“Frugivores, seed dispersal and tree regeneration along a human disturbance gradient in East African tropical rainforests”

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1 SUMMARY

Tropical forest mutualisms are under threat from increased rates of forest conversion and degradation. Seed dispersal and regeneration is important for maintenance of both trees and frugivores. To elucidate the effect of small-scale anthropogenic disturbance on frugivore community and the vital ecosystem process of seed dispersal and regeneration I investigated (1) the frugivore community and fruit removal rates of *Celtis durandii* (Ulmaceae) and (2), the relationship between fleshy-fruited tree species, frugivores and fleshy-fruited tree seedling establishment in three East African tropical rainforests. During frugivore community census I recorded 40 frugivorous birds and primates in the three forests. Moreover, I recorded more frugivores in little disturbed sites as compared to heavily disturbed sites. From observations on *C. durandii* trees I recorded more frugivore visitors on trees located in little disturbed than in heavily disturbed sites. This lead to marginally more seeds removed by frugivores in little disturbed than in heavily disturbed sites. The results did not differ among the three rainforests, suggesting that they were consistent at a regional scale. Therefore, it appears that small-scale forest disturbance has a more general negative impact on frugivores and their seed dispersal services than previously anticipated. During the vegetation survey I recorded 131 fleshy-fruited tree species in the three rainforests. Small-scale disturbance marginally significantly enhanced fleshy-fruited tree species richness with no direct effect on frugivore density and species richness of fleshy-fruited tree seedlings. Richness of fleshy-fruited trees had a marginally significant positive influence on frugivore density but not on seedlings. Correspondingly, the density of frugivores significantly increased the species richness of fleshy-fruited tree seedlings. Therefore, small-scale disturbance appear to have increased seedling establishment indirectly through increases in tree species richness and frugivore density. Most significantly, frugivore density played a more important role for forest regeneration than either small-scale disturbance or tree species richness. Thus, small-scale local disturbance seems to have both positive and negative effects on seed dispersal and regeneration. Therefore, further studies are required to clarify the effects of small-scale disturbance on tropical forest mutualisms.

2 GENERAL INTRODUCTION

Tropical rainforests are among the most ancient and diverse ecosystems in the world (Heywood 1995). They harbour the largest number of species, which participate in complex ecological interactions and processes; thus they play a crucial role in biodiversity conservation. The future of tropical forests and the animals they support is grim, however, and is linked to accelerating rates of forest conversion and degradation (Lewis 2006, Pimm 1995). Many interrelated forces cause forest conversion and degradation and compromise tropical forest existence. These threats often result from an expanding and uncontrolled demand on rainforest resources and from fragmentation, transformation and conversion of the forests to other types of land cover (Heywood 1995). The most important threats facing tropical rainforests world wide include rapid land use changes such as agricultural expansion, commercial logging, plantation development, mining, industry, urbanization and road building (Geist & Lambin 2002).

The rapid rates of global biodiversity loss are intensifying the need to understand the consequences for the ecosystem processes and functioning (Purvis & Hector 2000). Changes in the functioning of critical ecosystems, whether due to loss of keystone species or disruption of vital processes, threaten their regulatory functions. Many of these losses and changes are not easily reversible and can even persist for centuries (Chazdon 2003, Willis *et al.* 2004). Thus, understanding the diversity, maintenance, and functioning of tropical ecosystems is vital in order for conservation of tropical rainforests.

Among the most crucial processes maintaining the high diversity in tropical forests are pollination and seed dispersal (Howe & Westley 1988). The majority of tree and shrub species in the tropics depend on frugivores for their seed dispersal (Tabarelli & Peres 2002). Seed dispersal takes place at the final stage of each plant reproductive episode and therefore plays a key role in plant demography (Rey & Alcántara 2000). Various studies have shown that survival of seeds and seedlings is higher at far distances from parent plants (Connel 1971, Howe *et al.* 1985, Janzen 1970). Thus, to sustain the high diversity in tropical rainforests a better understanding of seed dispersal and regeneration in the face of human disturbance is necessary. This knowledge is urgently needed as the pressure on tropical forests imposed by anthropogenic disturbances has increased dramatically over the past decades with unclear effects on frugivores and tree populations.

2.1 Consequences of disturbance for frugivores, seed dispersal and tree regeneration

Mutualistic animal-plant interactions exist in a wide array in tropical forests (Bronstein 2001). One of the most important is the transport of seeds from parent plants by animals. In tropical forests, the seeds of the majority of tree species are dispersed by frugivorous animals (Tabarelli & Peres 2002). Two main advantages of seed dispersal have been suggested in the literature (Howe & Smallwood 1982). First, seed dispersal increases the probability that seeds encounter suitable sites for their establishment and subsequent development. Second, seed dispersal may help to escape from a higher probability of mortality below the parent tree. The latter advantage of seed dispersal is well captured by the Janzen-Connell hypothesis (Connell 1971, Janzen 1970). According to this hypothesis, the seed density will decrease with distance from the parent tree. However, due to species-specific predators and diseases, the seed and seedling mortality is expected to be highest near the parent tree. Consequently, seed dispersal by frugivores is thought to affect seedling establishment and composition of plant communities in general. On the other hand frugivores depend on fruits for their nourishment, thus any impact on fleshy-fruited trees for example from disturbance will ultimately affect frugivores (Moegenburg & Levey 2003).

Severe forms of disturbance such as fragmentation have been demonstrated to change the frugivore community leading to a loss of seed dispersers (Githiru *et al.* 2002). This loss of seed dispersers might lead to a breakdown in seed dispersal processes of concerned plants (Howe 1984, Pizo 1997). Previous studies have shown that low dispersal rates lead to reduced seedling establishment (Bleher & Böhning-Gaese 2001, Cordeiro & Howe 2003, Howe *et al.* 1985). Also recent studies have shown that seedlings and juveniles of many rainforest species suffer declines in forest fragments due to loss of seed dispersers (Cordeiro & Howe 2003, Githiru *et al.* 2002). Furthermore, severe disturbance has also been shown to trigger other deleterious processes that affect seedling diversity such as alteration in tree phenology, suppression of seedlings by increases in liana densities, infection of seedlings by fungal pathogens and increased seedling predation. On the other hand declines in abundance of fleshy fruits lead to a concomitant decline in frugivore abundance (Moegenburg & Levey 2003). Disturbance could therefore have consequences for frugivores, seedlings and trees.

Nevertheless, most previous studies focused on severe forms of forest disturbance such as forest loss and fragmentation (Laurance *et al.* 2001, Turner 1996). Thus, the consequences of less severe habitat disturbance, where some resemblance of forest remains (e.g., following selective logging, firewood collection, charcoal burning, grazing) are less clear (Hill & Hamer 2004). Since modified and degraded forests now form an increasingly large proportion of tropical landscapes (Peres *et al.* 2006) there is an urgent need to investigate the effect of this moderate disturbance on species diversity and ecosystem processes.

2.2 Aims of the thesis

In this thesis I investigated the impact of small-scale anthropogenic disturbance on the tree community, frugivore community, seed dispersal and seedling establishment in East African tropical rainforests from October 2004 to December 2006. My study sites were suited for this query because the three forests I worked on, i.e. Budongo, Mabira and Kakamega forest, share a similar history with sites that are heavily disturbed and sites of little or no disturbance. Furthermore, *Celtis durandii* which was my focal tree is found in high densities in all the three forests.

The first aim of the thesis was to determine the impact of small-scale anthropogenic disturbance on the frugivore community and seed dispersal. The second aim was to determine the impact of disturbance on fleshy-fruited tree species richness, frugivores and fleshy-fruited tree seedling establishment.

This thesis consists of two major chapters (Chapter 3 and 4) which can be read independently. Each of the two major chapters is organised like a journal publication containing an introduction, followed by methods used, a results and discussion section and a brief summary. The thesis closes with general conclusions.

In the first major chapter (chapter 3) I focused on effects of small-scale disturbance on the overall frugivore community and fruit removal by frugivores on *C.*

durandii. Specifically I quantified frugivorous birds and primates in little disturbed and heavily disturbed sections of the three forests. In addition I determined the frugivore assemblages and seed removal rates on 44 *C. durandii* trees. Lastly I quantified fruit availability in the vicinity of the study trees.

In the second major chapter (chapter 4) I quantified trees in one hectare plots, frugivores via point counts (birds) and line transects (primates) and seedling establishment in $1m^2$ subplots. Data for this chapter were collected in little disturbed sites, heavily disturbed sites and in a primary forest.

3 LOCAL DISTURBANCE OF TROPICAL FORESTS DIMINISHES FRUGIVORES AND SEED REMOVAL OF A SMALL-SEEDED AFROTROPICAL TREE

3.1 Introduction

The last few decades have seen an unprecedented destruction of global forest cover (Lewis 2006, Mayaux *et al.* 2005). The effects of severe forest loss and fragmentation on biodiversity and, to some degree, ecosystem processes have been extensively studied (Laurance *et al.* 2001, Lewis 2006, Turner 1996). However, forests can also be modified by small-scale disturbance, for example by selective logging, firewood collection, charcoal burning or cattle grazing. Degraded forests are on the increase and now form a large proportion of tropical landscapes (Foley *et al.* 2007, Peres *et al.* 2006). However, the impact of this less severe but widespread form of disturbance is still unclear (Hill & Hamer 2004). Therefore there is an urgent need to investigate the effect of this small-scale disturbance on biodiversity and ecosystem processes.

Effects of small-scale, local forest disturbance on biodiversity are comparatively well studied for birds and primates. So far, these studies indicate that not all species are equally vulnerable (Brook *et al.* 2003, Chapman *et al.* 2006, Sodhi *et al.* 2004). A recent meta-analysis of birds demonstrated that small-scale forest disturbance lead to increases in granivores and declines in insectivores and frugivores (Gray *et al.* 2006). With regard to habitat specialization, forest specialists were more negatively affected than forest generalists (Brook *et al.* 2003, Mason 1996, Peh *et al.* 2005, Raman 2001, Tejeda-Cruz & Sutherland 2005, Woltmann 2003). Also for primates, effects of local disturbance were species and site specific with some species being negatively affected in some areas while showing a marked increase in other areas (Chapman *et al.* 2000, Haugaasen & Peres 2005, Marshall *et al.* 2006, Onderdonk & Chapman 2000, Plumptre & Reynolds 1994). Primates that have low ecological flexibility, for example because they are food or habitat specialists, are more susceptible to disturbance than species with broader ecological niches (Chapman *et al.* 2006, Harcourt 2006).

Little is known about the indirect effects that small-scale, local disturbance might have on the relationship between biodiversity and ecosystem processes. Frugivorous birds and primates play a particularly important role for ecosystem functioning in tropical forests as they disperse seeds of up to 90% of the tree species (Howe & Smallwood 1982). Seed dispersal by frugivores is important for forest regeneration. Frugivores transport seeds away from areas of high mortality near the parent plant and towards vacant sites with a higher probability of seedling establishment (Herrera 2002, Wenny & Levey 1998). The decline and loss of birds and primates can lead to a breakdown of seed dispersal and seedling establishment (Bleher & Böhning-Gaese 2001, Böhning-Gaese, in press). However, most previous studies have focused on the impact of forest fragmentation (Cordeiro & Howe 2001, Cordeiro & Howe 2003, Farwig 2006, Graham 2002, Pizo 1997, Santos & Telleria 1994), and only few on small-scale disturbance (Farwig *et al.* 2006)

Regarding seed dispersal and regeneration, it is assumed that large-seeded tree species are more threatened than small-seeded tree species (Da Silva & Tabarelli 2000). Large seeded tree species are dispersed by fewer and larger-bodied bird and mammal species than small-seeded trees. Especially large-bodied mammals are vulnerable to disturbance, in particular to hunting (Peres & Nascimento 2006). Correspondingly, the loss of elephants and other large mammals, but also of large birds such as hornbills has lead to a decline of seed dispersal, seedling establishment and regeneration of a number of large-seeded tree species (Babweteera *et al.* 2007, Corlett 1998, Galetti *et al.* 2006, Forget & Jansen 2007, Wright *et al.* 2000). In addition, forest specialist species are particularly vulnerable to disturbance (Raman 2001, Woltmann 2003). However, in this case it could be expected that declines in forest specialists are compensated by increases in forest generalists leading to stability of their total ecosystem service (Brotons *et al.* 2003).

In this study I focused on the impact of small-scale, local forest disturbance on frugivorous birds and primates and on seed removal of the small-seeded tree *Celtis durandii* in three rainforests in East Africa. In general, Africa is studied much less frequently than the Neotropics and south-east Asia. For example, only 3 out of 57 studies reviewed in Gray *et al.* (2006) come from Africa. Nevertheless, Africa is expected to face a larger conservation crisis than the Neotropics and south-East Asia in the future because human population is expected to increase more severely (Laurance 2007, Wright & Muller-Landau 2006). For example it is estimated that the human population of the Democratic republic of Congo, a country that contains 21% of the tropical rainforests in Africa, will grow by 220% by the year 2030 (FAO 2000). My study areas, Budongo Forest and Mabira Forest in Uganda, and Kakamega Forest in Kenya lay along a west-east gradient across the East African highlands. By working in several rainforests I was able to test for effects of disturbance not only on a local but also on a regional scale. The three forests have been subjected to varying levels of past and present anthropogenic disturbances and it was possible to classify sites into little and heavily disturbed sites.

The objectives of the study were, first, to test whether small-scale, local disturbance affected the species richness and density of frugivorous birds and primates in the three forests. I tested whether disturbance affected forest specialists, generalists and visitors differently. Secondly I studied frugivore assemblages in and seed removal from *C. durandii* trees. I tested in particular for possible redundancy in seed removal among forest specialists, generalists and visitors. Due to the small fruits and seeds of *C. durandii* I expected that the tree was dispersed by a broad assemblage of frugivores and that potential declines in seed removal by forest specialists might be compensated by increases in seed removal by forest generalists and visitors.

3.2 Materials and methods

3.2.1 Study area

The study was carried out in three tropical rainforests in East Africa, Budongo and Mabira forests in Uganda and Kakamega Forest in Kenya (Fig. 3.1). Budongo Forest (1° 35'N – 1°55'N, 31°8'E – 31°42'E) lies 1100 m above sea level (asl) and covers an area of 428 km^2. Budongo Forest receives an average annual precipitation of about 1410 mm. The study was carried out in compartment N3 (selectively logged in 1947-52) herein referred to as little disturbed (LD) site, and W 22 (selectively logged in 1963-64 and again in 1996-97) herein referred to as heavily disturbed (HD) site. For more details on Budongo Forest see Eggeling (1947), Howard (1991), Plumptre (1996) and Plumptre & Reynolds (1994).

Mabira Forest (0° 23'N – 0°35'N, 32°50'E – 33°7'E) lies 1150 m asl and covers about 306 km^2. Mabira Forest is located in Mukono district of central Uganda and lies between Budongo and Kakamega Forest (Fig. 3.1). Mabira Forest receives an annual rainfall of 1640 mm. Mabira Forest reserve has been subjected to extensive anthropogenic disturbances including; encroachment, pit-sawing, charcoal burning and hunting both in the past and in the present. The study sites in Mabira were identified from land-use maps and Geographic Information System (GIS) coverages compiled by the Forest Department (verified by ground-truthing). Sites were grouped into LD sites characterized by relatively undisturbed forest without logging activity, although localized pit-sawing was evident and HD sites characterized by intensive past and present anthropogenic disturbances such as pit-sawing, charcoal burning, firewood collection, pole-wood harvesting and cattle grazing. For more details on Mabira Forest see Howard (1991) and Naidoo (2004).

Kakamega Forest (0º10´N – 0º21´N, 34º47´E – 34º58´E) lies 1550-1650 m asl. It is a mid-altitude tropical rainforest and is considered to be the eastern most outlier of the Congo-Guinean rainforest belt (Kokwaro 1988) (Fig. 3.1). The main forest area covers about 85 km^2 of near natural forest (BIOTA East 2004) that is surrounded and interspersed by secondary forest, clearings and glades, as well as tea and timber plantations (Bennun & Njoroge 1999). Kakamega Forest receives an average annual rainfall of between 1200 mm and 2100 mm per year (Emerton 1994). Kakamega Forest has experienced a long disturbance history including encroachment, commercial and selective logging, firewood collection, charcoal burning, etc. (Mitchell 2004, Tsingalia, 1990). Areas managed by the Kenya Wildlife Service have lower levels of human disturbance while those managed by the Forest Department have higher levels of disturbance (Bleher *et al.* 2006). Thus, study sites under the management of the Kenya Wildlife Service were defined as little disturbed (LD) and those under the management of the Forest Department as heavily disturbed (HD). For more details on Kakamega Forest see Kokwaro (1988), Mitchell (2004) and Tsingalia (1990).

The disturbance regimes in the three different forests are comparable because forest structure is mainly determined by selective logging. Little disturbed sites in the three forests had on average 73.4 % canopy cover while heavily disturbed sites had rather open canopies with an average cover of 51.3 %.

