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Can remnant frugivore species effectively disperse tree seeds in secondary tropical rain forests?

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Abstract Seed dispersal by frugivores in tropical rain forests is important for maintaining viable tree populations. Over the years, vertebrate assemblages in tropical forests have been altered by anthropogenic disturbances, leading to concerns about the ability of remnant vertebrates to substitute for the lost or declining vertebrate populations. We compared vertebrate composition and frugivore visitation rates as an indirect measure of rate of seed dispersal in three tropical rain forests in Uganda, namely Mabira, Budongo and Kibale Forests. Mabira is highly disturbed, Kibale is little and Budongo is intermediate. The aim was to determine whether vertebrate assemblages in differentially disturbed forests had comparable abilities to disperse seeds and whether tree species were equally vulnerable to loss of seed dispersers. Assemblages of forest generalist species were similar in all forests, but specialists were less abundant in the heavily disturbed forest. Remnant frugivores in the heavily disturbed forest were mainly small-bodied species that spat seeds beneath fruiting trees compared to large-bodied species observed in the less disturbed forests that ingested and carried away the seeds. We postulate that the quantity of seeds dispersed in heavily disturbed forests is much reduced due to low visitation rates of frugivores and the absence of large frugivores that consume large quantities of fruit. The quality of seed dispersal is affected as well by the distance over which seeds are moved. Assessment of vulnerability of trees shows no evidence for disperser substitution for trees producing large fruits. Fruit trees with low nutritional contents and digestibility were least visited in frugivore-impoverished forests. The loss of large specialist frugivores is likely to affect recruitment of many trees, especially of species that cannot establish beneath adult conspecifics.

Keywords Large vertebrates · Disturbance · Hunting · Fruit size · Visitation rate

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Introduction

Many tropical rain forests are faced with rapid fragmentation and heavy exploitation of flora and fauna (Fa et al. 2005; Laurance 1998). These human-induced changes threaten the survival of forest species because they disrupt ecological processes that are important in maintaining viable populations. One of the key processes is seed dispersal by frugivores (Howe and Miriti 2000). Frugivores disperse seeds of many tropical tree species. In some forests over 90% of trees are dependant on vertebrate animals for dispersal (Corlett 1996; da Silva and Tabarelli 2000; Gautier-Hion et al. 1985). Seed dispersal is crucial for reducing distance- or density-dependent mortality (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 superior sites (Howe and Smallwood 1982).

Given the potential role of vertebrates, it is likely that their extinction or a reduction in their abundance may severely hamper seed dispersal and subsequent tree recruitment. However, there is evidence of substantial dietary overlap among many rainforest vertebrates (Fleming 1979; Gautier-Hion et al. 1985), and this may mean that there is some functional redundancy in their roles as seed dispersers. Loss of some species can be compensated for by increases in the abundance of others in response to forest disturbance (Dranzoa 1998; Plumptre and Reynolds 1994). This density compensation phenomenon is thought to occur through remnant species expanding their diets and ranges (MacArthur et al. 1972). Consequently, the remnant vertebrate population may perform the seed dispersal roles of the lost species.

However, the risk of extinction following forest disturbance is often higher among large-bodied vertebrates (Pimm et al. 1988). This is because they often require large contiguous areas of habitat (Laidlaw 2000) and typically have a low reproductive rate. In addition, large-bodied vertebrates are more attractive to hunters and cannot adjust to persistent hunting pressure by becoming more behaviourally inconspicuous. Large vertebrates are less abundant and have fewer species in rain forest environments. This implies that there may be less functional redundancy among large vertebrates and hence a much reduced capacity for compensation. One function that large-bodied frugivores play that small ones cannot is the dispersal of large seeds. 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). Large seeds may be predated by animals of any size, but in order for an animal to act as a disperser, it must be large enough to swallow or carry the seed. This suggests that plants with large seeds may be more vulnerable to forest disturbance and loss of seed-dispersing animals than small-seeded species. However, there is a paucity of information on the scope of disperser substitution for trees with different fruit sizes and the effectiveness of the remnant frugivore population in seed dispersal.

Here we use empirical data to test the hypothesis that changes in vertebrate assemblages in tropical rain forests caused by anthropogenic disturbances affect the seed dispersal patterns with consequences for the long-term viability of tree populations in a forest landscape. By observing vertebrate assemblages on selected tree species with a range of fruit/seed sizes in three tropical rain forests, we sought to address three questions. First, we examine whether there are differences in seed-dispersing vertebrate communities in differentially disturbed forests. Second, we determine whether the rate of seed dispersal varies in differentially disturbed forests. Thirdly, we examine whether tree species are equally vulnerable to the effects of reduced seed dispersal in secondary forests. The effects of changes in vertebrate communities 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.

Methods

Study sites

This study compared vertebrate composition and frugivore visitation rate as an indirect measure of seed dispersal rate in three tropical rain forests in Uganda, namely: Mabira Forest Reserve, Budongo Forest Reserve and Kibale National Park. Although the three forests had similar faunal and floral compositions less than a century ago (Hamilton 1991; Howard 1991), they now represent a spectrum of disturbance ranging from the highly disturbed and fragmented Mabira Forest to the relatively undisturbed Kibale Forest. Budongo Forest is intermediate between the two (Hamilton 1991; Howard 1991). Mabira Forest Reserve is a medium altitude, moist, semi-deciduous forest (32°52′–33°07′E and 0°24′–0°35′N), covering an area of 306 km^2. The forest has been subjected to intense logging, hunting and conversion to agricultural land for several decades. For instance, 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% (Westman et al. 1989). This has resulted in severe fragmentation with an estimated 50,000 people living in the associated enclaves. Budongo Forest Reserve is also a medium altitude, moist, semi-deciduous forest (31°22′–31°46′E and 1°37′–2°03′N), covering an area of 853 km^2. Budongo has been selectively logged since the 1920s, with mahoganies (*Khaya* and *Entandrophragma* spp.) as the main harvested timber trees. The forest is made up of a production zone and a pristine nature reserve in which no exploitation is permitted (Karani et al. 1997). Although Budongo has been selectively logged for over 80 years, the forested area remains relatively intact. The 506 km^2 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. Parts of the forest were selectively logged (removing ~3 trees/km^2) during the early 1950s; however, this logging had minimal impact on the general forest structure (Kasenene 1987). Kibale was gazetted as a national park in the early 1990s and as a park where neither logging nor hunting is permitted; it is currently better protected than Budongo and Mabira.

