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Seed Dispersal and Tree Spatial Recruitment Patterns in Secondary Tropical Rain Forests

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1. Introduction

Many tropical rain forests are faced with rapid fragmentation and heavy exploitation of flora and fauna (Fa et al., 2005; Laurance, 1998). Studies on effects of forest disturbances, especially logging, have revealed incidental impacts such as damage to the seedlings, saplings and the canopy (e.g. Pereira et al., 2002; White, 1994). However, it is also recognised that the secondary effects of logging may in some cases outweigh the initial damage done by logging. For instance, logging is often accompanied by an increased incidence of hunting, fire and human occupation (Laurance et al., 2006). In addition, these human-induced changes disrupt the ecological processes that are important in maintaining viable populations thus threatening the very survival of forest species. The chain of damaging consequences of these exploitations are believed to lead to the loss of ecological services and loss of timber and non-timber forest products. These result in reduced conservation value of the remnant forests which in turn undermines their sustainability and land productivity.

With the increasing demand for timber and other forest products triggered by growing human populations in the developing countries where these forests are located, it is certain that sustainable management of these remnant forests will be a major challenge (Wright and Muller-Landau, 2006). There is therefore, a need to understand the dynamics of plant and animal populations in secondary tropical forest landscapes. Perhaps of great importance is the understanding of ecological processes that are vital for maintenance of viable tree and animal populations. One of the key ecological processes believed to be affected by forest disturbances and is vital in influencing plant community dynamics is seed dispersal (Barlow and Peres, 2006; Howe and Miriti, 2000). Seed dispersal is crucial for reducing distance- or density-dependent mortality of trees (Hardesty et al., 2006). In addition, within a forest landscape there are sites, such as gaps, that are more favourable for juvenile establishment than others. Consequently, the more widely the seeds of an individual species are dispersed, the greater the chances of the offspring reaching such favourable sites. In tropical rain forests, over 70% of tree species are dispersed by animals (Corlett, 1996; da Silva and Tabarelli, 2000; Gautier-Hion et al., 1985). Seed dispersing animals are believed to influence tree spatial distribution through the seed footprint patterns they create. The seed footprint is

determined by the distance over which seeds are dispersed and the density of seeds deposited at any site. Due to the diversity in behavioural ecology among seed dispersing animals, the resulting seed footprints are similarly diverse (Balcomb and Chapman, 2003; Kaplin and Moermond, 1998; Lambert, 2000; McConkey, 2000; Wrangham et al., 1994). Consequently, it is plausible that frugivore diversity in tropical forests may have a strong influence on tree recruitment and spatial distribution (Terborgh et al., 2002). Thus, implying that spatial recruitment of tree species in a forest landscape is altered following loss of some frugivore species.

This study examined seed dispersal and tree spatial recruitment patterns in three tropical forests whose vertebrate populations have been altered differently over the past few decades. The study uses empirical data to test the hypothesis that changes in vertebrate assemblages in tropical rain forests caused by anthropogenic disturbances affect the seed dispersal patterns and subsequent tree spatial recruitment patterns in secondary tropical rain forests. By observing vertebrate assemblages on selected tree species with a range of seed sizes in three tropical rain forests, I sought to address three questions. First, I examine whether there are differences in seed dispersing vertebrate communities in differentially disturbed forests. Second, I determine whether the rate of seed dispersal varies in differentially disturbed forests. Thirdly, I examine whether the observed frugivory patterns are correlated with the tree spatial recruitment patterns. The effects of changes in vertebrate seed disperser community on tree recruitment in secondary forest landscapes are discussed in the wider context of the effectiveness of remnant vertebrate populations in seed dispersal and the possible consequences for tree demography.

2. Methods

2.1 Study sites and tree species

The comparison of seed dispersal and tree recruitment patterns was conducted in three tropical rain forests in Uganda namely: Mabira, Budongo and Kibale Forests (Figure 1). Although these three forests had a similar faunal and floral composition less than a century ago (Hamilton, 1991; Howard, 1991), they now represent a spectrum of disturbance regimes ranging from a highly disturbed and fragmented Mabira Forest, to the moderately disturbed Kibale Forest while Budongo is intermediate. Mabira Forest Reserve is a medium altitude, moist, semi-deciduous forest in Central Uganda (32° 52' – 33° 07' E and 0° 24' – 0° 35' N), covering an area of 306 km². The forest has been subjected to intense anthropogenic disturbances such as logging and hunting which have led to loss of most of its animal populations (Howard, 1991). In addition, vast areas of formerly forested land have been converted to agriculture land. For example, over a period of 15 years (1973 – 1988) it is estimated that 29% of the forest cover was lost and the total forest edge-to-area ratio increased by 29% over the same period (Westman et al., 1989). This resulted in severe forest fragmentation with an estimated fifty thousand people living in the associated enclaves. Budongo Forest Reserve is also a medium altitude, moist, semi-deciduous forest in western Uganda (31° 22' – 31° 46' E and 1° 37' – 2° 03' N), covering an area of 753 km². Although Budongo has been selectively logged since the 1920s, it remains relatively intact with a large population of diurnal primates (Plumptre and Cox, 2006). Mabira and Budongo Forest Reserves are both believed to have had other large vertebrates such as elephants (*Loxodonta africana*) and leopards (*Panthera pardus*) but these were driven to extinction between 1950

and 1980 (Howard, 1991). As forest reserves, logging is still permitted in Mabira and Budongo. On the other hand, the 506 km² Kibale Forest National Park (30° 19' - 30° 32' E and 0° 13' - 0° 41' N) is a moist evergreen forest, transitional between lowland rain forest and montane forest. Kibale is habitat to approximately 280 elephants and has a higher primate biomass than Mabira and Budongo (Plumptre and Cox, 2006). As a national park, Kibale is granted a better protection status than Budongo and Mabira, given that neither logging nor hunting is permitted.