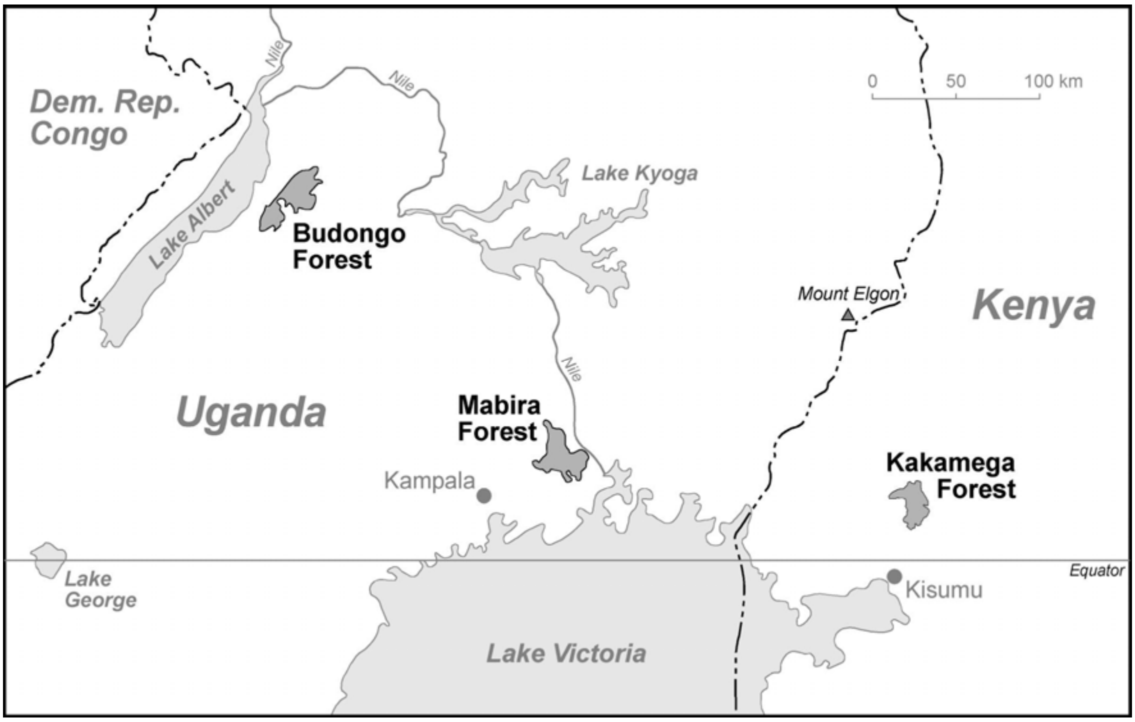

Figure 3.1: Map of Kenya and Uganda showing the location of Budongo, Mabira and Kakamega forests. Courtesy of G. Schaab.

3.2.2 Study species

Celtis durandii Engl. (Ulmaceae) (Struhsaker 1997), is widespread in Africa in low to medium altitude, mixed evergreen rainforest and riverine forest. *Celtis durandii* is an abundant tree in East Africa; I recorded an average of 27.3, 47.6 and 26.4 stems per hectare in Budongo, Mabira and Kakamega forests respectively. Trees grow to about 30 meters in height. It has small ovoid fruits that turn yellow to orange when ripe (Fruit size 6.09 ± 0.86 mm in diameter, N = 880 from 20 fruits collected from each of 44 trees). The fruits are classified as drupes and each fruit contain a single seed.

3.2.3 Sampling regime

Data were collected from November 2004 to December 2006, sampling the different forests and disturbance regimes in random order with regard to dry and wet season. For each site and season, surveys of birds, primates and fruits, and tree observations were conducted simultaneously (i.e. within two weeks). I established in Budongo Forest 6 one-hectare plots (3 plots in LD and 3 plots in HD sites) and in Kakamega and Mabira forests, 8 one-hectare plots each (4 plots in LD and 4 plots in HD sites respectively). Originally, I had planned to establish 8 plots in Budongo Forest as well. However, *C. durandii* did not develop any fruits between March 2006 and December 2006 in Budongo Forest and the two last plots had to be omitted. Each of the one-hectare plots consisted of 5 transects of 100 m length with neighbouring transects separated from each other by 20 m and the first and the last transect being 10m from the edge of the plot. All plots were at least 100 m from the forest edge in order to reduce edge effects.

3.2.4 Frugivore community

The frugivore community was quantified separately for birds and primates as both groups of species require different sampling designs. Birds were counted on the one-hectare plots using point counts. Point counts are widely used as a standard method for sampling forest birds (Bibby *et al*. 1992). I established nine point count locations within each one-hectare plot, with three points placed along the first transect (at 10, 50, and 90 m), three points along the third transect and three along the fifth transect. Birds were censused early in the morning (0700-0900 h). At each point count location, I recorded all birds heard or seen for ten minutes within a radius of 20 m. Bird species were identified according to Stevenson & Fanshawe (2002). For analysis I focused on frugivorous birds. I defined birds as frugivores if they were seen feeding on fruits during the study or have been described as being obligate or partial frugivores in the literature (Kissling *et al.* 2007). Bird species were classified according to their forest-dependency as either (1) *forest specialists*, for those bird species that occupy and breed in the interior of closed-canopy or little-disturbed forests; (2) *forest generalists* for those bird species that can occur and breed in both undisturbed and disturbed forest; or (3) *forest visitors* for those bird species which are recorded in forests but are more common in non-forest habitats, following Bennun *et al.* (1996). I calculated the number of species and of individuals of frugivorous birds by adding up all frugivorous bird species and individuals counted over the nine point count locations per plot. I calculated frugivorous bird density by dividing the total number of birds per plot by the area censused within each plot (9 x $(20\ \text{m})^2$ x Pi = 11304 m^2).

Primates were counted using a 500 m long line transect running through the centre of each plot. I used transects because primates generally live in groups and in low densities (National Research Council 1981). The transect extended 400 m beyond the edges of the plot. Primate censuses were carried out from 0900-1200 h recording all primate species and individuals heard or seen < 50 m on each side of the transect. Primate counts were repeated three times for each transect. Primates were identified according to Kingdon (1997). All primates were observed to be frugivores and classified into the same forest-dependency categories as birds (M. Cords and C. Chapman, personal communication). I calculated the number of species and individuals per transect by adding the species and individuals over the three censuses. Primate density was calculated by dividing the number of primate individuals counted in the three censuses by the area covered during census (3 x 500 m x 100 m= 150000 m^2). To obtain total frugivore species richness I added the number of bird species counted during the point counts and the number of primate species counted during transect counts. To test for potentially different effects of local disturbance on birds and primates I also analyzed the two groups of species separately. To obtain total frugivore density, frugivorous bird densities (calculated as number of bird individuals per hectare) and primate densities (calculated as number of primate individuals per hectare) were summed up.

3.2.5 Frugivore assemblage in *Celtis durandii*

I chose randomly two *C. durandii* trees per one-hectare plot for frugivore observations. The trees were either placed on the plot or, if this was not possible, in close vicinity to a plot (two trees were 50 m away from a plot). For each focal tree I estimated the crop size by counting representative parts of the crown and then extrapolating over the whole tree crown. Only trees bearing over 1000 fruits were selected for observations. For analyses, crop size was log-transformed.

To quantify the frugivore assemblage visiting the tree, each of the 44 trees was observed for two days from 0700 to 1400 h. All observations were carried out from a blind about 10-15 m away from the tree using a pair of binoculars (Nikon 10 x 50). Observations involved a scan sampling and a focal animal sampling procedure. Scan sampling was carried out every 15 minutes (58 times per tree) for a period of one minute recording all animal visitors in the tree. Focal animal sampling was carried out between the scan sampling sessions and involved random selection of an individual animal as it came into the tree and following it for as long as it stayed in the tree. I recorded the time of stay in the tree and the number of fruits eaten.

For identification and classification of frugivorous bird and primate species I followed the same methods as for the frugivore community. The number of species and individuals visiting a tree was calculated as the sum over the 58 scans corresponding to 58 minutes per day. In addition, visitation rates were calculated separately for species differing with regard to habitat specialization, i.e. for forest specialists, forest generalists and forest visitors. The numbers of individuals visiting a tree were log(x+1)-

transformed and the average for the two trees per one-hectare plot was calculated prior to statistical analyses.

3.2.6 Seed removal of *Celtis durandii*

To quantify the number of seeds removed per tree I combined scan and focal sampling data of all frugivores. First, I calculated for each species visiting the focal tree the sum of individuals per 58 minutes by adding the 58 scans per tree. Second, I assessed for each frugivorous species, using the focal animal sampling data, the average fruit consumption rate per minute, averaging over all focal observations of the respective frugivore species over all trees separately for each forest. I tested for potential differences in fruit consumption of a species between the two disturbance regimes within a forest, but these were not significant. Third, I multiplied for each species the number of individuals per 58 minutes with the average fruit consumption rate per minute. Fourth, these products were added over all species visiting the respective tree. The resulting number represents an estimate of the number of fruits eaten per 58 minutes per tree (58 scans x number of fruits consumed per minute). Since most of the fruits that were consumed by frugivores were removed away from the tree, these numbers represent estimates of the number of seeds removed per 58 minutes per tree. In addition, removal rates per 58 minutes per tree were calculated separately for birds and primates and for forest specialists, forest generalists and forest visitors. For analysis, number of fruits removed per tree was log(x+1)-transformed and then the average for the two trees was calculated.

3.2.7 Fruit availability

Birds may respond to variation in fruit abundance (Loisselle & Blake 1991, 1993). Hence, it was important to quantify fruit abundance within the vicinity of the focal trees. Therefore, data on general fruit availability of the forest surrounding the focal trees was recorded on the one-hectare plots with which the trees were associated. Within the one-hectare plots all fruiting plants which might be attractive to frugivorous animals were identified 10 m to the left and 10 m to the right of the five transects thereby covering the total area of 1 ha. Identification of plant species was carried according to Beentje (1994). For each plant the presence and number of ripe fruits were estimated in situ on a logarithmical scale (1-10, 10-100, 100-1 000, 1 000-10 000, >10 000 fruits) and the total number of fruits available per plot was calculated. For analysis, I used the log-transformed number of fruits.

3.2.8 Statistical analysis

The response variables in my study were at the level of the frugivore community, the total number of frugivore species and frugivore density and at the level of the trees, the total number of frugivore species, the number of frugivore individuals and the number of removed fruits. I tested the effects of local disturbance and forest identity on these response variables using Analysis of Covariance (ANCOVA). In the analyses, I treated local disturbance regime and forest identity and their interaction term as fixed effects whereby disturbance regime had two levels (little or heavily disturbed site) and forest identity had three levels (Budongo, Mabira or Kakamega Forest). Further, I included the covariates crop size and fruit availability in the model as well as all two-way interaction terms between disturbance regime, forest identity, crop size and fruit availability. I stepwise excluded first interaction terms and then covariates when they were not significant, starting with the least significant.

Furthermore, I ran the same analyses for birds and primates separately. The results were mainly similar to the ones of all frugivores combined. Thus, in general I restrict the presentation of the results to frugivores in general. In the few cases, in which the responses of birds and primates differed, however, I report these results separately. Finally, I ran all analyses separately for forest specialists, forest generalists and forest visitors. All analyses were performed using JMP (2001).

3.3 Results

3.3.1 Frugivore community

During the censuses of the frugivore community, I recorded 69 bird species, 35 of them frugivores, and five primate species, all of them frugivores (Appendix 7.1). Among the frugivores, 19 species were forest specialists, 18 were forest generalists and three were forest visitors (Appendix 7.1). I found significantly more frugivorous species and forest specialist species in LD than in HD sites, but no significant differences for forest generalists and forest visitors (Table 3.1, Fig. 3.2). This result was similar when I analyzed birds and primate species separately, except that I detected significantly more generalist primate species in LD sites ($F_{1,\ 18} = 9.87$ $P = 0.0056$). When frugivore densities between the LD and HD sites were compared, LD sites had significantly higher densities of all frugivores and of forest specialists. Densities of forest generalists and forest visitors did not differ between LD and HD sites (Table 3.1, Fig. 3.2). When bird and primate densities were analyzed separately, densities of generalist primates were significantly higher in LD than in HD sites (log(x+1) density: $F_{1,\ 18} = 8.73$, $P = 0.0085$). With regard to forest identity, Kakamega forest had the highest number of forest generalist species and Budongo Forest had the highest densities of forest generalists.

Table 3.1: Number of species and log(x+1) densities of all frugivores in the frugivore community, of forest specialists, forest generalists and forest visitors as a function of disturbance regime and forest identity. ANOVA, N = 22. Given are model and error DF-, *F*-, *P*- and R^2 values; ***P*<0.01, **P*<0.05, +0.05<*P*<0.1, ns = not significant.

Species	Model DF Error DF	All species	Forest specialists	Forest generalists	Forest visitors
Whole model	3,18	3.84*	3.18*	2.59+	0.76ns
Disturbance	1,18	4.69*	7.95*	0.42ns	0.0ns
Forest	2,18	3.41+	0.79ns	3.68*	1.13ns
R^2	-	0.39	0.35	0.30	0.11
Density					
Whole model	3,18	3.69*	3.43*	3.12+	0.04ns
Disturbance	1,18	4.86*	9.31**	0.08ns	0.06ns
Forest	2,18	3.11+	0.49ns	4.64*	1.53ns
R^2	-	0.38	0.36	0.34	0.15

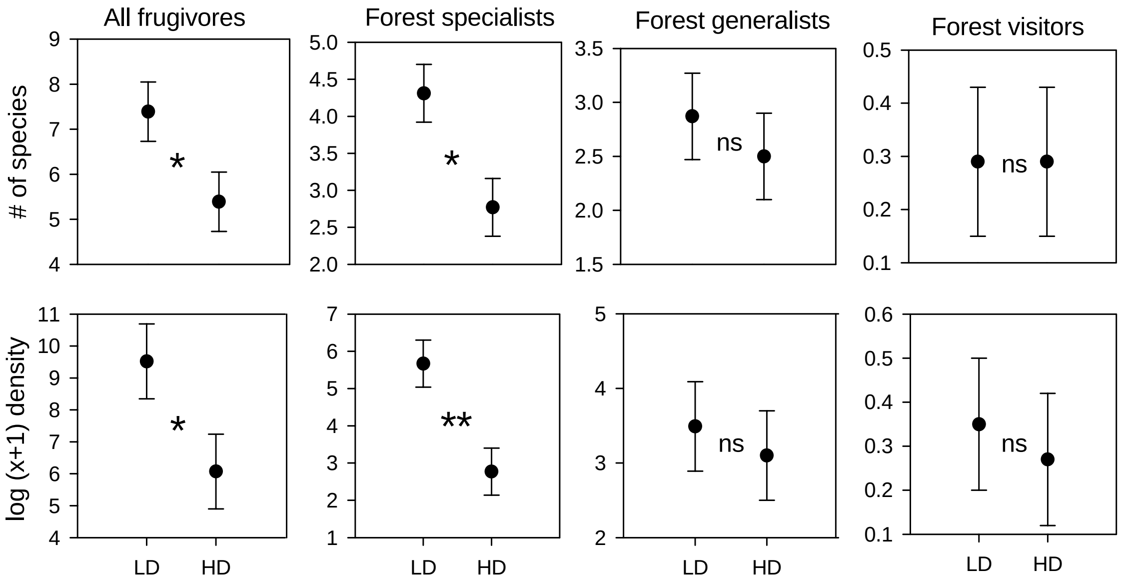

Figure 3.2: Number of species and log (x+1) densities of all frugivores in the frugivore community, of forest specialists, forest generalists and forest visitors in relation to disturbance regime (LD = little disturbed, HD = heavily disturbed). Given are least square means (± SE) controlling for forest identity (see Table 1), **$P<0.01$, *$P<0.05$, ns = not significant. Note different scaling of y-axis.

3.3.2 Frugivore assemblage

I recorded 42 frugivorous animal species over all *C. durandii* trees studied, 38 species of birds and four species of primates (Table 3.2). Among the frugivores, 19 species were forest specialists, 16 forest generalists and seven forest visitors (Table 3.2). I recorded significantly more frugivorous species and forest specialist species in trees located in LD than in HD sites (Table 3.3, Fig. 3.3), with no apparent differences for forest generalists and visitors. Mabira Forest had the highest number of forest visitor species while Kakamega Forest had the lowest.

Similarly, the numbers of all frugivorous individuals and of forest specialist individuals were significantly higher in LD than in HD sites, with no effect on forest generalists and visitors (Table 3.3, Fig. 3.3). When birds and primate individuals were analyzed separately, there were significantly more birds in LD than in HD sites ($F_{1, 13} = 14.8$, $p = 0.002$) whereas primate individuals did not differ between LD and HD sites ($F_{1, 18} = 1.3$, $p = 0.27$). The numbers of all frugivorous individuals and of forest specialist individuals were highest in Budongo Forest and lowest in Kakamega Forest. The covariate general fruit availability had a negative effect on the numbers of all frugivore individuals and of forest specialist individuals visiting the trees (Table 3.3). Furthermore, the numbers of all frugivorous individuals and of forest specialist individuals were influenced by a significant interaction between disturbance and fruit availability (declines in number of individuals with increasing fruit availability in heavily disturbed but not in little disturbed forest). Also, there was a significant interaction between forest and fruit availability (decrease in number of frugivores with increasing fruit availability in Budongo Forest, but not in Mabira and Kakamega Forest).

Table 3.2: Frugivore species visiting *Celtis durandii* trees during tree observations ordered by sum of individuals. Given is forest specialization, sum of individuals recorded over 58 scans per tree for the 44 trees, average number of seeds removed per minute over the three forests, and presence of frugivores during scan sampling in LD and HD sites for each forest.

