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Authors: McLennan, Matthew R. , and Plumptre, Andrew J.

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Research Article

Protected apes, unprotected forest: composition, structure and diversity of riverine forest fragments and their conservation value in Uganda

Matthew R. McLennan[1*] and Andrew J. Plumptre[2]

[1]Anthropology Centre for Conservation, Environment and Development, Oxford Brookes University, Oxford, UK. mmclennan@brookes.ac.uk

[2] Wildlife Conservation Society, PO Box 7487, Kampala, Uganda. aplumptre@wcs.org

*Corresponding Author: Faculty of Humanities & Social Sciences, Oxford Brookes University, Oxford, OX2 9AT, UK. Email: mmclennan@brookes.ac.uk Tel: +44(0) 1865 200416

Abstract

Small forest fragments are common in anthropogenic landscapes in the tropics. These have conservation value if they provide habitat for threatened wildlife and maintain connectivity between larger habitats. Riverine forests have particular 'corridor' potential due to their linear shape, but are under-studied in many regions. We surveyed trees in riverine fragments in Bulindi, an anthropogenic landscape 25 km south of the Budongo Forest in western Uganda, to determine their condition and assess their value for wildlife, particularly endangered chimpanzees *Pan troglodytes*. We assessed tree composition, structure and diversity and compared results with a previous survey made in Budongo, the nearest main forest block. Riverine fragments were considerably less species-dense and species-rich than Budongo. Community composition differed markedly between sites and there was virtually no overlap in common species. Common trees in fragments were characteristic of East African swamp and groundwater forests (e.g. the palm *Phoenix reclinata*) and the dominant tree family was the Moraceae, members of which produce fleshy fruits attractive to frugivores (e.g. figs). Important fruit foods for chimpanzees differed between habitats. While basal area of important fruit trees was comparable, overall density was greater in fragments. Our data suggest the riverine fragments offer a relatively food-dense habitat for chimpanzees and other frugivores. Small riverine forests have little or no protection regionally and are being extensively logged and cleared for agriculture. Species logged for timber in Bulindi included important chimpanzee fruit trees. Unless conservation projects successfully reverse current trends, the value of the riverine corridors for maintaining connectivity between main forest blocks is limited.

Keywords: chimpanzee, forest fragments, logging, riverine forest, species composition

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Introduction

Small remnant forest fragments are a common characteristic of anthropogenic landscapes in the tropics [1-4]. These often persist along waterways or in bottomland areas unsuitable for most agriculture. In densely populated landscapes where local people's access to well-protected forest is limited, forest patches provide multiple resources to local households including food, medicine, fuelwood and building materials [5, 6], and can be a source of income (e.g. from timber and charcoal sales) [7, 8]. Such fragments may also provide habitat for threatened wildlife [9-11]. The conservation value of small forest fragments rests in part on their utility to create habitat linkages and dispersal opportunities for wildlife through human-dominated landscapes. This 'corridor' value is especially true of riverine (or riparian) forests due to their linear shape [3, 12]. Tropical riverine forests may have particular value for frugivores because fruit seasonality can be less pronounced relative to terra firma forest, owing in part to higher densities of figs (*Ficus* spp.), which have asynchronous phenological cycles [12, 13]. On the other hand, small forest fragments (riverine or otherwise) might offer a poor quality habitat for frugivores due to human activities (e.g. timber harvesting) that reduce availability of fruit sources. Thus, basal areas or densities of large fruiting trees are often lower in fragments relative to continuous forest [14, 15]. In East Africa levels of human disturbance in small fragments, particularly those with little or no real protection, are typically high [10, 16, 17]. Evidently, where over-harvesting of resources and agricultural expansion leads to depletion and clearance, the conservation value of small unprotected forests including riverine corridors is limited [18, 19].

The forest blocks of western Uganda are fragmented and relatively small-sized (<1000 km^2; [20]). In compositional terms, the country's medium-altitude forests are drier, floristically impoverished outliers of the main Guineo–Congolean rainforest phytochorion [21-23]. Nevertheless, the Budongo Forest – the most northerly of Uganda's forest blocks – was richest for tree species of 22 sites surveyed within East Africa's Albertine Rift [24]. Budongo's flora and ecology is well-documented [e.g. 20, 25-28]. Bugoma Forest, 50 km southwest of Budongo, has been less well-studied but seems to support a less diverse flora [20, 24]. Both are classified as Forest Reserves, managed by the National Forest Authority for sustainable utilisation of forest resources. Both forests also support important populations of eastern chimpanzees (*Pan troglodytes schweinfurthii*) among other threatened wildlife [24, 29]. The long-term population viability of low density species like chimpanzees is enhanced if connectivity between fragmented forest blocks is maintained via wildlife corridors linking small forest reserves, private forests and grasslands in intervening landscapes [29, 30].

In Uganda, small remnant forests occur along watercourses and in waterlogged valleys. These are often highly degraded due to over-use by local people [17, 18, 31, 32]. Research at Budongo and elsewhere in mid-western Uganda (notably at Kibale National Park [33]) has yielded valuable data on the ecology of this region's main forests. Few studies have been made of outlying riverine forests, however, of which some have potential value for connecting important conservation areas. Since these forests are principally edaphic formations, associated with permanent swamps and riverine valleys, differences in tree composition (and therefore resources for wildlife) between riverine forests and main forest blocks are expected; however, this possibility has received little attention. Uganda's deforestation rate is currently among the highest in Africa (2.6% in 2000–2010 [34]), with most forest loss and degradation taking place outside of large gazetted areas on public or private land [35]. Given this high deforestation rate, studies of unprotected riverine forest are needed to determine their current condition and assess their value for wildlife.

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A survey of tree composition was undertaken as part of an 18-month ecological study of chimpanzees inhabiting riverine fragments in Bulindi, a forest–farm mosaic south of Budongo [36, 37]. Though exact numbers are unknown, recent surveys revealed the widespread occurrence of chimpanzees in small forest patches throughout the human-dominated landscape separating Budongo and Bugoma, as well as forest raptors and medium-sized carnivores, confirming this region's corridor potential [31, 38]. The aims of this study were to: (i) describe composition, structure and diversity of the forest tree community in riverine fragments in Bulindi and make comparisons with the nearest main forest block, Budongo; (ii) compare fruit tree abundance for chimpanzees in riverine fragments and Budongo as a measure of the quality of riverine forests for frugivorous wildlife; and (iii) assess the extent of timber harvesting in fragments as a measure of anthropogenic threat to riverine forests regionally.

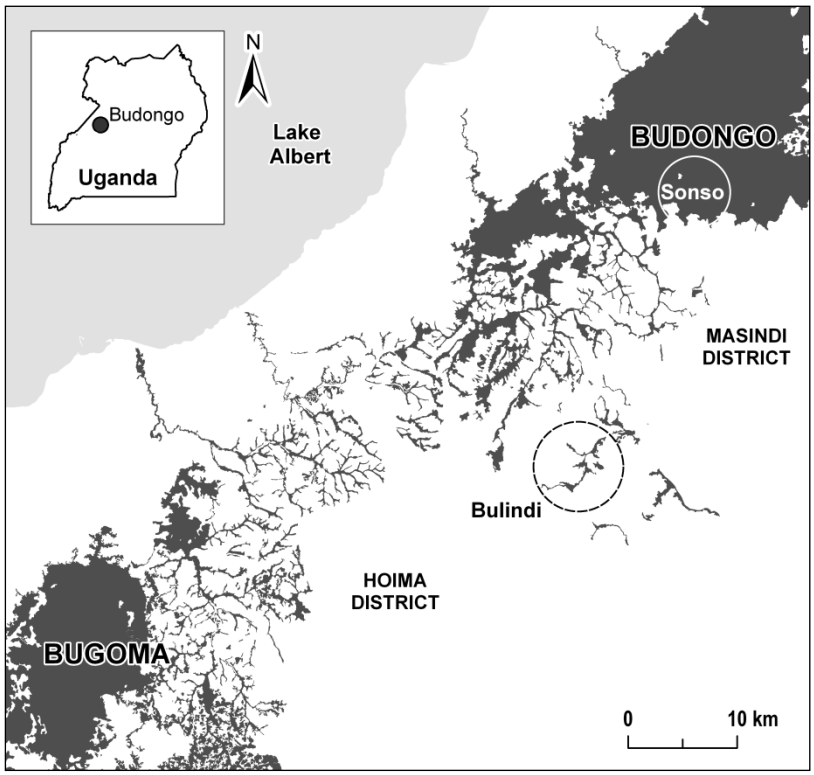


Fig. 1. Map showing the Budongo and Bugoma Forest Reserves (in Hoima and Masindi districts, respectively) and riverine forest fragments in the intervening region. Most fragments are on private or communal land. The study site in Bulindi is encircled. West of Bulindi is a proposed wildlife corridor linking Budongo and Bugoma. Also encircled is the Sonso region of Budongo Forest.

