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Woody Species Alpha-diversity and Species Abundance Distributions in an African Semi-deciduous Tropical Rain Forest

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ABSTRACT

Understanding plant species diversity patterns and distributions is critical for conserving and sustainably managing tropical rain forests of high conservation value. We analyzed the alpha-diversity, species abundance distributions, and relative ecological importance of woody species in the Budongo Forest, a remnant forest of the Albertine Rift in Uganda. In 32 0.5-ha plots, we recorded 269 species in 171 genera and 51 families with stems of ≥2.0 cm in diameter at breast height (dbh). There were 53 more species with stems of ≥2.0 cm dbh than with stems of ≥10 cm dbh, of which 33 were treelets and 20 were multi-stemmed shrubs. For both minimum stem diameter cut-offs (*i.e.*, ≥2 cm dbh vs. ≥10 cm dbh), the Fabaceae, Euphorbiaceae, Ulmaceae, and Meliaceae families and the species *Cynometra alexandri, Lasiodiscus mildbraedii,* and *Celtis mildbraedii* had the highest relative ecological importance. The relative ecological importance of some species and families changed greatly with the minimum stem diameter measured. Alpha-diversity, species richness, and species abundance distributions varied across historical management practice types, forest community types, and as a function of minimum stem diameter. Species richness and Shannon–Weiner diversity index were greater for species with stems of ≥2.0 cm dbh than of ≥10 cm dbh. The decrease in species evenness with an increasing number of plots was accompanied by an increase in species richness for trees of both minimum diameters. This forest is characterized by a small number of abundant species and a relatively large proportion of infrequent species, many of which are sparsely distributed and with restricted habitats. We recommend lowering the minimum stem diameter measured for woody species diversity studies in tropical forests from 10 cm dbh to 2 cm dbh to include a larger proportion of the species pool.

Key words: Albertine Rift Eco-region; alpha-diversity; familial importance value; minimum stem diameter; rarefaction diversity, relative ecological importance; SHE analysis.

TROPICAL RAIN FORESTS ARE THE MOST SPECIES RICH TERRESTRIAL BIOME OF THE WORLD, yet they are threatened with degradation and biodiversity loss. The ecological and environmental importance of these forests necessitates their conservation and sustainable management, which to a great extent depend on quantitative information on species distribution patterns and diversity (Buzas & Hayek 1996). In tropical rain forests, plant species richness and diversity are major criteria in nature conservation and ecology (*e.g.*, Ricotta *et al.* 2002). Because of increased anthropogenic disturbances, biodiversity loss, and climate change, reliable information about plant species diversity patterns, and distributions at the landscape scale is critical for protecting and conserving the remaining species (*e.g.*, Cadotte *et al.* 2002, Castillo-Campos *et al.* 2008).

Despite considerable research directed at characterizing tree alpha-diversity patterns in most tropical rain forests (Sheil 1999, ter Steege *et al.* 2001, Eilu *et al.* 2004, Parmentier *et al.* 2011), there is still much to understand. For example, only a few studies (*e.g.*, Galeano *et al.* 1998, Killeen *et al.* 1998, Pitman *et al.* 2001) have included trees with a minimum stem diameter at breast height (dbh) of <10 cm. These studies were conducted outside Africa and show that diversity is substantially enriched by treelets. Treelets have been classified as woody plants with stems of ≤5 cm dbh excluding palms, lianas, and hemi-epiphytes (Galeano *et al.* 1998), or as woody sub-canopy plants with stems of 5–10 cm dbh (Valencia *et al.* 1994). Treelets may also influence forest composition and structure (Pitman *et al.* 2001).

Although several studies have examined woody plant diversity, it remains to be determined how diversity is affected by minimum stem diameter, and if richness and evenness affect woody species diversity (H′) in an African semi-deciduous tropical rain forest like Budongo Forest Reserve (BFR) in Uganda. In addition, the relative ecological importance of plant families or species (based on importance value indices) and their relative contribution to the entire forest plant community composition has not been determined. Tree diversity is fundamental to tropical forest biodiversity, as trees support many forest species (Huston 1994). Thus, previous plant diversity studies in BFR focused on tree diversity and species turnover (*e.g.,* Plumptre 1996, Sheil 1996, Eilu *et al.* 2004), plant regeneration (*e.g.*, Mwavu & Witkowski 2009a,b), and providing broad vegetation classifications and descriptions (*e.g.,* Eggeling

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1947, Synnott 1985, Mwavu *et al.* 2008) based on trees of ≥10 cm dbh. However, in BFR several predominant woody species such as *Coffea euginioides* S. Moore and *Rinorea oblongiflora* C. Marquand flower at a diameter of <2.5 cm dbh, while others rarely attain a dbh of ≥10 cm at maturity (Mwavu *et al.* 2008).

In this study, we examined the alpha-diversity and species abundance distributions of woody plants (*i.e.*, trees, treelets, and shrubs excluding lianas) in BFR, and investigated the nature of species diversity in relation to the minimum stem diameter (i.e., ≥2 cm vs ≥10 cm dbh), forest community types (as determined by Mwavu *et al.* 2008), and historical management practices (HMPs). We explored the following questions: (1) Does species diversity differ for the ≥2.0 cm (this includes all diameters above 2 cm) and ≥10 cm stem dbh data? (2) If so, does the traditional use of only trees of ≥10 cm dbh underestimate the diversity? (3) Which woody plant families are the most species rich and which of these families are of high relative ecological importance? (4) What species abundance distribution types do the forest plant communities exhibit?

METHODS

STUDY AREA.—The study was conducted in Budongo Forest Reserve (BFR), a flagship reserve for primate conservation at the top of the escarpment east of Lake Albert (Howard 1991, Mwavu & Witkowski 2009a) in north-western Uganda. BFR has an area of 793 km^2 and lies between 1°37′ and 2°03′ N and 31°22′ and 31°45′ E (Fig. S1). The altitudinal range is 700–1270 m with a mean of 1050 m. BFR is a remnant forest of the Albertine Rift Eco-region, which consists of several forests and is believed to be one of Africa's most species rich and highly endemic regions, making it a region of global conservation value (Plumptre *et al.* 2007).