Common name Scientific name	Forest specialization[a]	Sum of individuals	Seeds[b] Removed min^{-1}	Budongo[c]		Mabira[c]		Kakamega[c]	
				LD	HD	LD	HD	LD	HD
Yellow-whiskered Greenbul *Andropadus latirostris*	FG	451	0.34	+	+	+	+	+	+
Yellow-throated Tinkerbird *Pogoniulus subsulphureus*	FS	316	0.66	+	+	+	+	-	-
Speckled Tinkerbird *Pogoniulus scolopaceus*	FG	285	0.67	+	+	+	+	-	-
Grey-headed Negrofinch *Nigrita canicapilla*	FG	283	0.60	+	+	+	+	+	+
Slender-billed Greenbul *Andropadus gracilirostris*	FS	251	0.89	+	+	+	+	+	+
Little Greenbul *Andropadus virens*	FG	153	0.92	+	+	+	+	+	+
Little grey Greenbul *Andropadus gracilis*	FS	129	0.84	+	+	+	+	-	-
Cameroon-sombre Greenbul *Andropadus curvirostris*	FS	99	0.79	+	+	+	+	+	+
Yellow-rumped Tinkerbird *Pogoniulus subsulphureus*	FG	70	0.64	-	-	-	-	+	+
Red-tailed Monkey *Cercopithecus ascanius*	FS	69	3.50	+	+	+	+	+	+
White-breasted Negrofinch *Nigrita fusconata*	FG	68	0.65	-	-	+	+	+	-
Blue Monkey *Cercopithecus mitis*	FS	54	3.49	+	+	-	-	+	+
Ansorge's Greenbul *Andropadus ansorgei*	FS	50	0.89	-	-	-	-	+	+
Spotted Greenbul *Ixonotus guttatus*	FS	46	1.19	+	+	-	-	-	-
Dark-backed Weaver *Ploceus bicolor*	FV	37	0.77	-	-	-	-	+	+
Black-necked Weaver *Ploceus nigricollis*	FV	32	0.76	-	-	+	+	+	-
White-throated Greenbul *Phyllastrephus albigularis*	FS	31	1.22	+	-	+	-	-	-
Shelley,s Greenbul *Andropadus masukuensis*	FS	29	0.91	-	-	-	-	+	+
Yellow White Eye *Zosterops senegalensis*	FV	27	0.42	+	-	+	+	-	-
Red-tailed Greenbul *Criniger calurus*	FS	26	0.9	+	-	+	-	-	-
Violet-backed Starling *Cinnyricinclus leucogaster*	FV	26	1.25	-	+	-	-	-	-
Grey-cheeked Mangabey *Lophocebus albigena*	FS	23	3.96	-	-	+	+	-	-

Common name Scientific name	Forest specialization[a]	Sum of individuals	Seeds[b] Removed min^{-1}	Budongo[c]		Mabira[c]		Kakamega[c]	
				LD	HD	LD	HD	LD	HD
Western Black-headed Oriole *Oriolus brachyrhynchus*	FG	20	1.17	+	-	+	+	+	+
Red-headed Malimbe *Malimbus rubricollis*	FS	19	1.18	+	+	+	-	+	+
Rufous Flycatcher Thrush *Stizorhina fraseri*	FS	19	0.58	+	-	+	-	-	-
Joyful Greenbul *Chlorocichla laetissima*	FG	17	0.85	-	-	-	-	+	+
Honey-guide Greenbul *Baeopogon indicator*	FS	15	1.1	-	-	+	-	+	+
Grosbeak Weaver *Amblyospiza albifrons*	FV	12	x	-	-	+	+	-	-
Grey-throated Barbet *Gymnobucco bonapartei*	FG	11	1.1	-	-	-	-	-	+
Red-tailed Bristlebill *Bleda syndactyla*	FS	10	1.21	-	-	+	-	+	+
Yellow-billed Barbet *Trachyphonus purpuratus*	FG	9	1.1	-	+	-	-	+	+
Yellow-spotted Barbet *Pogoniulus duchaillui*	FS	9	1	-	-	+	+	+	+
Vieillot's Black Weaver *Ploceus nigerrimus*	FV	8	x	-	-	+	+	-	-
Common Bulbul *Pycnonotus barbatus*	FV	7	0.67	-	-	+	+	-	-
Hairy-breasted Barbet *Tricholaema hirsute*	FG	7	0.86	-	-	+	-	+	-
Yellow-mantled Weaver *Ploceus tricolor*	FS	6	1.64	+	-	+	+	-	-
Black and white Colobus *Colobus guereza*	FG	5	x	+	-	-	-	-	-
Cabanis Greenbul *Phyllastrephus cabanisi*	FS	5	0.82	-	-	-	-	+	+
Purple-headed Starling *Lamprotornis. purpureiceps*	FG	5	1.39	+	+	-	+	-	-
Red-headed Blue Bill *Spermophaga ruficapilla*	FG	2	0.81	-	-	-	+	-	-
Great Blue Turaco *Corythaeola cristata*	FG	1	x	-	-	+	-	-	-
Tambourine Dove *Turtur tympanistra*	FG	1	x	+	-	-	-	-	-

[a] Forest specialization: FS = forest specialist, FG = forest generalists, FV = forest visitor according to Bennun *et al* (1996) for birds, and M. Cords and C. Chapman (pers. comm.) for primates.

[b] x = No data as the species had only been observed during scan sampling and not focal sampling.

[c] + = present, - = absent.

Table 3.3: Number of all frugivorous species and log(x+1) of all individuals visiting *C. durandii*, of forest specialists, forest generalists and forest visitors as a function of disturbance regime, forest identity, log fruit availability and two-way interaction terms. ANCOVA, N = 22. Given are Model and Error DF-, *F*-, *P*- and R^2 values; ****P*<0.001 ***P*<0.01, **P*<0.05, +0.05<*P*<0.1, ns = not significant.

Species	Model DF, error DF	All frugivores	Forest specialists	Forest generalists	Forest visitors
Whole model	3,18	3.47*	5.15**	1.27ns	2.98ns
Disturbance	1,18	7.51*	14.73**	0.76ns	0.0ns
Forest	2,18	1.46ns	0.36ns	1.52ns	4.48*
R^2	-	0.37	0.46	0.17	0.33
Individuals					
Whole model	7,14	5.61**	6.74**	0.29ns	0.83ns
Disturbance	1,14	16.77**	31.79***	0.32ns	1.22ns
Forest	2,14	13.39***	11.37**	0.32ns	0.05ns
Log fruit availability	1,14	20.11***	14.58**	-	-
Log fruit availability*disturbance	1,14	9.19**	4.85*	-	-
Log fruit availability*forest	2,14	6.93**	6.33*	-	-
R^2	-	0.74	0.77	0.05	0.12

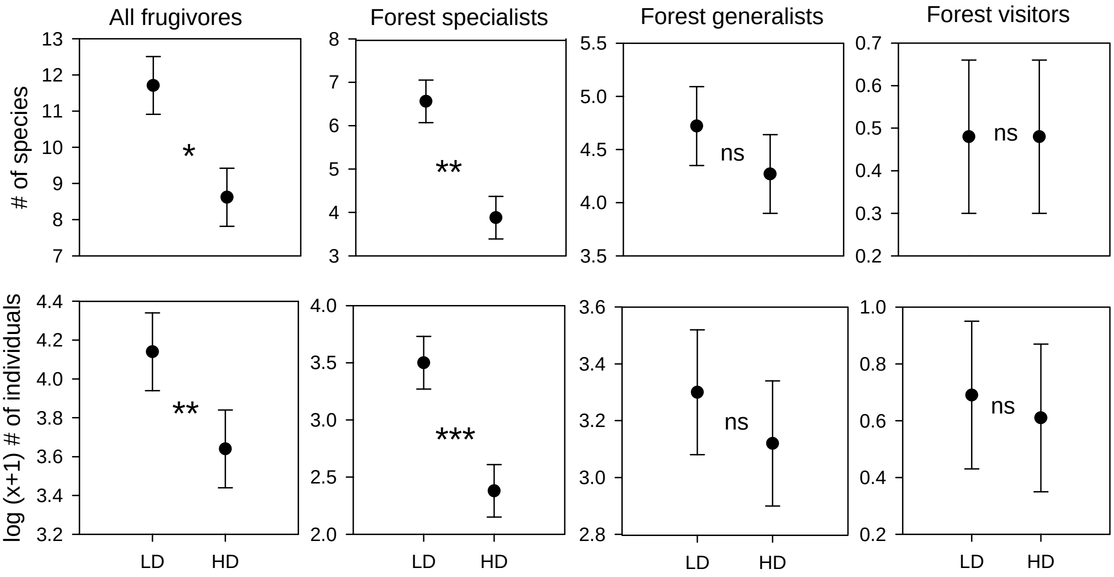

Figure 3.3: Number of species and log (x+1) individuals of all frugivores visiting *C. durandii*, of forest specialists, forest generalists and forest visitors in *C. durandii* trees recorded during 58 scan samples in relation to disturbance regime. For abbreviations see Fig. 2. Given are least square means (± SE) controlling for forest identity and potential covariates and interaction terms (see Table 3), ****P*<0.001, ***P*<0.01, **P*<0.05, ns = not significant. Note different scaling of y-axis.

3.3.3 Seed removal

The number of seeds removed in 58 minutes by frugivores differed marginally significantly between LD and HD sites with LD sites having a slightly higher number of seeds removed (Table 3.4, Fig. 3.4). When frugivorous birds and primates were analyzed separately, avian frugivores removed a significantly higher number of seeds in LD sites than in HD sites ($F_{1,\,14} = 15.42$, $P = 0.0015$) whereas there was no significant difference for number of seeds removed by primates between the two disturbance regimes ($F_{1,\,18} = 0.072$, $P = 0.93$). A significantly higher number of seeds were removed by forest specialists in LD than in HD sites with no apparent difference in those dispersed by generalists. Forest visitors removed slightly, but not significantly more seeds in HD than in LD sites (Table 3.4, Fig. 3.4).

Table 3.4: Log (x+1) number of seeds removed by all frugivorous species, by forest specialists, forest generalists and forest visitors as a function of disturbance regime and forest identity. ANOVA, N = 22. Given are Model and Error DF-, *F*-, *P*- and R^2 values; $**P<0.01$, $*P<0.05$, $+0.05<P<0.1$, ns = not significant.

	Model DF, error DF	All frugivores	Forest specialists	Forest generalists	Forest visitors
Whole model	3,18	1.63ns	3.20*	0.22ns	1.65ns
Disturbance	1,18	3.35+	8.66**	0.31ns	0.72ns
Forest	2,18	0.77ns	0.47ns	0.18ns	2.12ns
R^2	-	0.21	0.35	0.04	0.22

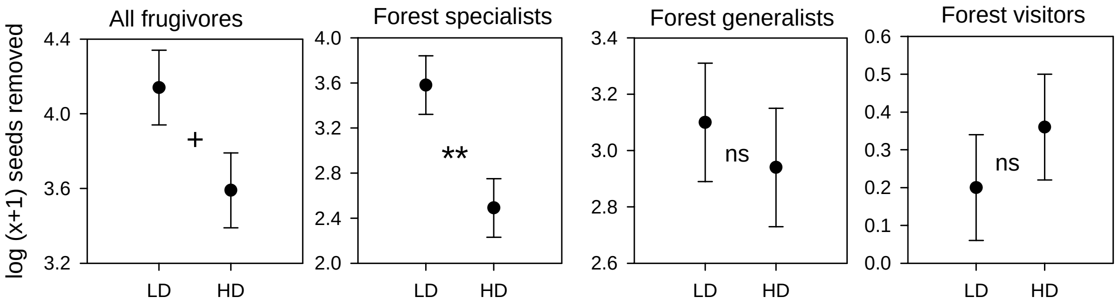

Figure 3.4: Log (x+1) number of seeds removed per tree in 58 minutes by all frugivorous species combined, by forest specialists, forest generalists and forest visitors in relation to disturbance regime. For abbreviations see Fig. 3.2. Given are least square means (± SE) controlling for forest identity (see Table 4), $**P<0.01$, $+0.05<P<0.1$, ns = not significant. Note different scaling of y-axis.

3.4 Discussion

This study is the first to demonstrate that small-scale forest disturbance had an impact on frugivores and their ecosystem function of seed removal. My results have shown that forest disturbance diminished the frugivore community in general, and forest specialists in particular. Furthermore, there was a significant reduction in frugivorous species and individuals visiting my study trees which led to a marginally significant decline in fruit removal by all frugivores and a significant reduction in removal by birds and by forest specialists.

My results on the frugivore community showed that frugivores were sensitive to small-scale forest disturbance (Fig. 3.2). This concurs with other studies that have reported declines in frugivores due to moderate disturbance (Chapman *et al.* 2000, Gray *et al.* 2006). When habitat specialization was considered, forest specialists were strongly affected by disturbance, while forest generalists and visitors seemed unaffected (Fig. 3.2). The high sensitivity of forest specialists to local disturbance might be due to their preference of closed canopy forests; they are rarely reported even in secondary forests (Bennun *et al.* 1996). This sensitivity of specialists to disturbance is not only restricted to birds (Brook *et al.* 2003, Mason 1996, Peh *et al.* 2005, Raman 2001, Tejeda-Cruz & Sutherland 2005, Woltmann 2003), but has also been reported in primates (Chapman *et al.* 2006). My results on forest generalists and forest visitors are in line with observations that these two groups forage and even breed in disturbed and secondary forests (Bennun *et al.* 1996).

Results for the frugivore assemblage visiting *C. durandii* trees matched well with the results on the frugivore community (Fig. 3.3). Such a pattern might be expected since frugivores visiting the trees are recruited from the pool of frugivores in the community. Therefore, any change in the frugivore community due to disturbance is expected to be reflected in the visitation rates of the trees. Thus, I recorded significantly fewer frugivore species and individuals visiting the trees in HD sites. Just like for the frugivore community results above, I documented significantly lower visitation rates by forest specialists (both species and individuals) in HD sites. In addition, visitation rates by both forest generalists and forest visitors did not differ significantly between LD and HD sites.

High fruit availability in the surrounding forest had a negative effect on frugivore visitation rates, i.e. the number of tree visitors declined with increasing fruit availability in the vicinity. Such an effect might be caused by competition among tree species for frugivores and indicate that frugivores are a limiting factor for seed removal. *Celtis durandii* appears to be affected negatively by such competition, possibly because the fruits might not be attractive for frugivores. Similarly, high fruit availability in the surrounding forest leads to low visitation rates in the tree *Ficus thonningii* in Kakamega Forest (Kirika *et al.*, submitted manuscript). In contrast, high fruit availability has a positive effect on frugivore visitations of the tree *Prunus africana* in the same forest (Farwig *et al.* 2006). Thus, in the latter study, high fruit availability appears to attract frugivores to the forest stand which then results in high visitations rates of *P. africana* (Farwig *et al.* 2006). These contrasting results could be due to different attractiveness of the fruits of the three species, with *C. durandii and F. thonningii* having low and *P. africana* having high attractiveness. The difference in attractiveness could emanate from fruit size (Alcántara & Rey 2003), fruit colour (Voigt *et al.* 2004) or chemical characteristics (Witmer & Soest 1998). Currently, it is not clear which of these factors influences frugivore choice in East African forests.

Local forest disturbance had a negative effect on frugivore visitation rates of *C. durandii* (this study) and of *F. thonningii* (Kirika *et al.*, submitted manuscript), but a positive effect on *P. africana* (Farwig *et al.* 2006). Trees with potentially unattractive fruits such as *C. durandii* and *F. thonningii* obviously suffer from small-scale forest disturbance and an impoverished frugivore community, whereas trees with potentially attractive fruits such as *P. africana* might even benefit. These differences in attractiveness of fruits could in the long term influence tree regeneration and community-wide tree species diversity. Crop size has also been reported to have an influence on visitation rates and hence fruit removal (Eshiamwata *et al.* 2006, Githiru *et* *al.* 2002, Korine *et al.* 2000, Nogales *et al.* 1999) but this was not evident in my study probably because I selected trees with large crop sizes in all the sites.

Patterns in seed removal followed the patterns in the frugivore community and in frugivore tree visitation rates (Fig. 3.4). I recorded a marginally lower number of seeds removed by all frugivores in HD than in LD sites. Still, seed removal by forest specialists was significantly reduced, clearly showing that dispersal services for *C. durandii* trees by forest specialists were impoverished in HD sites. A separate analysis of birds and primates revealed that significantly fewer seeds were removed by frugivorous birds in HD sites with no difference in seed removal by primates. The lack of significant differences in seed removal by primates was not surprising since primate individuals too did not differ between LD and HD sites.

Fewer numbers of removed seeds is expected to lead to less seed dispersal. Many studies demonstrated that seed dispersal is important for tree regeneration (Bleher & Böhning-Gaese 2001, Luck & Daily 2003, Makana & Thomas 2004). For example, seed passage through chimpanzee’s guts increases the percentage of seeds that germinate and shortens germination time of *C. durandii* (Wrangham *et al.* 1994). So with continued disturbance, regeneration of *C. durandii* could eventually be impaired in HD sites. First results on the seedling community in differently disturbed sites in the three forests demonstrated that the density of *C. durandii* seedlings is indeed lower in HD than in LD sites (mean number of seedlings in LD sites: 8.92 seedlings ha^{-1}, in HD sites: 4.25 seedlings ha^{-1}, J.M. Kirika, unpublished data). Frugivore density in the same study sites and forests is in general the most important factor determining species richness of tree seedlings (Kirika *et al.*, submitted manuscript).

With regard to habitat specialization, it has been postulated that forest generalists would compensate for the loss of forest specialists leading to stability of their total ecosystem service (Brotons *et al.* 2003). However, this was not evident in my study since removal rates by forest generalists did not differ significantly between LD and HD sites (Fig. 3.4). I recorded slightly more seeds removed by forest visitors in HD than in LD sites but this too was not significant (Fig. 3.4). Hence the expected compensation between the forest dependency groups was not apparent in my study. Consequently, the lower ecosystem service due to loss of forest specialists was not replaced by the services of forest generalists or visitors. Therefore in this system there seems to be no redundancy of species on a between-group level. Nevertheless, there might be some redundancy of species at the within-group-level. Within each forest dependency group, declines in the dispersal service of some species might have been partly substituted by other species. However, small sample sizes at the species-level did not allow for testing such effects.