Study species

Five tree species were selected on the basis of their fruit/seed size and availability of mature fruiting trees in all three forests. *Balanites wilsoniana* (*Zygophyllaceae*) is an upper canopy deciduous tree that reaches a height of 40 m. The tree produces single-seeded fruits ca. 90 mm in length and 60 mm in width. When mature, the fruits are green-brown with an unpleasant smell. The seeds measure ca. 88 mm in length and 47 mm in width (Chapman et al. 1992). *Chrysophyllum albidum* (*Sapotaceae*) is also an upper canopy tree of lowland medium-altitude mixed rain forest. The fruits are rounded green, ca. 40 mm across, turning yellow-orange upon ripening. Inside the fruits lie three to four shiny brown seeds 20 mm long in a sweet-acid edible pulp. The ripe fruits decay within 2–3 weeks of falling, and the seeds embedded in the pulp are often burrowed into by insects (Babweteera, personal observation). *Cordia millenii* (*Boraginaceae*) is an upper canopy tree producing green oval fruits ca. 40 mm in length that turn yellow when ripe. It is a rare tree whose fruit contains one oval seed ca. 30 mm embedded in a slimy pulp that makes it easy for frugivores to swallow. *Ricinodendron heudelotii* (*Euphorbiaceae*) is a secondary forest canopy tree that reaches a height of 40 m. The bilobed or trilobed fruits are ca. 30 mm × 40 mm, green turning yellowish upon ripening. Embedded in the fruit are two to three spherical hard seeds ca. 15 mm in diameter. *Ricinodendron* trees were not found in Kibale Forest. *Celtis zenkeri* (*Ulmaceae*) is a wide-spread dry forest tree species growing to a height of 25 m and producing ovoid green fruits ca. 10 mm in length that turn red upon ripening. Inside the fruit is one black seed measuring ca. 4 mm in length.

Vertebrate assemblage

We recorded vertebrates feeding on the five tree species in each of the three forests. Three mature fruiting individuals (hereafter referred to as ‘focal trees’) of each species per forest were identified and observed from time to time between March 2004 and December 2005. The focal trees of the five species were selected to be at least 1 km apart, and each one was observed at the peak of its fruit ripening for 45–75 h. We made the observations between 0600–1200 and 1500–1800 h, 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. 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 maximise 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 1.

Table 1 Total number of direct and camera trap observation hours for frugivory activities on selected tree species in Kibale, Budongo and Mabira Forests

	Balanites	*Chrysophyllum*	*Cordia*	*Ricinodendron*	*Celtis*
Kibale					
Direct	137	285	216	0	87
Camera traps	1,946	1,482	1,027	0	0
Budongo					
Direct	109	151	221	127	148
Camera traps	1,638	1,608	1,183	1,221	0
Mabira					
Direct	146	158	197	121	137
Camera traps	1,938	1,573	941	1,597	0

No observations were made on *Ricinodendron* trees in Kibale because they do not grow in this forest

Data analysis

To determine species richness, we compiled a matrix representing the abundance of frugivore species observed per hour (during direct observations) for each tree species in each forest. Each direct observation hour represented a sample. The samples for all tree species, except *Ricinodendron* and *Balanites*, in each forest were pooled in order to make comparisons of frugivore species richness among forests. *Ricinodendron* was excluded because the species was only found in Budongo and Mabira, and *Balanites* was excluded because no frugivores were directly observed feeding on this species in any of the three forests. We compiled a second matrix of the abundance of frugivore species captured by the camera trap each day for each tree species in each forest. As such, a day (24 h) represented a sample for camera trap observations. The use of a 'day' as the sampling unit for camera trap observations as opposed to the 'hour' sampling unit used for direct observations is due to the low number of frugivores captured by camera trap observations, possibly a result of a narrow field of view of camera traps compared to direct human observations. As with direct observations, the samples for all tree species, except *Ricinodendron*, in each forest were pooled to compare frugivore species richness between forests. Frugivore species richness for each forest was computed using the nonparametric Jackknife richness estimator based on 1,000 randomisations with replacement (Colwell and Coddington 1994; Palmer 1990). This extrapolation method was preferred because it estimates total species richness, including species not present in any sample. Separate species richness estimates were made for direct observations and camera trap observation because of the different sample units used. The Jackknife analysis was conducted using EstimateS (Colwell 2005).

Frugivorous vertebrates were categorised according to their forest dependency after Bennun et al. (1996) and Kingdon (1997), that is, forest specialists, forest generalists and forest visitors, to determine the impact of forest disturbances on these groups (for a full list of vertebrates see "Appendix"). Forest specialists are characteristic of the interior of undisturbed forest. They may persist in secondary forest and forest patches if their particular ecological requirements are met. They are rarely seen in non-forest habitats. Breeding is almost invariably within forests. Forest generalists may occur in undisturbed forest, but are also regularly found in forest strips, edges and gaps. They are likely to be more common in secondary forest than the interior of intact forest. Breeding is typically within forest. Forest visitors are often found in forests, but are not dependant on them. They are more common in non-forest habitats, where they are most likely to breed.

