicum	0.24	8.33	0.08	0.21	0.39	0.65	1.24
Tamarindus indica	0.13	8.33	0.08	0.21	0.21	0.65	1.06
Thespesia danis	0.13	8.33	0.08	0.21	0.21	0.65	1.06
Erythroxylum emarginatum	0.07	8.33	0.08	0.21	0.12	0.65	0.97
Combretum schumannii	0.03	8.33	0.08	0.21	0.05	0.65	0.91
Psydrax faulknerae	0.03	8.33	0.08	0.21	0.05	0.65	0.91
Adansonia digitata	0.02	8.33	0.08	0.21	0.03	0.65	0.88
Mimusops obtusifolia	0.01	8.33	0.08	0.21	0.01	0.65	0.87
Canthium glaucum	0.01	8.33	0.08	0.21	0.01	0.65	0.86
Total	**61.02**	**3966.67**	**12.92**	**100.00**	**100.00**	**100.00**	**300.00**

Appendix 3: Tree seedlings species sampled and their value in Primary forest

Given are species density, relative density, frequency, relative frequency and Relative abundance for each of the sampled tree species.

Species	No. of individuals	Density (Seedlings/m^2)	Frequency	Relative frequency	Relative density
Combretum schumannii	62	34.44	0.53	35.71	52.99
Lecaniodiscus fraxinifolius	38	21.11	0.32	21.43	32.48
Techlea trichocarpa	7	38. 89	0.06	17.86	5.98
Gyrocarpus americanus	3	16. 67	0.03	7.14	2.56
Drypetes natalensis	2	11.11	0.02	7.14	1.71
Drypetes reticulate	2	11.11	0.02	3.57	1.71
Synaptolypis kirkii	2	11.11	0.02	3.57	1.71
Diospiyros abyssinica	1	5. 56	0.01	3.57	0.85
Total	**117**		**1.00**	**100**	**100**

Appendix 4: Tree seedlings species sampled and their value in Secondary forest

Given are species density, relative density, frequency, relative frequency and Relative abundance for each of the sampled tree species.

Species	No. of individuals	Density (Seedlings/m^2)	Frequency	Relative frequency	Relative density
Azadiracta indica	14	11. 67	0.37	41.66667	36.84
Techlea trichocarpa	8	66. 67	0.21	20.83333	21.05
Diospiros squarrosa	5	41. 67	0.13	12.5	13.16
Lecaniodiscus fraxinifolius	5	41. 67	0.13	12.5	13.16
Suregada zanzibariensis	4	33. 33	0.11	8.333333	10.53
Turrea floribunda	2	16. 67	0.05	4.166667	5.26
Total	**38**	**31667**	**1.0**	**100**	**100**

Appendix 5: Tree saplings species sampled and their value in Primary forest

Given are species density, relative density, frequency, relative frequency and Relative abundance for each of the sampled tree species

Species	No. of individuals	Density (Seedlings/ha)	Frequency	Relative frequency	Relative density
Lecaniodiscus fraxinifolius	339	47083.33	0.94	19.77	69.18
Combretum schumannii	36	5000.00	0.78	16.28	7.35
Techlea trichocarpa	29	4027.78	0.56	11.63	5.92
Drypetes reticulata	18	2500.00	0.28	5.81	3.67
Asteranthe asterias	13	1805.56	0.28	5.81	2.65
Lepisanthes senegalensis	12	1666.67	0.28	5.81	2.45
Drypetes natalensis	8	1111.11	0.22	4.65	1.63
Suregada zanzibariensis	6	833.33	0.11	2.33	1.22
Azadiracta indica	4	555.56	0.11	2.33	0.82
Diospiros squarrosa	3	277.78	0.11	2.33	0.61
Monodora grandidieri	3	277.78	0.06	1.16	0.61
Deinbollia borbonica	2	277.78	0.11	2.33	0.41
Elaeodendron shweinfurthianum	2	277.78	0.11	2.33	0.41
Erythroxylum emarginatum	2	277.78	0.06	1.16	0.41
Salacia madagascariensis	2	277.78	0.11	2.33	0.41
Synaptolypis kirkii	2	277.78	0.06	1.16	0.41
Dalbergia melanoxylon	1	138.89	0.06	1.16	0.20
Erythrina sacluexii	1	138.89	0.06	1.16	0.20
Feretia apodanthera	1	138.89	0.06	1.16	0.20
Pleurostilia africana	1	138.89	0.06	1.16	0.20
Tarrena supra-axilaris	1	138.89	0.06	1.16	0.20
Terminalia spinosa	1	138.89	0.06	1.16	0.20
Trichilia emetica	1	138.89	0.06	1.16	0.20
Uvariodendron kirkii	1	138.89	0.06	1.16	0.20
Xylopia parviflora	1	138.89	0.06	1.16	0.20

Zanthoxylem chalybeum	1	138.89	0.06	1.16	0.20
Ziziphus mucronata	1	138.89	0.06	1.16	0.20
Total	**492**	**68055.56**	**4.7778**	**100**	**100.41**

Appendix 6: Tree saplings species sampled and their value in Secondary forest

Given are species density, relative density, frequency, relative frequency and Relative abundance for each of the sampled tree species