My results demonstrate that small-scale, local forest disturbance led to a decline in frugivorous animals and low visitation and seed removal rates of a small-seeded Afrotropical tree. My study was conducted in three East African rainforests, suggesting that these results apply not only to one forest in particular but are also consistent at a regional scale. Recently, a meta-analysis demonstrated that small-scale, local forest disturbance causes widespread, general declines of frugivorous birds in tropical forests (Gray *et al.* 2006). Thus, I expect that the seed removal service of frugivorous birds could be on the decline not only in East Africa but also in other similarly disturbed areas of the world. My results on the small-seeded Afrotropical tree *C. durandii* seem to contradict the notion that small-fruited and -seeded trees are less vulnerable to disperser failure because they are visited by a larger suite of dispersal agents than large-seeded trees (da Silva & Tabarelli 2000, Peres & van Roosmalen 2002). My study demonstrates that seed dispersal and seedling establishment of small-seeded trees may be as impaired by disturbance as those of large-seeded trees. So, disturbance-mediated frugivore declines can potentially disrupt seed dispersal and regeneration more generally than previously anticipated.

3.5 Summary

Small-scale local disturbance of tropical forests, for example through selective logging, is widespread, but its effects on biodiversity and ecosystem function are little studied. I investigated the effect of different levels of small-scale, local forest disturbance in three East African tropical rainforests, firstly, on the frugivore community and, secondly, on tree visitation and fruit removal rates of a small-seeded tree *Celtis durandii*. To characterize the frugivore community, I quantified birds and primates in little and heavily disturbed sites, distinguishing between forest specialists, forest generalists and forest visitors. I determined frugivorous tree visitors and seed removal rates of 44 *C. durandii* trees in the same sites. The results demonstrated that forest disturbance reduced the species richness and density of the frugivore community in general and of forest specialists in particular. I recorded a significant reduction in frugivorous species and individuals visiting the study trees which led to a marginally significant decline in fruit removal by all frugivores and a significant reduction in removal by birds and forest specialists. Lower rates of seed removal by forest specialists were not compensated by increases in those of forest generalists or visitors. The results did not differ among the three rainforests, suggesting that they were consistent at a regional scale. So, small-scale, local forest disturbance led not only to a loss of frugivores, but also to a decline of their seed removal services. This decline impacted not only large-seeded tree species, but also a tree with small fruits. Thus, small-scale forest disturbance appears to have a

more general negative impact on frugivores and their seed dispersal services than previously anticipated.

4 TREES, FRUGIVORES AND FOREST REGENERATION ALONG A HUMAN DISTURBANCE GRADIENT IN EAST AFRICAN RAINFORESTS

4.1 Introduction

Global forest destruction has accelerated in the last few decades with negative impact on forest-dependent plants and animals (Laurance 1999, Laurance & Bierregaard 1997, Pimm & Raven 2000, Whitmore 1997). Most previous studies focused on severe forms of forest disturbance such as forest loss and fragmentation (Laurance *et al.* 2001, Turner 1996). Thus, the consequences of less severe habitat disturbance, where some resemblance of forest remains (e.g. following selective logging, firewood collection, charcoal burning, grazing) are less clear (Hill & Hamer 2004). Since modified and degraded forests now form an increasingly large proportion of tropical landscapes (Peres *et al.* 2006) ecologists urgently need to investigate the effect of this moderate disturbance on species diversity and ecosystem processes.

Small-scale forest disturbance, for example in form of selective logging, fire-wood collection, charcoal burning and grazing, can have complex direct and indirect effects on forest ecosystems. Three particularly important and closely connected components of tropical forests are the tree community, the frugivores, and the seedling community (Fig. 4.1). Disturbance can have both direct and indirect effects on these components.

Small-scale forest disturbance, especially in the form of selective logging is expected to directly influence the species richness and composition of the tree community (Bleher *et al.* 2006, Sagar & Singh 2004, Shanker *et al.* 1998). Indeed this has been shown to be the case especially in fragmented landscapes (Hill & Curran 2003, Ross *et al.* 2002). However, there is a surprising lack of studies on the effects of forest disturbance on the tree community in continuous forests.

In addition to these direct effects of disturbance on the tree community, indirect and long-term effects can be expected because disturbance influences also other groups of species in the forest and can lead to changes in ecosystem processes. An important group of species and a process that links the tree community to forest regeneration is the frugivore community and seed dispersal (Fig. 4.1). Frugivorous animals are the dominant group of vertebrates in a number of tropical forests and can make up over 80% of the total mammalian and avian biomass (Estrada *et al.* 1997, Terborgh 1986). Correspondingly, seed dispersal by animals is one of the most important mutualistic interactions in tropical forests since up to 90% of all tree and shrub species produce fleshy fruits adapted to animal dispersal (Howe & Smallwood 1982). Disturbance in terms of forest fragmentation has been demonstrated to change the frugivore community and seed dispersal rates (Cordeiro & Howe 2001, 2003, Duncan & Chapman 1999, Githiru *et al.* 2002, Holl *et al.* 2000). In some studies also small-scale disturbance effects were detected (Farwig *et al.* 2006, Peh *et al.* 2005, Wunderle *et al.* 2006).

Finally, human disturbance affects forest regeneration. Regeneration is a central component of forest ecosystem dynamics (Swaine 1996). In tropical rainforests, seedlings are probably the most important regenerative pool of most long-lived tree species (Martînez-Ramos & Soto-Castro 1993). Disturbance of forests has been demonstrated to affect seedling diversity and abundance through alteration in tree phenology (Magnusson & Costa 2003), suppression of seedlings by increases in liana densities (Schnitzer & Carson 2001), infection of seedlings by fungal pathogens (García-Guzmán & Benítez-Malvido 2003) and increased seedling predation (Struhsaker 1997). In addition, changes in abiotic conditions such as light, temperature and humidity have an impact on seedling establishment (Ellison *et al.* 1993, Makana & Thomas 2005). These impacts of disturbance on seedling communities, in the long-term, probably lead to changes in the species richness and abundance of tree communities (Bond 1995, Hurtt & Pacala 1995).

Just focusing on trees, frugivores and seedlings demonstrates that it is difficult to disentangle direct and indirect effects of forest disturbance (Fig. 4.1). Disturbance can influence tree, frugivore, and seedling communities directly (Fig. 4.1, links between disturbance and trees, disturbance and frugivores, and disturbance and seedlings). Furthermore, tree communities themselves affect frugivores (Levey 1988a, Moegenburg & Levey 2003, link between trees and frugivores) and seedling communities (Dalling *et al.* 1998, Hubell *et al.*1999, link between trees and seedlings). Finally, frugivores can shape the pattern of regenerating seedlings (Bleher & Böhning-Gaese 2001, Chapman & Chapman 1996, link between frugivores and seedlings). Whereas a number of studies have investigated direct links in this network of interactions (e.g. between disturbance and tree species richness (Kariuki & Kooyman 2005) or disturbance and seedling species richness (Benítez-Malvido & Lemus-Albor 2005), to my knowledge, no study has tried to disentangle this more complex network of direct and indirect effects.

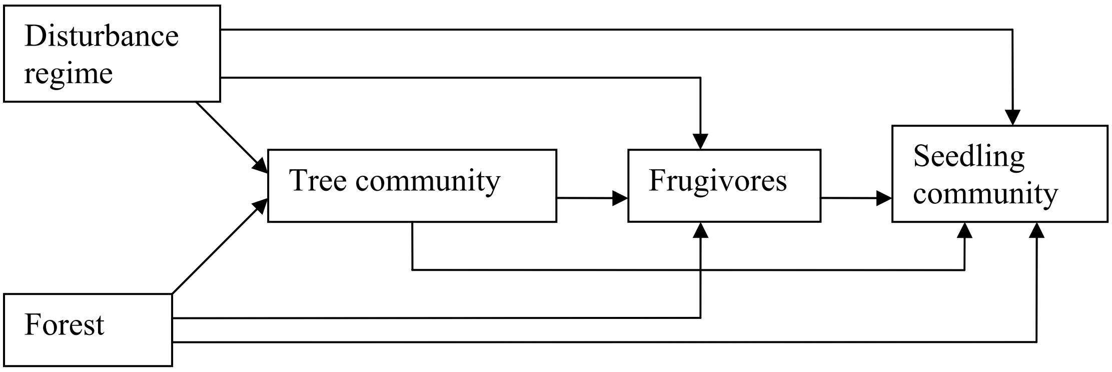

Figure 4.1: Links showing the assumed relationship between disturbance regime, forest identity, tree community, frugivore community and seedling community. Forest identity was included in the model, because in my study, disturbance regime was analysed within and between three East African rainforests (Budongo, Mabira, and Kakamega Forest).

In the present study, I investigated direct and indirect effects of small-scale, local forest disturbance on the species richness of fleshy-fruited trees, the density of frugivores (including birds and primates), and the species richness of fleshy-fruited seedlings. My study areas, Budongo Forest and Mabira Forest in Uganda, and Kakamega Forest in Kenya lay along a west-east gradient across the East African highlands. The three forests share almost similar present and past disturbance regimes and have little and heavily disturbed sites. In addition, a small section of Budongo Forest has been protected effectively from human disturbance and is considered a primary forest. I investigated direct effects of small-scale disturbance by testing the effect of disturbance on fleshy-fruited trees, on frugivores, and on fleshy-fruited seedlings. I investigated indirect effects, by testing whether tree communities affected frugivores and seedling communities and whether frugivores influenced seedling communities. In the case of indirect effects of disturbance on seedling communities I expected that small-scale disturbance would change tree species richness, which in turn would lead to changes in frugivore density, which would ultimately affect seedling species richness.

4.2 Materials and methods

4.2.1 Study area

The study was carried out in three tropical rainforests in East Africa, Budongo and Mabira forests in Uganda and Kakamega Forest in Kenya (Fig. 4.2). Budongo Forest (1° 35'N – 1°55'N, 31°8'E –31°42'E, 1100 m altitude, 428 km^2 area of forest cover) is the most western of the three forests and closest to the Congo-Guinean rainforest belt (Fig. 4.2). Average annual precipitation is about 1410 mm with rainfall mostly between April and May and between August and October. Budongo is described as a medium-altitude, semi-deciduous forest, with a tendency for *Cynometra alexandri* to become mono-dominant (Plumptre 1996). Selective logging and treatment with arboricides has altered the forest composition into a mosaic of forest types of which mixed forest is now the most common type (Plumptre 1996). The forest has about 465 species of trees and shrubs. The study was carried out in compartment N15 (never logged) herein referred to as primary forest (PF), N3 (selectively logged in 1947-52) herein referred to as little disturbed site (LD), and W22 (selectively logged in 1963-64 and again in 1996-97) herein referred to as heavily disturbed site (HD). For more details on Budongo forest see Eggeling (1947), Howard (1991), Plumptre (1996), and Plumptre & Reynolds (1994).

Mabira Forest (0° 23'N – 0°35'N, 32°50'E – 33°7'E, 1150 m altitude, about 306 km^2 forest cover) is located in Mukono district of central Uganda and lies between Budongo and Kakamega Forest (Fig. 4.2). Annual precipitation is 1640 mm. The vegetation can be broadly classified as medium-altitude, moist semi-deciduous forest (Howard 1991). Mabira Forest reserve has been subjected to extensive encroachment, pit-sawing, charcoal burning and hunting in the past and present. Study sites in Mabira were identified from land-use maps and Geographic Information System (GIS) coverages compiled by the Forest Department and were verified by ground-truthing. Sites were grouped into LD and HD sites depending on the level of anthropogenic disturbance. LD sites were characterised by relatively undisturbed forest with no large-scale logging activity, although localised pit-sawing was evident, HD sites were those close to past and present settlement areas and were characterised by intense anthropogenic disturbance. For more details on Mabira Forest see Howard (1991) and Naidoo (2004).

Kakamega Forest (0º10′N – 0º21′N, 34º47′E – 34º58′E, 1550-1650 m altitude; Bennun & Njoroge 1999) is a mid-altitude tropical rainforest and is considered to be the eastern most outlier of the Congo-Guinean rainforest belt (Kokwaro 1988) (Fig. 4.2). Kakamega Forest receives an average annual rainfall of between 1200 mm and 2100 mm per year (Emerton 1994). The main forest area covers about 85 km^2 of near natural forest (BIOTA East 2004) that is surrounded and interspersed by secondary forest, clearings and glades, as well as tea and timber plantations (Bennun & Njoroge 1999). Kakamega Forest is very diverse with over 380 species of plants having been identified of which over 150 species are woody trees, shrubs and vines, many of which are of Congolean lowland forest affinities (Kokwaro 1988). Kakamega Forest has experienced a long disturbance history including encroachment, commercial and selective logging, firewood collection, charcoal burning, etc. (Mitchell 2004, Tsingalia 1990). Areas managed by the Kenya Wildlife Service have lower levels of human disturbance while those managed by the Forest Department have higher levels of disturbance (Bleher *et al.* 2006). Thus, study sites under the management of the Kenya Wildlife Service were defined as little disturbed (LD) and those under the management of the Forest Department as heavily disturbed (HD). For more details on Kakamega Forest see Kokwaro (1988), Mitchell (2004) and Tsingalia (1990).

The disturbance regimes in the three different forests are comparable because forest structure is mainly determined by selective logging. Primary forest sites in Budongo Forest had an average of 81.7% closed canopy while little disturbed sites in the three forests had on average 72.7% canopy cover. Heavily disturbed sites in the three forests had rather open canopies with an average cover of 50.0%.

Figure 4.2: Map of Kenya and Uganda showing the location of Budongo, Mabira and Kakamega forests. Courtesy of G. Schaab.

4.2.2 Sampling regime

I established in Budongo Forest 12 one-hectare plots (6 plots in PF, 3 plots in LD and 3 plots in HD sites) and in Kakamega and Mabira Forests 6 one-hectare plots (3 plots in LD and 3 plots in HD sites, respectively). Plots were at least 100 m from the forest edge in order to reduce edge effects. Each of the one-hectare plots consisted of 5 transects of 100 m length with neighbouring transects separated from each other by 20 m and the first and the last transect placed 10m from the edge of the plot. Censuses of the tree, frugivore and seedling communities were carried out between November 2004 and

March 2006, sampling the different forests and disturbance regimes in random order with regard to dry and wet season. For each site and season, birds, primates, fruits and seedlings were counted simultaneously (i.e. within two weeks).

4.2.3 Tree community

I identified and counted all trees > 10 cm dbh on the one-hectare plots by walking along the 5 transects recording all trees within 10 m to the left and 10 m to the right of the transect (thereby covering the total area of one-hectare). I defined as trees all woody plants, but excluding shrubs, herbs and climbers. In the analysis, I focused on fleshy-fruited tree species dispersed by frugivorous birds and primates because I expected significant links between trees and these frugivores, and between frugivores and seedlings only for tree species dispersed by birds and primates. Thus, tree species were classified as either fleshy-fruited and dispersed by birds and/or primates, or as non-fleshy fruited and dispersed by other means (e.g. ungulates, wind, explosive mechanism, gravity). I defined trees as fleshy-fruited if fruits were berries, drupes or dehiscent and had fleshy arils. For this classification I used data compiled from studies in Malawi (Dowsett-Lemaire 1988), South Africa (Bleher *et al.* 2003) and Kenya (B. Bleher, unpublished data) and tree field guides for South Africa (Pooley 1994) and Kenya (Beentje 1994). For analysis I compiled the number of fleshy-fruited tree species per plot.

In addition to the tree community, fruit availability might influence the frugivore community. Thus, I recorded fruit availability on the one-hectare plots by walking along the 5 transects in each plot and recording all trees and shrubs bearing ripe fruits which might be consumed by frugivorous animals 10 m to the left and 10 m to the right of the transect (again, covering the total area of one-hectare). For each tree the presence and number of ripe fruits were estimated *in situ* on a logarithmical scale (1 to 10, 10 to 100, 100 to 1 000, 1 000 to 10 000, >10 000 fruits) and the total number of fruits per plot was calculated.

4.2.4 Frugivore community

The frugivore community was quantified separately for birds and primates as both groups of species require different sampling designs. Birds were counted on the one-hectare plots using point counts. Point counts are widely used as a standard method for sampling forest birds (Bibby *et al*. 1992). I established nine point count locations within each one-hectare plot, with three points placed along the first transect (at 10, 50, and 90 m), three points along the third transect and three along the fifth transect. Point count locations were 40 m distant from each other. Birds were censused early in the morning (0700-0900 h). At each point count location, I recorded all birds heard or seen for ten minutes within a radius of 20 m. Bird species were identified according to Stevenson & Fanshawe (2002). For analysis I focused on frugivorous birds. I defined birds as frugivores if they were seen feeding on fruits during the study or have been described as being obligate or partial frugivores in the literature (Kissling *et al*. 2007). For seed dispersal and seedling establishment, I assumed that the number of frugivorous animals was more important than the species richness of frugivorous animals (Farwig *et al*. 2006). Hence, I calculated the number of frugivorous birds by adding up all frugivorous bird individuals counted over the nine point count locations per plot. I then calculated frugivorous bird density by dividing the total number of birds per plot by the area censused within each plot ($9 \times (20\ \text{m})^2 \times \pi = 11304\ \text{m}^2$).

Primates were counted using a 500 m long line transect running through the center of each plot. I used transects because primates generally live in groups and in low densities (National Research Council 1981). The transect extended 400 m beyond the edges of the plot. Primate censuses were carried out from 0900–1200 h recording all primate species and individuals heard or seen < 50 m on each side of the transect. Primate counts were repeated three times for each transect, again to account for the patchy distribution and low density of primates. Primates were identified according to Kingdon (1997). All primates recorded in this study are considered to be at least partly frugivorous. Primate density was calculated by dividing the number of primate individuals counted in the three censuses by the area covered during census (3 counts × 500 m length × 100 m width = 150000 m^2). To obtain overall frugivore density, frugivorous bird densities (calculated as number of bird individuals per hectare) and primate densities (calculated as number of primate individuals per hectare) were added up and frugivore density was log-transformed.