Methods

Study Area

The Budongo Forest Reserve (1°37'–2°00'N, 31°22'–31°46'E) is situated in Uganda's Masindi District (Fig. 1). The reserve covers 793 km^2 of moist semi-deciduous forest and grassland, of which 428 km^2 is forested, with an average altitude of 1100 m. Descriptions of the forest are found in Eggeling [25], Howard [20] and Plumptre [27]. Four main forest types are discernable: *Cynometra*-dominated forest, mixed forest, colonising forest and swamp forest [25]. Rainfall averages 1600 mm per annum [39] and exhibits a bimodal pattern with a main annual dry season occurring during December–February. Minimum temperatures average 21°C but daily temperatures reach 32°C in the dry season [40]. The forest has been logged on a sustainable yield basis since the 1920s up to the present day [27], although illegal logging is widespread [41]. Human communities bordering the reserve also harvest other wood-based products (e.g. fuelwood and building poles) [39].

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Bulindi Parish (1°28'N, 31°28'E) is located in Hoima District, 25 km south of Budongo and 40 km northeast of Bugoma Forest (Fig. 1). Bulindi lies to the east of a proposed wildlife corridor linking these two forest blocks [30]. The 40 km^2 study area comprises a mosaic of riverine forest fragments (altitude range: 1100–1150 m), papyrus (*Cyperus papyrus*) swamp and wooded grassland, intermixed with farmland and village areas. The climate at Bulindi is somewhat drier than at Budongo: mean annual precipitation was 1461 mm during 2001–2007. Chimpanzees in Bulindi are sympatric with four other diurnal nonhuman primates: *Cercopithecus mitis stuhlmanni*, *Chlorocebus tantalus budetti*, *Colobus guereza occidentalis* and *Papio anubis*. Elsewhere in the district, *Cercopithecus ascanius schmidti* occurs in riverine fragments while *Lophocebus ugandae* is present in patches at the eastern edge of Bugoma [31, 38]. In addition, Golden cat *Profelis aurata* has been recorded south of Bugoma as well as side-striped jackals *Canis adustus*. Forest raptors occurring at low density such as the crowned eagle *Stephanoaetus coronatus* have also been recorded [38].

Forest patches in Bulindi are physiognomically representative of riverine fragments elsewhere in the Budongo–Bugoma landscape (M.M. pers. obs.). These small forests are owned by local households according to traditional customary tenure. In the 1960s–1970s cocoa gardens (*shambas*) were established in some parts of forest in Bulindi, as occurred in private forests regionally. The *shambas* were abandoned when the cocoa market declined in the 1980s [42]. Residents rely heavily on forests for firewood and building materials among other resources; studies in 2004 indicated forests contribute about 16% of annual household income to people living in this area [43]. Since approximately 2000 riverine forests throughout Hoima and Masindi districts have been extensively logged with handsaws (pitsawing) or by freehand milling using chainsaws [31]. In Bulindi many households are involved in harvesting, buying, and/or selling timber trees from local forests to varying degrees. Human population density in Hoima District was 95.4 individuals per km^2 at the most recent census in 2002, and the average annual growth during 1991–2002 was 4.7% [44].

Data Collection

Forest trees in Bulindi were surveyed by the first author (M.M.) during 2006–2007. Sampling was conducted in fragments utilised by chimpanzees comprising five riverine patches (ranging from 16–50 ha in area) and one drier forest–thicket (14 ha). Transects were positioned to run the length of the longest straight line within each patch. Since riverine forests grow around waterbodies, transects tended to run parallel to streams or swamps. However, floral composition changes along a gradient from swampy low-lying centres to better drained soils at forest edges. To ensure sufficient sampling of all forest types, shorter transects were placed at 100 m intervals perpendicular to main transects, running to the forest edge. Total transect length was 9475 m. 185 plots measuring 10 x 20 m (200 m^2) were established randomly along transects, equivalent to one plot per 51 m. The total area sampled was 3.70 ha (2.2% of the combined area of forest patches). Plots were assigned to one of four physiognomic forest types:

Swamp forest – seasonally inundated or permanently waterlogged forest growing around papyrus swamps or alongside low-lying streams, characterised by aggregations of *Phoenix reclinata* palms;
Mixed forest – habitat that grades from swamp forest where the ground rises away from low-lying waterbodies. No single species dominates the stand;
Ecotone forest – regenerating or colonising forest on well-drained soil, typically along forest edges, transitional in composition between forest and grassland species;
Cocoa forest – forest associated with abandoned cocoa *shambas*. When *shambas* were established, understory vegetation was cleared but medium to large trees were left for shade. Cocoa forest is an artificial variant of other forest types.

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Diameter at breast height (DBH) was measured at 1.3 m for all stems ≥10 cm DBH. Buttressed trees were measured immediately above buttresses. In the case of strangling figs, the measure was taken around the central root structure, excluding outlying roots. Tree height was calculated by measuring to the tree base and treetop at fixed distances from the tree with a clinometer (Silva Clino Master). Distance was measured with a laser rangefinder (Bushnell Yardage Pro Sport 450; accurate to 1 m). Artificially short stems (e.g. broken by felled timber trees) were not measured. Preliminary species identification was made with reference to field guides [45, 46], while formal identification of voucher specimens was performed by botanists at Makerere University's herbarium. Several unresolved specimens were identified at Kew Gardens Herbarium in 2008.

To assess the impact of timber harvesting, data on the size and species of cut stumps were collected in July 2007, 2–15 months following tree surveys (depending on forest patch). Stumps were recorded within 5 m on either side of transects because recent logging in some areas made it difficult to precisely locate older plots. The length of transects surveyed was 7390 m giving a sample area of 7.39 ha (some sections of original transect were not sampled due to understorey regeneration). Because trees are often cut below 1.3 m it was frequently not possible to measure DBH precisely. Therefore DBH was estimated to the nearest 1 cm (for small trees; 10–20 cm), 5 cm (medium-sized trees; 21–50 cm) or 10 cm (large trees; >50 cm), by examining the stump and, in the case of sawn specimens, leftover logs. Data were collected by the first author with an experienced field assistant, both of whom had measured hundreds of stems during ecological surveys and were thus familiar with diameter sizes. Timber cutters typically target large trees. We considered large stumps (>50 cm DBH) to have been felled for timber if unequivocal evidence showed the tree was cut with a chainsaw or handsaw. Smaller stumps were considered to have been logged only if sawn planks from the tree were additionally present. We identified species from the leaves of coppice growth and from wood and bark characteristics.

An inventory of Budongo Forest's tree species was made by the second author (A.P.) in 1992 [27]. Five 2-km transects were established in a stratified random manner in each of eight compartments (B4, B1, N15, N3, N11, W21, K4, and K11–13) subject to varying management histories; six had previously been selectively logged while two were unlogged (see Plumptre [27] for details). Trees ≥10 cm DBH were recorded in 820 x 7 m-radius circular plots (154 km^2) situated at 50 m intervals along transects (total area sampled = 12.63 ha). DBH of strangling figs was not measured. A sub-sample of the same plots in compartment N3 have been monitored for tree phenology since 1992 up to the present day. Also, in 2000 tree DBH was measured again in six compartments (B4, B1, N15, N3, W21 and K11-13) to assess tree growth over the previous 8 years. While considerable mortality has occurred, particularly in smaller trees, the composition of the forest has not noticeably changed since 1992 at any compartment up to 2000 or at N3 over the past 19 years to the present, with recruitment coming from similar species in the forest (A.P. unpubl. data).