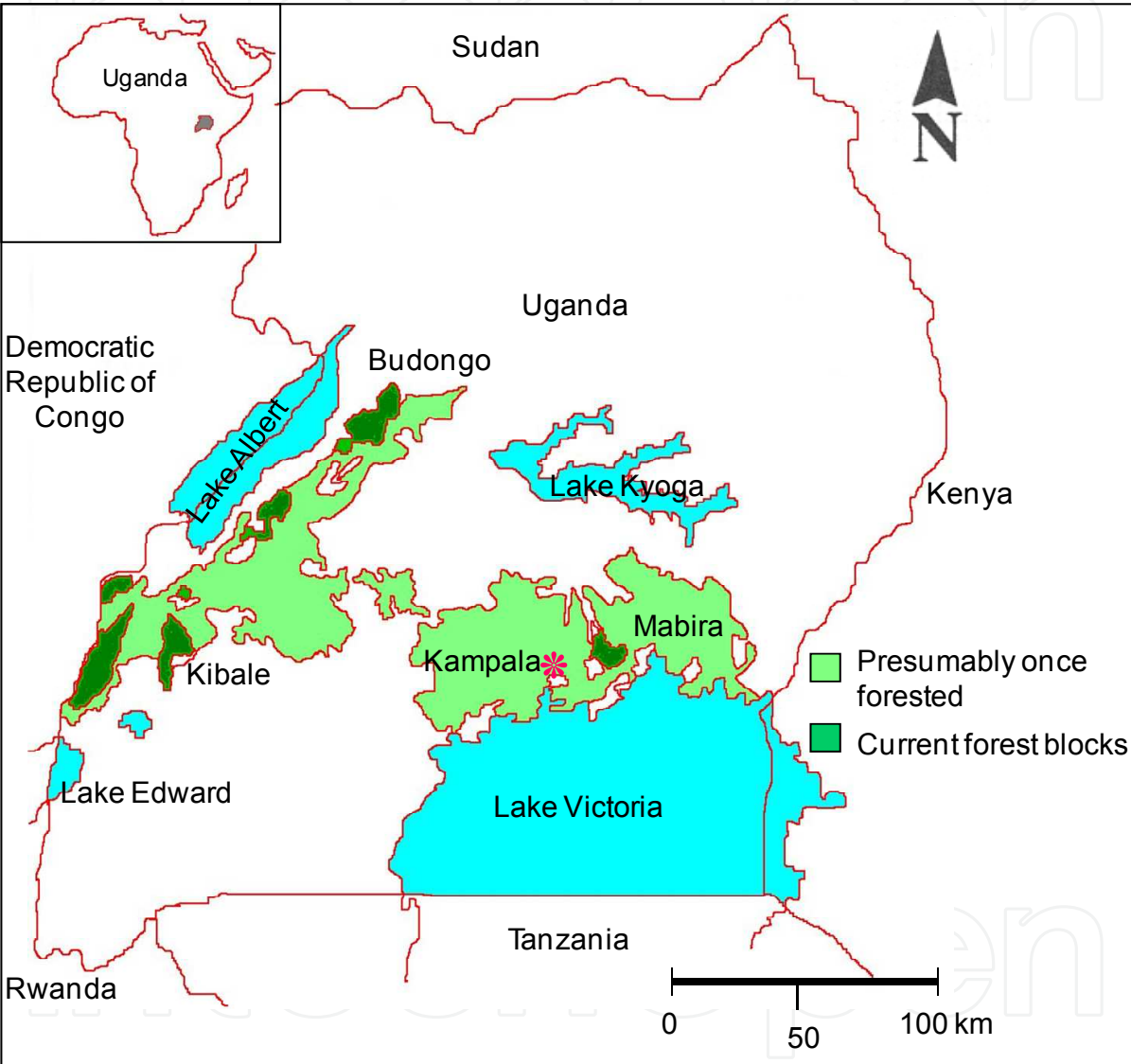


Fig. 1. Map of Uganda showing the forests studied and the areas presumably once forested before 1950s (Hamilton, 1984). Inset is the location of Uganda in Africa

To study seed dispersal and tree spatial recruitment patterns, five tree species were selected on the basis of their fruit/seed size and their occurrence in the three study sites. Fruit/seed size is the major factor limiting vertebrates feeding on fruits and/or seeds of a particular tree (Bollen et al., 2004; Githiru et al., 2002). All five tree species occur in the three forests except for *Ricinodendron heudelotii* that does not grow in Kibale Forest. A brief description of each species is presented in Table 1.

Species	Family	Fruit size (mm)	No of seeds per fruit	Vertebrate dispersers
<i>Balanites wilsoniana</i> Dawe & Sprague	Zygophyllaceae	90	1	Elephants ¹
<i>Chrysophyllum albidum</i> G. Don	Sapotaceae	40	3-4	Large primates and ungulates
<i>Cordia millenii</i> Baker	Boraginaceae	40	1	Primates and ungulates
<i>Ricinodendron heudelotii</i> (Baill.) Pierre ex Pax	Euphorbiaceae	30	2-3	Primates and ungulates ²
<i>Celtis zenkeri</i> Engl.	Ulmaceae	10	1	Most primates and birds

¹(Babweteera et al., 2007; Chapman et al., 1992);

²(Feer, 1995; Plumptre et al., 1994).

Table 1. A description of the study tree species

2.2 Vertebrate assemblage and seed dispersal rate

Seed dispersal rate was inferred from the frugivore visitation rates. Vertebrates feeding on the five tree species in each of the three forests were recorded. Three mature fruiting individuals (hereafter referred to as ‘focal trees’) of each species per forest were identified and observed from time to time for a period of one year. The focal trees of the five species were selected to be at least one kilometre apart and each one was observed at the peak of its fruit ripening for 45 – 75 hours. The observations were made between 0600 – 1200 hrs and 1500 – 1800hrs, recording information on the vertebrate species visiting the tree and the time that each spent feeding. All individual vertebrates visiting the focal trees and observed to be eating the fruits and/or seeds were recorded. Focal sampling was done for each frugivorous species recorded in order to determine the number of fruits consumed per unit time. In addition to the direct observations, camera traps (DSC-P32 Digital Camtrakkers) were mounted beneath the fruiting trees to record animals feeding on fallen fruits. Camera traps have been used successfully to study animal populations (e.g. Carbone et al., 2001; Silveira et al., 2003) and their use is thought to overcome some of the limitations of direct observation such as failure to observe nocturnal feeders or shy frugivores. The camera traps were not mounted to make observations on *Celtis* trees because of the difficulty in ascertaining whether the photographed animals were feeding on the tiny *Celtis* fruits. The camera traps were set to make observations during both day and night. The fruiting trees on which they were placed were different from the set used for direct observation. This was done in order to maximize the total observation period for each species, given that the fruiting season for some trees is of short duration. The direct and camera trap observation period for each tree in each forest is summarized in (Table 2).

In addition to the estimate of fruit consumption by arboreal frugivores, an estimate of the rate of fruit removal by vertebrate seed dispersers that feed on fallen fruits were also made. To quantify this, six fruiting trees of each species except for *Celtis*, were selected in each forest. *Celtis* was excluded from the assessment of rate of fruit removal because of the difficulty in ascertaining the fate of the fruit, given its small size. For each individual tree,

two fruit piles were randomly placed at 10m (hereafter categorised as NEAR) and 100m (FAR) from the edge of the fruiting tree crown. Fruit piles were placed NEAR and FAR to assess effect of proximity to fruiting tree on rate of fruit removal. Each fruit pile (referred to as ‘fruit station’) contained 10 ripe fruits. The fruit stations were monitored daily until all the fruits were removed or rotten. An individual fruit was considered ‘removed’ if the whole fruit was missing or partially eaten with the seed missing.

	<i>Balanites</i>	<i>Chrysophyllum</i>	<i>Cordia</i>	<i>Ricinodendron</i>	<i>Celtis</i>
Kibale					
Direct	137	285	216	0	87
Camera traps	1946	1482	1027	0	0
Budongo					
Direct	109	151	221	127	148
Camera traps	1638	1608	1183	1221	0
Mabira					
Direct	146	158	197	121	137
Camera traps	1938	1573	941	1597	0

Table 2. Summary of the direct and camera trap observation hours for frugivory activities on selected tree species in Kibale, Budongo and Mabira Forests. No observations were made on *Ricinodendron* trees in Kibale because they do not exist in this forest

To compare seed dispersal patterns by frugivores in different forests, variations in frugivore body size in the three forests were analysed. The body size is of utmost importance because it is a strong correlate to the quantity of seed dispersal and the distance over which seeds are moved (Lambert, 1998; Lambert, 1999). Limited variation in the body size of frugivores at a particular site causes stereotyped dispersal patterns distinctive of the seed handling and movement patterns of frugivores. In addition, frugivore visitation rates and number of frugivore species visiting each tree species in the three forests were computed as implicit measures of rate of seed dispersal and frugivore preference. The number of individual frugivores visiting each tree species per hour was computed in each forest and ANOVA (SPSS v12) used to test for differences in visitation rate between trees species and forest. The hourly visitation rate data for individual conspecific focal trees in each forest was pooled because there was no significant difference in visitation rates among them for all species. Trees with low visitation rates and narrow ranges of frugivorous species are deemed to be the most vulnerable. To augment the estimated arboreal seed dispersal rate, the rate of ground fruit removal per fruit station was assessed by calculating finite removal rates using the Kaplan-Meier method (Krebs, 1999). The finite removal rate ranges between 0 (0% removal) and 1 (100% removal). To test for differences in fruit removal rates, the calculated finite removal rates were arcsine transformed and used in an ANOVA general linear model procedure. The model included forest type, tree species and distance from the fruiting tree (NEAR or FAR) as the main effects.