4.2.5 Seedling community

I quantified the seedling community by establishing on each one-hectare plot, 90 × 1 m^2 subplots following the design by Harms *et al.* (2000). The 1 m^2 subplots were established in groups of three with 6 groups along each transect (at 0, 20, 40, 60, 80, and 100 m). Groups of three subplots were separated from the respective transect by 2 m. During mapping wire frames were laid down to demarcate the area. All seedlings of tree species were identified to species level and their numbers were counted. I defined as seedlings all plant individuals that had cotyledons and/or first or second sets of true leaves. Seedling species were classified according to the fruits of their parent trees as either fleshy-fruited or non-fleshy fruited using the same classification as for trees (see above). I calculated the species richness of fleshy-fruited seedling species per plot by pooling the species over all 90 × 1 m^2 subplots.

4.2.6 Data analysis

In this study I assumed that disturbance regime influenced directly the species richness of fleshy-fruited trees, the density of frugivores, and the species richness of fleshy-fruited seedlings (Fig. 4.1). In addition, I assumed that fleshy-fruited trees affected frugivores and fleshy-fruited seedlings, and that frugivores had an impact on fleshy-fruited seedlings (Fig. 4.1). Finally, I assumed that forest identity (Budongo Forest, Mabira Forest, and Kakamega Forest) may influence trees, frugivores and seedlings (Fig. 4.1) because the three forests lay along a west-east gradient with Budongo Forest being the closest and Kakamega Forest the most distant to the Congo-Guinean rainforest belt.

I tested the direct and potential indirect influence of disturbance and forest identity on three response variables, the species richness of fleshy-fruited trees, the log-transformed density of frugivores, and the species richness of fleshy-fruited seedlings. I did this by conducting three separate statistical analyses. I first tested the influence of disturbance and forest on species richness of fleshy-fruited trees (using ANOVA). Secondly, I tested the impact of disturbance, forest and fleshy-fruited tree species richness on log (frugivore density) and, thirdly, the effects of disturbance, forest, fleshy-fruited tree species richness and log (frugivore density) on species richness of fleshy-fruited seedlings (using two ANCOVAs). In all three analyses, disturbance regime and forest were treated as fixed factors. For all analyses, I first included all two-way interaction terms between the predictor variables (e.g. in the analysis of log (frugivore density), between disturbance and forest, between disturbance and trees, and between forest and trees). However, none of the interaction terms turned out to be significant and, hence, they were removed from the models. In addition, I verified that the residuals of all analyses were normally distributed. In preliminary analyses I also included log-transformed fruit availability into the models. However, this variable was never significant and I removed it from the final analyses. All statistical analyses were performed using JMP (2001).

The reasoning behind this statistical analysis was derived from path analysis. Complex relationships which include both direct links (such as between disturbance and frugivores) as well as indirect links (such as between disturbance and frugivores via trees) can be visualized using a path diagram (Fig. 4.1) and analysed statistically using path analysis. In path analysis, the links connecting different components of the path diagram, i.e. the path coefficients, are standardised partial regression coefficients from a multiple regression analysis that includes all variables as predictor variables that have direct links with a specific response variable. Thus, in path analysis the influence of disturbance, forest and tree community on frugivores would be tested by a multiple regression with disturbance, forest and tree community as predictor, and frugivores as response variable. However, in my case path analysis could not be applied since disturbance regime and forest identity were categorical variables and path analyses allow only for the use of continuous variables. Nevertheless, I adapted the logical reasoning behind path analysis for my purposes.

4.3 Results

4.3.1 Tree community

I recorded a total of 161 tree species in the three forests, 131 (81.4%) of these were fleshy-fruited, whereas 30 (18.6%) were non-fleshy fruited (Appendix 7.2). Disturbance had a marginally significant effect on the species richness of fleshy-fruited trees (Fig. 4.3, Table 4.1) with LD and HD sites having higher species richness than PF (Contrast between PF and LD: *F* = 6.81, *P* = 0.017, Contrast between PF and HD: *F* = 4.57, *P* = 0.046). Fleshy-fruited tree species richness differed marginally significantly between the three forests (Fig. 4.3, Table 4.1) with Budongo Forest having a slightly higher species richness than Mabira Forest (Contrast between Budongo and Mabira: *F* = 3.05, *P* = 0.097) and no significant differences between Mabira and Kakamega Forest (Contrast between Mabira and Kakamega: *F* = 0.43, *P* = 0.52).

Table 4.1: Species richness of fleshy-fruited trees as a function of disturbance regime and forest identity. ANOVA, $R^2 = 0.31$, N = 24. Given are model and error DF-, *F*- and *P*- values.

	Model, Error DF	*F*	*P*
Whole model	4,19	2.16	0.11
Disturbance	2,19	3.48	0.052
Forest	2,19	3.08	0.069

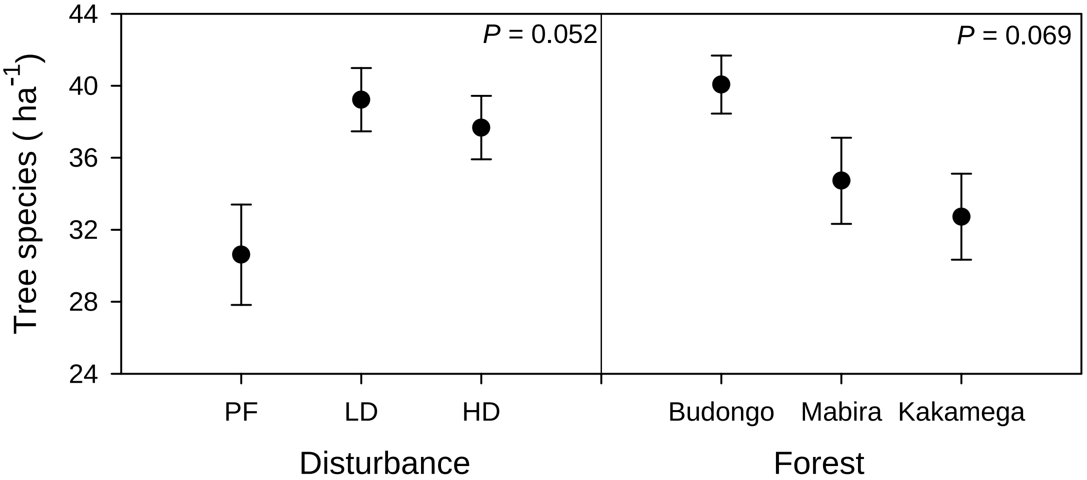

Figure 4.3: Fleshy-fruited tree species richness in relation to disturbance regime and forest identity in three East African rainforests. Given are the *P* values and the least square means (± 1 SE) of a two-factor ANOVA while controlling for the respective other factor (see Table 4.1).

4.3.2 Frugivore community

A total of 71 bird and five primate species were recorded in the three forests. Thirty-eight bird species and all primate species were classified as frugivores (Appendix 7.1). Neither disturbance regime nor forest identity had a significant direct effect on frugivore density. However, species richness of fleshy-fruited trees showed a marginally significant positive influence on frugivore density (Fig. 4.4, Table 4.2). A separate analysis of frugivorous birds and primates alone yielded similar results.

Table 4.2: Frugivore density (log transformed) as a function of disturbance regime, forest identity, and species richness of fleshy-fruited trees. ANCOVA, $R^2 = 0.45$, N = 24. Given are model and error DF-, *F*- and *P*-values.

	Model DF, Error DF	*F*	*P*
Whole model	5,18	9.8	0.042
Disturbance	2,18	2.08	0.15
Forest	2,18	1.89	0.18
Fleshy-fruited tree species	1,18	3.84	0.066

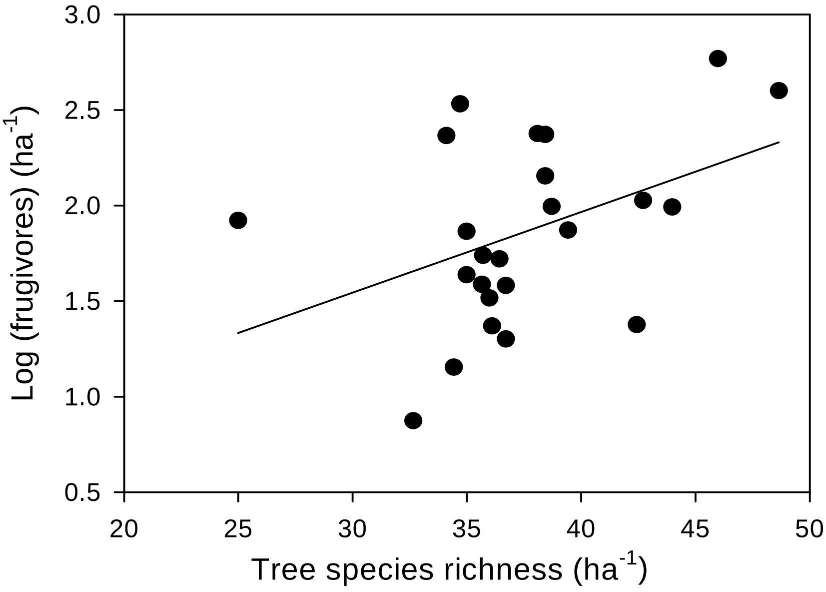

Figure 4.4: Frugivore density (log-transformed) in relation to species richness of fleshy-fruited trees in three East-African rainforests. Leverage plot after controlling for the effects of disturbance regime and forest identity (see Table 4.2).

4.3.3 Seedling community

A total of 70 seedling species were recorded in the three forests, out of these 62 (88.6%) were of fleshy-fruited tree species and 8 (13.4%) belonged to non-fleshy fruited tree species (Appendix 7.2). Neither disturbance regime and forest type, nor the species richness of fleshy-fruited trees had significant direct effects on the species richness of fleshy-fruited seedlings. However, the density of frugivores significantly increased the species richness of fleshy-fruited seedlings (Fig. 4.5, Table 4.3). The influence of log (frugivore density) on species richness of fleshy-fruited seedlings was also significant in a simple regression analysis (t = 2.63, P = 0.015, R^2 = 0.23, N = 24). As expected, the species richness of frugivores had no significant influence on the species richness of fleshy-fruited seedlings (ANCOVA, species richness of frugivores: $F_{1,\ 17}$ = 0.16, P = 0.69).

Table 4.3: Species richness of fleshy-fruited seedling species as a function of disturbance regime, forest identity, species richness of fleshy-fruited trees and log (frugivore density). ANCOVA, $R^2 = 0.58$, N = 24. Given are model and error DF-, *F*- and *P*- values.

	Model, error DF	*F*	*P*
Whole model	6,17	3.97	0.011
Disturbance	2,17	2.44	0.12
Forest	2,17	2.37	0.12
Fleshy-fruited tree species	1,17	0.88	0.36
Log (frugivore density)	1,17	5.42	0.032

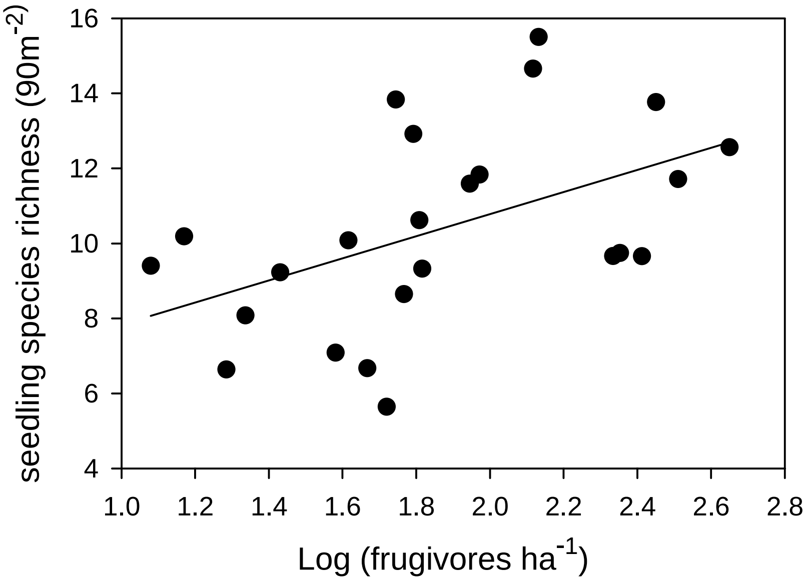

Figure 4.5: Species richness of fleshy-fruited seedlings in relation to frugivore density (log-transformed) in three East-African rainforests. Leverage plot after controlling for the effects of disturbance regime, forest type and species richness of fleshy-fruited trees (see Table 4.3).

4.4 Discussion

My study presents evidence that small-scale, local disturbance slightly enhanced the species richness of fleshy-fruited trees with no apparent effects on frugivore density and the species richness of fleshy-fruited seedlings. However, there was an indirect link between disturbance and seedling communities mediated through tree and frugivore communities, with disturbance slightly increasing the species richness of fleshy-fruited trees, this species richness of trees slightly increasing frugivore density and a significant impact of frugivore density on the species richness of fleshy-fruited seedlings.

My study demonstrated that the little disturbed forest had the highest richness of fleshy-fruited tree species while the primary forest had the lowest. These results are consistent with those of Cannon *et al.* (1998), Kessler (2001), Molino & Sabatier (2001), Plumptre (1996) and Sheil (2001) who reported higher tree species richness in little disturbed forests as compared to undisturbed forests in East African as well as other rainforests. Thus, my findings agree with the intermediate disturbance hypothesis that proposes that biodiversity peaks under intermediate disturbance regimes (Connell 1978). Currently the relationship between disturbance and tropical forest diversity is a hotly debated topic with some researchers claiming that high local richness is a temporary successional property that can only be maintained by an appropriate disturbance regime (Connell 1978, Huston 1994), while others argue that such richness is characteristic of late-successional equilibrium communities (Peet 1978, Phillips *et al.* 1997). My results seem to support the proponents of disturbance-maintained diversity. However, I have to point out that my study included only one forest that still contained a section of primary forest, i.e. Budongo Forest. In Budongo Forest, forest succession tends to lead towards mono-dominance of *Cynometra alexandri* (Plumptre 1996). Since the 1940s, foresters artificially increased the disturbance regime in Budongo Forest with the aim to obtain a species-rich “mixed forest” (Plumptre 1996, Plumptre & Reynolds 1994). Therefore, further studies are required especially in forests that do not develop towards mono-dominance.

There was no direct effect of disturbance or forest identity on frugivore density. This is in contrast to a study by Wunderle *et al.* (2006) that reported a positive effect of disturbance on frugivores. However, their study took place between 20–40 months after selective logging. Generally frugivores are known to be positively affected by disturbance in the short term. This is due to increased flowering and fruiting associated with increased light levels after tree felling (Peh *et al.* 2005, Wunderle *et al.* 2006). However, I did not record any differences in fruit production between differently disturbed sites in my study ($F_{2, 19}$ =1.32, P = 0.29) and this could have contributed to the similarities in frugivore densities recorded. In addition, frugivores are well known for being highly mobile and tracking fruit resources also at larger, landscape scales (Levey 1988b, Loiselle & Blake 1993, Saracco *et al.* 2004). Thus, frugivores could easily move within and among either of the plots within each forest in my study.

Neither disturbance regime nor forest identity had direct effects on the species richness of fleshy-fruited seedlings. Similarly, no difference in seedling establishment was found in Kibale Forest between logged and unlogged areas (Chapman & Chapman 1997). However, Chapman & Chapman (1997) reported an influence of disturbance on sapling densities and concluded that disturbance is impairing the recruitment into the sapling stage. This could be true in my study area too although I did not record sapling densities. Elsewhere anthropogenic fragmentation of forests and the creation of forest edges formation have been reported to lead to a decrease in density and diversity of seedlings (Benítez-Malvido & Lemus-Albor 2005, Benítez-Malvido & Martínez-Ramos 2003, Sizer & Tanner 1999) due to edge effects that result in high seedling mortality and reduction in seedling establishment.

Whereas, I did not find a direct effect of disturbance on frugivores and the species richness of fleshy-fruited seedlings I detected an indirect link between the two. Disturbance slightly increased the species richness of fleshy-fruited trees, this richness slightly increased the density of frugivores and this density significantly increased the species richness of fleshy-fruited seedlings. Thus, my study suggests a link between fleshy-fruited tree species richness, frugivores and seedling species richness. Such a chain of effects is expected in tropical forests. As a consequence, a number of studies have investigated this network of interactions. However, most studies have looked at the different links in isolation, for example at the link between fleshy-fruited tree species and frugivores (Hamann & Curio 1999, Price 2004) or at the link between frugivores and fleshy-fruited seedling species (Bleher & Böhning-Gaese 2001, Herrera *et al.* 1994, Houle 1998, Rey & Alcántara 2000). In the present study, I tested the different links together and I provided correlative evidence that light levels of disturbance appear to have an indirect positive effect on the species richness of fleshy-fruited seedlings. These results suggest that the relationship between disturbance and forest regeneration is very complex and I call for more in-depth studies to unravel the underlying mechanisms behind these relationships.

Considering the network of interactions I tested in my study (Fig. 4.1), of all the links, the relationship between frugivore density and the species richness of fleshy-fruited seedlings was the most significant. This relationship was more significant than the effect of disturbance or tree species richness on the seedling community (Table 4.3). In my study frugivore density significantly increased fleshy-fruited seedling species richness possibly because frugivores are highly mobile species with large territories (Restrepo & Gomez 1998, Westcott & Graham 2000) that can carry seeds from other areas into my study plots. A high density of frugivores appears to generate a widespread and diverse seed shadow. The finding that frugivores influence tree seedling communities, with increases in frugivore density leading to increases in fleshy-fruited seedling species richness, has been reported by many authors (e.g. Bleher & Böhning-Gaese 2001, Cardoso da Silva & Tabarelli 2000, Cordeiro & Howe 2001, Hamilton 1999). The surprising result from the present analysis is that this relationship appears to be more important than any other of the links developed in Fig. 4.1. This result emphasises the important role that frugivores play in shaping seedling communities and forest regeneration.