To determine whether the vertebrate assemblages observed in the different forests formed distinct groups, vertebrates observed feeding on fruits and seeds of *Balanites*, *Chrysophyllum*, *Cordia* and *Celtis* in each forest were pooled and used in an analysis of similarity (ANOSIM). Similarity percentages (SIMPER) were used to reveal the percentage contributions of species to the average dissimilarity between the forests [CAP v3.0 (Seaby and Henderson 2004)]. Vertebrates feeding on *Ricinodendron* were omitted from the ANOSIM and SIMPER analyses because there were no trees of this species in Kibale Forest. The tests were based on a Bray–Curtis rank similarity matrix (Clarke 1993). The test statistic, *R*, compares the degree of separation of the vertebrate assemblage by comparing the differences between forests to the differences among the replicates in each forest using the average rank similarities. An *R* near zero indicates that there is little or no separation among the groups, whereas an *R* near 1 indicates complete separation. ANOSIM was also used to analyse the vertebrate assemblage similarities between trees. In addition, non-metric multidimensional scaling (NMDS) (CAP v3.0) was used to display relative differences between tree species in their vertebrate assemblages. NMDS is a non-parametric ordination method, which attempts to make the Euclidean distance between samples on a scatterplot proportional to their rank dissimilarity.

Variations in frugivore body size in the three forests were analysed to assess the possible similarities of seed dispersal patterns by frugivores in different forests. The body size is of utmost importance because it is strongly correlated with the quantity and distance of seed dispersal (Lambert 1998, 1999). Limited variation in the body size results in a restricted range of seed dispersal. In addition, frugivore visitation rates and the 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 forests. 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.

Results

In the three forests a total of 44 frugivore species that may disperse seeds were recorded, of which 31 were birds, 8 primates and 5 ungulates/omnivores. Five species of rodent seed predators were recorded as well (“Appendix”).

Species richness and body size comparison among forests

Assuming an infinite number of samples for the combined vertebrate assemblage on the selected tree species in each forest, the jackknife procedure, using direct observations (sampling with replacement), predicted a species richness of 30, 35 and 18 species in Kibale ($N = 646$ individuals observed), Budongo ($N = 1{,}275$) and Mabira ($N = 695$), respectively (Fig. 1a). Similarly, the Jackknife procedure for camera trap observations predicted a species richness of 9 species each for Kibale ($N = 101$) and Budongo ($N = 145$), and 6 species for Mabira ($N = 68$) (Fig. 1b). Most species (4 out of 5) observed with camera traps in Mabira were rodent seed predators and not frugivores. In addition to fewer 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 2). Mabira had the lowest proportion of forest specialists.

Similarity of vertebrate assemblages between forests

Analysis of similarity (ANOSIM) of vertebrate assemblages between forests shows significant differences in assemblages ($R = 0.27$, $P = 0.02$), although the low R value implies that the groups were not clearly separated. Pairwise ANOSIM of vertebrate assemblages between the forests indicates that the greatest differences in assemblages were between Budongo and Mabira ($R = 0.63$, $P = 0.05$; Table 3), followed by Kibale and Mabira ($R = 0.23$, $P = 0.05$; Table 4), while Budongo and Kibale were not significantly different ($R = 0.16$, $P = 0.2$). The low dissimilarity between forests was due to a high proportion (63%) of species that were found in at least two of the three forests, while 29% were common to all three forests.

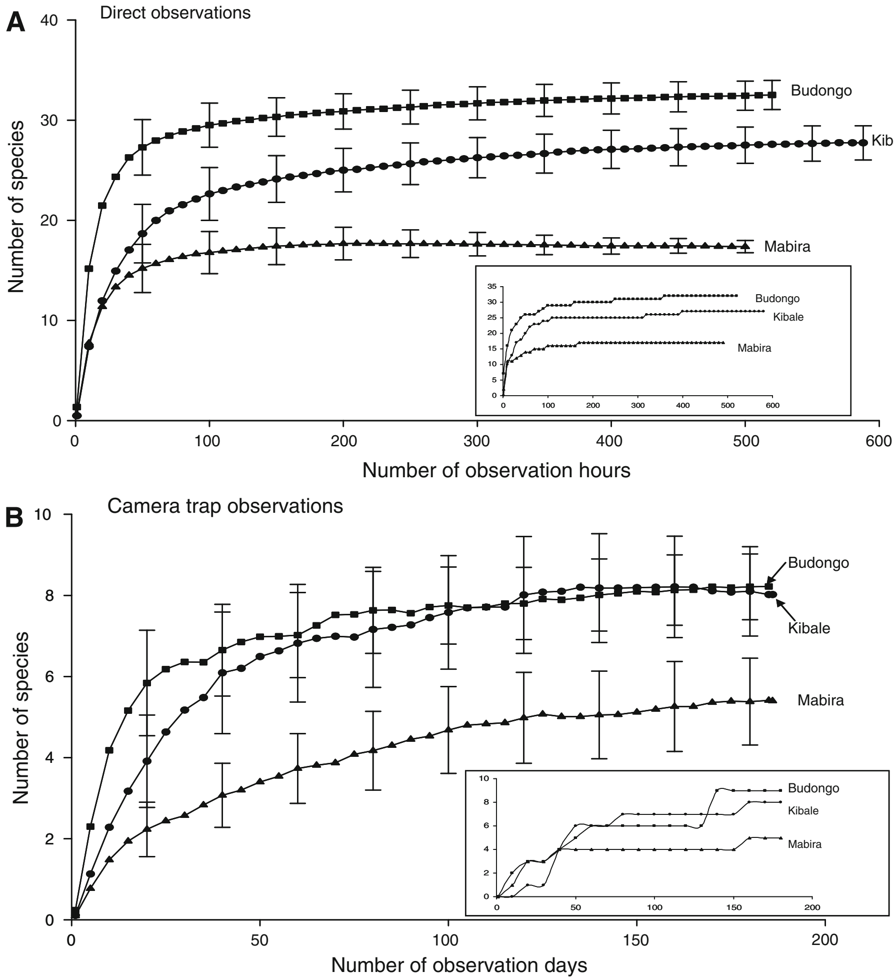

Fig. 1 Species accumulation curves based on a jackknife procedure using **a** direct observations and **b** camera trap observations for Kibale (●), Budongo (■) and Mabira (▲) Forests. *Inset* within each panel represents empirical species accumulation curves