2.3 Spatial recruitment of juvenile trees

Spatial juvenile tree recruitment was assessed in square 1-ha plots established around adult conspecific trees for each of the study species. Three plots were established in each of the three forests for each tree species. The selected plots for each species had approximately

equal numbers of adult trees of the study species. In each plot, a search for all juveniles (seedlings 0-50 cm in height; sapling 51-400 cm; and poles >400 cm in height but less than 10 cm DBH) of the corresponding tree species was made and the distance to the nearest adult tree was measured. *Balanites* that propagates both sexually and vegetatively, an effort was made to determine whether juveniles originated from root sprouts or seed. Individuals confirmed to be developing from sprouts were omitted from the analysis. To compare the relative dispersion between forests, the cumulative distributions of distances from juveniles to adult trees for each species in each forest were computed (Hamill and Wright, 1986). Pairwise Kolmogorov-Smirnov tests (Dytham, 2003) were then conducted between conspecific plots within each forest to determine whether there were significant differences in the spatial distributions among plots within each forest. Thereafter, the spatial distribution data were pooled for each forest to obtain a single distribution function to enable comparisons between forests using Kolmogorov-Smirnov tests.

3. Results

3.1 Frugivore assemblage and seed dispersal rates

In the three forests a total of 44 frugivore species were recorded, of which 31 were birds, 8 primates, 5 ungulates/omnivores. Five species of rodent seed predators were recorded as well. An overview of the distribution of species and abundance per forest is presented in Appendix. In general, Mabira Forest had the least number of frugivorous species and number of individual frugivores (Figure 2). In addition to fewer frugivore species, there was less variation in the body weight of frugivores in Mabira, whereas the highest variation was in Kibale Forest due to the presence of elephants (Table 3). Mabira also had the highest number of seed predating rodent species (Figure 2).

Frugivore visitation rates were significantly different between the forests ($F = 65$, $df = 2$, $P < 0.001$). The mean hourly visitation rate was higher in Budongo (2.2 individuals/hr) than in Kibale (1.6 individuals/hr) and Mabira (0.9 individuals/hr). The high visitation rate in Budongo was particularly due to the high frequencies of blue monkeys *Cercopithecus mitis*. The low frugivore visitation rate in Mabira could be an explicit indicator of low vertebrate densities. In addition, small-fruited *Celtis* trees were visited more frequently in all three forests whereas, *Ricinodendron* was the least visited tree (ANOVA; $F = 270$, $df = 3$, $P < 0.001$; Figure 3). The high visitation rate to *Celtis* compared to the large-fruited trees was mainly due to the large number of frugivorous birds visiting *Celtis* and a preference for large-fruited trees by large frugivores. *Ricinodendron* was the least visited tree and this could be due to the fibrous characteristic of its fruits. Pairwise comparisons of visitation rates to conspecific trees show significant differences between Budongo and Mabira for all tree species whereas visitation rates in Budongo and Kibale were not different except for *Celtis* (Figure 3). *Balanites* was not included in the pairwise comparisons of frugivore visitation rates because, the only observations of frugivores feeding on this species were made by camera traps, for which I could not determine the hourly visitation rate.

A comparison of the estimated quantity of fruit handled by arboreal frugivores (frugivores feeding in the canopy) shows that they handled 20, 36 and 2 fruits per hour in Kibale, Budongo and Mabira respectively. The low quantity of fruit handled in Mabira compared to Budongo and Kibale is due to the low visitation rate and fewer fruits eaten per visiting

frugivore. The high quantity handled in Budongo compared to Kibale is attributed to a higher number of chimpanzees and blue monkeys visiting fruiting trees in Budongo (Table 4). Chimpanzees were the most important frugivores in both Kibale and Budongo Forests where they handled over 80% of the fruit. This was largely due to their longer visitation period coupled with a larger quantity of fruit eaten per hour. Chimpanzees and baboons were the only frugivores regularly observed to ingest whole fruits. Other smaller primates ate the pulp and discarded the seed beneath the fruiting trees. However, some of the smaller primates especially the blue monkeys were occasionally seen carrying away a few fruits from the fruiting tree and feeding in the neighbouring trees.

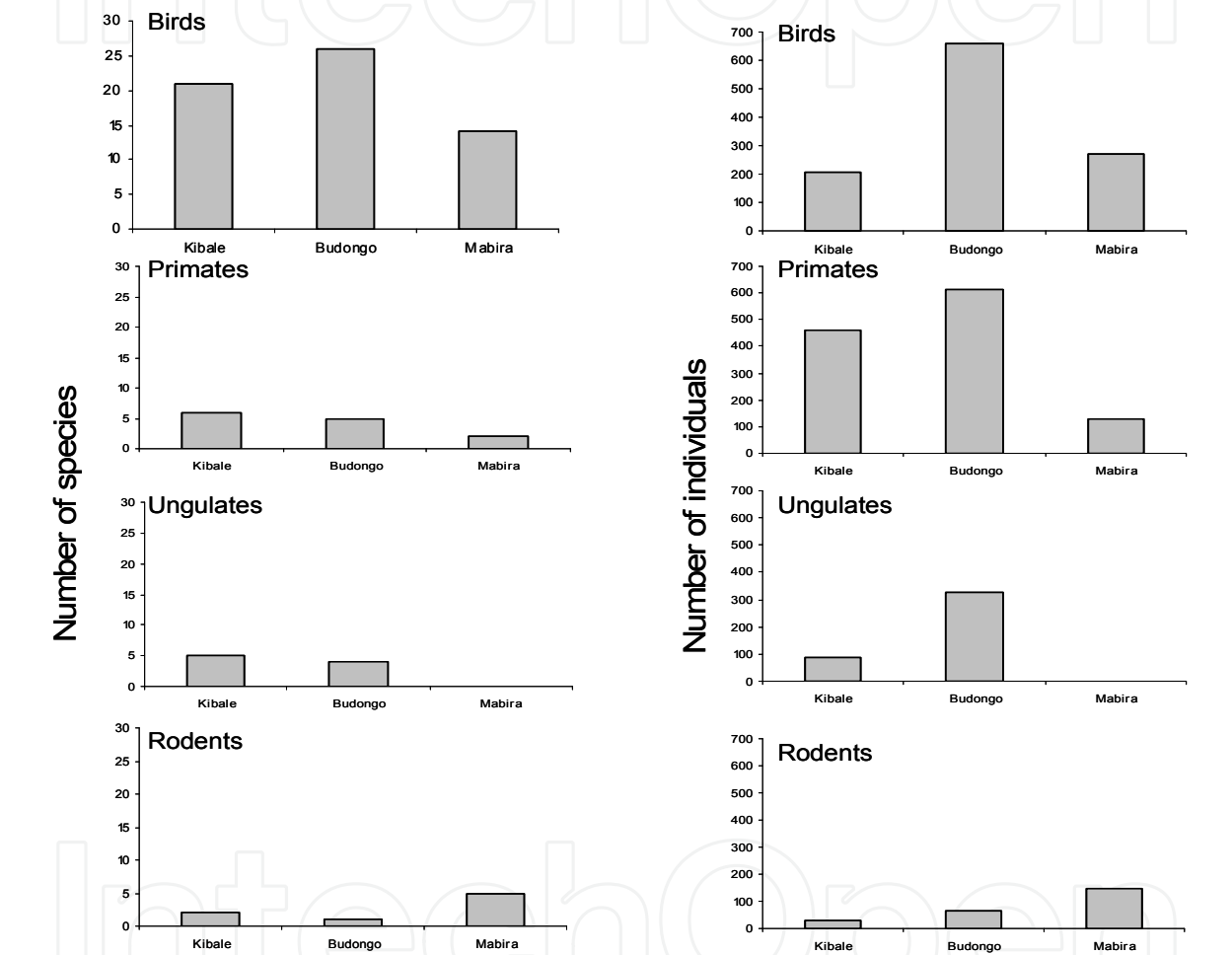


Fig. 2. Species richness and abundance of guilds of vertebrates observed feeding on fruits and seeds of *Celtis*, *Ricinodendron*, *Cordia*, *Chrysophyllum* and *Balanites* in Mabira, Budongo and Kibale Forests.