In general, this study suggests that a moderate use and the slight disturbance of tropical forests maybe compatible with high tree and seedling diversity and high density of frugivores. My results suggest that human activities need not to be completely excluded to achieve the conservation and regeneration of tropical rainforests. However, in this study I focused on species richness of the complete tree and seedling community and the density of frugivores not taking into account the specialization or threat status of each species. Although local disturbance seems to cause high species richness of trees and seedlings there is evidence suggesting that common species benefit at the expense of species specialised to primary forests (Tabarelli & Peres 2002). A number of studies demonstrated that late-successional species are more negatively affected by continued disturbance and are therefore more in need of conservation (Sheil & Burslem 2003, Tabarelli & Peres 2002). Similarly, among the birds, habitat specialists are more significantly influenced by persistent human disturbance than habitat generalists (Raman 2001, Woltmann 2003). In my study six climax tree species (*Chrysophylum muerense, Heisteria pervifolia*, *Suregada procera*, *Xylopia pervifolia* and *Zanthoxylum leprieurii*), two avian frugivores (*Phyllastrephus xavieri* and *Phyllastrephus icterinus*) and three climax seedling species (*Celtis zenkeri, Memecyon jasminoides* and *Pancovia turbinata*) were only found in the primary forest. Subjecting the primary forest to disturbance would lead to the local extinction of such species or even to their total extinction in case they are endemics (Cordeiro & Howe 2003, Svenning 1998). Thus my findings should not diminish the importance of preserving undisturbed forest areas, which include distinct species and communities and different biological interactions and processes than disturbed forests (Connell 1978, Laurence & Bierregaard 1997, Martin *et al.* 2004).

4.5 Summary

Tropical forest mutualisms are under threat from increased rates of forest conversion and degradation. In this study I investigated the effect of varying levels of small-scale human disturbance on fleshy-fruited tree species, frugivores and fleshy-fruited seedling establishment in three East African tropical rainforests. In a total of 24 one-hectare plots along a disturbance gradient, I identified and counted all trees > 10 cm diameter at breast height (dbh). To characterise the frugivores community point counts for avian frugivores and line transect counts for primates were carried out. In addition, I established 90 1m² subplots per one-hectare plots to quantify seedling species richness. Small-scale disturbance marginally significantly enhanced fleshy-fruited tree species richness but had no effect on frugivore density and species richness of fleshy-fruited seedlings. Richness of fleshy-fruited trees had a marginally significant positive influence on frugivore density but not on seedlings. The density of frugivores significantly increased the species richness of fleshy-fruited seedlings. Thus, small-scale disturbance appear to have increased seedling establishment indirectly through increases in tree species richness and frugivore density. Most significantly, frugivore density played a more important role for forest regeneration than either small-scale disturbance or tree species richness.

5 GENERAL CONCLUSIONS

Anthropogenic disturbance has increased tremendously in the last few decades posing a serious threat to processes and functioning of tropical rainforests. Among the most vital processes maintaining tropical forest diversity is seed dispersal by frugivores and subsequent regeneration. Frugivores too depend on the forest for their sustenance and survival. Thus any impact on the forest will have direct or indirect effects on frugivores and this will consecutively affect regeneration. In this thesis I studied the effects of small-scale anthropogenic disturbance on frugivore community, seed dispersal and tree regeneration in three East African tropical rainforests.

Firstly, I focused on general frugivore community and seed removal from *C. durandii* in heavily and little disturbed sites of the three forests. To answer this question I counted frugivorous birds and primates in the three forests. I also carried out tree observations to determine the frugivore assemblage and seed removal rates of *C. durandii*. Moreover, I considered the level of forest dependency by frugivores. Since it has been reported that crop size and fruit availability generally affects frugivores; I estimated the crop size and quantified fruit availability in the neighbourhood of *C. durandii.* Census data yielded 35 avian frugivores and 5 frugivorous primates. Small-scale disturbance had a negative effect on frugivore community in general, and forest specialists in particular. The general frugivore community did not differ significantly between the three forests; however, Kakamega Forest had the highest number of forest generalist species while Budongo Forest had the highest densities of forest generalists.

Observations on *C. durandii* trees yielded 38 frugivorous bird species and four frugivorous primate species. Among the frugivores, 19 species were forest specialists, 16 forest generalists and seven forest visitors. I recorded fewer numbers of frugivorous species and individuals visiting *C. durandii* in heavily disturbed sites. Furthermore, fruit availability of surrounding trees had a strong negative influence on frugivore visitors; nevertheless, crop size seemed to have no effect. The reduction in number of all frugivores and forest specialist frugivores lead to a decrease in seeds removed in heavily disturbed sites. Thus, in general frugivore communities and seed dispersal process could be under threat from small-scale disturbance.

Secondly, I focused on fleshy-fruited tree communities, frugivore community and fleshy-fruited seedling establishment along a disturbance gradient. I quantified all trees species with a diameter at breast height of >10 cm in a total of 24 one-hectare plots along a disturbance gradient. To characterise the frugivores community I carried out point counts for avian frugivores and line transect counts for primates. Furthermore, I established 90 $1m^2$ subplots per one-hectare plots to quantify seedling species richness. I recorded marginally higher number of fleshy-fruited trees in disturbed sites but no differences were found for frugivore density and species richness of fleshy-fruited seedlings between the disturbance regimes. Nevertheless, richness of fleshy-fruited trees had a marginally significant positive influence on frugivore density but not on seedlings. Correspondingly, density of frugivores significantly increased the species richness of fleshy-fruited seedlings. Thus, my results suggest that small-scale disturbance led to increased seedling establishment indirectly through increases in tree species richness and frugivore density. Nonetheless, frugivore density played a more important role for forest regeneration than either small-scale disturbance or tree species richness.

Results from this study are relevant to the conservation of rainforest forest biodiversity. I have shown that frugivores and especially forest specialists are highly sensitive to small-scale disturbance. Thus the ecosystem service by frugivores and especially by forest specialists is under threat from small-scale disturbance. Furthermore I succeeded in proving the impact of disturbance on tree species, frugivores and seedlings in tropical rainforests. Above all I have shown that small-scale disturbance effects are not restricted to a single forest but are consistent on a regional scale. Thus the decline in frugivores especially in heavily disturbed sites resulted into lower visitations in *C. durandii* trees in all the three forests. The lower visitations in turn led to few seeds removed from *C. durandii* trees and correspondingly, few seedlings of this particular tree establishing in the same sites. Despite the fact that *C. durandii* produces small fruits which essentially should attract a large frugivore assemblage this was not the case especially in heavily disturbed sites. Therefore the assumption that trees such as *C. durandii* should not suffer declines in seed dispersal due to disturbance should be viewed with caution. Furthermore, the notion that forest generalists generally compensate for decline or loss of forests specialists especially in regard to dispersal services is not apparent from this study.

Small-scale disturbance seems to increase fleshy fruited tree species richness. This is in line with the intermediate disturbance hypothesis. Thus, small-scale disturbance seems to enhance seedling establishment indirectly through mediation by trees and frugivores. This happens through opening up of the forests which enables “weak” tree species to survive in areas that they otherwise would have been out-competed by the dominant species. This increase in tree species richness leads to availability of more fruits for frugivores which in turn increases frugivore species richness. High frugivore species richness leads to dispersal of a wide range of seed species translating into establishment of more seedling species. However, this should be taken with caution since the slight increase in tree species richness is generally at the expense of trees specialized to old growth forests. Furthermore, this seems to apply only in forests that climax into monodominant stands. However, there seems to be a possibility of maintaining high biodiversity in such forests by adoption of an appropriate disturbance regime similar to natural background disturbance. Nevertheless, for this to be applicable more studies are required especially in such forests.

To conclude, it is clear that small-scale anthropogenic disturbance is not an isolated event but rather pervasive in nature. Therefore, results from this study could apply in similarly disturbed areas across the globe. The strong response by frugivores especially forest specialists to small-scale disturbance means that they can be used as indicators of general forest health. Furthermore, the importance of frugivores to general seedling establishment is amplified by this study. Thus conservation of frugivores is necessary and a must in order to maintain the process of seed dispersal and regeneration in tropical rainforests.

Whether or not changes reported in this study affects the long term sustainability of tropical forest ecosystems requires further studies. For example other vital groups such as pollinators need to be considered. In addition, observations need to be carried out on more trees species in order to generalize the results across tree species. Furthermore, studies on the other aspects of seed dispersal mutualism such as secondary dispersal and predation need to be carried out.

6 REFERENCES

ALCÁNTARA, J. M. & REY, P. J. 2003. Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *Journal of Evolutionary Biology* 16:1168–1176.

BABWETEERA, F., SAVILL, P. & BROWN, N. 2000. *Balanites wilsoniana*: Regeneration with and without elephants. *Biological Conservation* 137:40–47.

BEENTJE, H. 1994. *Kenya's trees, shrubs and lianas*. National Museums of Kenya, Nairobi, Kenya.

BENÍTEZ-MALVIDO, J. & LEMUS-ALBOR, A. 2005.The seedling community of tropical rain forest edges and its interaction with herbivores and pathogens. *Biotropica* 37:301–313.

BENÍTEZ-MALVIDO, J. & MARTÍNEZ-RAMOS, M. 2003. Influence of edge exposure on tree seedling species recruitment in tropical rainforest fragments. *Biotropica* 35:530–541.

BENNUN, L. A. & NJOROGE, P. 1999. *Important bird areas in Kenya*. The East Africa Natural History Society, Nairobi, Kenya.

BENNUN, L. A., DRANZOA, C. & POMEROY, D. 1996. Forest birds of Kenya and Uganda. *Journal of East African Natural History* 85:23–48.

BIBBY, C. J., BURGESS, N. D. & HILL, D. A. 1992. *Bird census techniques*. Academic Press, London.

BIOTA EAST AFRICA. 2004. BIOTA East Africa. Biodiversity in conversion: The influence of fragmentation and disturbance on the biodiversity of East African highland rain forests. *Final Report Phase* I (2001–2004).

BLEHER, B., & BÖHNING-GAESE, K. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129:385–394.

BLEHER, B., POTGIETER, C. J., JOHNSON, D. N. & BÖHNING-GAESE, K. 2003. The importance of figs for frugivores in a South African coastal forest. *Journal of Tropical Ecology* 19:375–386.

BLEHER, B., USTER, D. & BERGSDORF, T. 2006. Assessment of the threat status and management effectiveness in Kakamega Forest, Kenya. *Biodiversity Conservation* 15:1159–1177.

BOND, W. J. 1995. Assessing the risk of plant extinction due to pollinator and disperser failure. Pp.131−146 in Lawton, J. H., and May, R. M., eds. *Extinction rates*. Oxford.

BRONSTEIN, J. L. 2001. The exploitation of mutualisms. *Ecology Letters* 4:277–287.

BROOK, B.W., SODHI, N. S. & NG, P. K. L. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* 424:420–423.

BROTONS, L., MØNKKØNEN, M. & MARTIN, J. L. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *American Naturalist* 162:343–357.

CANNON, C. H., PEART, D. R. & LEIGHTON, M. 1998. Tree species diversity in commercially logged Bornean rainforest. *Science* 281:1366–1368.

CARDOSO DA SILVA, J. M. & TABARELLI, M. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404:72–74.

CHAPMAN, C. A & CHAPMAN, L. J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29:396–412.

CHAPMAN, C. A. & 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. & ONDERDONK, C. A. 1998. Forests without primates: primate/plant co-dependency. *American Journal of Primatology* 45:127–141.

CHAPMAN, C. A., BALCOMB, S. R., GILLESPIE, T. R., SKORUPA, J. P. & STRUHSAKER, T. T. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology* 14:207–217.

CHAPMAN, C.A., LAWES, M. J. & EELEY, H. A. C. 2006. What hope for African primate diversity? *African Journal of Ecology* 44:116–133.

CHAZDON, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6:51–71.

CONNELL J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298–312 in den Boer P.J. and Gradwell G.R. eds. *Dynamics of Populations*. Centre for Agricultural Publishing and Documentation, Wageningen, the Netherlands.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.

CORDEIRO, N. J. & HOWE, H. F. 2001. Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* 15:1733–1741.

CORDEIRO, N. J. & 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.

CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73:413–448.

DA SILVA, J. M. C. & TABARELLI, M. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404:72–74.

DALLING, J. W., HUBBELL, S. P. & SILVERA, K. 1998. Seed dispersal, seedling establishment, and gap partitioning among pioneer trees. *Journal of Ecology* 86:674–689.

DOWSETT-LEMAIRE, F. 1988. Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Revue d'Ecologie* (*Terre et Vie*) 43:251–281.

DUNCAN, R. S. & CHAPMAN, C. A. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* 9:998–1008.

EGGELING, W. J. 1947. Observations on the ecology of the Budongo rainforest, Uganda. *Journal of Ecology* 34:20–87.

ELLISON, A. M., DENSLOW, J. S., LOISELLE, B. A. & BRENES, M. D. 1993. Seed and seedling ecology of neotropical Melastomataceae. *Ecology* 74:1733–1749.

EMERTON, L. 1994. *Utilisation of Kakamega Forest Reserve by Adjacent Households*. KIFCON Socio-Economic Report, Forest Department, Karura, Kenya.

ESHIAMWATA, G. W., BERENS, D. G., BLEHER, B., DEAN, W. R. J. & BÖHNING-GAESE, K. 2006. Bird assemblages in isolated *Ficus* trees in Kenyan farmland. *Journal of Tropical Ecology* 22:723–726.

ESTRADA, A. COATES-ESTRADA, R. & MERITT, D. A. Jr. 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 6:19–43.

FAO. 2000. Global forest resource assessment 2000—Main report. FAO Forestry Paper 140, United Nations Food and Agricultural Organization, New York.

FARWIG, N., BÖHNING-GAESE, K. & BLEHER, B. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests. *Oecologia* 147:238–252.

FOLEY, J. A., ASNER, G. P., COSTA, M. H., COE, M. T., DEFRIES, R., GIBBS, H. K., HOWARD, E. A., OLSON, S., PATZ, J., RAMANKUTTY, N. & SYNDER, P. 2007. Amazon revealed: Forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment* 5:25–32.

FORGET, P. M. & JANSEN, P. A. 2007. Hunting increases dispersal limitation in the tree *Carapa procera*, a non-timber forest product. *Conservation Biology* 21:106–113.

GALETTI M, DONATTI, C. I., PIRES, A. S., GUIMARAES, P. R. & 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 Society* 151:141–149.

GARCÍA-GUZMÁN, G. & BENÍTEZ-MALVIDO, J. 2003. Effect of litter cover on the incidence of leaf fungal pathogens and herbivory in seedlings of a tropical tree *Nectandra ambigens*. *Journal of Tropical Ecology* 19:171–177.

GEIST, H. J. & LAMBIN, E. F. 2002 Proximate causes and underlying driving forces of tropical deforestation. *BioScience* 52:143–150.

GITHIRU, M., LENS, L., BENNUN, L. A. & OGOL, C. P. K. O. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afro-tropical forest. *Oikos* 96:320–330.

GRAHAM, C., MARTINEZ-LEYVA, J. E. & CRUZ-PAREDES, L. 2002. Use of fruiting trees by birds in continuous forest and riparian forest remnants in Los Tuxtlas, Veracruz, Mexico. *Biotropica* 34:589–597.

GRAY, M. A., BALDLAUF, S. L., MAYHEW, P. J. & HILL, K. J. 2006. Response of avian feeding guilds to tropical forest disturbance. *Conservation Biology* 21:133–141.

HAMANN, A. & CURIO, E. 1999. Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. *Conservation Biology* 13:766–773.

HAMILTON, M. B. 1999. Tropical tree gene flow and seed dispersal. *Nature* 401:129–130.

HARCOURT, A. H. 2006. Rarity in the tropics: biogeography and macroecology of the primates. *Journal of Biogeography* 33:2077–2087.

HARMS, K. E., WRIGHT, S. J., CALDERÓN, O., HERNÁNDEZ, A. & HERRE, E. A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.

HAUGAASEN, T. & PERES, C. A. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. *American Journal of Primatology* 67:243–258.

HERRERA, C. M., JORDANO, P., LÓPEZ-SORIA, L. & AMAT, J. A. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* 64:315–344.

HEYWOOD, V. H. editor. 1995. *Global biodiversity assessment*. Cambridge University Press, Cambridge, London, United Kingdom.

HILL, J. K. & HAMER, K. C. 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* 41:744–754.

HILL, L. & CURRAN, P. J. 2003. Area shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *Journal of Biogeography* 30:1391–1403.

HOLL, K. D., LOIK, M. E., LIN, E. H. V. & SAMUELS, I. A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* 8:339–349.

HOULE, G. 1998. Seed dispersal and seedling recruitment of *Betula alleganiensis*: spatial inconsistency in time. *Ecology* 79:807–818.

HOWARD, P. C. 1991. *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland, Switzerland.

HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.

HOWE, H. F. SCHUPP, E. W. & WESTLEY, L. C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66:781–791.

HOWE, H. F. & WESTLEY, L. C. 1988. *Ecological Relationships of Plants and Animals*. Oxford University Press, Oxford.

HUBBELL, S. P., FOSTER, R. B. & O'BRIEN, S. T. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557.

HURTT, G. C. & PACALA, S. W. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.