Data Analysis

Our analysis was primarily concerned with describing tree species richness, density and composition in riverine fragments in Bulindi, making comparisons with the main Budongo forest block, and assessing compositional similarity between sites. We also tested for differences in density and basal area of trees that provide an important fruit source for chimpanzees in the two habitats. Finally, we examined the impact of recent logging in riverine forests by comparing densities of live and logged stems.

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To compare species richness (alpha diversity) between Bulindi and Budongo, the EstimateS freeware application (Version 8.2 [47]) was used to generate expected species accumulation (rarefaction) curves with 95% confidence intervals [48]. These were scaled by individuals to account for potential differences in tree density between sites [49]. Species density was calculated for each site by extracting the expected number of species encountered in a sampling area equal to 1 ha (50 plots at Bulindi, 65 plots at Budongo).

Structural composition of tree communities in Bulindi and Budongo were compared in terms of overall tree density and basal area (BA) per hectare (ha^{-1}), and mean DBH. Data on DBH and BA of strangling figs in Bulindi were excluded in comparisons with Budongo. Taxonomic composition at Bulindi was quantified at family and species level, following Mori and Boom [50]. For each family and species, the total number of stems, stems ha^{-1}, and BA ha^{-1} were calculated. Based on these totals the following values were calculated for family: *relative diversity* (the % species per family of the total number of species); *relative density* (the % stems per family of the total number of stems ha^{-1}); and *relative dominance* (the % BA per family of the total BA ha^{-1}). For species, the same values were calculated except *relative frequency* replaces relative diversity. The relative frequency is the number of plots in which each species occurred as a percentage of the sum of occurrences of all species. *Importance Values* (IV) for each species were calculated by summing the relative frequency (i.e. how often a species is encountered throughout the forest), relative density (its abundance) and relative dominance (an indicator of the relative size of individuals), as a measure of the overall ecological importance of each species in the community. A *Family Importance Value* (FIV) was similarly calculated for each family except relative diversity substitutes for relative frequency [50]. Equivalent data for Budongo are not presented; detailed analyses of forest composition at Budongo are published elsewhere [e.g. 25].

Species diversity was assessed via the widely-used Shannon diversity index (*H'*), which incorporates information about the number of species and the abundance distribution of individuals in those species [51]. *H'* is calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of the sample belonging to the *i*th species. A greater number of species and a more even distribution increase the value of *H'*, which usually falls between 1.5 and 3.5 (rarely surpassing 4.5).

A further measure of evenness (Pielou's index, *J'*) was calculated as the ratio of observed diversity (*H'*) to maximum possible diversity (H_{max}):

$$J' = H' / H_{max} = H' / \ln S$$

where *S* is species richness. *J'* is constrained between 0 and 1.0 with 1.0 representing a situation in which all species are equally abundant [51]. Values of *H'* and *J'* were calculated from the Budongo data for comparison. Species richness, density and diversity in Budongo are marginally underestimated because *Albizia* spp. were not differentiated.

Species turnover between Bulindi and Budongo (beta diversity) was assessed using the Morisita–Horn (*MH*) index, which incorporates information about the relative abundance of individuals per species when comparing communities. While it is insensitive to species richness and sample size, it is sensitive to changes in abundances of the most common species [52]. Therefore abundance data were square-root transformed. The index is calculated as follows:

$$MH = 2\sum (a_i \cdot b_i) / (d_a + d_b) * (N_a * N_b)$$

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where N_a = the total number of individuals at site A; N_b = the total number of individuals at site B; a_i = the number of individuals of the *i*th species in A; b_i = the number of individuals of the *i*th species in B; and d_a (and d_b) are calculated as:

$$d_a = \sum a_i^2 / N_a^2$$

The index returns a value between 0 and 1, with the maximum value attained by two identical communities [51].

Balcomb et al. [53] and Plumptre [54] demonstrated a relationship between chimpanzee nest density and density of trees producing large fleshy fruits in Kibale National Park and Budongo Forest, respectively. To assess the potential value of riverine forests for frugivores, we compared the density and BA of trees that produce fruits (of any size) important in the chimpanzee diet at Bulindi with that at Budongo. Chimpanzees in Bulindi were unhabituated and therefore diet was determined from analysis of faeces (N = 1436) collected between January 2007 and January 2008 (see McLennan [36] for details). Ten species of forest tree, the seeds of which occurred most frequently in chimpanzee dung, were included in the analysis (cultivated fruits growing predominantly outside forest were excluded). Chimpanzees of the Sonso community in Budongo have been studied continuously since 1990 [39]. We identified ten species most commonly eaten at Sonso from observational studies of feeding behaviour [55-58]. Because tree species composition varies spatially in Budongo [27], we used a subset of tree data from two compartments located wholly (N3) and partially (N15) within the Sonso chimpanzees' home range for the analysis (sample area = 3.2 ha; Fig. 1). The sum of the DBH values of all trees producing fruits in these two compartments is relatively large compared to other surveyed compartments, suggesting high food availability [54]. We conducted Mann–Whitney tests to assess whether densities and BAs per hectare of the ten important fruit trees differed between Bulindi and the Sonso region in Budongo. Fig species were lumped because the seeds were not distinguished to species level in dung at Bulindi.

To assess the impact of logging on densities of timber trees in riverine forests in Bulindi, we calculated the density ratio of stumps to living stems in the large diameter class (>50 cm) for all recorded timber species. Tree species nomenclature follows the *Flora of Tropical East Africa* [59]. Data were analysed using SPSS Version 19. All statistical tests reported were two-tailed and $p<0.05$ was considered significant.

Results

A total of 79 tree species belonging to 61 genera and 27 families was recorded in forest plots in Bulindi (Appendix 1). Fig. 2 compares expected species accumulation curves for Bulindi and Budongo. Neither curve has levelled off completely. In particular, the Bulindi curve is still rising, implying that new species would be encountered with further sampling. In fact, 19 additional species not recorded in plots were identified during the study, bringing the total number of known forest tree species in Bulindi to 98. Evident from Fig. 2 is that riverine patches were considerably less species-rich compared to the main Budongo forest block: an equivalent number of species encountered after 1729 individuals in Bulindi (n = 79) is reached after just 450 individuals are sampled in Budongo. Tree species occurred at an expected density of 53 species ha^{-1} (± 3.4 SD), considerably lower than the corresponding value for Budongo (78 ± 4.3 species ha^{-1}).

Forest tree density in Bulindi was 467.5 individuals ha^{-1} and basal area (BA) was 25.5 m^2 ha^{-1} (or 26.5 m^2 including strangling figs). These values are similar to those calculated for Budongo (density: 446.1 individuals ha^{-1}; BA: 27.9 m^2 ha^{-1}). Likewise, mean DBH (± SD) was equivalent at both sites (Bulindi: 22.2 ± 14.4 cm, Budongo: 22.1 ± 17.6 cm; strangling figs excluded). The distribution of stems in different diameter classes in Bulindi and Budongo are compared in Fig. 3. Stem distribution

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at both sites displays an inverse 'J-shape' or negative exponential curve characteristic of tropical forests [60]. Although the overall distribution of stems differed significantly between sites (χ^2 = 47.24, df = 9, p<0.001), the discordance between observed and expected values was slight for most diameter classes. A smaller proportion of stems were in the 10–19 cm class in Bulindi compared to Budongo, whereas the opposite was true for stems measuring 20–29 cm diameter. Stems >100 cm DBH were rarer than expected in riverine fragments; only five such individuals occurred in the sample. The most commonly encountered trees >80 cm DBH in Bulindi were *Pseudospondias microcarpa*, *Ficus* spp. and *Albizia* spp. With the exception of *Albizia coriaria* these trees were rarely targeted by timber cutters (see below). Average tree height in Bulindi was 14.5 ± 8.4 m. Most stems (78%) were <20 m tall and only 6% of stems reached ≥30 m. Tree height was positively correlated with DBH (Spearman rank test: r_s = 0.696, p<0.001). The commonest trees ≥40 m in height were *Albizia* spp. Other tall, emergent trees occurring at lower densities in riverine fragments were *Parkia filicoidea* and *Piptadeniastrum africanum*.