Table 2 Proportion of forest specialists and variation in body weight (quartile ranges and minimum and maximum) of frugivores in Kibale, Budongo and Mabira Forests

Forest	Percentage of forest specialist (%)	Body weight (kg)			
		25%	75%	Minimum	Maximum
Kibale	50	0.05	6.8	0.02	5,000
Budongo	43	0.03	4.0	0.01	65
Mabira	33	0.03	0.4	0.02	9

Among the feeding guilds, primates contributed over 60% to the total dissimilarities among all three forests. Of the individual species that contributed most to the dissimilarities, blue monkeys *Cercopithecus mitis* and blue duikers *Cephalophus monticola*

Table 3 Results of ANOSIM (*R* values and significance levels) and SIMPER analysis of abundance of discriminating forest species contributing up to 75% of total dissimilarity between Budongo and Mabira Forests

ANOSIM			Guild	SIMPER		
R	*P*	Average dissimilarity (%)		Contribution of discriminating species (%)	Abundance in Budongo	Abundance in Mabira
0.63	0.05	90.8	Primate	*Cercopithecus mitis* (20)	102.7	0.0
			Ungulate	*Cephalophus monticola* (13.8)	60.7	0.0
			Primate	*Pan troglodytes* (10.9)	60.3	0.0
			Rodent	*Cricetomys gambianus* (7.6)	16.3	31.0
			Primate	*Cercopithecus ascanius* (4.9)	31.3	26.7
			Bird	*Andropadus latirostris* (4.5)	19.7	22.7
			Bird	*Pogoniulus scolopaceus* (3.4)	27.3	1.7
			Primate	*Lophocebus aterrimus* (3.4)	0.0	15.3
			Bird	*Andropadus virens* (3.4)	8.7	17.3
			Bird	*Andropadus gracilirostris* (3.1)	17.0	7.7

Table 4 Results of ANOSIM (*R* values and significance levels) and SIMPER analysis of abundance of discriminating forest species contributing up to 75% of total dissimilarity between Kibale and Mabira Forests

ANOSIM			Guild	SIMPER		
R	*P*	Average dissimilarity (%)		Contribution of discriminating species (%)	Abundance in Kibale	Abundance in Mabira
0.23	0.05	90.0	Primate	*Cercopithecus ascanius* (12.4)	32.8	26.7
			Rodent	*Cricetomys gambianus* (11.5)	0.3	31.0
			Ungulate	*Loxodonta africana* (9.5)	15.5	0.0
			Primate	*Papio anubis* (8.7)	29.8	0.0
			Bird	*Andropadus latirostris* (7.7)	16.0	22.7
			Primate	*Lophocebus aterrimus* (7.5)	0.0	15.3
			Primate	*Pan troglodytes* (5.5)	16.5	0.0
			Bird	*Andropadus virens* (4.8)	4.3	17.3
			Primate	*Cercocebus albigena* (4.4)	13.8	0.0
			Primate	*Procolobus badius* (3.2)	10.3	0.0

typified Budongo, whereas red tail monkeys *Cercopithecus ascanius*, baboons *Papio anubis* and elephants *Loxodonta africana* were most common in Kibale. Mabira was mostly characterised by the abundance of the seed-predating Gambian rat *Cricetomys gambianus* and two bird species, Yellow-whiskered Greenbul *Andropadus latirostris* and Little Greenbul *Andropadus virens* (Tables 3, 4).

Similarity of vertebrate assemblages between tree species

ANOSIM results show that vertebrate assemblages between some tree species were distinct ($R = 0.56$, $P < 0.001$). Assemblages on the small-fruited *Celtis* trees were different from

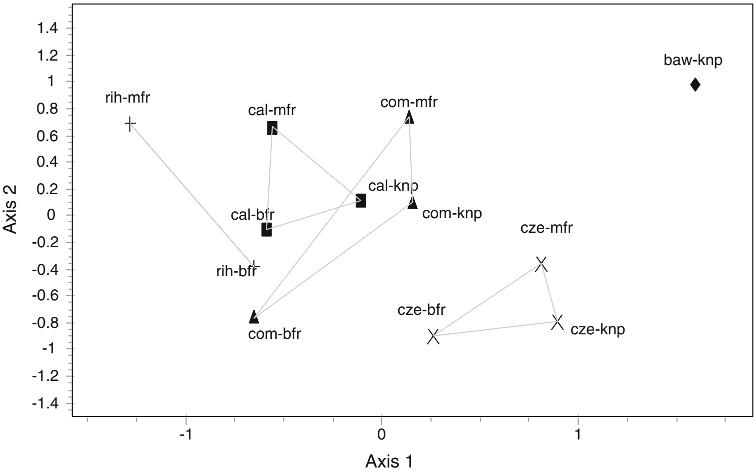

Fig. 2 MDS ordination of vertebrates feeding on *Celtis* (X), *Ricinodendron* (+), *Cordia* (▲), *Chrysophyllum* (■) and *Balanites* (◆) in Kibale (*KNP*), Budongo (*BFR*) and Mabira Forests (*MFR*)

those on large-fruited species. Similarly, assemblages on *Balanites* were different from other large-fruited species because fruits of *Balanites* are consumed only by elephants. However, frugivore assemblages among the other large-fruited trees were not different. An NMDS ordination scatterplot (Fig. 2) shows distinct separation between frugivores feeding on the small-fruited *Celtis* and the large-fruited tree species. The limited separation of vertebrate assemblages on *Chrysophyllum*, *Cordia* and *Ricinodendron* in all forests, except for *Ricinodendron* in Mabira, suggests the potential for limited disperser substitution. *Ricinodendron* in Mabira was eaten by Cuvier's tree squirrels *Funiscurius pyrrhopus* and Gambian rats *Cricetomys gambianus* only. The fibrous nature of fruits of *Ricinodendron* may cause low digestibility in many frugivores, and for this reason they are less favoured. However, in Budongo the fruits were mainly consumed by blue duikers, and the absence of duikers in Mabira could imply a loss of frugivores that are key dispersers of *Ricinodendron*. Similarly, elephants *Loxodonta africana* were the only frugivores observed feeding on *Balanites* in Kibale Forest (Fig. 2). The large fruit of *Balanites* excludes most other frugivores, including primates.