The general ecology, environment, management, and history of BFR have been described elsewhere and this area is well known for the conservation of chimpanzees (see Eggeling 1947, Synnott 1985, Howard 1991). Most of the forest's compartments have been treated with arboricides and logged at least once, except for a few that have been set aside as nature reserves since 1932. During the 1950s and early 1960s, the arboricides trichlorophenoxyacetic (2,4,5, T-D) and dichlorophenoxyacetic acid (2,4-D) were mixed with diesel (1:2) and applied to trees that were assumed to be of no commercial value (so called 'weed' species) to open up the canopy, reduce the extent of monodominant forest stands, and encourage the spread of mixed forest (Phlip 1964). This treatment ceased in the 1970s, when more tree species became marketable and it became difficult to import chemicals (Synnott 1985). This forest is broadly classified as a mid-altitude, semi-deciduous moist tropical rain forest, because several of the dominant species (*e.g., Celtis* spp., *Ficus* spp., *Maesopsis eminii* Engl. etc.) are at least briefly deciduous (Eggeling 1947, Sheil 1997). A more recent numerical classification (Mwavu *et al.* 2008) revealed four forest community types: (1) *Pseudospondias microcarpa* swamp forest; (2) *Funtumia elastica-Pouteria altissima* secondary dry forest; (3) *Celtis mildbraedii-Lasiodiscus mildbraedii* mixed forest; and (4) *Cynometra alexandri-Rinorea ilicifolia* forest. The soil of the whole forest area is well weathered, slopes are mostly gradual, and the intervening ridges rounded. The valley bottoms have streams, many of which trickle through rattan (*Calamus deerratus* Mann & Wendl.) swamps with no apparent flow during the dry months (Eggeling 1947).

SAMPLING AND DATA COLLECTION.—In BFR, there are three general historical management practice (HMP) types: logging and arboricide treatment, logging without arboricide treatment (hereafter 'logged only'), and nature reserve. These practices formed the basis for stratifying the forest and choosing sites for vegetation sampling. An attempt was made to capture the main forest types (as described by Mwavu *et al.* 2008) and the environmental variations as much as possible within the sampled compartments. We sampled vegetation of the three HMP types using 50 m × 100 m (0.5 ha) plots consisting of five (50 m × 20 m; 0.1 ha) contiguous sub-plots established and laid along transects following a topographic gradient. Along each transect, at least three 0.5-ha plots were laid following topographic position categories (*i.e.*, lower slope, mid-slope, upper slope, flat/ridgetop), and oriented at right angles to this gradient, with the long side of the plot parallel to the contour. A total of 32 plots, six in the nature reserve, 19 in the logged and arboricide-treated area, and seven in the logged only areas, were laid. The variation in the number of plots per HMP type is related to their corresponding size in the BFR.

We systematically counted stems, measured stem diameter at breast height (dbh; 1.3 m aboveground), and identified all treelets, trees, and shrubs (hereafter referred to as woody plants) with ≥2.0 cm dbh and blazed each stem to prevent accidental re-measurement. We define treelets as woody species with a stem diameter of 2.0–10 cm at breast height, excluding shrubs, lianas, palms, and hemi-epiphytes. We classify a shrub as a woody plant of relatively low height having several perennial stems (*i.e.*, none dominant) arising from the base and lacking a single trunk, with some species (*e.g., Alchornea laxiflora*) attaining a stem dbh of ≥10 cm. We measured the diameter of the stem at breast height, unless there were irregularities at this height or trees were shorter than 1.3 m. For individuals with buttresses or other stem irregularities at breast height, stem diameter was measured immediately above the irregularity. For each multi-stemmed individual of a shrub, we counted the number of stems, measured the diameter of three 'average' stems and calculated the mean dbh and mean basal area of a single stem. The latter value was multiplied by the number of stems to calculate the basal area of the individual. We identified species in the field using identification guides, primarily Flora of Tropical East Africa (FTEA; Polhill 1952 *et seq.*), and with the help of a botanist familiar with the flora. For species that could not be confidently identified in the field, vegetative structures and, if available, flowering or fruiting samples, were collected and pressed, and vouchers were subsequently identified at the Botany Department Herbarium (MHU), Makerere University, Kampala, Uganda.

DATA ANALYSIS.—The total number of species recorded in the sampling plots (species richness), rarefaction (measure of diversity; Smith & Grassle 1977), Shannon–Wiener Index (H′), Fisher's alpha (α) diversity (Fisher *et al.* 1943), and SHE analysis (Hayek & Buzas 1998) were used to quantify and characterize species diversity and species abundance distributions of the plant communities. Alpha-diversity indices (*i.e.*, H′ and α) were quantified for both ≥2.0 cm and ≥10 cm dbh data sets at the 0.5-ha scale, using all individuals and species per plot. The Fisher's α-diversity index is relatively insensitive to sample size and performs well with data within forest plots (Condit *et al.* 1998, ter Steege *et al.* 2001) and if the abundance of plants varies considerably among plots (Laurance *et al.* 2001). By contrast, H′ incorporates evenness and, therefore, describes the distribution of individuals among the species in addition to the number of species in a plot (Magurran 2004). H′ was calculated using the formula:

$$H' = -\sum_{i=1}^{S}(p_i)(\mathrm{In} p_i)$$

where s = the number of species; p_i = the proportion of individuals or abundance of the i^{th} species.

Rarefaction diversity ($E(S_n)$) was also computed to compare species numbers from different sized samples among the community types. It is used to estimate the number of species expected ($E(S_n)$) to be present in a random sample of individuals taken from any given collection, and provides confidence limits of species richness (Hsieh & Li 1998). $E(S_n)$ is expressed as:

$$E(S_n) = 1 - \frac{(N - N_i)/n}{N/n}$$

where N is the total number of individuals in the sample, and N_i the number of individuals belonging to the i^{th} species (Tokeshi 1999).