HUSTON, M. A. 1994. *Biological diversity: The coexistence of species on changing landscapes*. Cambridge University Press, New York.

ISABIRYE-BASUTA, G. 1989. Feeding ecology of chimpanzees in the Kibale Forest, Uganda. Pp. 116–127 in P. N. Heltne and L. Marquardt, eds. *Understanding Chimpanzees*. Cambridge, MA: Harvard University Press.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.

JMP 2001. *JMP statistics and graphic guide*. Version 4.0. SAS Institute, Cary, North Carolina.

KARIUKI, M. & KOOYMAN, M. R. 2005. Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology* 30:844–855.

KESSLER, M. 2001. Maximum plant-community endemism at intermediate intensities of anthropogenic disturbance in Bolivian montane forests. *Conservation Biology* 15:634–641.

KINGDON, J. 1997. *The Kingdon field guide to African mammals*. Academic press, London.

KISSLING, W. D., RAHBEK, C. & BÖHNING-GAESE, K. 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society London B* 274:799–808.

KOKWARO, J. O. 1988. Conservation status of the Kakamega Forest in Kenya. The Eastern most relic of the equatorial rainforest of Africa. *Monographs of Systematic Botany of the Missouri Botanic Gardens* 25:471–489.

KORINE, C., KALKO, E. K. & HERRE, E. A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123:560–568.

LAURANCE, W. F. & BIERREGAARD, R. O. Jr. (eds) 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press.

LAURANCE, W. F. 1999. Reflections on the tropical deforestation crisis. *Biological Conservation* 91:109–117.

LAURANCE, W. F. 2007.Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution* 22:65–70.

LAURANCE, W. F., LOVEJOY, T. E., VASCONCELOS, H. L., BRUNA, E. M., DIDHAM, R. K., STOUFFER, P. C., GASCON, C., BIERREGAARD, R. O, LAURANCE, S. G. & SAMPAIO, E. 2001. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.

LEVEY, D. J. 1988a. Tropical wet forest treefall gaps and distributions of understorey birds and plants. *Ecology* 69:1076–1089.

LEVEY, D. J. 1988b. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251–269.

LEWIS, S. L. 2006. Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society London* B 361:195–210.

LOISELLE, B. A. & BLAKE, J. G. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. *Vegetatio* 107/108:177–189.

LOISSELLE, B.A. & BLAKE, J. G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72:180–193.

LUCK, G. W. & DAILY, G. C. 2003. Tropical countryside bird assemblage: richness, composition and foraging differ by landscape context. *Ecological Applications* 13:235–247.

MAGNUSSON, W. E. & COSTA, F. R. C. 2003. Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in a central Amazonian forest. *Biotropica* 35:103–114.

MAKANA, J. & THOMAS, J. C. 2005. Effects of light gaps and litter removal on seedling performance of six African Timber Species. *Biotropica* 37:227–237.

MAKANA, J. R. & THOMAS, J. C. 2004. Dispersal limits natural recruitment of African mahoganies. *Oikos* 106:67–72.

MARSHALL, A. J., NARDIYONO, ENGSTRÖM, L. M., PAMUNGKAS, B., PALAPA, J., MEIJAARD, E. & STANLEY, A. S. 2006. The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans *Pongo pygmaeus morio* in the forests of East Kalimantan. *Biological Conservation* 129:566–578.

MARTIN, P. H., SHERMAN, R. E. & FAHEY, T. J. 2004. Forty years of tropical forest recovery from agriculture: Structure and floristics of secondary and old growth riparian forests in the Dominican Republic. *Biotropica* 36:297–317.

MARTÎNEZ-RAMOS, M. & SOTO-CASTRO, A. 1993. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* 108:299–318.

MASON, D. 1996. Response of Venezuelan understory birds to selective logging, enrichment strips and vine cutting. *Biotropica* 28:296–309.

MAYAUX, P., HOLMGREN, P., ACHARD, F., EVA, H., STIBIG, H. J. & BANTHOMME, A. 2005. Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society London B* 360:373–384.

MITCHELL, N. 2004. The exploitation and disturbance history of Kakamega Forest, western Kenya. In Bleher, B. and Dalitz, H. eds BIOTA Report No. 1. Bielefelder Ökologische Beiträge, 20, Bielefield.

MOEGENBURG, S. M. & LEVEY, D. J. 2003. Do frugivores respond to fruit harvest? An experimental study of short-term responses. *Ecology* 84:2600–2612.

MOLINO, J. F. & SABATIER, D. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294:1702–1704.

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

NATIONAL RESEARCH COUNCIL. 1981. *Techniques for the study of primate population ecology*. National Academy Press, Washington, D.C.

NOGALES, M., VALIDO, A., MEDINA, F. M. & DELGADO, J. D. 1999. Frugivory and factors influencing visitation by birds at ‘Balo’ (*Plocama pendula* Ait., Rubiaceae) plants in the Canary Islands. *Ecoscience* 6:531–538.

ORDENDONK, A. & CHAPMAN, C. A. 2000. Coping with forest fragmentation: the primates of Kibale National Park Uganda. *International Journal of Primatology* 21:587–611.

PEET, R. K. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* 37:65–78.

PEH, K. S. H., DE JONG, J., SODHI, N. S., LIM, S. L. H. & YAP, C. A. M. 2005. Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biological Conservation* 123:489–505.

PERES, C. A. & NASCIMENTO, H. S. 2006. Impact of game hunting by the Kayapo´ of south-eastern Amazonia: implications for wildlife conservation in tropical forest indigenous reserves. *Biodiversity and Conservation* 15:2627–2653.

PERES, C. A. & VAN ROOSMALEN, M. 2002. Primate frugivory in two species-rich neotropical forests: Implications for the demography of large-seeded plants in overhunted areas. Pp 407–421 in D. J. Levey, W. R. Silva, and M. Galetti, eds. *Seed dispersal and frugivory: evolution and conservation*. CAB International.

PERES, C. A., BARLOW, J. & LAURENCE, F. W. 2006. Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology and Evolution* 21:227–229.

PHILLIPS, O. L., HALL, P., GENTRY, A. H., SAWYER, S. A. & VASQUEZ, R. 1997. Species richness, tropical forest dynamics, and sampling: response to Sheil. *Oikos* 79:183–187.

PIMM, S. L. & RAVEN, P. 2000. Extinction by numbers. *Nature* 403:843–845.

PIMM, S. L.,RUSSELL, G. J., GITTLEMAN, J. L. & BROOKS, T. M. 1995. The future of biodiversity. *Science* 269:347–350.

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

PLUMPTRE, A. J. & REYNOLDS, V. 1994. The effects of selective logging on primate populations in Budongo Forest reserve. *Uganda Journal of Applied Ecology* 31:631–641.

PLUMPTRE, A. J. 1996. Changes since sixty years of selective timber harvesting in Budongo forest reserve, Uganda. *Forest Ecology and Management* 89:101–113.

POOLEY, E. 1994. *The complete field guide to the trees of Natal, Zululand and Transkei*. Natal Flora Publications Trust, Durban, South Africa.

PRICE, O. F. 2004. Indirect evidence that frugivorous birds track fluctuating fruit resources among rainforest patches in the Northern Territory, Australia. *Austral Ecology* 29:137–144.

PURVIS, A. & HECTOR, A. 2000. Getting the measure of biodiversity. *Nature* 405: 212–219.

RAMAN, T. R. S. 2001. Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, north-east India. *Conservation Biology* 15:685–698.

RESTREPO, C. & GÓMEZ, N. 1998. Responses of understory birds to anthropogenic edges in a Neotropical montane forest. *Ecological Applications* 8:170–183.

REY, J. & ALCÁNTARA, J. M. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology* 88:622–633.

ROSS, K. A., FOX, B. J. & FOX, M. D. 2002. Changes to plant species richness in forest fragments: fragment age, disturbance and fire history may be as important as area. *Biogeography* 29:749–765.

SAGAR, R. & SINGH, J. S. 2004. Local plant species depletion in a tropical dry deciduous forest of northern India. *Environmental Conservation* 31:55–62.

SANTOS, T. & TELLERIA, J. L. 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish Juniper *Juniperus thurifera*. *Biological Conservation* 70:129–134.

SARACCO, J. F., COLLAZO, J. A. & GROOM, M. J. 2004. How do frugivores track resources? Insights from spatial analyses of birds foraging in a tropical forest. *Oecologia* 139:235–245.

SCHNITZER, S. A., & CARSON W. P. 2001 Tree fall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–19.

SHANKAR, U., MURALI, K. S., SHAANKER, R. U., GANESHAIAH, K. N. & BAWA, K. S. 1998. Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 4. Impact on floristic diversity and population structure in a thorn scrub forest. *Economic Botany* 52:302–303.

SHEIL, D. & BURSLEM, D. F. R. P. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution* 18:18–26.

SHEIL, D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* 155:183–199.

SIZER, N. & TANNER, E. V. J. 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation* 91: 135–142.

SODHI, N. S., LIOW, L. H. & BAZZAZ, F. A. 2004. Avian extinctions from tropical and subtropical forests. *Annual Review of Ecology, Evolution and Systematics* 35:323–345.

STEVENSON, T. & FANSHAWE, J. 2002. *Field guide to the birds of East Africa*. T. and A. D Poyser, London.

STRUHSAKER, T. T. 1997. *Ecology of an African rain forest: Logging in Kibale and the conflict between conservation and exploitation.* University Press of Florida.

SVENNING, J. C. 1998. The effect of land-use on the local distribution of palm species in an Andean rain forest fragment in northwestern Ecuador. *Biodiversity and Conservation* 7:1529–1537.

SWAINE, M. D. 1996. *The Ecology of Tropical Forest Tree Seedlings*. Parthenon, New York.

TABARELLI, M. & PERES, C. A. 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: Implications for forest regeneration. *Biological Conservation* 106:165–175.

TEJEDA-CRUZ, C. & SUTHERLAND, W. J. 2005.Cloud forest bird responses to unusually severe storm damage. *Biotropica* 37:88–95.

TERBORGH, J. 1986. Keystone plant resources in the tropical forest. Pp 330–344 in Soule, M.E. ed. *Conservation biology: The source of scarcity and diversity*. Sinauer Associates, Sunderland, Massachussets, USA.

TSINGALIA, M. H. 1990. Habitat disturbance, severity and patterns of abundance in Kakamega forest, Western Kenya. *African Journal of Ecology* 28:213–226.

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

VOIGT, F. A., BLEHER, B., FIETZ, J., GANZHORN, J. U, SCHWAB, D. & BÖHNING-GAESE, K. 2004. A comparison of morphological and chemical fruit traits between two sites with different frugivore assemblages. *Oecologia* 141:94–104.

WENNY, D. G. & LEVEY, D. J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the Natural Academy of Sciences USA*. 95:6204–6207.

WESTCOTT, D. A. & GRAHAM, D. L. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122:249–257.

WHITMORE, T. C. 1997. Tropical forest disturbance, disappearance and species loss. Pp 3–12 in Laurence, W.L. and Bieregaard Jr. R.O. eds, *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*. University of Chicago Press.

WILLIS, K. J., GILLSON, L. & BRNCIC, T. M. 2004. How “virgin” is virgin rainforest? *Science* 304:402–403.

WITMER, M. C. & SOEST, P. J. V. 1998. Contrasting digestive strategies of fruit eating-birds. *Functional Ecology* 12:728–741.

WOLTMANN, S. 2003. Bird community responses to disturbance in a forestry concession in lowland Bolivia. *Biodiversity and Conservation* 12:1921–1936.

WRANGHAM, R. W., CHAPMAN, C. A. & CHAPMAN, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10:355–368.

WRIGHT S. J. & MULLER-LANDAU, H. C. 2006. The future of tropical forest species. *Biotropica*. 38:287–301.

WRIGHT, S. J., ZEBALLOS, H., DOMINGUEZ, I., GALLARDO, M. M., MORENO, M. C. & IBANEZ, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14:227–239.

WUNDERLE, J. M., HENRIQUES, L. M. P. & WILLIG, M. R. 2006. Short-term responses of birds to forest gaps and understory: An assessment of reduced-impact logging in a lowland Amazon forest. *Biotropica* 38:235–255.

7 APPENDIXES

Appendix 7.1: List of frugivorous bird and primate species recorded during point counts. Given is forest specialization and present (+) or absent (-) in PF, LD and HD sites for each forest. FG = forest generalist, FS = forest specialist, FV = forest visitor, PF = primary forest, LD = little disturbed and HD = heavily disturbed.

Common name Scientific name	Forest specialization	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
Birds								
African green Pigeon *Treron calva*	FG	-	+	-	-	-	-	-
African grey Parrot *Psittacus erithacus*	FS	+	+	-	-	-	-	-
African pied Hornbill *Tockus fasciatus*	FV	-	+	-	-	-	-	-
Ansorge's Greenbul *Andropadus ansorgei*	FS	-	-	-	-	-	+	+
Black and white casqued Hornbill *Bycanistes subcylindricus*	FG	+	+	-	-	+	+	+
Cabanis Greenbul *Phyllastrephus cabanisi*	FS	-	-	-	-	-	+	+
Cameroon-sombre Greenbul *Andropadus curvirostris*	FS	+	-	-	-	-	+	-
Common Bulbul *Pycnonotus Barbatus*	FV	-	-	-	-	+	+	+
Dark-backed Weaver *Ploceus bicolor*	FG	-	-	-	-	-	-	+
Crested Malimbe *Malimbus malimbicus*	FG	-	-	+	-	-	-	-
Green Sunbird *Anthreptes rectirostris*	FS	-	-	-	+	+	-	-
Grey-headed Negrofinch *Nigrita canicapilla*	FG	-	-	-	-	+	+	+
Grey-throated Barbet *Gymnobucco bonapartei*	FG	-	-	-	+	-	-	-
Honeyguide Greenbul *Baeopogon indicator*	FS	-	-	-	-	-	+	+

Common name Scientific name	Forest specialization	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
Birds								
Icterine Greenbul *Phyllastrephus icterinus*	FS	+	-	-	-	-	-	-
Joyful Greenbul *Chlorocichla laetissima*	FG	-	-	-	-	-	+	+
Little Greenbul *Andropadus virens*	FG	-	+	+	+	+	+	+
Little grey Greenbul *Andropadus gracilis*	FS	-	+	+	+	+	-	-
Olivaceous Warbler *Hippolais pallida*	FV	-	-	-	-	-	+	-
Red-capped Robinchat *Cossypha natalensis*	FG	-	-	-	-	-	+	-
Red-headed Blue bill *Spermophaga ruficapilla*	FG	+	-	+	-	-	-	-
Red-headed Malimbe *Malimbus rubricollis*	FS	-	+	-	-	-	-	-
Red-tailed Bristlebill *Bleda syndactyla*	FS	-	+	+	+	+	+	-
Red-tailed Greenbul *Criniger calurus*	FS	-	+	-	-	+	-	-
Rufuous Flycathcher-thrush *Stizorhina fraseri*	FS	+	+	-	+	-	-	-
Slender-billed Greenbul *Andropadus gracilirostris*	FS	+	-	-	+	-	+	-
Speckled Tinkerbird *Pogoniulus scolopaceus*	FG	+	+	-	+	+	-	-
Splendid Starling *Lamprotornis purpureus*	FG	+	-	-	-	-	-	-
Spotted Greenbul *Ixonotus guttatus*	FS	-	-	+	-	-	-	-
Tambourine Dove *Turtur tympanistra*	FG	+	-	-	-	+	-	-
Western black-headed Oriole *Oriolus brachyrhynchus*	FG	+	+	-	-	+	-	+
White-breasted Negrofinch *Nigrita fusconata*	FG	-	-	+	-	-	-	-
White-thighed Hornbill *Bycanistes cylindricus*	FS	-	+	-	-	-	-	-
White-throated Greenbul *Phyllastrephus albigularis*	FS	+	+	-	+	-	-	-
Xavier's Greenbul *Phyllastrephus xavieri*	FS	+	-	-	-	-	-	-

Common name Scientific name	Forest specialization	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
Birds								
Yellowbill *Ceuthmochares aereus*	FV	-	+	+	+	+	-	-
Yellow-billed Barbet *Trachyphonus purpuratus*	FG	-	-	-	-	-	-	+
Yellow-throated Tinkerbird *Pogoniulus subsulphureus*	FS	-	+	-	-	+	-	-
Yellow-whiskered Greenbul *Andropadus latirostris*	FG	-	-	+	+	+	+	+
Primates								
Black and white Colobus *Colobus guereza*	FG	+	+	+	-	-	+	+
Blue Monkey *Cercopithecus mitis*	FS	+	+	+	-	-	+	+
Grey-cheeked Mangabey *Lophocebus albigena*	FS	-	-	-	+	+	+	+
Olive Baboon *Papio anubis*	FG	-	+	-	-	-	-	-
Red -tailed Monkey *Cercopithecus ascanius*	FS	+	+	-	-	+	+	+

Appendix 7.2: List of tree and seedling species recorded during the study. Given for each species are means of dispersal, succession type and where present (+) or absent (-) in the three forests. PF = primary forest, LD = little disturbed and HD = heavily disturbed.