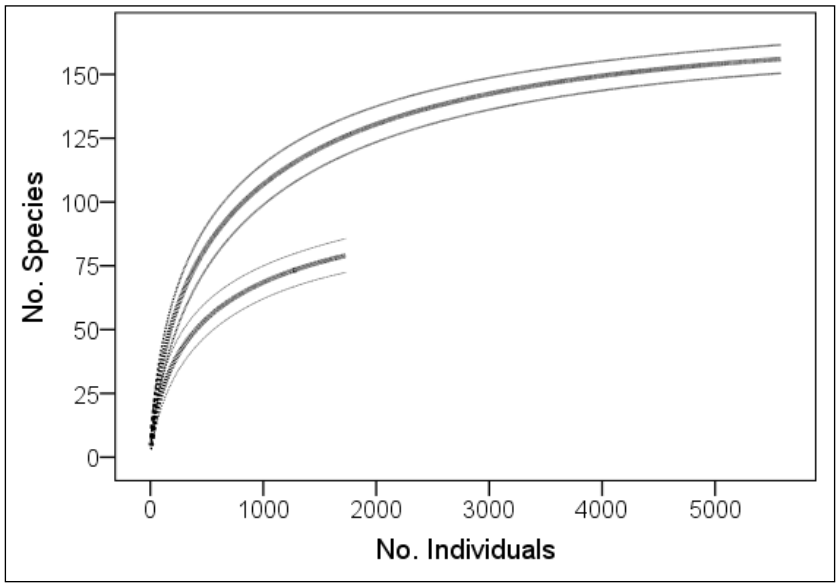


Fig. 2. Expected species accumulation curves for trees ≥10 cm DBH in riverine fragments in Bulindi (lower solid line) and the main Budongo forest block (upper solid line) with 95% confidence intervals (thin lines). Number of individuals sampled: Bulindi = 1729, Budongo = 5581.

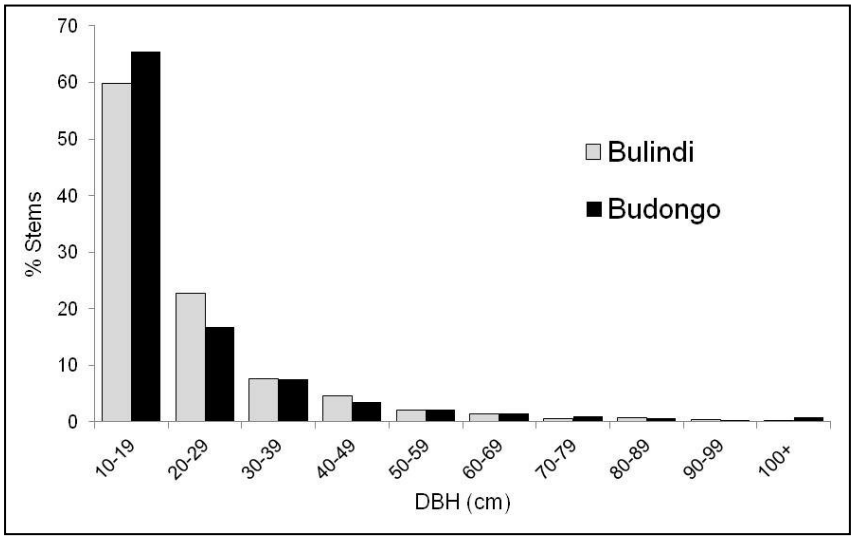


Fig. 3. Comparative distribution of stems ≥10 cm DBH in different diameter size classes in riverine fragments in Bulindi and the main Budongo forest block.

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Ten families with the highest ranked importance value in Bulindi are listed in Appendix 2. The dominant family was the Moraceae: it was most species-rich (11 species; 14% of all species), had the highest stem density, and accounted for nearly one-third of total BA. By contrast, the second ranked family Arecaceae (the palms) was represented by just two species of which the wild date palm *Phoenix reclinata* accounted for all but one of its 395 stems. Predominant forest types in Bulindi were mixed forest and swamp forest, accounting for 46% and 34% of plots, respectively. Ecotone and cocoa forest were comparatively minor habitats (11% and 9% of plots, respectively) (Fig. 4).

Appendix 3 lists the 20 most important species in Bulindi. The highest ranked species was the *Phoenix reclinata* palm. While this palm exhibits a narrow diameter range (maximum diameter = 28 cm), it occurred at a density of 106.5 stems ha $^{-1}$ (23% of all stems) and in 46% of plots, principally in swamp forest. The second ranked species, *Trilepisium madagascariensis*, had the highest BA ha $^{-1}$ and occurred in 48% of plots, particularly in mixed forest. Notably, the fourth commonest species was the exotic cocoa tree *Theobroma cacao*. Almost exclusively confined to abandoned forest *shambas* where it dominated the understorey, cocoa occurred in only 12% of plots and had a relatively low BA.

Results of the Shannon diversity index indicate lower diversity in the tree community in Bulindi (H' = 3.1) compared to Budongo (H' = 3.8). Even so, the index suggests riverine forest patches were moderately diverse. Species evenness was similar at both sites, though slightly lower in Bulindi (Bulindi: J' = 0.71, Budongo: 0.75). These values point to overall low ecological dominance at both sites. The Morisita–Horn index returned a value of 0.238, indicating relatively low similarity between sites. Of 180 species recorded in plots from both sites (*Albizia* spp. were lumped because they were not differentiated at Budongo), only 52 (28.9%) were shared. Whereas 68.4% of 76 species in Bulindi were recorded in Budongo plots (though almost all have been recorded there previously), only 33.3% of 156 species encountered in Budongo occurred in Bulindi plots. Moreover, none of the most abundant species at Bulindi were common at Budongo (Appendix 3). Notably, among 24 species not encountered in Budongo plots was the commonest species in Bulindi, *Phoenix reclinata* (however, it is known to occur but is confined to swamp forest and is therefore rare; A.P. pers. obs.). Conversely, only five of 20 most abundant species in Budongo were recorded in the riverine fragments. In particular, the top nine species were entirely absent from Bulindi (Appendix 4).

Ten forest fruit trees identified as particularly important for chimpanzees in Bulindi and at Sonso in Budongo are listed in Appendix 5. Aside from figs, there is little overlap in important fruit foods. The overall density of important fruit trees was three times higher in Bulindi fragments compared to Budongo (Sonso). However, median species density did not differ significantly between sites (Mann–Whitney: U = 38.5, p = 0.39). The combined BA ha $^{-1}$ of important fruit trees was similar at both sites, and median BA was not significantly different (U = 43.5, p = 0.62).

In total, 616 stumps ≥10 cm DBH were recorded along transects at Bulindi (83.4 stumps ha $^{-1}$). 75.6% were in the smallest diameter class, and were cut for poles or firewood. However, 98 (15.9%) were sawn for timber (13.3 logged trees ha $^{-1}$). (A further 14 specimens were most likely logged, but this could not be confirmed unequivocally). Logged specimens belonged to ≥16 species (Appendix 6). *Antiaris toxicaria* was most frequently represented (36% of logged trees), followed by *Albizia coriaria* (13%) and *Trilepisium madagascariensis* (12%). Chimpanzees fed on at least eight of the 16 logged species, and four were important fruit trees. Though most logged trees (85%) were large-sized, some were harvested at smaller diameters (i.e. <50 cm DBH). The smallest tree unequivocally sawn for timber was a specimen of *Lovoa trichilioides*, estimated at 30 cm DBH. For six species, the density of large stumps exceeded that of living specimens (Appendix 6). For four other species, fewer than two

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large living stems remained to each large stump. For all logged species, the overall ratio of large stumps to living trees was 1:1.5.