Importance value index (IVI), the relative ecological importance of each plant family or species to the entire forest community (Curtis & McIntosh 1951, Wittmann *et al.* 2006), was used to compare the relative contribution of each family and species to forest woody plant composition. For both the ≥2.0 cm and ≥10 cm dbh data, IVI for each species was determined for the total forest community, and calculated as:

$$\mathrm{IVI} = \frac{(\text{Relative density} + \text{Relative basal area})}{2}$$

Family Importance Value (FIV) was calculated as the average of the values of relative dominance (RDo), relative density (RDe), and relative diversity (RDi):

$$\frac{\mathrm{RDo} + \mathrm{RDe} + \mathrm{RDi}}{3},$$

where

$$\mathrm{RDo} = \frac{\text{Basal area of family}}{\text{Total basal area}} \times 100$$

$$\mathrm{RDe} = \frac{\text{Number of individuals in a family}}{\text{Total number of woody individuals}} \times 100$$

$$\mathrm{RDi} = \frac{\text{Number of species in a family}}{\text{Total number of species}} \times 100$$

To characterize species abundance distribution and to decompose diversity, a SHE analysis (Hayek & Buzas 1998) using the equation $H = \ln S + \ln E$ was used, where S is species richness and E is evenness. The values of lnS and lnE were calculated because the pattern of H′, lnS, lnE, and lnE/lnS during the accumulation of individuals is characteristic of the underlying species abundance distributions (Hayek & Buzas 1998, Magurran 2004). The pattern of H′, lnS, lnE, and lnE/lnS in relation to the number of samples was graphically displayed and examined for the specific species abundance distribution (*e.g.,* log series, log normal, broken stick). With the broken stick distribution, both lnS and H′ increase while lnE remains constant; for log normal, lnS and H′ increase while lnE/lnS remains constant; and for the log series lnS increases and lnE decreases while H′ remains constant (*e.g.,* Hayek & Buzas 1998, Magurran 2004).

The richness, alpha-diversity indices, rarefaction, and SHE analysis calculations were performed using the Species Diversity and Richness (SDR)® version IV software (Seaby & Henderson 2006). Differences in species richness and diversity between sample plots, historical management practice types, forest community types, and topographic positions were compared by one-way ANOVA, followed by a Tukey's HSD test for unequal sample sizes. A paired *t*-test was also performed to determine if diversity values for the two stem diameter size data sets were statistically different.

RESULTS

SPECIES COMPOSITION AND RICHNESS.—*Community composition.*—We enumerated 36 468 woody plant stems of ≥2.0 cm dbh, representing 269 species in 171 genera and 51 families, within 32 0.5-ha plots, and for 7390 stems of ≥10 cm dbh, representing 216 of the 269 species (*i.e.*, excluding 53 (19.7%) species in the species pool). The 53 species consisted of 33 treelet and 20 shrub species. The species-accumulation curves for the ≥2.0 cm and ≥10 cm dbh data sets, at both 0.1-ha subplot and 0.5-ha plot sizes, were all approaching an asymptote, showing that species richness was not far from being completely recorded for this forest (Fig. 1). The species-accumulation curves were below the rarefaction curves, suggesting heterogeneity among the samples (*i.e.*, patchiness).

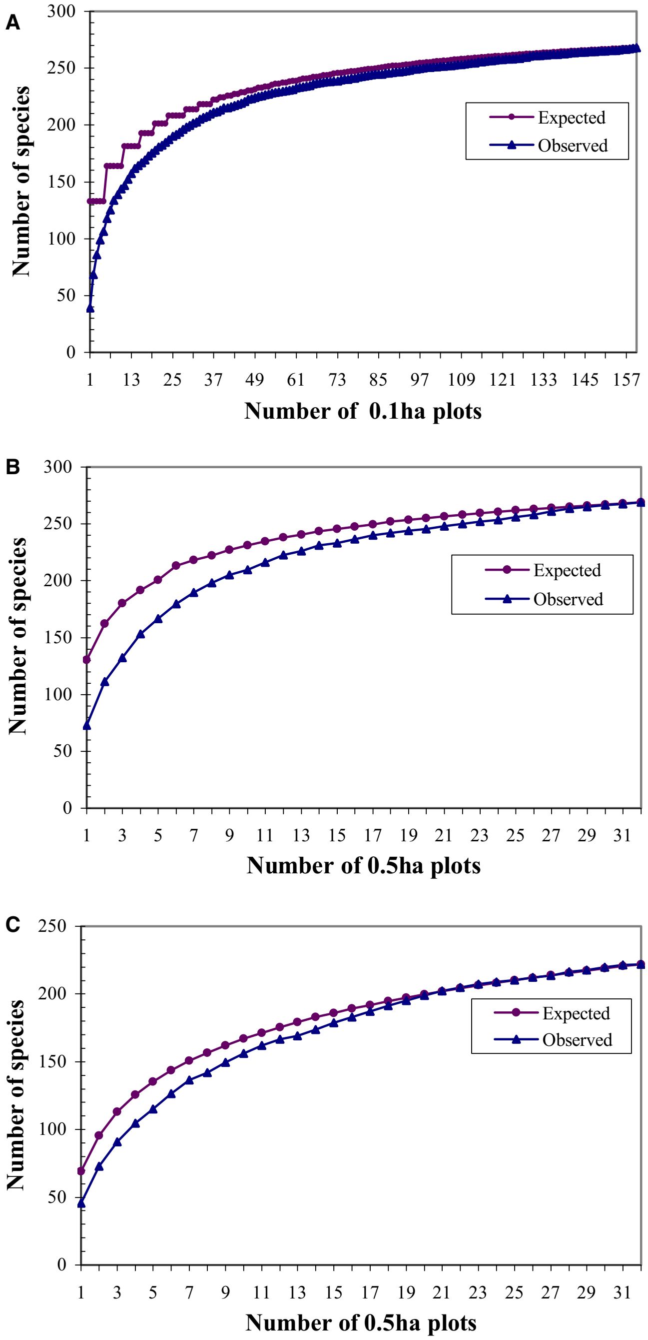

FIGURE 1. Rarefaction (expected) and species-accumulation (observed) curves for woody species. Data are from plants of (A) ≥2.0 cm dbh including values presented for "C", measured in 160 0.1-ha plots and (B) ≥2.0 cm and (C) ≥10 cm dbh, measured in 32 0.5-ha plots in Budongo Forest Reserve, Uganda. The finite version of the rarefaction was used where resampling is done without replacement.