Species	No. of individuals	Density (Seedlings/ha)	Frequency	Relative frequency	Relative density
Lecaniodiscus fraxinifolius	95	19791.67	13.57	76.87	42.79
Techlea trichocarpa	38	7916.67	0.50	2.83	17.12
Suregada zanzibariensis	20	4166.67	0.42	2.36	9.01
Turrea floribunda	17	3541.67	0.42	2.36	7.66
Trichilia emetica	10	2083.33	0.42	2.36	4.50
Azadiracta indica	9	1875.00	0.42	2.36	4.05
Carpolobia goetzei	6	1250.00	0.25	1.42	2.70
Sorindeia madagascariensis	6	1250.00	0.25	1.42	2.70
Diospiros squarrosa	4	833.33	0.25	1.42	1.80
Grewia plagiophylla	4	833.33	0.25	1.42	1.80
Feretia apodanthera	3	625.00	0.25	1.42	1.35
Antiaris toxicaria	2	416.67	0.08	0.47	0.90
Combretum schumannii	2	416.67	0.08	0.47	0.90
Allophyllus rubifolius	1	208.33	0.08	0.47	0.45
Lepisanthes senegalensis	1	208.33	0.08	0.47	0.45
Lonchocarpus bussei	1	208.33	0.08	0.47	0.45
Terminalia boivinii	1	208.33	0.08	0.47	0.45
Thevetia peruviana	1	208.33	0.08	0.47	0.45
Xylopia parviflora	1	208.33	0.08	0.47	0.45
Total	**222.00**	**46250.00**	**17.65**	**100.00**	**100.00**

Appendix 7: Tree species dispersed through seed rain

Below the canopies	Away from the canopies	Fecal dispersal
Diospyros squarrosa	*Diospyros squarrosa*	*Grewia forbesii*
Tamarindus indica	*Tamarindus indica*	*Diospyros squarrosa*
Combretum schumannii	*Combretum schumannii*	*Cassia Sylvicola*
Lecaniodiscus fraxinifolius	*Lecaniodiscus fraxinifolius*	*Lannea schweinfurthii*
Gyrocarpus americanus	*Gyrocarpus americanus*	
Lannea schweinfurthii	*Lannea schweinfurthii*	
Cissus rotundifolia	*Cissus rotundifolia*	
Carpolobia goetzei	*Terminalia spinose*	
Antiaris toxicaria	*Mimusops obtusifolia*	
Terminalia spinosa	*Cassia Sylvicola*	
Mimusops obtusifolia	*Species 15*	
	Araucaria araucana	

Appendix 8: Seed dispersal through egestion

Frequency of distribution of seeds in a fecal sample, total number of seeds extracted from the dung and average number of seeds per fecal sample per species collected during the study.

Species	**Frequency**	**Total no. seeds**	**Average seeds/fecal sample**
Adansonia digitata	17	27	1.6
Antiaris toxicaria	27	36	1.3
Azadiracta indica	14	31	2.2
Cassia afrofistula	5	6	1.2
Cissus rotundifolia	41	135	3.3
Cissus integrifolia	4	6	1.5
Cissus sylvicola	4	8	2
Diospyros squarrosa	42	195	4.6
Ficus	48		
Grewia forbesii	73	343	4.7
Grewia plagiophylla	2	3	1.5
Haplocoelum inoploeun	6	10	1.7
Lannea schweinfurthii	153	743	4.9
Lecaniodiscus fraxinifolius	32	148	4.6
Mimusops obtusifolia	53	122	2.3
Opilia amenteacea	1	3	3
sp 1	1	1	1
Grewia truncata	1	1	1
sp 11	1	2	2
sp 13	1	1	1
sp 14	1	1	1
sp 16	2	2	1
sp 18	1	1	1
sp 3	1	1	1
sp 5	1	1	1
sp 8	1	3	3
sps 12	2	14	7
sps 4	1	1	1
sps 7	2	7	1
sps9	1	1	1
Suregada zanzibariensis	2	2	1
Tamarindus indica	43	61	1.4
Vitex strikeri	1	1	1
Total		1917	

Appendix 9: Germination success as the percentages of ingested, spat and control seeds that germinated in the trials

Tree species	**Percentage of seeds germinating**		
	Fecal	**Spat**	**Dropped**
Adansonia digitata	40	0	0
Antiaris toxicaria	40	40	20
Azadiracta indica	100	20	100
Cassia afrofistula	60	40	0
Cissus integrifolia	60	80	0
Cissus rotundifolia	80	80	80
Cissus sylvicola	0	0	0
Diospiros squarrosa	80	80	60
Grewia forbesii	20	0	0
Grewia plagiophyla	80	40	60
Grewia truncata	40	40	20
Haplocoelum inopleum	80	40	20
Lannea schweinfurthii	40	20	0
Lecaniodiscus fraxinifolius	0	0	0
mimusops obtusifolia	40	0	0
Opilia amentacea	80	80	80
Mean percentage of seeds that germinated	**52.5**	**35**	**27.5**

PLATES

Plate 1: Dung beetle activity: Dung rolling and seed cleaning

Plate 2: Seed trap design used in the study for seed rain estimation

Plate 3: Germination trials

Plate 4: Sykes monkey feeding on *Tamarindus indica* fruit

Plate 5: Provisioning of study monkeys with banana, candy and biscuits