Forest	Body weight (Kg)			
	25%	75%	Min	Max
Kibale	0.05	6.8	0.02	5000
Budongo	0.03	4.0	0.01	65
Mabira	0.03	0.4	0.02	9

Table 3. Variation in body weight (minimum, maximum and quartile ranges) of frugivores in Kibale, Budongo and Mabira Forests

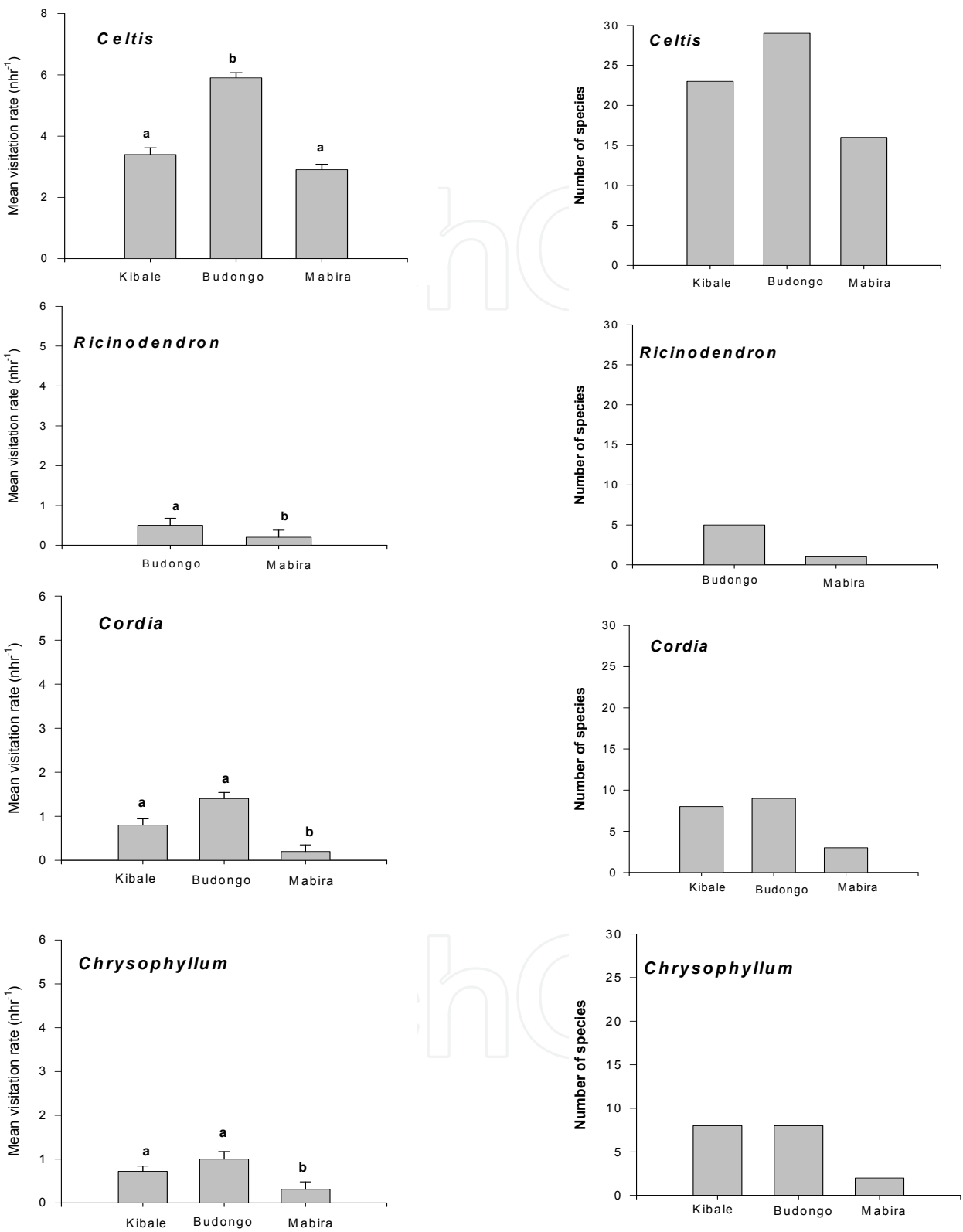


Fig. 3. Frugivore visitation rates (left) and number of frugivorous species visiting (right) different tree species in Kibale, Budongo and Mabira Forests. Bars labelled with different letters represent significantly different mean hourly visitation rates (Tukey HSD) at $P < 0.01$ (ANOVA). There were no *Ricinodendron* trees in Kibale.

Species (number of observation hours)	Visits (n)	Duration of visit			Fruits eaten (n/hr-1)	% of fruits (Total number of fruits) handled
		(hr)				
		Mean	25%	75%		
Kibale (501)						
Chimpanzee*	76	1.33	0.78	1.92	81	80.5 (8187)
Red tailed monkey**	131	0.13	0.05	0.18	52	8.7 (886)
Baboon*	70	0.12	0.07	0.12	78	6.4 (655)
Grey cheeked mangabey**	27	0.23	0.13	0.42	42	2.6 (260)
Red Colobus**	24	0.12	0.03	0.15	48	1.4 (138)
Black and white colobus**	22	0.08	0.03	0.15	28	0.5 (49)
Budongo (372)						
Chimpanzee*	138	1.25	0.85	1.6	84	89 (11490)
Blue monkey**	230	0.17	0.07	0.25	29	7 (1134)
Red tailed monkey**	68	0.15	0.05	0.2	51	3.2 (520)
Black and white Colobus**	26	0.08	0.05	0.13	42	0.5 (87)
Baboon*	2	0.02	0.02	0.02	63	0.3 (3)
Mabira (355)						
Black mangabey**	46	0.2	0.13	0.32	31	57 (524)
Red tailed monkey**	49	0.1	0.03	0.12	44	43 (216)

* Ingest whole fruit;
** Eat pulp and discard seeds at feeding point

Table 4. Quantity of *Cordia* and *Chrysophyllum* fruits consumed in Kibale, Budongo and Mabira Forests. Duration of visit is represented by mean and quartile ranges.

Estimates of dispersal rates by vertebrates feeding on fruits on the ground at the fruit stations revealed that the rate of removal was significantly affected by the tree species ($F = 61.2$, $df = 3$, $P < 0.001$) and the forest ($F = 451.6$, $df = 2$, $P < 0.001$) but not the distance of the fruit station from the fruiting tree. Given that removal rates were not influenced by the proximity of the fruit station to the fruiting tree, the observed ground fruit removal rates at all the fruit stations for each species in each forest were pooled in order to analyse for differences in the rate of fruit removal between forests for each tree species. The pooled data showed that fruit removal rates were higher in both Budongo and Kibale than Mabira (Figure 4). There were no differences in fruit removal rates between Budongo and Kibale for all species except for *Balanites* where hardly any fruits were eaten in Budongo due to the absence of the elephants, the only known frugivores feeding on the fruits. The few fruits of *Balanites* that were removed in Mabira and Budongo were probably eaten by bush pigs or rodents.

Although over 90% of all the fruit was removed in both Kibale and Budongo, the mean duration for 75% of fruits to be removed was significantly lower in Kibale compared to Budongo (6 and 10 days respectively, ANOVA $F = 198$, $P < 0.001$). The faster removal rate in Budongo compared to Kibale may be attributed to a higher density of duikers in Budongo (Appendix). It was further observed that animals consuming the fruit in Budongo and

Kibale ingested the whole fruit since there were no signs of fruit husks or seeds left at the station. In Mabira, 4 out of 96 fruit stations had at least 75% of the fruit removed. Overall 90% of the fruit in Mabira rotted after 3 weeks. It is possible that the few fruits removed in Mabira were consumed by rodent seed predators as I observed fruit husks left at the station. Unlike the arboreal frugivores that preferred *Chrysophyllum* and *Cordia* to *Ricinodendron*, the frugivores feeding on fallen fruits (probably ungulates) did not show any preference for particular fruits.