Based on the ≥2.0 cm dbh data, nine families with the highest number of genera were Euphorbiaceae (22 genera), followed by Fabaceae (18), Rubiaceae (16), Rutaceae (8), Sapindiaceae (8), Meliaceae (8), Annonaceae (7), Moraceae (7), and Flacourtiaceae (7). Of the remaining 42 families, 16 were represented by only one genus each. The eight most species rich families were Euphorbiaceae (34 species), Fabaceae (24 species), Rubiaceae (24 species), Moraceae (18), Meliaceae (17), Rutaceae (12), Annonaceae (10), and Flacourtiaceae (10), accounting for 147 (54.6%) woody species. The remaining 43 families had low representation, with 19 having only one species each. On the other hand, based on FIVs, the ecologically most important families were Fabaceae (FIV = 17.5), followed by Eurphobiaceae (16.33), Ulmaceae (8.35), Meliaceae (6.57), Rhamanaceae (6.11), and Apocynaceae (5.49) (Table 1). Fabaceae, Eurphobiaceae, and Rubiaceae had both high generic and species representation and the most species rich genera were *Ficus* (12 species), *Celtis* (5), *Rinorea* (5), and *Albizia* (5). For the ≥10 cm dbh data, the families with the highest FIV (*i.e.*, >6.0%) were Fabaceae, followed by Ulmaceae, Meliaceae, Euphorbiaceae, Moraceae, and Apocynaceae (Table 1). The FIV for these families (except Euphorbiaceae) were higher for the ≥10 cm than for the ≥2.0 cm dbh data. Generally, the two data sets showed a similar suite of families with a high FIV, with the exception of Rubiaceae and Violaceae, which showed greater values (>3.0) for only the ≥2.0 cm dbh data set (Table 1). The family Violaceae was mainly represented by treelets (*e.g.*, *Rinorea ilicifolia*, *Rinorea oblongifolia*, and *Rinorea dentata*) and other species that rarely attain a ≥10 cm dbh (*e.g.*, *Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze and *Rinorea brachypetala*). Similarly, Rubiaceae was represented by a number of treelets (*e.g.*, *Coffea euginioides*, *Coffea spathcalyx,* and *Rothmannia whitfieldi*), and other species with few individuals (mainly 1-9) that barely had a >10 cm dbh. Hence, these families did not exhibit a high FIV.

Based on the ≥2.0 cm dbh data, the nine most highly represented species were *Lasiodiscus mildbraedii* Engl., *Acalypha*

TABLE 1. *Woody plant families with the highest familial importance values (FIV) (i.e., FIV ≥3.0) and stem diameters of ≥2.0 cm and ≥10 cm measured in 32 0.5-ha plots in Budongo Forest Reserve, Uganda. Families are included if FIV is ≥3.0 percent for either minimum stem diameter.*

	FIV (%)	
Family	≥2.0 cm dbh	≥10 cm dbh
Fabaceae	17.50	20.85
Euphorbiaceae	16.33	7.39
Ulmaceae	8.35	11.51
Meliaceae	6.57	8.34
Rhamnaceae	6.11	5.64
Apocynaceae	5.49	6.73
Moraceae	4.98	7.04
Rubiaceae	3.69	2.74*
Violaceae	3.61	1.54*
Sapotaceae	3.04	3.36
Total	75.67%	70.91%

*Values not included in the calculation of Total FIV percent because they are <3.0 percent.

neptunica Muell. Arg*.*, *Acalypha ornata* Hochst. ex A. Rich., *Celtis mildbraedii* Engl*.*, *Senna spectabilis* (DC.) Irwin & Barneby, *Funtumia elastica* (Preuss) Stapf., *Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze, *Thecacoris lucida* (Pax) Hutch., and *Cynometra alexandri* C.H. Wright*,* and these accounted for 20,647 (56.6%) of the individuals in the 32 sample plots. Although these species exhibited both high abundance and high frequency, with the exception of *S. spectabilis*, 101 species were represented by <10 individuals, of which 28 were each represented by a single individual (*i.e.*, singletons). The most ecologically important species (*i.e.*, with high IVIs) were *Cynometra alexandri, Lasiodiscus mildbraedii, Celtis mildbraedii, Senna spectabilis, Acalypha neptunica, Acalypha ornata,* and *Funtumia elastica* (Table 2). The composition of species with the highest IVIs (*i.e.*, IVI ≥1.0%) differed little for the ≥2.0 cm and ≥10 cm dbh data (Table 2). *Cynometra alexandri, Lasiodiscus mildbraedii,* and *Celtis mildbraedii* were the species with the highest IVIs, both in the ≥2.0 cm and ≥10 cm dbh data sets (Table 2), although *Lasiodiscus mildbraedii* and *Celtis mildbraedii* had the second and third highest IVIs, respectively, in the ≥2.0 cm dbh data set, but the third and second highest IVIs in the ≥10 cm dbh. The shrubs *Acalypha neptunica, A. ornata*, and *Thecacoris lucida* had high IVIs for the ≥2.0 cm data set, but very low for the ≥10 cm.

Species richness.—Species richness at the 0.5-ha level varied with topographic position and HMP type, ranging from 24–111 for the ≥2.0 cm dbh data set and from 12–61 for the ≥10 cm dbh (Table 3). Species richness values differed significantly ($t_{(31)}$ = 20.16, $P < 0.001$) between the ≥2.0 cm and ≥10 cm dbh data sets. At the 0.5-ha level, species richness was highest in plots that were both logged and treated with arboricide, and lowest in those with higher densities of large *Cynometra alexandri* and *Senna spectabilis* trees (data not shown). Lower-slope plots, and those from the "nature reserve" were the most species rich, compared to other plots in the same topographic category (Table 3). Species richness was significantly different among HMPs for both the ≥2.0 cm (ANOVA, $F_{2,29}$ = 16.98, $P < 0.0001$) and ≥10 cm dbh data sets (ANOVA, $F_{2,29}$ = 37.27, $P < 0.0001$). Species richness also varied significantly (ANOVA, $F_{3,28}$ = 13.3, $P < 0.0001$) among forest communities, with the *Pseudospondias microcarpa* swamp forest having the highest value, followed by *Funtumia elastica-Pouteria altissima* and *Lasiodiscus mildbraedii-Khaya anthotheca*, and the *Cynometra alexandri-Rinorea ilicifolia* forest community having the lowest (Table 4). Species richness did not significantly vary among the topographic position groupings for either data set (Table 4).