Frugivore visitation rates

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/h) than in Kibale (1.6 individuals/h) and Mabira (0.9 individuals/h). The high visitation rate in Budongo was due to the high frequencies of blue monkeys *Cercopithecus mitis* and blue duikers *Cephalophus monticola*, which accounted for over 30% of the observed individual visitors in this forest. The low frugivore visitation rate in Mabira could be an indicator of low vertebrate densities.

Small-fruited *Celtis* trees were visited more frequently in all three forests, whereas *Ricinodendron* was the least visited tree (ANOVA; $F = 270$, $df = 3$, $P < 0.001$; Fig. 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

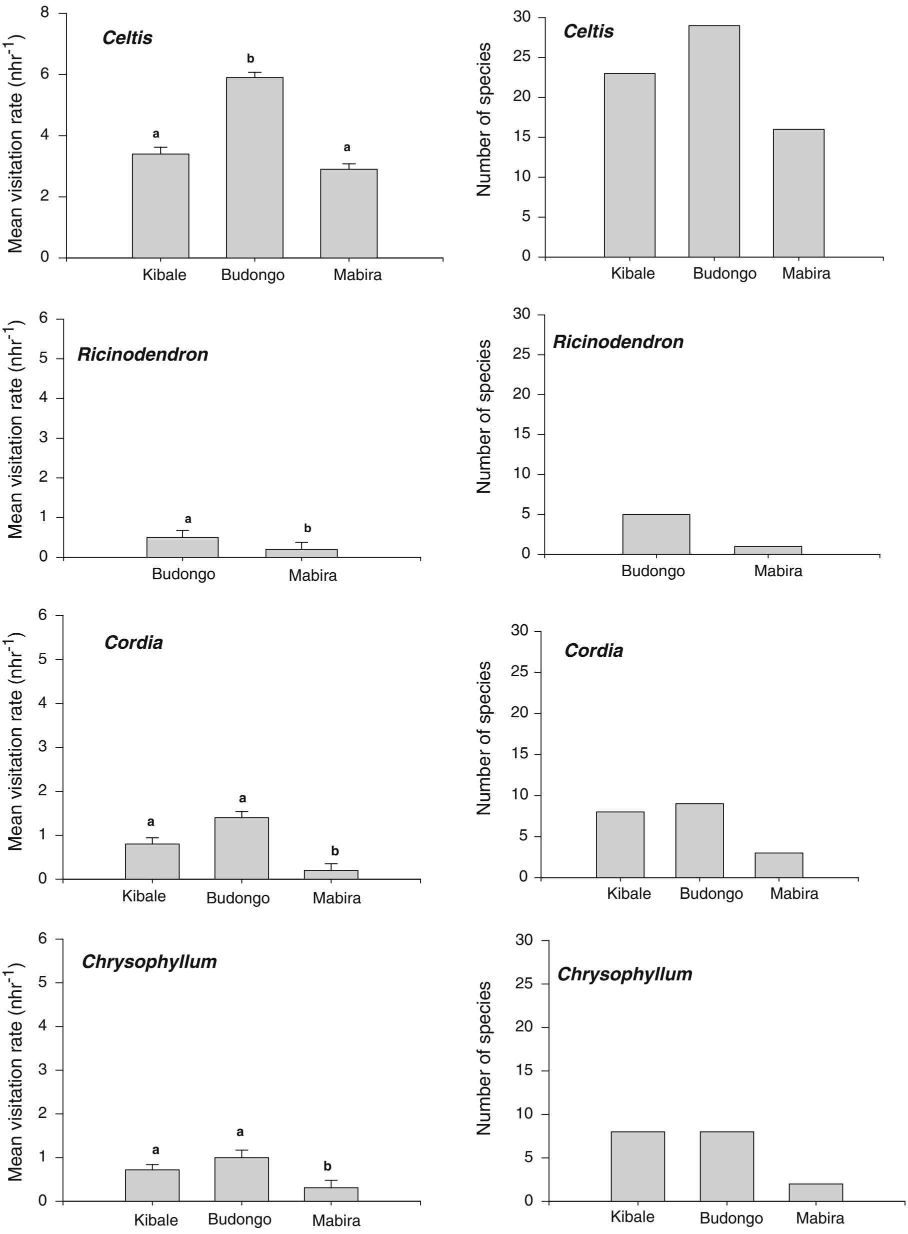

Fig. 3 Frugivore visitation rates (*left*) and number of frugivorous species visiting (*right*) different tree species in Kibale, Budongo and Mabira Forests. *Bars* labelled with different letters represent significantly different mean hourly visitation rates (Tukey HSD) at $P < 0.01$ (ANOVA). There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

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 in Budongo and Kibale visitation rates were not different except for *Celtis* (Fig. 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 we could not determine the hourly visitation rate.

Discussion

Direct and camera trap observations showed a higher species richness and abundance in both Kibale and Budongo than Mabira. Forest specialist species were also least common in Mabira. This conforms with the predicted adverse effects of past anthropogenic disturbances in Mabira on vertebrate diversity and abundance. Although vertebrates visiting *Ricinodendron* were excluded from the analysis to determine species richness, it is likely that their exclusion did not affect the results because there were no vertebrates visiting this species exclusively in either Budongo or Mabira.