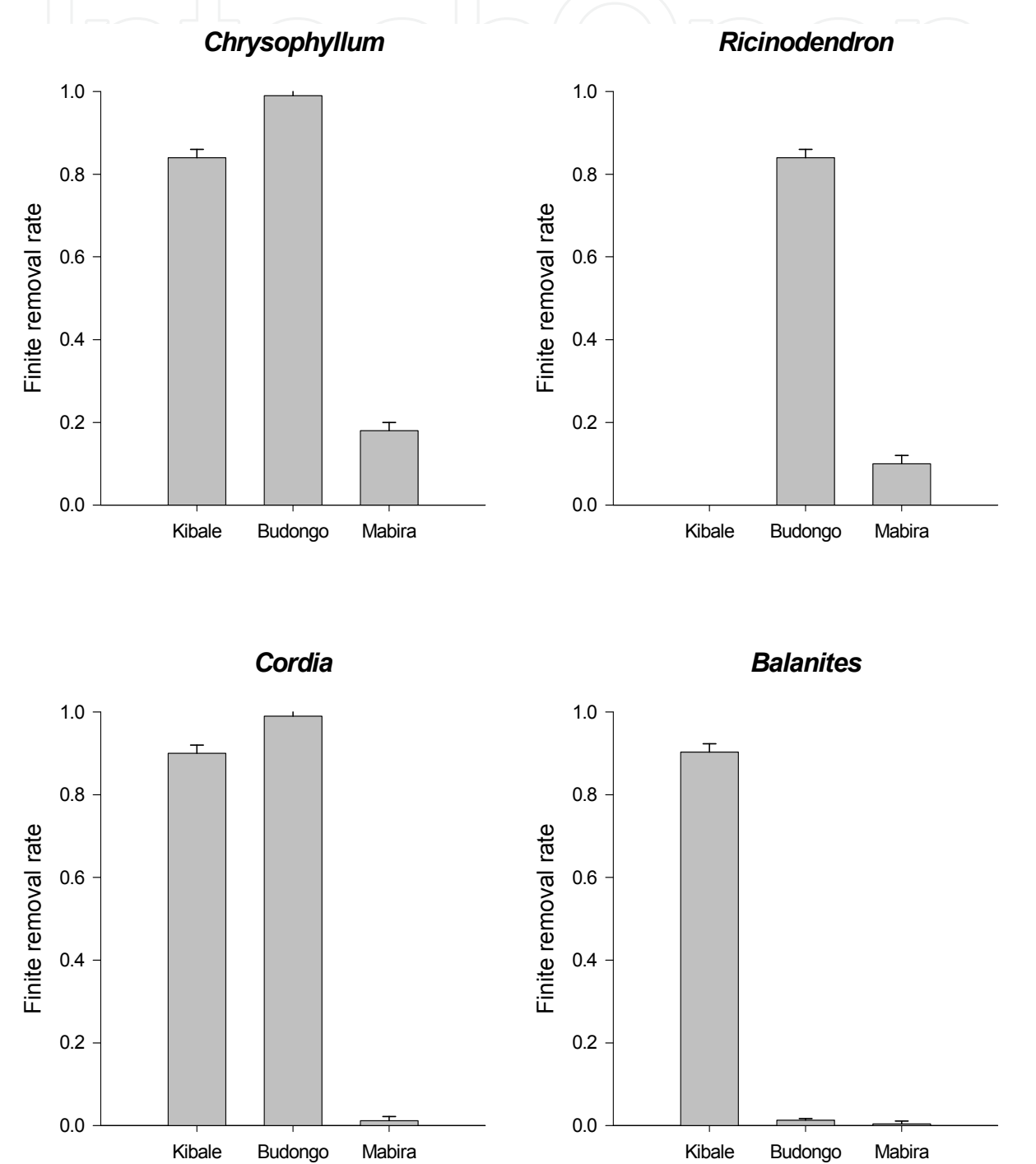


Fig. 4. Fruit removal rates in Kibale, Budongo and Mabira Forests. There were no *Ricinodendron* trees in Kibale.

3.2 Spatial recruitment of juvenile trees

Juveniles of *Cordia* and *Ricinodendron* were not found in any of the plots established in the three forests. The abundance of *Celtis* juveniles was similar between forests whereas juvenile densities of *Chrysophyllum* and *Balanites* varied significantly between forests (Figure 5). *Chrysophyllum* densities were high in both Budongo and Kibale compared to Mabira. In contrast, densities of *Balanites* were highest by a huge margin in Mabira.

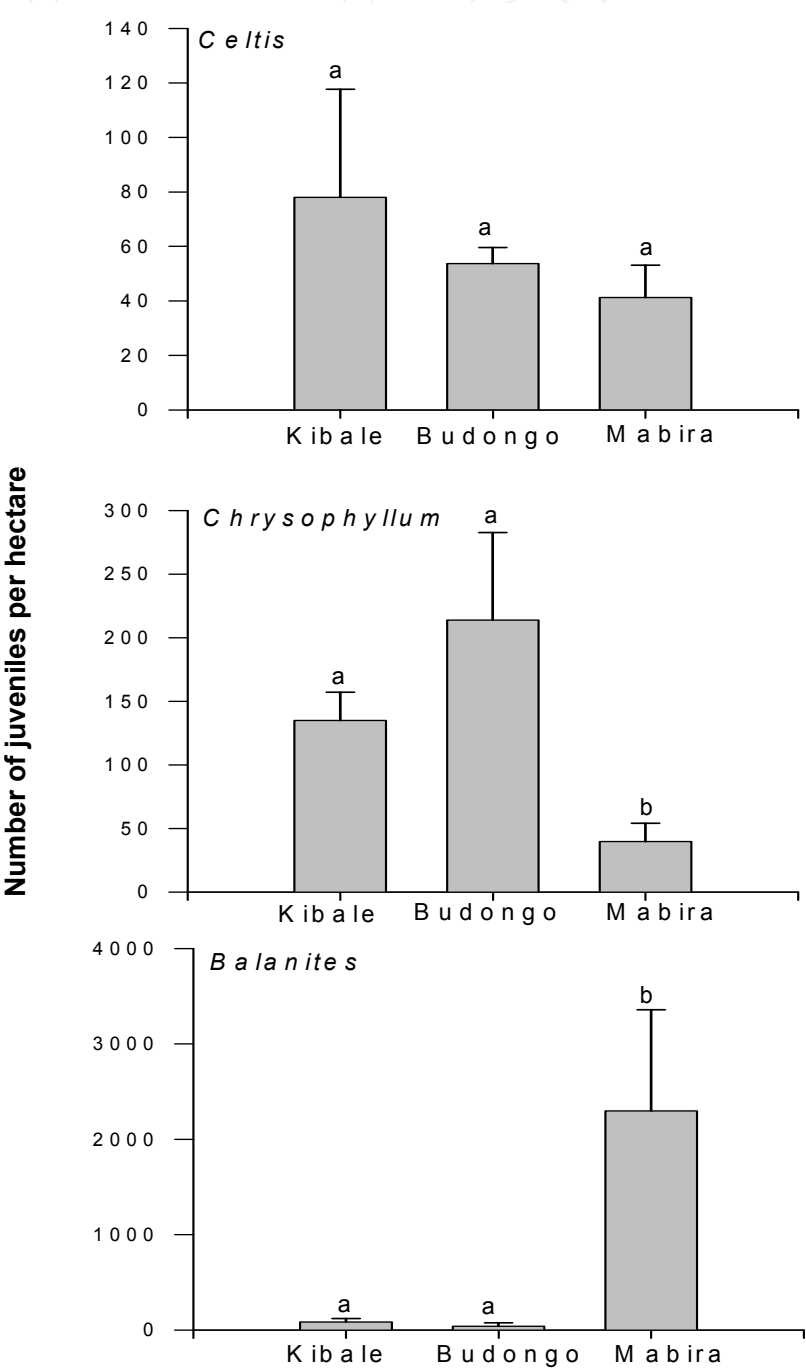


Fig. 5. Juvenile densities (mean + SE) of *Celtis*, *Chrysophyllum* and *Balanites* in Kibale, Budongo and Mabira Forests. Different lower-case letters indicate significant differences (Mann-Whitney U-test; (Dytham, 2003), $P < 0.05$)