ALPHA-DIVERSITY AND SPECIES ABUNDANCE DISTRIBUTIONS.—*Alpha-diversity.*—The Fisher's α-diversity values were relatively low, from 4.45–30.59 for the ≥2.0 cm dbh data set, and 3.07–29.7 for the ≥10 cm dbh (Table 3). Using the ≥2.0 cm dbh data resulted in higher Fisher's α-diversity values for 28 of the plots (or 87.5%), compared with the ≥10 cm dbh data. However, some plots with higher α-diversity values did not have higher H' values (Table 3). Fisher's α-diversity was significantly higher for the ≥2.0 cm dbh

TABLE 2. *Species with the highest importance value (IV) (i.e., IV ≥1.0) for woody plants with a stem diameter of ≥2.0 cm and ≥10 cm dbh measured in 32 0.5-ha plots in Budongo Forest Reserve, Uganda. Species are included if IV is ≥1.0 percent for either minimum stem diameter.*

Family	Species	Species IV (%)	
		≥2.0 cm dbh	≥10 cm dbh
Fabaceae	*Cynometra alexandri* C.H. Wright	14.17	16.35
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	7.74	6.67
Ulmaceae	*Celtis mildbraedii* Engl.	6.37	7.48
Fabaceae	*Senna spectabilis* (DC.) Irwin & Barneby	4.89	5.15
Euphorbiaceae	*Acalypha neptunica* Muell. Arg.	4.64	0*
Euphorbiaceae	*Acalypha ornata* Hochst ex. A.	4.12	0*
Apocynaceae	*Funtumia elastica* (Preuss) Stapf	4.09	6.13
Meliaceae	*Khaya anthotheca* (Welw.) C.DC.	2.92	4.26
Violaceae	*Rinorea ardiisiflora* (Welw.ex Oliv.) Ktze.	2.57	1.55
Euphorbiaceae	*Thecacoris lucida (Pax.)* Hutch	2.45	0.34*
Ulmaceae	*Celtis zenkeri* Engl.	2.33	4.18
Euphorbiaceae	*Alchornea laxiflora (Bench)* Pax & K. Hoffm	2.01	1.12
Apocynaceae	*Alstonia boonei* De Wild	1.85	2.32
Anacardiaceae	*Pseudospondias microcarpa* (A. Rich.) Engl.	1.51	2.04
Ulmaceae	*Celtis gomphophylla* Baker	1.32	2.40
Tiliaceae	*Glyphaea brevis* (Spreng.) Manachino	1.12	0.14*
Violaceae	*Rinorea brachypetala* (Turcz.) O. Ktze.	1.1	0.05*
Rhamnaceae	*Maesopsis eminii* Engl.	1.05	1.37
Meliaceae	*Trichilia rubescens* Oliv.	0.96*	1.51
Moraceae	*Trilepisium magadascariense* Dc.	0.78*	1.27
Moraceae	*Myrianthus holstii* Engl.	0.76*	1.23
Sapotaceae	*Pouteria altissima* (A. Chiev.) Aubrev. & Pellegr.	0.92*	1.11
Euphorbiaceae	*Croton macrostachyus* Hochst. Ex Del.	0.62*	1.03
Capparidaceae	*Maerua duchesnei* (De Wild.) F. White	0.62*	1.00
Moraceae	*Antiaris toxicaria* (Pers.) Lesch.	0.71*	1.00
	Total	66.25%	69.16%

*Values not included in the calculation of Total IV percent because they are <1.0 percent.

TABLE 3. *Tree and shrub species richness (S), and Fisher's alpha (α) and Shannon–Wiener (H′) diversity in 32 0.5-ha plots for the (i) ≥2.0 cm dbh and (ii) ≥10 cm dbh stem diameter data from Budongo Forest Reserve, Uganda. Sample plots are arranged by sample for the three categories of historical management practice, topography of plots, and forest community types. A: Pseudospondias microcarpa swamp; B: Funtumia elastica-Pouteria altissima, C: Lasiodiscus mildbraedii-Khaya anthotheca, and D: Cynometra alexandri-Rinorea ilicifolia Forest.*

				≥2.0 cm dbh data			≥10.0 cm dbh data		
Management practice	Sample plot	Forest community type	Topography of plots	S	α	H′	S	α	H′
Logging and arboricide treatment	1	A	Lower slope	106	30.59[†]	3.49	61[†]	29.27[†]	3.51[†]
	2	C	Mid slope	111[†]	29.90	3.65[†]	55	21.55	3.22
	3	C	Upper slope	71	15.85	2.97	42	14.92	2.87
	4	C	Ridgetop	64	14.56	2.75	46	17.58	3.13
	5	A	Lower slope	94	25.92	3.61	45	22.71	3.33
	6	C	Mid slope	98	23.15	3.14	54	18.75	3.30
	7	C	Upper slope	77	16.27	2.85	45	16.24	3.09
	8	C	Ridgetop	72	15.12	2.81	43	14.02	2.88
	15	B	Upper slope	85	20.59	2.75	40	14.14	2.53
	17	B	Upper slope	71	19.34	2.72	42	14.03	2.69
	18	B	Upper slope	71	14.66	2.00[†]	38	11.65	2.14
	19	A	Lower slope	83	21.41	3.00	49	21.61	3.23
	20	C	Mid slope	91	23.68	3.53	56	23.51	3.37
	21	C	Upper slope	92	24.71	3.38	55	24.89	3.27
	22	C	Ridgetop	76	18.23	3.24	46	15.44	3.11
	29	A	Lower slope	78	22.59	3.61	46	20.65	3.22
	30	B	Mid slope	83	22.35	3.47	50	17.81	3.26
	31	B	Upper slope	92	23.40	3.77	52	17.35	3.19
	32	B	Ridgetop	94	24.77	3.51	57	22.64	3.38
Nature Reserve	9	A	Lower slope	87	27.21	3.53	42	16.85	2.99
	10	C	Mid slope	77	18.71	2.74	43	13.51	2.35
	11	C	Upper slope	67	14.97	2.91	34	10.19	2.50
	12	A	Lower slope	103	28.43	3.71	48	19.85	3.18
	13	C	Mid slope	66	15.36	2.80	33	9.72	2.30
	14	C	Upper slope	59	13.26	2.59	24	6.08	1.98
Logging	16	B	Mid slope	67	17.83	2.79	22	7.08	1.61[†]
	23[*]	D	Lower slope	47	10.02	2.34	18	4.90	2.00
	24[*]	D	Mid slope	24[†]	4.45[†]	2.14	12[†]	3.07[†]	1.83
	25[*]	D	Upper slope	56	11.61	3.05	31	9.70	2.81
	26[*]	D	Lower slope	50	10.50	2.37	29	8.89	2.18
	27[*]	D	Mid slope	59	13.14	2.48	26	10.07	2.50
	28[*]	D	Upper slope	43	10.80	2.82	17	5.26	2.23
	Overall	$\bar{X}$		75.44	18.86	3.02	40.66	15.12	2.79
		SD		19.51	6.40	0.48	12.77	6.50	0.53