Discussion

The composition, structure and current status of riverine fragments outside of main forests in mid-western Uganda, and their value for frugivores including endangered chimpanzees, has not previously been reported. These data are needed because some such forests have been identified by conservation organisations as having potential value as wildlife corridors linking fragmented protected areas [29, 30, 38]. Anthropogenic activities in forests such as logging and plantation establishment cause a reduction in species richness and density [32, 33, 61]. Therefore degradation of unprotected forest fragments is expected to result in low species diversity. Nevertheless, expected tree species density in riverine patches in Bulindi (53 species ha $^{-1}$) was similar to densities reported from 1-ha plots in main forests elsewhere in Uganda [62]. This is probably because several physiognomic forest types were distinguishable in the fragments. For example, regular burning of bush and grassland at forest edges increases compositional complexity through maintenance of ecotone habitat, which was the most species-rich forest type in Bulindi [36]. As expected, however, riverine fragments were considerably less diverse than Budongo, the nearest main forest block, and overall species richness was much lower.

In most respects, the structure of riverine fragments conformed to a typical tropical forest. The stem density of 467.5 trees ha $^{-1}$ was within the range of 300–700 stems given by Richards [60], and was equivalent to average stem density in four major Ugandan forests including Budongo [62]. While similar to Budongo, BA ha $^{-1}$ in Bulindi (26.5 m^2 including strangling figs) was at the lower end of the range of values for a selection of tropical forests given in Swaine et al. [63], which mostly fall between 30 and 50 m^2 ha $^{-1}$. (Previous studies reported higher BA in Budongo plots [28, 62]). Very large trees were rarer than expected in Bulindi, and BA had probably decreased due to recent removal of large stems for timber; even light-to-moderate logging causes marked reductions in BA [33, 64]. The relatively low BA also reflects the fact that sections of Bulindi forests were young, having regenerated on previously cultivated land. However, stems in the smallest diameter class (10–19 cm) were also rarer than expected. This is probably related to local people's frequent cutting of small trees and saplings for poles (particularly, during this research, for constructing tobacco drying barns). Physiognomically, the riverine fragments showed features characteristic of disturbed secondary forest: a dense understorey of shrubs, small trees and climbers, and an irregular, low and broken canopy, with frequent large gaps created by logging.

Common trees in Bulindi were characteristic of damp waterlogged conditions [59]. The most abundant species – the *Phoenix reclinata* palm – occurred at an overall density of >100 stems ha $^{-1}$, and at much higher densities in stretches of swamp forest (e.g. 271 stems ha $^{-1}$ in one forest patch). Aggregations of these palms are a common structural feature in groundwater and swamp forest in East Africa [65-67]. Other common trees indicative of swampy conditions in Bulindi were *Pseudospondias microcarpa* and *Macaranga schweinfurthii*. The overall ecological dominance of the Moraceae family (the figs and mulberries) is notable since it appears to be relatively uncommon in African tropical forests [22]. Members of the Moraceae produce fleshy drupaceous fruits attractive to frugivores. Figs, for example, are an important resource for many tropical vertebrates [68, 69] including chimpanzees [40, 70], due to their asynchronous fruiting. High densities of certain species (e.g. *Antiaris toxicaria, Trilepisium madagascariensis* and some figs) could result, in part, from the feeding preferences of frugivores in fragments, including chimpanzees, and subsequent seed dispersal [71]. Even so, many African representatives of the Moraceae also favour wet forest types including riverine forest [59]. Additionally, the dominance of Moraceae in Bulindi could be

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influenced by light conditions associated with anthropogenic disturbance and edge effects [68, 72]. To what extent it has been influenced by human activities such as logging is difficult to assess, however. While large specimens of families including the Meliaceae are cut for timber, so too are members of the Moraceae (notably *Antiaris toxicaria*), though figs are usually ignored (Appendix 6).

While tree species in Bulindi are characteristic of the region generally [20, 66], community composition differed markedly from Budongo, the nearest main forest block. Long-term shifts in tree community composition and climatic changes have been documented at Kibale National Park [73]. At Budongo, while successional processes affecting forest composition are occurring, these changes are gradual [28], and forest composition has not changed noticeably since 1992 (A.P. unpubl. data). Additionally, there have been no clear trends in rainfall or temperature in and around Budongo Forest over the past 20 years [74]. Therefore, the major compositional differences between Budongo and riverine fragments in Bulindi could not be attributed to the 15-year gap between surveys. The riverine fragments support a groundwater-dependant vegetation community, whereas similar forest occurs only in narrow waterlogged valleys in Budongo and is a relatively unimportant habitat type [25].

Given these differences it is unsurprising that trees providing important fruit sources for chimpanzees also differed between riverine fragments and Budongo. The Sonso region of Budongo is rich in primate food trees [54]. However, food supply in outlying forest patches has been assumed to be inadequate for chimpanzees year-round [39]. Data from Bulindi indicate that is not necessarily the case. The BA ha $^{-1}$ of important chimpanzee fruit trees at Bulindi was similar to Sonso, while their overall density was considerably greater. In part, this is because fruits of the superabundant *Phoenix* palm and spatially clumped cocoa trees (which both exhibit a narrow range of trunk diameters) were important foods for Bulindi chimpanzees [36] (Fig. 5). In addition, figs were the most commonly eaten fruit in the chimpanzee diet at Bulindi [36], as at Sonso [40, 56]. Riverine forests in Bulindi contained a higher density of fig trees (16.8 individuals ha $^{-1}$) than many tropical forests [cf. 33, 69 and references therein], including Budongo (5.9 ha $^{-1}$ overall, 9.1 ha $^{-1}$ at Sonso). This suggests that reduced densities of large fruit-producing trees in small, disturbed fragments can be compensated by greater abundances of palms and figs, which also represent important resources for frugivores [see also 15, 67].

Our comparison of potential food abundance between sites is crude, however. It fails to account for possible differences in nutritional quality of important fruit foods and their seasonal availability. Furthermore, it overlooks the dietary importance of non-tree fruits or non-fruit foods such as leaves. For example, young leaves of the most abundant tree in Budongo, *Celtis mildbraedii*, are a major food for Sonso chimpanzees [39]. On the other hand, fruits of certain forest herbs, shrubs and vines (e.g. *Aframomum* spp. and *Monanthotaxis ferruginea*) were heavily exploited by Bulindi chimpanzees; qualitative observations suggested such non-tree fruit sources were abundant in riverine fragments [36]. Overall, our data indicate that the riverine forests offer a relatively food-dense habitat for frugivores. Inasmuch as Bulindi forests are physiognomically representative of riverine fragments elsewhere in the Budongo–Bugoma landscape (M.M. pers. obs.), these results may explain the unexpected widespread occurrence of chimpanzees in forest patches regionally [31].

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Fig. 4. Some forest types in Bulindi. Left to right: Thin forest dominated by *Phoenix reclinata* palms growing around a papyrus swamp; degraded mixed forest including trees of *Albizia* sp.,*Trilepisium madagascariensis* and *Funtumia africana* (the logged tree in the garden is *Antiaris toxicaria*); fresh chimpanzee night nest in a cocoa tree (*Theobroma cacao*) in an abandoned forest plantation. Photo credit: M. McLennan.





Fig. 5. Important fruit foods for chimpanzees in riverine forest in Bulindi. Left to right: *Phoenix reclinata* palm with clusters of ripe fruit; cocoa tree in an abandoned forest plantation with unripe pods; fruiting fig tree (*Ficus sur*). Photo credit: M. McLennan.





Fig. 6. Unlicensed timber extraction in riverine fragments. Left to right: Pitsaw structure (the log is *Trilepisium madagascariensis*); freshly chainsawn *Antiaris toxicaria* in heavily-logged forest – all large trees have been felled (note *Phoenix* palms remaining); adult male chimpanzees in a clearing made by logging in Bulindi. Photo credit: M. McLennan.