However, an analysis of the juvenile age/size classes shows that juveniles of *Balanites* in Budongo and Mabira were mainly seedlings. In Budongo, none of the seedlings survived to later life stages, whereas 1.4% and 0.3% survived to sapling and pole stages respectively in Mabira. Significant proportions of both *Celtis* and *Chrysophyllum* survived beyond the seedling stage in all three forests.

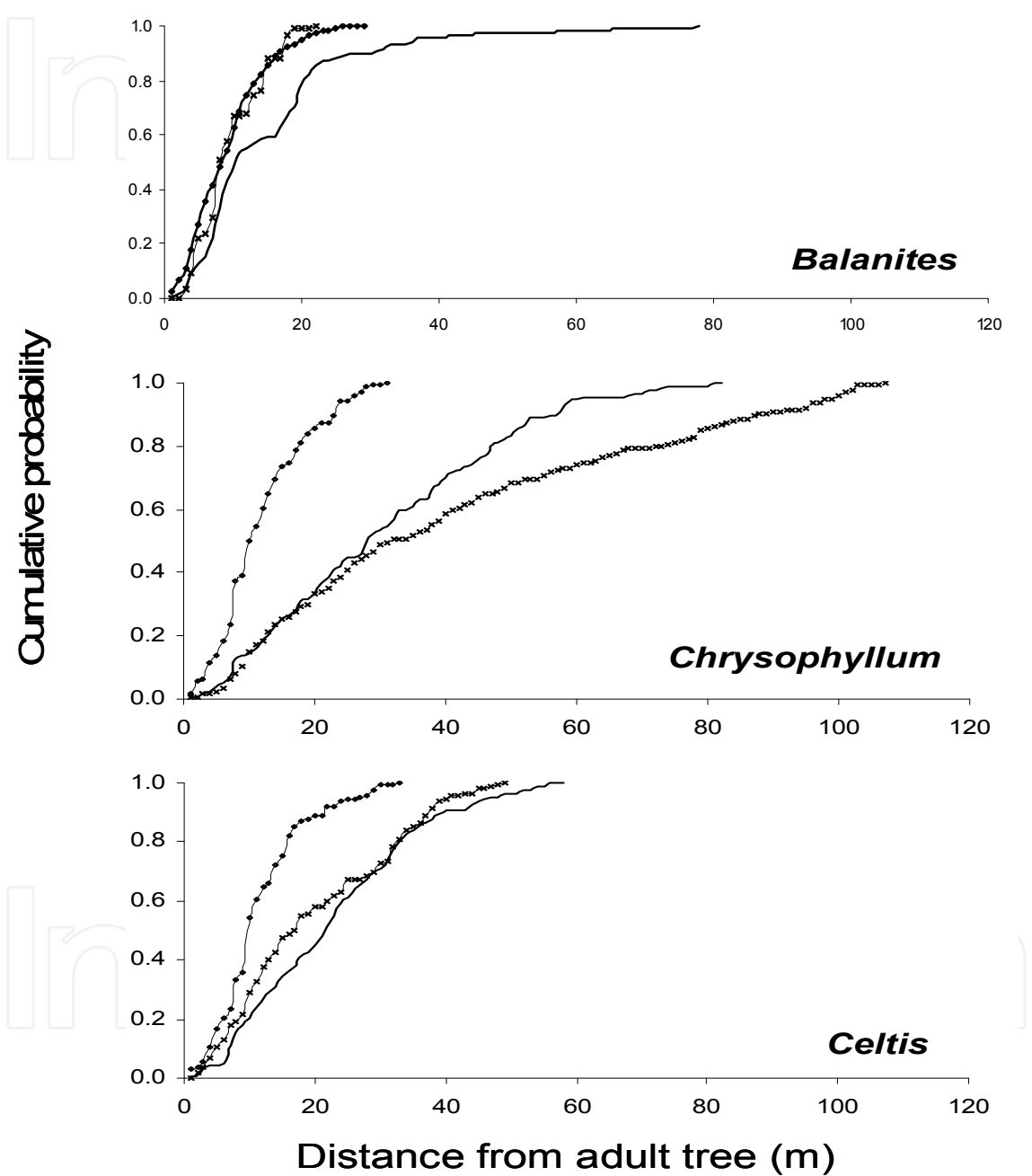


Fig. 6. Observed spatial distribution of juveniles of *Balanites*, *Chrysophyllum* and *Celtis* in Kibale (—), Budongo (xxx) and Mabira (•••) Forests

Pairwise comparison of the pooled data of spatial distributions for conspecific tree plots in each forest shows that the proportions of *Celtis* and *Chrysophyllum* juveniles established beneath adult conspecifics in Kibale and Budongo were not significantly different

(Kolmogorov-Smirnov test $P > 0.05$). However, a larger proportion of juveniles of the two species were established beneath adult conspecifics in Mabira than in Budongo and Kibale ($P < 0.001$). Similarly, the maximum recruitment distance from the mother trees for the two species was lower in Mabira than in Budongo and Kibale (Figure 6). For the large-fruited *Balanites*, the distribution was similar in Mabira and Budongo (Kolmogorov-Smirnov test, $Z = 0.6$, $P > 0.05$) where over 90% of juveniles were established beneath the adult trees (Figure 6). Although the majority of *Balanites* juveniles in Kibale were equally established beneath the adult trees, the spatial distribution was significantly different from that observed in Budongo ($Z = 4.5$, $P < 0.001$) and Mabira ($Z = 4.2$, $P < 0.001$) because of the longer maximum distances over which some juveniles were found (Figure 6).

4. Discussion

4.1 Vertebrate assemblage and seed dispersal rate

Direct and camera trap observations showed a higher species richness and abundance in the less disturbed Kibale and Budongo Forests compared to the heavily disturbed Mabira Forest (Table 2 and Figure 2). Primates are an important frugivorous guild and they contributed most to the frugivore visitation rate and proportion of fruits consumed. The remnant primates in the heavily disturbed Mabira Forest were mainly small-bodied monkeys that often spat seeds beneath the mother trees while feeding compared to the large-bodied primates observed in Kibale and Budongo that ingested the whole fruit. Similarly, ungulates were conspicuously absent in Mabira where they are the favoured bush meat for hunting communities (personal observation).