Tree species	Mode of dispersal	Succession	Budongo			Mabira		Kakamega	
			PF	LD	HD	LD	HD	LD	HD
Acacia abyssinica	other	pioneer	-	-	-	+	-	-	-
Alangium chinense	animal	pioneer	+	+	+	+	+	+	+
Albizia grandibracteata	other	climax	-	-	-	-	+	-	-
Albizia gummifera	other	climax	+	+	+	+	+	+	+
Alchornea laxiflora	animal	climax	+	+	+	+	-	-	-
Allophyllus abyssinica	animal	climax	-	-	+	-	-	-	-
Allophyllus dummeri	animal	climax	+	+	-	-	-	-	-
Alstonia boonei	animal	climax	+	+	+	+	+	-	-
Aningeria altissima	animal	climax	+	+	+	+	-	+	+
Antiaris toxicaria	animal	climax	+	+	+	+	+	+	+
Baphia wollastonii	other	climax	+	-	+	+	-	-	-
Beilschmidia ugandensis	animal	climax	-	-	-	-	+	-	-
Bequaertiodendron oblanceolatum	animal	climax	+	+	-	+	+	+	+
Bersame abyssinica	animal	pioneer	-	-	-	-	-	-	+
Bischoffya javonica	animal	pioneer	-	-	-	-	-	-	+
Blighia unijugata	animal	climax	+	+	+	+	+	+	+
Bridelia micrantha	animal	pioneer	-	-	-	-	+	-	-
Broussonetia pypefera	animal	pioneer	-	+	-	+	+	-	-
Caloncoba schweinfurthii	other	climax	+	+	+	-	-	-	-
Canarium schweinfurthii	animal	climax	+	+	-	+	+	-	-
Casaeria englevi	animal	pioneer	+	-	-	-	-	-	-
Cassaeria battiscombei	animal	climax	+	-	+	-	-	+	+
Cassaeria gladiiformis	animal	climax	+	+	-	+	+	+	+
Cassipourea ruwensorensis	animal	climax	-	+	-	-	-	+	+
Celtis africana	animal	climax	-	-	-	+	+	+	+
Celtis durandii	animal	climax	+	+	+	+	+	+	+
Celtis mildbraedii	animal	climax	+	+	+	+	+	+	+
Celtis philippensis	animal	climax	+	+	+	+	+	-	-
Celtis zenkeri	animal	climax	+	+	+	+	+	-	-
Chaetacme aristata	animal	climax	-	-	-	+	+	+	+
Chrysophyllum albidum	animal	climax	+	+	+	+	+	+	+
Chrysophyllum muerense	animal	climax	+	-	-	-	-	-	-

Tree species	Mode of dispersal	Succession	Budongo			Mabira		Kakamega	
			PF	LD	HD	LD	HD	LD	HD
Chrysophyllum perpulchrum	animal	climax	+	+	+	-	-	-	-
Chrysophyllum viridifolium	animal	climax	-	-	-	+	+	+	+
Clausena anisata	animal	pioneer	+	-	+	+	+	+	+
Cleistopholis patens	animal	pioneer	+	-	-	-	-	-	-
Coffea comephora	animal	climax	-	-	-	-	+	-	-
Cordia africana	animal	climax	-	-	-	-	-	+	+
Cordia mellenii	animal	climax	+	+	+	+	+	-	-
Craibia brownii	other	climax	+	+	-	-	+	+	-
Croton macrostachyus	animal	pioneer	+	-	-	+	+	+	-
Croton megalocarpus	animal	pioneer	-	+	-	-	-	+	+
Croton sylvaticus	animal	pioneer	+	+	+	-	+	+	+
Cynometra alexandri	animal	climax	+	+	+	-	-	-	-
Deinbollia kilimandscharica	animal	climax	-	-	-	-	-	-	+
Desplatsia dewevrei	animal	climax	+	+	+	-	-	-	-
Diospyros abyssinica	animal	climax	-	+	-	+	+	+	+
Dovyalis macrocalyx	animal	climax	-	-	-	-	+	+	-
Dracaena stendneri	animal	pioneer	-	-	-	-	+	-	-
Drypetes ugandensis	animal	climax	+	+	+	+	-	-	-
Dryptes gerradi	animal	climax	-	-	-	-	-	+	+
Ehretia cymosa	animal	climax	+	+	+	+	+	+	+
Ekebergia capensis	animal	climax	-	-	+	-	-	-	-
Entandrophragma angolense	other	climax	-	-	-	+	+	-	-
Entandrophragma utile	other	climax	+	+	+	-	-	-	-
Erythrina abyssinica	other	pioneer	+	-	-	-	-	-	-
Erythrophleum suaveolens	other	climax	+	+	-	-	+	-	-
Fagaropsis angolensis	animal	pioneer	+	-	+	+	+	-	+
Ficus cyathistipula	animal	climax	-	-	-	-	-	+	-
Ficus exasperata	animal	climax	+	+	+	+	+	+	+
Ficus lutea	animal	climax	-	-	-	-	+	+	+
Ficus mucoso	animal	climax	-	-	-	-	+	-	-
Ficus natalensis	animal	climax	+	-	-	+	+	-	-
Ficus spp	animal	climax	-	-	-	-	-	-	+
Ficus sur	animal	climax	-	+	+	+	+	+	+
Ficus sycomoras	animal	climax	+	+	-	+	-	-	-
Ficus thonningii	animal	climax	-	-	-	-	+	+	+
Ficus urceolaris	animal	pioneer	-	-	-	+	-	-	-

Tree species	Mode of dispersal	Succession	Budongo			Mabira		Kakamega	
			PF	LD	HD	LD	HD	LD	HD
Ficus vallis-choudae	animal	climax	-	-	-	-	+	+	-
Funtumia africana	other	pioneer	+	+	+	+	+	+	+
Glyphaea brevis	animal	climax	+	+	+	+	+	-	-
Grewia mildbraedii	animal	climax	-	+	+	+	+	-	-
Harungana madagascariensis	animal	pioneer	-	-	+	-	-	+	+
Heinsenia diervilleoides	animal	climax	-	-	-	-	-	+	+
Heisteria pervifolia	animal	climax	+	-	-	-	-	-	-
Holoptelea grandis	other	climax	+	+	+	+	+	-	-
Khaya anthotheca	other	climax	+	+	+	+	+	-	-
Kigelia africana	other	climax	-	-	-	-	-	+	+
Kleinedoxa gabonensis	other	climax	+	-	+	-	-	-	-
Lannea welwitschii	animal	climax	-	-	-	+	+	-	-
Lasiodiscus mildbraedii	animal	climax	+	+	+	+	-	-	-
Lepisanthes senegalensis	animal	climax	-	+	+	+	-	+	-
Lovoa trichilioides	other	climax	-	-	-	-	+	-	-
Lychnodiscus cerospermus	other	climax	+	+	+	+	-	-	-
Macaranga schweinfurthii	other	climax	-	-	-	-	+	-	-
Macaranga spinosa	other	pioneer	+	-	-	-	+	-	-
Maerua duchensei	animal	climax	-	-	+	+	+	-	-
Maesa lanciolata	animal	pioneer	-	-	-	-	+	-	-
Maesopsis eminnii	animal	pioneer	+	+	+	+	+	-	+
Majidea zanguebarica	animal	climax	+	-	-	+	+	-	-
Mallotus oppositifolius	animal	climax	+	+	-	-	-	-	-
Mamea africana	animal	climax	+	+	+	-	-	-	-
Manilkara butugi	animal	climax	-	-	-	-	-	+	-
Margaritaria discoideus	animal	pioneer	+	+	+	+	+	-	-
Margaritaria pachysiphon	animal	climax	-	-	-	+	+	-	+
Markhamia lutea	other	pioneer	-	+	-	+	+	+	+
Maytenus heterophylla	animal	pioneer	-	-	-	-	-	-	-
Mildbraediodendron excelsum	other	climax	+	+	-	-	-	-	-
Milicia excelsa	animal	climax	-	+	+	+	+	-	+
Milletia eetveldeana	animal	pioneer	-	-	-	+	-	-	-
Monodora angolense	animal	climax	+	-	+	+	-	+	-
Monodora myristica	animal	climax	+	+	+	-	-	-	-
Morus mesozygia	animal	climax	+	+	+	+	+	+	+
Myrianthus holstii	animal	climax	+	+	+	+	+	-	-

	Mode of dispersal		Budongo			Mabira		Kakamega	
Tree species		Succession	PF	LD	HD	LD	HD	LD	HD
Ochna bracteosa	animal	climax	+	-	-	-	-	-	-
Olea capensis	animal	climax	-	-	-	-	-	+	+
Oncoba spinosa	animal	climax	-	-	-	-	-	+	-
Ouratea densiflora	animal	climax	-	-	+	-	-	-	-
Oxyanthus specious	animal	climax	+	-	-	+	+	+	+
Pancovia turbinata	animal	climax	-	+	+	-	-	+	-
Parkia filicoidea	animal	climax	+	-	-	+	-	-	-
Piptadeniastrum africanum	other	climax	-	-	-	-	+	-	-
Polyathia suaoveolens	animal	climax	+	+	+	-	-	-	-
Polyscias fulva	other	pioneer	-	-	-	+	+	+	+
Premna angolensis	animal	climax	-	+	-	-	-	+	-
Prunus africana	animal	climax	-	-	-	-	+	+	+
Pseudospondias microcarpa	animal	climax	+	+	+	+	+	+	-
Psidium guajava	animal	pioneer	-	+	+	-	-	-	-
Pterygota mildbraedii	other	climax	+	+	-	+	+	-	-
Pycnianthus angolensis	animal	climax	+	+	-	-	-	-	-
Raphia farinifera	other	pioneer	+	-	-	-	-	-	-
Rauvolfia vomitoria	animal	pioneer	-	+	+	-	+	-	-
Rawsonia lucida	animal	climax	+	+	-	+	-	+	-
Ricinodendron heudelotii	animal	climax	+	+	+	-	-	-	-
Rinorea ardisiaeflora	animal	climax	+	+	+	-	-	-	-
Rinorea dentata	animal	climax	+	-	-	-	-	-	-
Ritchiea albersii	animal	climax	-	+	-	+	-	-	+
Rothamannia urcelliformus	animal	climax	-	-	+	-	+	+	-
Rytigynia umbellulata	animal	climax	-	-	-	-	+	-	-
Sapium ellipticum	animal	climax	-	-	-	+	+	+	+
Schrebera arborea	other	climax	-	-	+	+	+	+	-
Spathodea campanulata	other	pioneer	-	-	-	-	+	+	+
Sterculia dawei	animal	climax	+	-	+	+	+	-	-
Strombosia scheffleri	animal	climax	+	+	+	+	-	-	+
Strychnos usambarensis	animal	climax	+	-	-	-	-	+	+
Suregada procera	animal	climax	+	-	-	-	-	-	-
Syzygium guineensis	animal	climax	-	-	-	-	-	+	+
Tabernaemontana pachysiphon	animal	climax	+	+	+	+	+	-	-
Tabernaemontana stapfiana	other	climax	+	-	-	+	+	-	-
Tapura fischeri	animal	pioneer	+	+	+	+	+	-	-

Tree species	Mode of dispersal	Succession	Budongo			Mabira		Kakamega	
			PF	LD	HD	LD	HD	LD	HD
Tarenna pavetoides	animal	climax	-	-	-	-	+	-	-
Teclea nobilis	animal	climax	+	+	+	+	-	+	+
Terminalia ivorensis	other	climax	-	-	-	-	+	+	-
Tetrapleura tetraptera	other	climax	+	+	+	+	+	-	-
Tetrarchidium didymonstemon	animal	pioneer	+	+	-	-	-	-	-
Treculia africana	animal	climax	-	-	-	+	+	-	-
Trema orientalis	animal	pioneer	-	-	-	-	+	+	-
Trichilia emetica	animal	climax	+	+	-	+	+	+	+
Trichilia prieuriana	animal	climax	+	+	+	+	+	-	-
Trichilia rubescens	animal	climax	+	+	+	+	-	-	-
Trilepisium madagascariense	animal	climax	+	+	+	+	+	+	+
Turraea floribunda	animal	climax	+	-	-	-	-	+	+
Turraea holstii	animal	climax	+	+	+	+	+	-	-
Turraeanthus africanus	animal	climax	+	+	+	-	+	-	-
Uvariopsis congensis	animal	climax	+	+	+	+	+	-	-
Vangueria apiculata	animal	pioneer	-	-	+	+	-	+	+
Vitex doniana	animal	climax	-	-	-	-	-	-	+
Vitex ugandensis	animal	climax	+	+	-	-	-	-	-
Xylopia parviflora	animal	climax	+	-	-	-	-	-	-
Zanthoxylum gillettii	animal	climax	+	-	+	-	-	-	+
Zanthoxylum leprieurii	animal	climax	+	-	-	-	-	-	-
seedling species									
Alangium chinense	animal	climax	-	+	-	+	+	-	-
Albizia gummifera	other	climax	-	+	+	+	+	+	+
Allophyllus abyssinicus	animal	climax	-	-	-	+	+	+	+
Alstonia boonei	animal	climax	-	-	-	+	-	-	-
Aningeria altissima	animal	climax	+	+	+	-	-	+	+
Antiaris toxicaria	animal	climax	+	+	+	+	+	+	+
Argomuellera macrophylla	other	climax	+	+	+	+	-	-	-
Baphia wollastonii	other	climax	-	-	+	-	-	-	-
Bequaertiodendron oblanceolatum	animal	climax	+	+	+	+	+	+	+
Blighia unijugata	animal	climax	-	-	+	+	+	-	+
Bridelia micrantha	animal	pioneer	-	+	-	-	-	-	-
Cassaeria battiscombei	animal	climax	-	-	-	-	-	-	+
Cassipourea ruwensorensis	animal	climax	-	-	-	-	+	-	-

Seedling species	Mode of dispersal	Succession	Budongo PF	Budongo LD	Budongo HD	Mabira LD	Mabira HD	Kakamega LD	Kakamega HD
Celtis africana	animal	climax	-	-	-	-	-	+	-
Celtis durandii	animal	climax	+	+	+	+	+	+	+
Celtis mildbraedii	animal	climax	+	+	+	+	+	+	-
Celtis philippensis	animal	climax	-	-	-	+	-	-	-
Celtis zenkerii	animal	climax	+	-	-	-	-	-	-
Chaetacma aristata	animal	climax	-	-	+	+	-	-	-
Chrysophyllum albidum	animal	climax	+	+	+	-	-	+	+
Chrysophyllum perpulchrum	animal	climax	-	+	+	-	-	-	-
chrysophyllum viridifolium	animal	climax	-	-	-	+	-	-	-
Clausena aniseta	animal	pioneer	-	-	-	-	+	-	-
Coffea eugenioides	animal	climax	-	-	-	-	-	+	-
Cordia africana	animal	climax	-	+	-	-	-	-	-
Croton macrostachyus	animal	pioneer	-	-	-	+	-	-	-
Croton sylvaticus	animal	pioneer	-	-	+	-	-	+	+
Cynometra alexandri	animal	climax	+	+	+	-	-	-	-
Diospyros abyssinica	animal	climax	+	+	+	-	-	+	+
Dovyalis macrocalyx	animal	climax	-	-	-	-	-	-	+
Erythroccoca trichogyne	animal	climax	-	-	-	-	+	-	-
Ficus asperifolia	animal	climax	-	-	+	+	-	-	-
Ficus spp			-	-	-	+	-	-	-
Ficus exasperata	animal	climax	-	+	-	+	-	-	-
Funtumia africana	other	pioneer	-	+	+	-	-	+	+
Khaya anthotheca	other	climax	+	+	+	-	-	-	+
Lasiodiscus mildbraedii	animal	climax	+	+	+	-	-	-	-
Lecaniodiscus fraxinifolius	animal	climax	+	-	-	-	-	-	-
Maesa lanciolata	animal	pioneer	-	+	-	-	+	-	-
Maesopsis eminii	animal	pioneer	-	+	+	-	-	-	-
Margaritaria discoideus	animal	pioneer	-	+	-	+	-	-	-
Markhamia lutea	other	pioneer	-	-	-	-	-	+	-
Memecyon jasminoides	animal	climax	+	-	-	-	-	-	-
Monodora angolensis	animal	climax	+	-	-	+	+	-	-
Morus mesozygia	animal	climax	-	-	-	-	-	-	+
Myrianthus holstii	animal	climax	+	+	+	-	-	-	-
Ouratea densiflora	animal	climax	+	-	+	-	-	-	-
Pancovia turbinata	animal	climax	+	-	-	-	-	-	-
Peddea fischeri	animal	climax	-	-	-	-	-	+	-

Seedling species	Mode of dispersal	Succession	Budongo			Mabira		Kakamega	
			PF	LD	HD	LD	HD	LD	HD
Polyathia suaveoleus	animal	climax	+	-	+	-	-	-	-
Polyscias fulva	other	pioneer	-	-	-	-	-	-	+
Prunus africana	animal	climax	-	-	-	+	+	+	+
Psidium guajava	animal	pioneer	-	-	+	-	-	-	-
Psychotria peduncularis	animal	climax	-	-	-	-	+	-	-
Pterigota mildbraedii	other	climax	-	-	-	-	+	-	-
Rawsonia lucida	animal	climax	-	+	+	-	-	-	+
Rinorea ardisiaeflora	animal	climax	+	+	+	-	-	-	-
Rinorea brachypetala	animal	climax	+	+	+	-	-	-	-
Rinorea dentata	animal	climax	+	-	+	+	-	-	-
Rinorea ilicifolia	animal	climax	-	-	+	+	+	-	-
Streculia dawei	animal	pioneer	-	-	-	-	+	-	-
Strombosia scheffleri	animal	climax	+	+	+	+	+	-	+
Strychnos usambarensis	animal	climax	-	-	-	+	-	+	-
Tabernaemontana pachysiphon	animal	climax	+	-	-	-	+	-	-
Teclea nobilis	animal	climax	-	+	-	+	+	+	+
Trichilia emetica	animal	climax	-	-	-	-	-	-	-
Trilepisium madagascariense	animal	climax	+	-	+	+	+	+	+
Turraea floribunda	animal	climax	-	-	+	-	-	+	-
Uvariopsis congensis	animal	climax	-	-	+	+	-	-	-
Vangueria apiculata	animal	pioneer	-	-	+	-	-	-	-