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Implications for Conservation

Our study underscores the importance of protecting tropical riverine forest fragments for conservation of threatened wildlife, including great apes. Given that riverine corridors provide many ecosystem services (e.g. watershed protection), as well as a diversity of products valued by people, their protection is beneficial to both humans and wildlife. However, this study also highlights the substantial threats to these neglected and frequently unprotected habitats from anthropogenic activities – in this case from agricultural expansion and unregulated commercial logging (Fig. 6). The high density of logged stems at Bulindi was likely an underestimate. Gaps created by logging are invaded by a dense cover of vines and shrubs, and some stumps were probably missed in heavily logged areas. Additionally, decaying stumps older than about 2–3 years were rarely recorded because of difficulties establishing whether they had been cut or died naturally. This extensive timber extraction – mostly unlicensed – meant fragments were in the process of becoming cutovers. Following removal of big trees, forest land is cleared for subsistence and/or commercial agriculture. This process is underway throughout the Budongo–Bugoma landscape [31], and is representative of broader land-use changes taking place around large protected areas across western Uganda [4, 8, 75, 76].

Extensive loss of habitat and resources such as large fruit-producing trees will inevitably cause wildlife population declines, including chimpanzees. Among species targeted by timber cutters in Bulindi were important chimpanzee fruit trees (Appendix 6). For example, *Antiaris toxicaria* was logged to such an extent that by 2008 most large specimens with straight trunks were felled (M.M. pers. obs.). This species is one of several forest trees being promoted in Uganda as substitutes for more valuable hardwoods, which have become scarce due to over-exploitation [77]. Along with certain other species (e.g. *Trilepisium madagascariensis* and *Sterculia dawei*), *Antiaris toxicaria* was targeted because large specimens of greater economic importance (e.g. the mahoganies *Khaya anthotheca* and *Entandrophragma* spp., and *Lovoa trichilioides*) were already harvested (Fig. 6).

These findings have clear implications for conservation projects aiming to maintain habitat connectivity and dispersal opportunities for chimpanzees and other wildlife among Uganda's main forest blocks [30]. Unless projects are successful in reversing present trends most riverine fragments will be severely depleted if not cleared completely in the near-future, negating their value as corridors for endangered wildlife. Currently, the feasibility of using carbon funds, among other alternative income-generating projects, as incentive for private forest owners in the Budongo–Bugoma landscape to maintain forest on their land is being explored [38].

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Appendix 1. Tree species recorded in riverine forest plots in Bulindi. Columns show for each species: the total no. of stems (≥10 cm DBH), stem density ha $^{-1}$, basal area (BA) ha $^{-1}$ and mean DBH (+ standard error). Tree species nomenclature follows the *Flora of Tropical East Africa* [59]; synonyms commonly used in the literature are given for some species.

Family	Species (Synonym)	No. Stems	Density	BA (m^2)	Mean DBH (SE)
Anacardiaceae	*Lannea barteri* (Oliv.) Engl.	1	0.3	0.020	30.8
	Lannea schimperi (A. Rich.) Engl.	4	1.1	0.031	17.8 (4.2)
	Pseudospondias microcarpa (A. Rich.) Engl.	69	18.6	2.539	34.9 (2.8)
	Rhus natalensis Krauss	1	0.3	0.006	17
Annonaceae	*Annona senegalensis* Pers.	5	1.4	0.015	11.7 (0.8)
Apocynaceae	*Funtumia africana* (Benth.) Stapf (syn. *F. latifolia*)	104	28.1	1.312	22.3 (1.0)
	Rauvolfia vomitoria Afzel	2	0.5	0.098	47.1 (9.9)
Arecaceae	*Phoenix reclinata* Jacq.	394	106.5	2.804	18.0 (0.2)
	Raphia farinifera (Gaertn.) Hylander	1	0.3	0.083	62.5
Bignoniaceae	*Markhamia platycalyx* (Baker) Sprague (syn. *M. lutea*)	1	0.3	0.002	10.2
	Spathodea campanulata P. Beauv.	6	1.6	0.022	13.0 (1.2)
Bombacaceae	*Bombax buonopozense* P. Beauv.	1	0.3	0.004	14.3
Celastraceae	*Gymnosporia heterophylla* (Eckl. & Zeyh.) Loes (syn. *Maytenus heterophylla*)	9	2.4	0.026	11.7 (0.3)
Combretaceae	*Combretum collinum* Fresen.	12	3.2	0.043	12.8 (0.7)
	Combretum molle G. Don	6	1.6	0.069	21.3 (4.2)
	Terminalia glaucescens Benth. (syn. *T. veluntina*)	1	0.3	0.003	12.8
Dracaenaceae	*Dracaena steudneri* Engl.	4	1.1	0.022	15.4 (2.8)
Euphorbiaceae	*Bridelia ndellensis* Beille	1	0.3	0.032	39.1
	Croton macrostachyus Del.	8	2.2	0.085	21.9 (1.9)
	Croton sylvaticus Krauss	2	0.5	0.020	20.2 (7.6)
	Macaranga schweinfurthii Pax	58	15.7	0.861	22.4 (1.9)
	Margaritaria discoidea (Baill.) Webster (syn. *Phyllanthus discoideus*)	17	4.6	0.260	24.1 (3.0)
	Neoboutonia melleri (Muell. Arg.) Prain	24	6.5	0.284	20.8 (2.3)
	Sapium ellipticum (Krauss) Pax	16	4.3	0.852	46.8 (4.6)
Fabaceae (Caesalpinioideae)	*Senna spectabilis* (DC.) Irwin & Barneby (syn. *Cassia spectabilis*)	3	0.8	0.086	36.6 (1.7)
(Faboideae)	*Erythrina abyssinica* DC.	2	0.5	0.008	13.2 (2.2)
(Mimosoideae)	*Albizia coriaria* (Welm. ex) Oliv.	14	3.8	1.349	63.5 (6.3)
	Albizia glaberrima (Schumach. & Thonn.) Benth.	12	3.2	0.439	34.8 (6.8)
	Albizia grandibracteata Taub.	2	0.5	0.334	88.5 (6.0)
	Albizia zygia (DC.) Macbr.	20	5.4	0.546	32.0 (3.7)
	Parkia filicoidea (Welw. ex) Oliv.	15	4.1	0.396	31.2 (4.4)
	Piptadeniastrum africanum (Hook. f.) Brenan	15	4.1	0.333	27.5 (4.5)
Flacourtiaceae	*Lindackeria schweinfurthii* Gilg	1	0.3	0.002	10.8
	Oncoba spinosa Forssk.	3	0.8	0.009	11.9 (0.9)
Guttiferae	*Harungana madagascariensis* Poir.	5	1.4	0.036	16.6 (3.9)