The frugivore visitation rate and hence rate of seed dispersal was lowest in Mabira and highest in Budongo. The low visitation rate in Mabira is an indicator of low frugivore densities. Low densities of frugivores results in satiation of the disperser community and many mature fruits remain unconsumed (Bas et al., 2006). Although many frugivores were observed in Mabira, almost all were small; 75% of the frugivores weighed less than 0.4kg (Table 3). The loss of large-bodied vertebrates may result in reduced seed dispersal and probably limit the distance over which seeds are moved. Body size is a strong correlate of quantity of seed dispersed and distance over which seeds are moved. The lack of variation in body size implies that frugivore-generated seed footprints in Mabira are likely to be small and homogeneous. A diversity of frugivore-generated seed footprints may be an important means of enhancing the probability of successful tree regeneration through delivery of seed to a variety of safe sites or escaping density dependent mortality. Consequently recruitment of trees in Mabira will not only be impaired by the effects of reduced dispersal rate but also the characteristic short distance dispersal by remnant small-bodied frugivores. In addition to the loss of large vertebrates in Mabira, the forest was characterised by a high frequency of rodent seed predators compared to Kibale and Budongo. This finding is similar to that of Basuta and Kasenene (1987), and Stanford (2000) who found that rodent diversity and abundance increased with logging intensity. Rodent populations are thought to increase in heavily disturbed landscapes due to dense undergrowth in secondary forests that provide safe cover against predators. The increased rodent population in disturbed forests could significantly lower the seed survival probability by increasing seed predation (Kozłowski, 2002). The high density of un-dispersed seeds underneath fruiting trees may exacerbate predator losses. Trees are known to survive seed predation effects through seed predator

satiation mechanisms (Fenner and Thompson, 2005). It is possible that the rodents may disperse some seeds in the process of scatter hoarding (Forget, 1990). The significance of seed dispersal by scatter hoarding rodents is not well understood and is an important research subject in heavily disturbed forest landscapes.

Regardless of the vertebrate assemblage differences between forests, the vertebrate assemblage varied between tree species according to the fruit size (Figure 3). This implies that tree species are not equally vulnerable to the loss of vertebrate seed dispersers. The small-fruited *Celtis* was mainly dispersed by birds, many of which are ubiquitous in all three forests. Similar small-fruited trees may not be adversely affected by forest disturbances. In contrast, large-fruited trees are more vulnerable to disturbance because they depend on large vertebrates that are vulnerable too. *Balanites* is a notable example of this effect. This species is believed to be dispersed exclusively by elephants (Babweteera et al., 2007; Chapman et al., 1992). In Budongo and Mabira where elephants have become extinct over the past few decades, there were no substitute dispersers of *Balanites*. There is probably very limited capacity for disperser substitution for large-fruited trees in the disturbed forests.

4.2 Spatial recruitment of juvenile trees

Tree species showed varied recruitment success in different forests. Although, the study did not directly test the factors limiting or enhancing recruitment, implicit inferences indicate that life history, tree fecundity and post dispersal seed and juvenile predation could be the major factors limiting seedling recruitment (Kozlowski, 2002). Establishment of seedlings is a major hurdle for tree regeneration. Early theories suggested coevolution of trees and animal dispersers for which the latter enhance the establishment success of seedlings through gut seed treatment (e.g. Temple, 1977). More recently an experiment on germination of *Balanites* showed that elephant gut treatment enhance germination by over 50% (Cochrane, 2003). However, significant recruitment of *Balanites* seedlings in forests where elephants are now extinct was also observed in this study (Figure 5). This provides evidence that germination can also be significant without animal gut treatment. Germination of tree seedlings in tropical forests is influenced by a number of factors including light and moisture regimes, predators, pathogens, forest floor litter and soil disturbance. Experiments that have looked exclusively at the effect of gut passage may have ignored other more important factors influencing seed germination (Robertson et al., 2006).

Recruitment of light demanders (*Cordia* and *Ricinodendron*) was limited by unfavourably low light regimes characteristic beneath a closed canopy. *Cordia* and *Ricinodendron* are occasionally found in forest gaps in Budongo (personal observation). The two species require high light intensities for establishment and the absence of their juveniles in closed canopy forest underscores the inability of light demanders to recruit outside the forest gaps. Consequently, light demanders require dispersal to enhance their chance of reaching open habitats within a landscape. In Mabira Forest, the seeds of *Cordia* are dispersed by two small bodied primates; red tail monkey (*Cercopithecus ascanius*) and black mangabey (*Lophocebus aterrimus*) while, *Ricinodendron* was visited by rodent seed predators and no frugivores. The small-bodied vertebrates are likely to disperse the seeds over short distances, thus limiting the probability of seeds reaching open habitats, ultimately leading to lowered recruitment of *Cordia* and *Ricinodendron*. On the other hand, low seed production could be the cause of low

juvenile densities of *Chrysophyllum* in Mabira. Juveniles of *Chrysophyllum* are shade tolerant and can establish beneath adult conspecifics. They are rarely browsed by ungulates or attacked by insect defoliators. Hence the most likely cause for low recruitment in Mabira compared to Kibale and Budongo is seed limitation which could be a result of low tree fecundity and/or high seed predation rates. Seeds of *Chrysophyllum* are eaten mostly by Gambian rats (*Cricetomys gambianus*) in all three forests. The frequency of visitation by these rodents is highest in Mabira, probably implying a higher seed predation rate (Appendix). Variations in seed dispersal and seed/seedling predation rates of *Balanites* in the three forests accounts for the vast abundance of juveniles in Mabira. *Balanites* trees produce fruit gregariously every 2-3 years (Chapman et al., 1999). Indeed the focal trees observed during this study in all three forests fruited gregariously prior to the commencement of the study. Consequently, the low recruitment in Budongo and Kibale compared to Mabira cannot be attributed to differences in adult tree fecundity. Instead, it could be due to (a) trees in Budongo and Kibale produce less viable fruits, or (b) the absence of predators in Mabira permits the massive recruitment of juveniles. There is no data to support the first hypothesis. The second hypothesis is supported by the fact that *Balanites* seeds are crushed by bush pigs (*Potamochoerus porcus*, (Cochrane, 2003) and the seedlings are browsed mostly by blue duikers (*Cephalophus monticola*, (Babweteera et al., 2007). Consequently, the absence of these potential predators in Mabira (Appendix 1) probably favours the recruitment of *Balanites*. Furthermore, the low density in Kibale could be attributed to dispersal by elephants. A study of seed dispersal by elephants in Kibale showed that elephants visited over 60% of fruiting *Balanites* trees and consumed over 35% of available fruit (Cochrane, 2003). In this study recruitment was assessed in plots around adult conspecifics. Ultimately, it is likely that plots placed at random throughout the forest may have revealed a higher density in Kibale than in Mabira and Budongo where there is no dispersal at all.

With the exception of *Balanites* in Budongo and Mabira, a significant number of seedlings of all study species survive to later life stages. A decrease in number of individuals with increasing age or size is expected for most plant populations (Peet and Christensen, 1987). However, the proportion of *Balanites* juveniles progressing from seedling to pole stage in Mabira (less than 2%) and Budongo (0%) may be insufficient to maintain stable populations in the long-term because, in the event of stochastic mortality, smaller populations are more vulnerable than large populations. In Budongo, although animals capable of dispersing *Balanites* have been lost, the seed and seedling predator populations are intact. This exposes seeds and seedlings to density and/or distance driven mortality factors. Similarly, in Mabira there are no elephants to disperse *Balanites* seeds. However, the survival of a few individuals could be attributed to a lack of seed and seedling predators.