[*] Indicates *Cynometra alexandri*-dominated plots.

[†] Indicates the highest and lowest species number and diversity values.

data than for the ≥10 cm dbh ($P = 0.0239$), while the H′ was not ($P = 0.075$).

Using the ≥2.0 cm dbh data, the plots within previously logged and arboricide-treated compartments had the highest α and H′ diversity values, followed by those from the nature reserve, and lastly the *Cynometra alexandri*-dominated areas (Community D). Both the α and H′ values were significantly higher for the previously logged and arboricide-treated areas than for the nature reserve and logged only areas, and values were higher for the nature reserve than for the logged only areas, for both the ≥2.0 cm (α: $P = 0.00032$; H′: $P = 0.0134$), and ≥10 cm (α: $P < 0.0001$; H′: $P < 0.0001$) dbh data (Table 4). Forest communities also differed significantly ($P < 0.01$) in α-diversity for both the ≥2.0 cm and ≥10 cm dbh data. Generally, α-diversity was highest in the *Pseudospondias microcarpa* swamp forest, followed by *Funtumia elastica-Pouteria altissima*, *Lasiodiscus mildbraedii-Khaya anthotheca,* and the *Cynometra alexandri-Rinorea ilicifolia* forest community (Table 4). The α-diversity did not significantly vary among

TABLE 4. *Mean ± SE of species richness (S), and Fisher's alpha (α) and Shannon–Wiener (H′) diversity indices calculated separately for sites with different historical management practice, forest community type, and topography using the ≥2.0 cm and ≥10 cm dbh stem diameter data at the 0.5-ha plot scale from Budongo Forest Reserve. The diversity values are the means of the plot values for each site. Species richness and diversity values in the same column under each grouping and dbh size data set accompanied by the same superscript letters do not differ significantly (Tukey,* $P < 0.05$*).*

		≥2.0 cm dbh			≥10.0 cm dbh data		
Grouping	No. of plots	S	α	*H′*	S	α	*H′*
Management practice type							
Logging and arboricide treatment	19	84.68 ± 2.95^{a}	21.43 ± 1.10^{a}	3.17 ± 0.10^{a}	48.53 ± 1.48^{a}	18.88 ± 1.04^{a}	3.09 ± 0.08^{a}
Nature reserve	6	76.50 ± 6.63^{a}	19.66 ± 2.68^{a}	3.05 ± 0.19^{ab}	37.33 ± 3.53^{b}	12.70 ± 2.06^{b}	2.55 ± 0.18^{b}
Logging	7	49.43 ± 5.2^{b}	11.19 ± 1.51^{b}	2.57 ± 0.12^{b}	22.14 ± 2.61^{c}	6.99 ± 1.01^{c}	2.17 ± 0.15^{b}
Forest community type							
Pseudospondias microcarpa swamp (A)	6	91.8 ± 4.56^{c}	26.03 ± 1.43^{c}	3.49 ± 0.10^{c}	48.5 ± 2.69^{c}	21.82 ± 1.70^{c}	3.24 ± 0.07c
Funtumia elastica-Pouteria altissima (B)	7	80.4 ± 4.09^{c}	20.42 ± 1.31^{cd}	3.00 ± 0.23^{cd}	43.0 ± 4.37^{c}	14.96 ± 1.87^{c}	2.69 ± 0.25^{cd}
Lasiodiscus mildbraedii-Khaya anthotheca (C)	13	78.5 ± 4.21^{c}	18.75 ± 1.40^{d}	3.03 ± 0.09^{cd}	44.3 ± 2.68^{c}	15.88 ± 1.52^{c}	2.88 ± 0.12^{c}
Cynometra alexandri-Rinorea ilicifolia (D)	6	46.5 ± 5.09^{d}	10.09 ± 1.21^{e}	2.53 ± 0.14^{d}	22.2 ± 3.09^{d}	6.98 ± 1.20^{d}	2.26 ± 0.14^{d}
Topographic position of plot							
Lower slope	8	81.00 ± 22.18^{e}	22.08 ± 7.87^{e}	3.21 ± 0.57^{e}	42.25 ± 13.18^{e}	18.09 ± 7.82^{g}	2.96 ± 0.55^{h}
Mid slope	9	75.11 ± 25.33^{e}	18.73 ± 7.33^{e}	2.99 ± 0.51^{e}	39.00 ± 16.32^{e}	13.90 ± 6.94^{g}	2.64 ± 0.67^{h}
Upper slope	11	71.27 ± 15.11^{e}	16.86 ± 4.60^{e}	3.04 ± 0.45^{e}	38.18 ± 11.28^{e}	13.13 ± 5.52^{g}	2.67 ± 0.43^{h}
Ridgetop	4	76.50 ± 12.69^{e}	18.17 ± 0.4.69^{e}	3.08 ± 0.36^{e}	48.00 ± 6.16^{e}	17.42 ± 3.78^{g}	3.13 ± 0.20^{h}

the topographic position groupings for either of the data sets (Table 4).