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Lamiaceae	*Vitex doniana* Sweet	1	0.3	0.005	16
Meliaceae	*Entandrophragma angolense* (Welw.) C.DC.	15	4.1	0.187	22.2 (2.6)
	Entandrophragma cylindricum (Sprague) Sprague	2	0.5	0.006	11.8 (1.5)
	Entandrophragma utile (Dawe & Sprague) Sprague	4	1.1	0.020	14.5 (2.8)
	Khaya anthotheca (Welw.) C.DC.	3	0.8	0.029	20.9 (2.7)
	Lovoa trichilioides Harms (syn. *L. brownii*)	45	12.2	0.537	21.8 (1.4)
	Trichilia dregeana Sond.	25	6.8	0.484	26.6 (2.9)
	Trichilia prieureana A. Juss.	8	2.2	0.049	16.0 (2.1)
	Trichilia rubescens Oliv.	3	0.8	0.014	14.2 (3.4)
Moraceae	*Antiaris toxicaria* Leschen.	129	34.9	2.286	24.4 (1.4)
	Ficus exasperata Vahl	9	2.4	0.155	26.0 (4.1)
	Ficus mucuso Ficalho	5	1.4	0.164	28.2 (13.7)
	Ficus natalensis Hochst.	17	4.6	1.012	43.8 (7.5)
	Ficus ovata Vahl (syn. *F. brachypoda*)	3	0.8	0.226	56.5 (13.4)
	Ficus sur Forssk. (syn. *F. capensis*)	21	5.7	0.446	27.3 (3.6)
	Ficus vallis-choudae Del.	6	1.6	0.034	15.9 (1.8)
	Ficus variifolia Warb.	1	0.3	0.007	18.1
	Milicia excelsa (Welw.) C.C. Berg	2	0.5	0.459	82.5 (63.3)
	Morus mesozygia Stapf (syn. *M. lactea*)	12	3.2	0.437	31.5 (8.1)
	Trilepisium madagascariensis DC. (syn. *Bosqueia phoberos*)	224	60.5	3.144	22.1 (0.9)
Myristicaceae	*Pycnanthus angolensis* (Welw.) Warb.	10	2.7	0.131	22.6 (3.5)
Ochnaceae	*Ochna afzelii* Oliv.	3	0.8	0.026	20.1 (2.2)
Olacaceae	*Strombosia scheffleri* Engl.	1	0.3	0.011	23.1
Phyllanthaceae	*Antidesma membranaceum* Muell. Arg.	2	0.5	0.011	15.8 (0.1)
Pittosporaceae	*Pittosporum mannii* Hook. f.	4	1.1	0.010	10.9 (0.4)
Rhamnaceae	*Maesopsis eminii* Engl.	6	1.6	0.153	32.1 (5.9)
Rubiaceae	*Aidia micrantha* (K. Schum.) F. White	1	0.3	0.006	17.2
	Dictyandra arborescens Hook. f.	11	3	0.053	14.7 (0.9)
	Multidentia crassa (Hiern) Bridson & Verdc. (Syn. *Canthium crassum*)	1	0.3	0.007	17.8
	Oxyanthus speciosus DC.	14	3.8	0.056	13.4 (0.9)
	Rothmannia urcelliformis (Hiern) Robyns	2	0.5	0.007	12.5 (0.3)
	Vangueria apiculata K. Schum.	1	0.3	0.004	13.5
	Vangueria madagascariensis Gmelin	2	0.5	0.014	17.5 (4.5)
Rutaceae	*Fagaropsis angolensis* (Engl.) Dale	5	1.4	0.107	28.3 (7.2)
	Teclea nobilis Del.	64	17.3	0.587	19.4 (0.9)
Sapindaceae	*Allophylus africanus* P. Beauv.	9	2.4	0.042	14.1 (1.6)
	Allophylus ferrugineus Taub. (syn. *A. macrobotrys*)	2	0.5	0.004	10.3 (0.3)
	Glenniea africana (Radlk.) Leenh. (syn. *Crossonephelis africanus*)	76	20.5	1.338	24.5 (1.7)
	Zanha golungensis Hiern	4	1.1	0.142	37.5 (9.5)
Sterculiaceae	*Dombeya kirkii* Mast. (syn. *D. mukole*)	4	1.1	0.019	15.1 (1.0)
	Sterculia dawei Sprague	7	1.9	0.509	48.5 (13.3)
	Theobroma cacao L.	115	31.1	0.419	12.8 (0.3)

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Ulmaceae	*Celtis africana* Burm. f.	4	1.1	0.039	20.4 (3.5)
	Trema orientalis (L.) Bl.	7	1.9	0.062	17.5 (4.3)
Total:		1729	467.5	26.489	22.4 (0.4)

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Appendix 2. Ten tree families with the highest ranked Family Importance Values (FIV) in riverine forest fragments in Bulindi. The FIV is the sum of the relative diversity (RDi), relative density (RD) and relative dominance (RDo). Also shown for each family is the total no. of species, the total no. of stems (≥10 cm DBH), stem density and basal area (BA) ha^{-1}.

Family	No. Species	No. Stems	Density	BA (m^2)	RDi	RD	RDo	FIV
1. Moraceae	11	429	116	8.4	13.9	24.8	31.6	70.3
2. Arecaceae (Palmae)	2	395	107	2.9	2.5	22.8	10.9	36.3
3. Fabaceae (Leguminosae)	8	83	22	3.5	10.1	4.8	13.2	28.1
4. Euphorbiaceae	7	126	34	2.4	8.9	7.3	9.0	25.2
5. Meliaceae	8	105	28	1.3	10.1	6.1	5.0	21.2
6. Anacardiaceae	4	75	20	2.6	5.1	4.3	9.8	19.2
7. Sapindaceae	4	91	25	1.5	5.1	5.3	5.8	16.1
8. Sterculiaceae	3	126	34	0.9	3.8	7.3	3.6	14.7
9. Apocynaceae	2	106	29	1.4	2.5	6.1	5.3	14.0
10. Rubiaceae	7	32	9	0.1	8.9	1.9	0.6	11.3
Remaining Families (n = 17)	23	161	44	1.4	29.1	9.3	5.3	43.7
Total:	79	1729	468	26.5	100	100	100	300

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Appendix 3. Twenty tree species with the highest ranked Importance Values (IV) in riverine fragments in Bulindi. The IV is the sum of the relative frequency (RF), relative density (RD) and relative dominance (RDo) of each species. For each species the total no. of stems, the percentage of plots (n = 185) in which the species occurred, basal area (BA) and density ha $^{-1}$ is shown; for comparison, species densities in Budongo are given in parenthesis.

Species	Family	No. Stems	% Plots	BA (m^2)	Density (Budongo) [a]	RF	RD	RDo	IV
1. *Phoenix reclinata* Jacq.	Arecaceae	394	45.9	2.8	106.5 (–)	10.0	22.8	10.6	43.4
2. *Trilepisium madagascariensis* DC.	Moraceae	224	47.6	3.1	60.5 (6.4)	10.4	13	11.9	35.2
3. *Antiaris toxicaria* Leschen.	Moraceae	129	38.9	2.3	34.9 (1.9)	8.5	7.5	8.6	24.6
4. *Pseudospondias microcarpa* (A. Rich.) Engl.	Anacardiaceae	69	26.5	2.5	18.6 (0.9)	5.8	4.0	9.6	19.4
5. *Funtumia africana* (Benth.) Stapf	Apocynaceae	104	30.3	1.3	28.1 (3.4)	6.6	6.0	5.0	17.6
6. *Glenniea africana* (Radlk.) Leenh.	Sapindaceae	76	28.6	1.3	20.5 (2.2)	6.3	4.4	5.1	15.7
7. *Theobroma cacao* L.	Sterculiaceae	115	11.9	0.4	31.1 (–)	2.6	6.7	1.6	10.8
8. *Teclea nobilis* Del.	Rutaceae	64	16.8	0.6	17.3 (1.7)	3.7	3.7	2.2	9.6
9. *Macaranga schweinfurthii* Pax	Euphorbiaceae	58	10.3	0.9	15.7 (0.8)	2.2	3.4	3.2	8.8
10. *Lovoa trichilioides* Harms	Meliaceae	45	17.3	0.5	12.2 (0.5)	3.8	2.6	2.0	8.4
11. *Albizia coriaria* (Welm. ex) Oliv.	Fabaceae	14	6.5	1.3	3.8 (*)	1.4	0.8	5.1	7.3
12. *Ficus natalensis* Hochst.	Moraceae	17	6.5	1.0	4.6 (0.3)	1.4	1.0	3.8	6.2
13. *Sapium ellipticum* (Krauss) Pax	Euphorbiaceae	16	7.6	0.9	4.3 (0.3)	1.7	0.9	3.2	5.8
14. *Trichilia dregeana* Sond.	Meliaceae	25	10.3	0.5	6.8 (0.2)	2.2	1.4	1.8	5.5
15. *Albizia zygia* (DC.) Macbr.	Fabaceae	20	10.3	0.5	5.4 (*)	2.2	1.2	2.1	5.5
16. *Ficus sur* Forssk.	Moraceae	21	7.6	0.4	5.7 (2.3)	1.7	1.2	1.7	4.6
17. *Parkia filicoidea* (Welw. ex) Oliv.	Fabaceae	15	7.0	0.4	4.1 (0.2)	1.5	0.9	1.5	3.9
18. *Piptadeniastrum africanum* (Hook. f.) Brenan	Fabaceae	15	7.0	0.3	4.1 (0.2)	1.5	0.9	1.3	3.7
19. *Margaritaria discoidea* (Baill.) Webster	Euphorbiaceae	17	7.0	0.3	4.6 (5.2)	1.5	1.0	1.0	3.5
20. *Albizia glaberrima* (Schumach. & Thonn.) Benth.	Fabaceae	12	4.9	0.4	3.2 (*)	1.1	0.7	1.7	3.4
Remaining Species (n = 59)	–	279	–	4.6	75.4	23.8	16.1	17.2	57.1
Total:		1729	–	26.5	467.5	100	100	100	300

[a] A dash indicates the species was not recorded in Budongo plots; * individual *Albizia* spp. were not differentiated in the Budongo survey. *Albizia* occurred at an overall density of 13.0 and 3.0 individuals ha $^{-1}$ in Bulindi and Budongo, respectively.