The spatial distribution of juveniles was strongly correlated to the frugivory patterns (Figure 6). The study did not establish the exact parentage of juveniles. Instead it assumed that the observed juveniles were the offspring of the nearest adult tree. There is evidence that seeds can be dispersed hundreds of metres from the mother tree and that germinated seedlings may not be produced by the nearest reproductive adult (Hardesty et al., 2006). However, the noticeable differences between observed juvenile spatial distributions in different forests presented here indicate a strong correlation with the observed frugivory patterns. Consequently, this study provides a meaningful assessment of how forest disturbances affect frugivore activity, which in turn affects the spatial recruitment of trees. In the vertebrate impoverished Mabira Forest, most juveniles were observed recruiting beneath

adult conspecifics. This denotes lack of dispersal away from the parent tree. Frugivore species in Mabira were mainly small bodied individuals that often spat seeds beneath or near fruiting trees. Consequently, juveniles of the three tree species were clumped underneath or a few metres from the adult trees in Mabira. Moreover, clumped dispersal footprints are more prominent among the large-fruited trees. For instance *Balanites* is exclusively dispersed by elephants because the fruits and seeds are too large for other frugivores to eat them. The loss of elephants in Budongo and Mabira has obviously left no substitute disperser. Ultimately, the recruitment is restricted to an area immediately beneath adult trees in the two forests. However, even in Kibale where elephants are still present, the spatial distribution of *Balanites* is clumped (Figure 6). This could be due to disperser satiation as a result of mast fruiting and the dependence of the species on a single frugivore (Cochrane, 2003). The observation of clumped distribution patterns in forests with and without animal seed dispersers of *Balanites* probably suggests that studies of seed dispersal should not focus exclusively on the level of juvenile aggregation but instead incorporate a measure of the maximum dispersal distances. In Budongo and Kibale where the large bodied frugivore community is still intact, juveniles of trees that are dispersed further away may have a higher chance for establishment than those dispersed near parent trees or those not dispersed at all.

In conclusion, this study provides evidence of reduced frugivory and seed dispersal activities in heavily disturbed forests due to loss of large vertebrates. However, all tree species are not equally affected by these changes. There is limited capacity for disperser substitution for the large-fruited/seeded trees. Small-fruited/seeded trees dispersed by avian frugivores are unlikely to suffer a major impact on dispersal because many bird species are generalists, resilient to the disturbances. Large-fruited trees should therefore be of particular conservation concern because of the likelihood that they will lose their potential animal dispersers. In addition, this study demonstrates the link between loss of vertebrate seed dispersers and subsequent spatial recruitment patterns of trees. The results underscore the problem about generalising the resilience of tree species to forest disturbances. It is apparent that light demanding species are most vulnerable to the loss of vertebrate seed dispersers given that they are not capable of establishing in closed canopy forest. Consequently, they require a dispersing agent to reach open habitats. Even though open habitats may be common in secondary forests, loss of frugivore species or reduction in their abundance reduces the chance for light demanding tree seeds reaching these sites. In forests where large frugivores are extinct or their populations are reduced, it is plausible that continuous short distance dispersal will lead to spatially clumped tree populations. The long-term population viability of tropical tree species that have clumped distributions resulting from restricted recruitment beneath adult conspecifics is not well understood and could be an important research subject in the future.

5. Appendix

Number of individual vertebrates (direct plus camera trap) and their body weights observed feeding on *Balanites*, *Chrysophyllum*, *Cordia*, *Ricinodendron* and *Celtis* fruits and seeds in Kibale, Budongo and Mabira Forests. Primate, ungulate and rodent body weights after (Kingdon, 1997) and bird body size after Fry et al. (1988; 2000), Fry and Keith (2004), Urban et al. (1986; 1997) and Keith et al. (1992).

Species (common/ <i>scientific name</i>)	Body weight (Kg)	Number of individuals		
		Kibale	Budongo	Mabira
Primates				
Chimpanzee <i>Pan troglodytes</i>	45	77	181	0
Baboon <i>Papio anubis</i>	24	119	7	0
Black and white colobus <i>Colobus guereza</i>	13	13	22	0
Grey cheeked mangabey <i>Cercocebus albigena</i>	10	55	0	0
Black mangabey <i>Lophocebus aterrimus</i>	9	0	0	46
Red Colobus <i>Procolobus badius</i>	8	41	0	0
Blue monkey <i>Cercopithecus mitis</i>	7	0	308	0
Red tailed monkey <i>Cercopithecus ascanius</i>	4	156	94	80
Birds				
Yellow-throated Tinkerbird <i>Pogoniulus subphulphureus</i>	0.01	0	62	0
Speckled Tinkerbird <i>Pogoniulus scolopaceus</i>	0.02	1	82	25
Little Grey Greenbul <i>Andropadus gracilis</i>	0.02	0	17	9
Little Greenbul <i>Andropadus virens</i>	0.02	17	26	52
Spotted-flanked Barbet <i>Tricholaema lachrymose</i>	0.02	0	7	0
Grey-headed Negrofinch <i>Nigrita canicapilla</i>	0.02	0	14	4
Cameroon Sombre Greenbul <i>Andropadus curvirostris</i>	0.03	8	50	27
Yellow-whiskered Greenbul <i>Andropadus latirostris</i>	0.03	64	59	68
Slender-billed Greenbul <i>Andropadus gracilirostris</i>	0.03	13	51	23
Spotted Greenbul <i>Ixonotus guttatus</i>	0.04	0	33	0
Common Bulbul <i>Pycnonotus barbatus</i>	0.04	13	31	0
Black-billed Barbet <i>Lybius guifsobalito</i>	0.04	11	17	0
Green-tailed Bristlebill <i>Blenda eximia</i>	0.04	0	0	17
Yellow-spotted Barbet <i>Buccanodon duchaillui</i>	0.04	2	2	0
Hairy-breasted Barbet <i>Lybius hirsutus</i>	0.05	2	19	7
Violet-backed Starling <i>Cinnyricinclus leucogaster</i>	0.05	5	86	0
Grey-throated Barbet <i>Gymnobucco bonapartei</i>	0.06	0	1	1
Narina Trogon <i>Apaloderma narina</i>	0.06	1	0	0
Red-headed Malimbe <i>Malimbus rubricollis</i>	0.06	1	18	0
Purple-headed Glossy Starling <i>Lamprotornis purpureiceps</i>	0.07	22	25	19
Yellow-billed Barbet <i>Trachylaemus purpuratus</i>	0.09	1		1
Splendid starling <i>Lamprotornis splendidus</i>	0.11	12	0	0
Red-eyed dove <i>Streptopelia semitorquata</i>	0.2	4	0	0
African Green Pigeon <i>Treron calva</i>	0.22	0	6	4
Black-billed Turaco <i>Tauraco schuetti</i>	0.24	1	1	0
Crowned Hornbill <i>Tockus alboterminatus</i>	0.24	7	2	0
Pied Hornbill <i>Tockus fasciatus</i>	0.28	0	9	0

Grey Parrot <i>Psittacus erithacus</i>	0.4	0	1	0
Ross’s Turaco <i>Musophaga rossae</i>	0.4	2	0	0
Great Blue Turaco <i>Corythaeola cristata</i>	0.98	16	21	12
Black and white-casqued Hornbill <i>Ceratogymna subcylindricus</i>	1.31	2	17	0
Ungulates/omnivores				
Elephant <i>Loxodonta africana</i>	5000	62	0	0
Bush pig <i>Potamochoerus porcus</i>	65	4	1	0
Weyns duiker <i>Cephalophus weynsi</i>	15	2	5	0
Blue duiker <i>Cephalophus monticola</i>	5.5	4	307	0
Civet cat <i>Civetticus civetta</i>	5	12	14	3
Rodents				
Gambian rat <i>Cricetomys gambianus</i>	1.2	1	65	144
Elephant shrew <i>Rhynchocyon spp</i>	0.45	0	0	1
Cuvier’s tree squirrel <i>Funiscurius pyrrhopus</i>	0.25	28	0	1
Long-footed rat <i>Malacomys longipes</i>	0.07	0	0	1
Jackson’s rat <i>Praomys jacksoni</i>	0.04	0	0	1

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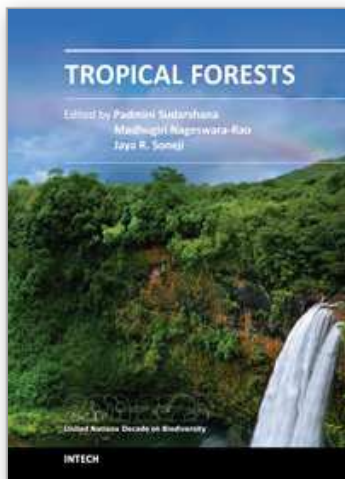
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The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

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