Primates are an important forest specialist guild, and they contributed most to the dissimilarities observed between forests. 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 that are equally forest specialists were conspicuously absent in Mabira where they are the favoured bush meat for hunting communities (personal observation). Some studies (e.g., Cordeiro and Howe 2001) have compared the effects of anthropogenic disturbances on vertebrate populations and seed dispersal without taking their dependency on undisturbed forest habitat into account. Pooling all species regardless of their habitat requirements and ecological niches may distort the interpretation of consequences of forest disturbances on seed dispersal. For instance, two bird species *Andropadus virens* and *Andropadus latirostris* were most abundant in Mabira compared to Kibale and Budongo. However, the two species are forest generalists and can survive in heavily modified forest habitats (Dranzoa 1998). In this study, a consideration of forest dependency shows the lowest frequency of forest specialists was in the heavily disturbed Mabira Forest. This reflects the magnitude of disturbances that have led to declines in forest specialist populations and the extinction of some species. Although there was no significant difference in assemblages between Kibale and Budongo, there was a higher abundance of forest specialist frugivores (especially blue monkeys and blue duikers) in Budongo than Kibale, although the latter is relatively less disturbed. It can therefore be assumed that with the exception of elephants, the disturbance regimes in Budongo have not exceeded the threshold level that have an impact on forest specialist populations. Instead, it can be argued that low-impact forest management activities in Budongo may have created a greater diversity of microhabitats for these species (Plumptre 1996).

The frugivore visitation rate and hence rate of seed dispersal were lowest in Mabira and highest in Budongo. The low visitation rate in Mabira is an indicator of low frugivore densities. Low densities of frugivores result 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 <0.4 kg. 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 is 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.

The observations of higher frugivore visitation rate in Budongo compared to Kibale may not imply a higher frugivore density in the former. Recent surveys of primate populations show a higher mean biomass of primates in Kibale (1,411 kg/km^2) compared to Budongo (845 kg/km^2) (Plumptre and Cox 2006). The higher frugivore visitation rate in Budongo may be due to differences in food preference. Plumptre et al. (1994) showed that colobus monkeys, red tail monkeys and blue monkeys in Kibale ate much more leaf material and less fruit than the same species in Budongo. In this study, we recorded only those frugivores that were observed consuming fruits. Secondly, there is evidence that intraspecific competition for seed dispersers between trees may result in individual trees having fewer fruits removed when there are large numbers of conspecific fruiting trees in the neighbourhood (Manasse and Howe 1983; Saracco et al. 2005). In this study, we did not assess the spatial distribution of fruiting conspecifics, although there seemed to be a higher density of *Chrysophyllum* fruiting trees in Kibale than Budongo. The low visitation rate at the focal trees in Kibale could be due to the competition between individual conspecific trees for frugivores. If correct, this observation further emphasises the importance of dispersal to avoid intraspecific competition given that conspecific trees exhibit synchronous fruiting (Chapman et al. 1999).

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 because of dense undergrowth in secondary forests that provides safe cover against predators. The increased rodent population in disturbed forests could significantly lower the seed survival probability by increasing seed predation. 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 fruit size. 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 disturbed forests.

Apart from fruit size, the fruit structure and composition also appear to affect the types of frugivores that will take fruit. *Ricinodendron* was not a popular fruit with any frugivore, probably because of the fibrous fruit pulp (Fig. 3). In Mabira only rodent seed predators were seen to feed on them, giving this species a distinctive frugivore community (Fig. 2).

Frugivores exhibit interspecific competition for high value foods, and there are indications that large frugivores often dominate foraging of high quality foods and chase away smaller frugivores (French and Smith 2005). Given that frugivore body size determines dominance (French and Smith 2005), trees providing high quality fruits may benefit more from dispersal by large frugivores. Trees with poor quality fruits are thus dispersed by the less dominant smaller-bodied frugivores. However, in frugivore-impoverished forests, such as Mabira, there is a likelihood of reduced interspecific and intraspecific competition for quality food. This implies that less dominant frugivores may have access to high quality fruits as well. As a consequence, trees such as *Ricinodendron* with low nutritional content and digestibility will be less favoured and consequently less well dispersed.

Vulnerability of trees to seed predation by rodents is unequal. In this study, there were high seed predation rates on *Chrysophyllum* and *Ricinodendron*, but none on *Cordia*. There is insufficient knowledge about the risk of seed predation among tropical trees. Several studies suggest that the seed size influences the risk of predation (Hulme 1998; Moles and Westoby 2006). However, this study also suggests that seed predation may be strongly linked to the mechanical texture of the seed coat and the nutritional value of the seed. Rodents appear to select for *Chrysophyllum* with soft seed coats and the highly nutritious *Ricinodendron* seeds (Manga et al. 2000).

In conclusion, these results indicate reduced frugivory and seed dispersal activities in heavily disturbed forests due to loss of large vertebrates. However, 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 disturbances. Large-fruited trees should therefore be of particular conservation concern because of the likelihood that they will lose their animal dispersers.

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Appendix

See Table 5.