Species abundance distributions.—The SHE analysis also showed greater richness (lnS) and higher H′ diversity for the ≥2.0 cm than ≥10 cm dbh data set (Fig. 2). A graphical presentation of species evenness and richness data showed that decreases in evenness are accompanied by increases in richness for both the ≥2.0 cm and ≥10 cm dbh data sets. The H′ was greater for the ≥2.0 cm data set, suggesting that H′ resulted from greater richness (*i.e.*, a higher lnS curve) rather than evenness (lnE). The cumulative lnE/lnS remained relatively constant for both data sets, indicating that the data are best fitted by a log-normal species abundance distribution. However, the cumulative H′ for both data sets revealed that H′ becomes relatively constant with an increasing number of samples (N), which is characteristic of a log-series distribution. The cumulative lnE decreased for both minimum stem diameters, although only slightly, which is characteristic of both the log-normal and log-series distributions. Thus, these data fit between the log-normal and log-series species abundance distributions.

Widely distributed species (present in ≥30 out of the 32 (93.8%) plots) were *Acalypha neptunica*, *A. ornata*, *Funtumia elastica*, *Celtis zenkeri*, *Chrysophyllum albidum*, *Vepris nobilis,* and *Tapura fischeri*, with only *A. neptunica* present in all plots. By contrast, 171 (63.6%) species were each recorded in <10 of 32 plots (<31.3%), of which 51 were recorded in only one plot. Thus, many of the species are sparsely distributed, with some having restricted habitats. For example, *Pseudospondias microcarpa*, *Alangium chinense* (Lour.) Harms., *Glyphaea brevis*, *Cleistophilis patens* (Benth.) Engl. & Diels, and *Neoboutonia melleri* (Muell. Arg.) Pain were mostly recorded in the lower slope plots, while *Neoboutonia melleri*, *Raphia farinifera* (Gaertn.) Hylander, *Euphorbia teke* Schweinf. ex Pax, and *Leea guineensis* G. Don. were only recorded in the lower slope plots.

DISCUSSION

SPECIES DIVERSITY AND RICHNESS PATTERNS.—Species-accumulation and rarefaction curves for both stem diameters and plot sizes almost reached an asymptote, indicating that most of the species in the forest had been sampled. This suggests that the selected sampling design successfully unveils the woody species diversity of semi-deciduous tropical rain forests like BFR. Fifty-three more species (19.7% of the total species richness) were found in the ≥2.0 cm dbh than in the ≥10 cm dbh data set. Using ≥2.0 cm as the stem diameter cut-off may be more suitable for woody species studies in such forests as many of the species found are generally smaller in dbh than the more commonly used 10 cm dbh. Some studies in tropical rain forests (*e.g.,* Gentry & Dodson 1987, Valencia *et al.* 1994, Galeano *et al.* 1998, Neider *et al.* 2000) have shown that non-tree woody species also exhibit high levels of species richness. Some woody plants with a dbh of much smaller than 10 cm (*i.e.*, treelets) may contribute significantly to the overall species diversity, and influence forest composition and structure (Pitman *et al.*2001), as revealed in this study. Tree species of ≥10.0 cm dbh make up only 15–20 percent of the complete floras of many Neotropical sites (Gentry & Dodson 1987) and scarcely account for 10–30 percent of the total number of species in many Amazonian forests (Duivenvoorden 1994) and 17 percent of the forest flora on Mt. Kilimanjaro (Hemp 2010). Therefore, it is a shortcoming to characterize tropical forests based on woody species with a mini-

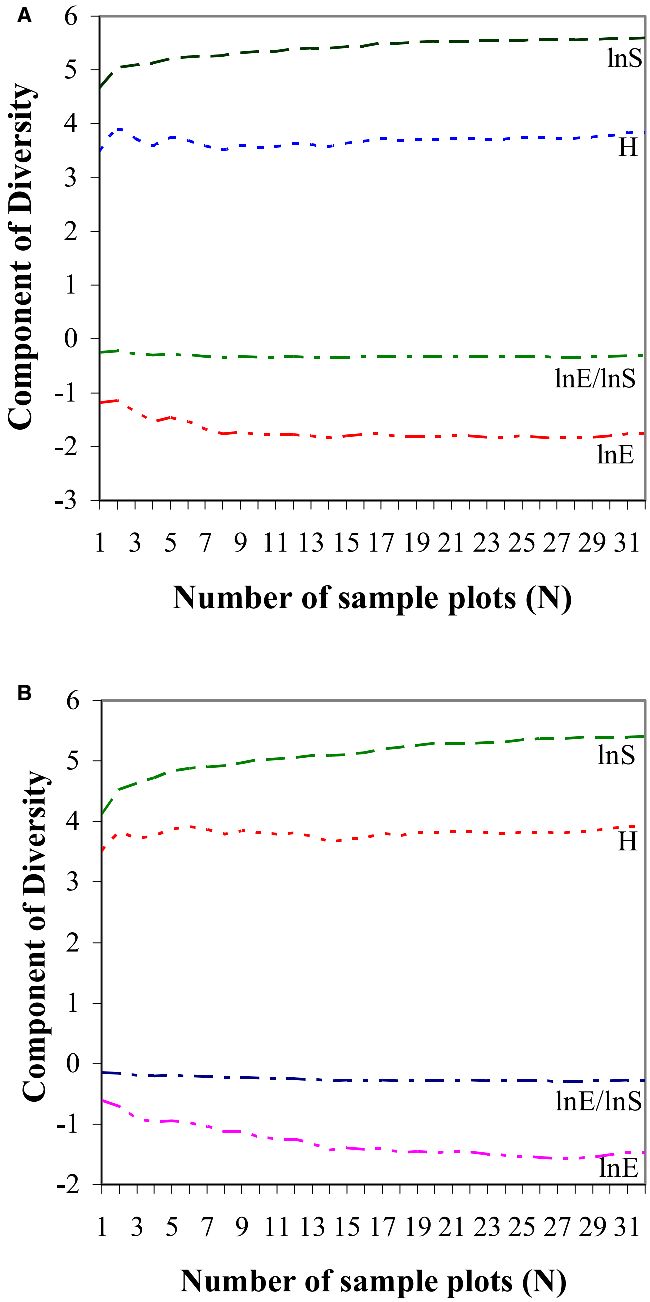

FIGURE 2. Plot of H, lnS, lnE, and lnE/lnS (SHE analysis) with increasing number of sampling plots (N). Plots show data for trees and shrubs of stem diameter (A) ≥2.0 cm and (B) ≥10 cm dbh from 32 0.5-ha plots in Budongo Forest Reserve, Uganda.

mum dbh of 10 cm, particularly in places where treelets, shrubs, and non-tree woody plants might exhibit high levels of species richness (Gentry & Dodson 1987). Inventories attempting to assess woody species α-diversity for conservation goals should consider growth forms other than large trees, as this will ensure that the bulk of species contributing to richness are considered (Galeano *et al.* 1998).