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Appendix 4. The 20 most common tree species (≥10 cm DBH) and their densities (stems ha $^{-1}$) in Budongo Forest Reserve. Species are listed in descending order of abundance. Densities in Bulindi are shown for comparison; a dash indicates the species was not recorded in Bulindi plots.

Species	Family	Density	
		Budongo	Bulindi
1. *Celtis mildbraedii* Engl.	Ulmaceae	47.3	–
2. *Funtumia elastica* (Preuss) Stapf.	Apocynaceae	41.0	–
3. *Lasiodiscus mildbraedii* Engl.	Rhamnaceae	28.5	–
4. *Celtis zenkeri* Engl.	Ulmaceae	26.5	–
5. *Rinorea ardisiiflora* (Welw. ex Oliv.) Kuntze	Violaceae	24.5	–
6. *Celtis wightii* Planch.	Ulmaceae	22.3	–
7. *Cynometra alexandri* C.H. Wright	Fabaceae	18.9	–
8. *Celtis gomphophylla* Baker	Ulmaceae	17.3	–
9. *Uvariopsis congensis* Robyns & Ghesq.	Annonaceae	14.7	–
10. *Khaya anthotheca* (Welw.) C.DC.	Meliaceae	11.5	0.8
11. *Tapura fischeri* Engl.	Dichapetalaceae	11.4	–
12. *Trichilia rubescens* Oliv.	Meliaceae	10.9	0.8
13. *Croton macrostachyus* Del.	Euphorbiaceae	7.0	2.2
14. *Holoptelea grandis* (Hutch.) Mildbr.	Ulmaceae	6.7	–
15. *Trilepisium madagascariensis* DC.	Moraceae	6.4	60.5
16. *Alchornea laxiflora* (Benth.) Pax & K. Hoffm.	Euphorbiaceae	5.6	–
17. *Margaritaria discoidea* (Baill.) Webster	Euphorbiaceae	5.2	4.6
18. *Chrysophyllum albidum* G. Don	Sapotaceae	5.0	– [a]
19. *Alstonia boonei* De Wild.	Apocynaceae	4.4	–
20. *Apodytes dimidiata* E. May. Ex Arn.	Icacinaceae	4.3	–

[a] While *Chrysophyllum albidum* was not recorded in plots at Bulindi it occurs at a very low density.

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Appendix 5. Density and basal area (BA) ha $^{-1}$ of 10 tree species that are important fruit foods for (a) chimpanzees in riverine fragments in Bulindi, and (b) chimpanzees of the Sonso community in Budongo Forest. Figs (*Ficus* spp.) are lumped. Values for Budongo were calculated from a subset of tree data including the two surveyed compartments within or overlapping the Sonso chimpanzees' home range. Fruit foods at Bulindi are listed in descending order of importance based on their frequencies in chimpanzee dung; emboldened species occurred in ≥10% of dungs (N = 1436) [36]. Important fruit foods at Sonso were identified from four observational studies of diet [55-58]. While their relative importance differed between studies, emboldened species are those ranked among the top five fruit foods in two or more studies; figs were always top-ranked. A dash indicates the species was not encountered in plots.

(a) Bulindi	Family	Density	BA (m^2)	(b) Budongo (Sonso)	Family	Density	BA (m^2)
***Ficus* spp.**	Moraceae	16.8	2.046	***Ficus* spp.**	Moraceae	9.1	0.969 [a]
Phoenix reclinata Jacq.	Arecaceae	106.5	2.804	***Broussonetia papyrifera*** (L.) Vent.	Moraceae	1.9	0.199
Pseudospondias microcarpa (A. Rich.) Engl.	Anacardiaceae	18.6	2.539	***Cynometra alexandri*** C.H. Wright	Fabaceae	16.3	5.442
Theobroma cacao L.	Sterculiaceae	31.1	0.419	***Maesopsis eminii*** Engl.	Rhamnaceae	4.7	1.518
Caloncoba crepiniana (De Wild. & T. Dur.) Gilg	Flacourtiaceae	–	–	***Celtis gomphophylla*** Baker	Ulmaceae	23.4	1.800
Parkia filicoidea (Welw. ex) Oliv.	Fabaceae	4.1	0.396	*Cordia millenii* Bak.	Boraginaceae	3.8	0.444
Antiaris toxicaria Leschen.	Moraceae	34.9	2.286	*Morus mesozygia* Stapf	Moraceae	–	–
Morus mesozygia Stapf	Moraceae	3.2	0.437	*Mildbraediodendron excelsum* Harms	Fabaceae	0.3	0.008
Annona senegalensis Pers.	Annonaceae	1.4 [b]	0.015	*Desplatsia dewevrei* (De Wild. & T. Dur.) Burret	Tiliaceae	2.2	0.078
Zanha golungensis Hiern	Sapindaceae	1.1	0.142	*Croton macrostachyus* Del.	Euphorbiaceae	6.3	0.352
Total:		217.7	11.084	Total:		67.8	10.811

[a] The BA of *Ficus* spp. in Budongo (Sonso) is marginally lower than the true value because three strangling figs were not measured; [b] *Annona senegalensis* occurs at higher densities in regenerating and woodland habitat outside forest patches.

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Appendix 6. Tree species harvested for timber in Bulindi. Columns show for each species: the no. of logged stumps recorded along transects; the diameter (DBH) range of logged specimens; the density of stumps and living stems in the large diameter class (>50 cm DBH); and the density ratio of large stumps to live stems. Emboldened ratios indicate species for which the density of large stumps exceeded that of living trees. * Species followed by an asterisk were recorded in the chimpanzee diet at Bulindi [36]; emboldened species were identified as important fruit sources for this population.

Species (family) [a]	No. logged trees	DBH range (cm)	Density (ha $^{-1}$)		Density ratio (Stump : Live stem)
			Large stumps	Large live stems	
***Antiaris toxicaria* (Moraceae) ***	35	45–120	4.2	2.7	**1:0.6**
Albizia coriaria (Fabaceae)	13	45–100	1.5	2.4	1:1.6
Trilepisium madagascariensis (Moraceae)	12	40–90	0.9	3.5	1:3.9
Glenniea africana (Sapindaceae)	8	50–100	0.9	1.4	1:1.6
Lovoa trichilioides (Meliaceae)	7	30–90	0.5	0.0	**1:0.0**
Sterculia dawei (Sterculiaceae) *	5	70–100	0.7	0.8	1:1.1
Albizia sp. (Fabaceae)	4	50–120	0.4	1.6	1:4.0
Entandrophragma sp. (Meliaceae)	2	70–80	0.3	0.0	**1:0.0**
***Pseudospondias microcarpa* (Anacardiaceae) ***	2	100–120	0.5 [b]	4.1	1:8.2
Trichilia dregeana (Meliaceae) *	2	70	0.3	0.3	1:1.0
Funtumia africana (Apocynaceae)	1	70	0.1	0.0	**1:0.0**
Khaya anthotheca (Meliaceae)	1	70	0.1	0.0	**1:0.0**
Maesopsis eminii (Rhamnaceae) *	1	70	0.1	0.0	**1:0.0**
***Parkia filicoidea* (Fabaceae) ***	1	60	0.1	0.8	1:8.0
Pycnanthus angolensis (Myristicaceae) *	1	40	0.0	0.0	–
***Zanha golungensis* (Sapindaceae) ***	1	130	0.1	0.3	1:3.0
Unidentified sp.	2	60–70	–	–	–
Total:	98	30–130	11.2	17.3	1:1.5

[a] One or more individuals of the following low-density species were logged for timber during this study but stumps were not recorded along transects: *Cordia millenii*, *Milicia excelsa* and the figs *Ficus mucuso*, *F. ovata* and *F. variifolia*; [b] The density of large *Pseudospondias microcarpa* stumps includes two unlogged specimens that were cut to free felled timber trees caught in their crowns.

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