Table 5 Number of individual vertebrates (direct plus camera trap), body weights and forest dependency observed feeding on *Balanites*, *Chrysophyllum*, *Cordia*, *Ricinodendron* and *Celtis* fruits and seeds in Kibale, Budongo and Mabira Forests

Species (common/scientific name)	Forest dependency	Body weight (kg)	Kibale	Budongo	Mabira
Primates					
Chimpanzee *Pan troglodytes*	FF	45	77	181	0
Baboon *Papio anubis*	FF	24	119	7	0
Black and white colobus *Colobus guereza*	FF	13	13	22	0
Grey cheeked mangabey *Cercocebus albigena*	FF	10	55	0	0
Black mangabey *Lophocebus aterrimus*	FF	9	0	0	46
Red Colobus *Procolobus badius*	FF	8	41	0	0

Table 5 continued

Species (common/scientific name)	Forest dependency	Body weight (kg)	Kibale	Budongo	Mabira
Blue monkey *Cercopithecus mitis*	FF	7	0	308	0
Red tailed monkey *Cercopithecus ascanius*	FF	4	156	94	80
Birds					
Yellow-throated Tinkerbird *Pogoniulus subphulphureus*	F	0.01	0	62	0
Speckled Tinkerbird *Pogoniulus scolopaceus*	F	0.02	1	82	25
Little Grey Greenbul *Andropadus gracilis*	FF	0.02	0	17	9
Little Greenbul *Andropadus virens*	F	0.02	17	26	52
Spotted-flanked Barbet *Tricholaema lachrymose*	F	0.02	0	7	0
Grey-headed Negrofinch *Nigrita canicapilla*	F	0.02	0	14	4
Cameroon Sombre Greenbul *Andropadus curvirostris*	FF	0.03	8	50	27
Yellow-whiskered Greenbul *Andropadus latirostris*	F	0.03	64	59	68
Slender-billed Greenbul *Andropadus gracilirostris*	FF	0.03	13	51	23
Spotted Greenbul *Ixonotus guttatus*	F	0.04	0	33	0
Common Bulbul *Pycnonotus barbatus*	f	0.04	13	31	0
Black-billed Barbet *Lybius guifsobalito*	F	0.04	11	17	0
Green-tailed Bristlebill *Blenda eximia*	F	0.04	0	0	17
Yellow-spotted Barbet *Buccanodon duchaillui*	FF	0.04	2	2	0
Hairy-breasted Barbet *Lybius hirsutus*	F	0.05	2	19	7
Violet-backed Starling *Cinnyricinclus leucogaster*	f	0.05	5	86	0
Grey-throated Barbet *Gymnobucco bonapartei*	F	0.06	0	1	1
Narina Trogon *Apaloderma narina*	F	0.06	1	0	0
Red-headed Malimbe *Malimbus rubricollis*	FF	0.06	1	18	0
Purple-headed Glossy Starling *Lamprotornis purpureiceps*	F	0.07	22	25	19
Yellow-billed Barbet *Trachylaemus purpuratus*	F	0.09	1	1	1
Splendid starling *Lamprotornis splendidus*	F	0.11	12	0	0
Red-eyed dove *Streptopelia semitorquata*	f	0.2	4	0	0
African Green Pigeon *Treron calva*	F	0.22	0	6	4
Black-billed Turaco *Tauraco schuetti*	FF	0.24	1	1	0
Crowned Hornbill *Tockus alboterminatus*	f	0.24	7	2	0
Pied Hornbill *Tockus fasciatus*	F	0.28	0	9	0
Grey Parrot *Psittacus erithacus*	F	0.4	0	1	0
Ross's Turaco *Musophaga rossae*	F	0.4	2	0	0
Great Blue Turaco *Corythaeola cristata*	F	0.98	16	21	12
Black and white-casqued Hornbill *Ceratogymna subcylindricus*	F	1.31	2	17	0
Ungulates/omnivores					
Elephant *Loxodonta africana*	FF	5,000	62	0	0
Bush pig *Potamochoerus porcus*	FF	65	4	1	0

Table 5 continued

Species (common/scientific name)	Forest dependency	Body weight (kg)	Kibale	Budongo	Mabira
Weyns duiker *Cephalophus weynsi*	FF	15	2	5	0
Blue duiker *Cephalophus monticola*	FF	5.5	4	307	0
Civet cat *Civetticus civetta*	FF	5	12	14	3
Rodents					
Gambian rat *Cricetomys gambianus*	FF	1.2	1	65	144
Elephant shrew *Rhynchocyon spp*	FF	0.45	0	0	1
Cuvier's tree squirrel *Funiscurius pyrrhopus*	FF	0.25	28	0	1
Long-footed rat *Malacomys longipes*	FF	0.07	0	0	1
Jackson's rat *Praomys jacksoni*	FF	0.04	0	0	1

FF Forest specialists, *F* forest generalists, *f* forest visitors after Bennun et al. (1996) and Kingdon (1997). 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)

References

Babweteera F, Savill P, Brown N (2007) *Balanites wilsoniana*: regeneration with and without elephants. Biol Conserv 134:40–47. doi:10.1016/j.biocon.2006.08.002

Bas JM, Pons P, Gomez C (2006) Exclusive frugivory and seed dispersal of *Rhamnus alaternus* in the bird breeding season. Plant Ecol 183:77–89. doi:10.1007/s11258-005-9008-0

Basuta IG, Kasenene JM (1987) Small rodent populations in selectively felled and mature tracts of Kibale Forest, Uganda. Biotropica 19:260–266. doi:10.2307/2388345

Bennun L, Dranzoa C, Pomeroy D (1996) The forest birds of Kenya and Uganda. J East Afr Nat Hist 85: 23–48. doi:10.2982/0012-8317(1996)85[23:TFBOKA]2.0.CO;2

Bollen A, Van Elsacker L, Ganzhorn JU (2004) Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. J Trop Ecol 20:599–612. doi:10.1017/S0266467404001853

Carbone C et al (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim Conserv 4:75–79. doi:10.1017/S1367943001001081

Chapman LJ, Chapman CA, Wrangham RW (1992) *Balanites wilsoniana*—elephant dependent dispersal. J Trop Ecol 8:275–283

Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. J Trop Ecol 15:189–211. doi:10.1017/S0266467499000759

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. V 7.5

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond B Biol Sci 345:101–118. doi:10.1098/rstb.1994.0091

Cordeiro NJ, Howe HF (2001) Low recruitment of trees dispersed by animals in African forest fragments. Conserv Biol 15:1733–1741. doi:10.1046/j.1523-1739.2001.99579.x