The woody plant species diversity (*i.e.*, 24–122-ha^{-1} for trees with ≥10 cm dbh) in BFR, although higher than that in other Albertine Rift (see Eilu *et al.* 2004) and West African forests (Hall & Swaine 1981, Davies 1987), is lower than that of forests with high rainfall, like those in Amazonia (Gentry 1988, Valencia *et al.* 1994, Duivenvoorden 1995, ter Steege *et al.* 2001, Primack & Corlett 2005). However, comparisons among studies are complicated as different plot sizes were used. Furthermore, these forests may differ in terms of edaphic, climatic, and anthropogenic factors, resource availability, and evolutionary history of the regional species pools that may contribute to the variation in species diversity (Huston 1994, Pärtel *et al.* 2007, Wilson *et al.* 2008).

BFR has diverse forest communities, from relatively species rich *Pseudospondias microcarpa* Swamp forest (Community A) to almost monodominant stands of *Cynometra alexandri—Rinorea ilicifolia* (Community D). The *Pseudospondias microcarpa* swamp forest experiences longer periods of soil moisture availability than the drier upper slope communities, suggesting the influence of water availability. Tree species richness and species diversity decline along a water availability gradient (Segura *et al.* 2003), and increase from ridges to valley bottoms, along a topographic gradient (Tanner 1977). Furthermore, the relatively high degree of variation in species diversity between plots, even for those within the same historical management practice or forest community, highlights the heterogeneous nature of the BFR environment, and the limited species dispersal ability (Hubbell 2001, Tuomisto *et al.* 2003). In BFR, there is variation in edaphic and light gradients and stand age, as well as anthropogenic disturbances and historical management practices that have implications for species diversity and distributions (Mwavu & Witkowski 2008, 2009a,b). Anthropogenic disturbance may cause fragmentation and habitat loss and generally affect forest structure, composition, and diversity (Huston 1994, Williams-Linera & Lorea 2009). Nevertheless, results from the ≥2.0 cm dbh data set indicated that most logged and arboricide-treated sampling plots (>47%; Table 3) had higher species diversity than did nature reserve or logged only plots. Logging and arboricide treatment removes some trees from the canopy, creating gaps that may favor the emergence and existence of pioneer species within the canopy gaps. Thus, disturbance in mature forests with closed canopies may favor increased species diversity. Our results differ from those of Chittabablu and Parthasarathy (2000), who recorded reduced diversity and altered species composition in disturbed, relative to undisturbed, plots in a tropical evergreen forest in Ghats, India. This contrast, however, may be attributed to differences in the time when the disturbance last occurred and the severity of the disturbance experienced. BFR experiences few and patchy anthropogenic disturbances due to the chimpanzee conservation initiatives, regulated logging, and effective law enforcement against illegal activities in the forest. However, not all disturbance agents maintain species diversity in tropical forests, since species differ in the extent of canopy disturbance from which they can successfully regenerate (*e.g.,* Swaine &

Whitmore 1988). For instance, the creation of gaps resulting in patchy canopy coverage and associated parameters may lead to low or high levels of species α, β, and γ diversity (Leach & Givnish 1999), while a closed canopy limits understorey development, leading to a simplified forest structure and lower diversity of plants (Franklin *et al.* 1993). This may explain the low species richness and diversity in the *Cynometra alexandri-Rinorea ilicifolia* forest in BFR, where *Cynometra alexandri* maintains an almost closed canopy throughout the year.

Relative ecological importance.—The relative ecological importance of the most ecologically important families in BFR is attributed mainly to high species richness and abundance of the constituent species. For example, Euphorbiaceae is included among the families with high relative ecological importance because it was the most species rich and the constituent species were frequent, whereas Rhamnaceae was included because of the combined high abundance and frequency of its constituent species. In BFR, like the forests of Peru and Ecuador (Pitman *et al.* 2001), a few common species dominate the tree community, accounting for over 50 percent of individuals.

The BFR shares a suite of woody plant families rich in species and high relative importance values with other lowland Albertine Rift forests and tropical forests in other continents (except Dipterocarpaceae dominance in Asia; Ashton 1988, Bunyavejchewin *et al.* 2003). For example, Fabaceae, Rubiaceae, Euphorbiaceae, Sapotaceae, and Apocynaceae are among the ten most important families in BFR, and are also the most important and diverse families in the dry tropical forests and fragments of Madagascar, Mexico, and Amazonian Ecuador (Valencia *et al.* 1994, Cadotte *et al.* 2002, Williams-Linera & Lorea 2009). Euphorbiaceae, Meliaceae, and Rubiaceae are also among the most species rich families in other Albertine Rift forests of Uganda (Eilu *et al.* 2004) and New Caledonia (Gillespie & Jaffré 2003). The ranking of Fabaceae as second in terms of its high number of genera and species in BFR agrees with findings from the Amazonia lowland primary forests where Fabaceae is the most diverse family (Gentry & Ortiz 1993, Valencia *et al.* 1994).

Species abundance distributions.—The finding that species evenness generally decreased with increasing sample size may reflect changes in species diversity and abundance patterns (Small & McCarthy 2002). The small change in H′ diversity with increasing sample size may be attributed to decreases in evenness that parallel increases in species richness. This suggests that the added species tend to be relatively rare (Small & McCarthy 2002, Magurran 2004). The log-normal species abundance distribution for both minimum stem diameter data sets indicates that some of BFR communities are mature and diverse, with a high proportion of rare species (Hayek & Buzas 1998, Magurran 2004). Although the BFR has been historically disturbed, resulting in a mosaic of forest types at different seral stages, it is still a robust plant community exhibiting a small number of abundant, and a relatively large proportion of rare species (Magurran 2004).

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material.

FIGURE S1. Location and map of Budongo Forest Reserve, Uganda, showing all management compartments.

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