Corlett RT (1996) Characteristics of vertebrate-dispersed fruits in Hong Kong. J Trop Ecol 12:819–833

da Silva JMC, Tabarelli M (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404:72–74. doi:10.1038/35003563

Dranzoa C (1998) The avifauna 23 years after logging in Kibale National park, Uganda. Biodivers Conserv 7:777–797. doi:10.1023/A:1008892419940

Fa JE, Ryan SF, Bell DJ (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. Biol Conserv 121:167–176. doi:10.1016/j.biocon.2004.04.016

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

Fleming TH (1979) Do tropical frugivores compete for food? Am Zool 19:1157–1172

Forget PM (1990) Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. J Trop Ecol 6:459–468

French AR, Smith TB (2005) Importance of body size in determining dominance hierarchies among diverse tropical frugivores. Biotropica 37:96–101

Fry CH, Keith S (2004) The birds of Africa, vol VII. Christopher Helm, London

Fry CH, Keith S, Urban EK (1988) The birds of Africa, vol III. Academic Press, London

Fry CH, Keith S, Urban EK (2000) The birds of Africa, vol VI. Academic Press, London

Gautier-Hion A et al (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65:324–337. doi:10.1007/BF00378906

Githiru M, Lens L, Bennur LA, Ogol C (2002) Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. Oikos 96:320–330. doi:10.1034/j.1600-0706.2002.960214.x

Hamilton A (1991) A field guide to Uganda forest trees. Makerere University Printery, Kampala

Hardesty BD, Hubbell SP, Bermingham E (2006) Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. Ecol Lett 9:516–525. doi:10.1111/j.1461-0248.2006.00897.x

Howard PC (1991) Nature conservation in Uganda's tropical forest reserves. IUCN, Gland

Howe HF, Miriti MN (2000) No question: seed dispersal matters. Trends Ecol Evol 15:434–436. doi:10.1016/S0169-5347(00)01965-0

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228. doi:10.1146/annurev.es.13.110182.001221

Hulme PE (1998) Post-dispersal seed predation and seed bank persistence. Seed Sci Res 8:513–519. doi:10.1017/S0960258500004487

Karani P, Kiwanuka LS, Sizomu-Kagolo ME (1997) Forest management plan for Budongo Forest Reserve July 1997–June 2007. Uganda Forest Department, Kampala

Kasenene JM (1987) The influence of mechanised selective logging, felling intensity and gap size on the vegetation of tropical moist forest reserve, Uganda. PhD Dissertation, Michigan State University, USA

Keith S, Urban EK, Fry CH (1992) The birds of Africa, vol IV. Academic Press, London

Kingdon J (1997) The Kingdon guide to African mammals. Academic Press, London

Laidlaw RK (2000) Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. Conserv Biol 14:1639–1648. doi:10.1046/j.1523-1739.2000.99073.x

Lambert JE (1998) Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evol Anthropol 7:8–20. doi:10.1002/(SICI)1520-6505(1998)7:1<8::AID-EVAN3>3.0.CO;2-C

Lambert JE (1999) Seed handling in chimpanzees (*Pan troglodytes*) and red tail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. Am J Phys Anthropol 109:365–386. doi:10.1002/(SICI)1096-8644(199907)109:3<365::AID-AJPA6>3.0.CO;2-Q

Laurance WF (1998) Forest fragmentation: another perspective. Trends Ecol Evol 13:75. doi:10.1016/S0169-5347(97)01310-4

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330–342. doi:10.2307/1934090

Manasse RS, Howe HF (1983) Competition for dispersal agents among tropical trees: influences of neighbors. Oecologia 59:185–190. doi:10.1007/BF00378836

Manga TT, Fondoun JM, Kengue J, Thiengang C (2000) Chemical composition of *Ricinodendron heudelontii*: an indigenous fruit tree in southern Cameroon. Afr Crop Sci J 8:195–201

Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. Oikos 113:91–105. doi:10.1111/j.0030-1299.2006.14194.x

Palmer MW (1990) The estimation of species richness by extrapolation. Ecology 71:1195–1198. doi:10.2307/1937387

Pimm SL, Jones HL, Diamond J (1988) On the risk of extinction. Am Nat 132:757–785. doi:10.1086/284889

Plumptre AJ (1996) Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. For Ecol Manage 89:101–113. doi:10.1016/S0378-1127(96)03854-6

Plumptre A, Cox D (2006) Counting primates for conservation: primate surveys in Uganda. Primates 47:65–73. doi:10.1007/s10329-005-0146-8

Plumptre AJ, Reynolds V (1994) The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. J Appl Ecol 31:631–641. doi:10.2307/2404154

Plumptre A, Reynolds V, Bakuneeta C (1994) The contribution of fruit eating primates to seed dispersal and natural regeneration after selective logging. Final report to ODA. R4738. Budongo Forest Project, Oxford

Saracco JF, Collazo JA, Groom MJ, Carlo TA (2005) Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. Biotropica 37:81–87

Seaby RMH, Henderson PA (2004) Community Analysis Package. 3.0. Pisces Conservation Ltd

Silveira L, Jacomo ATA, Diniz-Filho JAF (2003) Camera trap, line transect census and track surveys: a comparative evaluation. Biol Conserv 114:351–355. doi:10.1016/S0006-3207(03)00063-6

Stanford A (2000) Rodent ecology and seed predation in logged and unlogged forest, Uganda. DPhil Dissertation, University of Bristol

Urban EK, Fry CH, Keith S (1986) The birds of Africa, vol II. Academic Press, London

Urban EK, Fry CH, Keith S (1997) The birds of Africa, vol V. Academic Press, London

Westman WE, Strong LL, Wilco BA (1989) Tropical deforestation and species endangerment: the role of remote sensing. Landsc Ecol 3:97–109. doi:10.1007/BF00131173