
Spatial variability in the vegetation structure and composition of an East African rain forest

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Abstract

We conducted a study of spatial variation in tree community structure and composition in the Kakamega Forest of western Kenya. We compared the tree communities at two sites, Buyangu and Isecheno, separated by approximately 11 km of contiguous forest. All trees ≥ 15 cm d.b.h. were censused along transects covering 4.95 ha at Buyangu and 4.15 ha at Isecheno. The structure of the forest at the two sites was similar as mean d.b.h. was comparable and stem size class distribution did not differ significantly. However, species richness and stem density were both much higher at Buyangu. The disparity in stem density may be because of the greater abundance at Isecheno of a semi-woody undergrowth species, *Brillantaisia nitens* Lindau, believed to inhibit the establishment of tree seedlings. Floristic composition varied strikingly between sites, with 52% of the species occurring only at one site. Densities of those species present at both sites often differed markedly between sites. Potential sources of these intersite differences in floristic composition include small disparities in rainfall, soil composition, elevation, and temperature as well as past differences in anthropogenic disturbance and in large mammal distribution and abundance. Floristic differences between Buyangu and Isecheno appear to be at least partly responsible for the substantial dietary differences between redtail monkeys (*Cercopithecus ascanius* Audebert) at these sites.

Key words: *Brillantaisia nitens*, *Cercopithecus ascanius*, disturbance, Kakamega Forest, logging, tropical forest

Résumé

Nous avons réalisé une étude de la variation spatiale de la structure et de la composition des communautés d'arbres

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dans la forêt de Kakamega, à l'ouest du Kenya. Nous avons comparé les communautés d'arbres à deux endroits, Buyangu et Isecheno, séparés par ~11 km de forêt contiguë. Tous les arbres de ≥ 15 cm de diamètre à hauteur de poitrine (DBH) étaient recensés le long de transects couvrant 4,95 ha à Buyangu et 4,15 ha à Isecheno. La structure de la forêt était semblable aux deux endroits puisque le DBH était comparable et que les classes de distribution par taille des plants n'étaient pas significativement différentes. Cependant, la richesse en espèces et la densité des troncs étaient beaucoup plus élevées à Buyangu. La disparité de densité des troncs pourrait être due à la plus grande abondance à Isecheno d'une espèce semi-ligneuse de sous-bois, *Brillantaisia nitens* Lindau, dont on croit qu'elle inhibe l'établissement de jeunes plants d'arbres. La composition floristique différait étonnamment entre les sites, 52% des espèces ne se trouvant qu'à un d'eux. La densité des espèces présentes aux deux endroits différait souvent nettement entre les sites. Les sources potentielles de ces différences dans la composition floristique incluent de légères différences de chutes de pluie, de la composition des sols, de l'altitude et de la température, ainsi que des différences anciennes relevant des perturbations anthropogènes et de la distribution et l'abondance des grands mammifères. Les différences floristiques entre Buyangu et Isecheno semblent être au moins en partie responsables des différences substantielles du régime alimentaire des cercopithèques ascagnes (*Cercopithecus ascanius* Audebert) de ces endroits.

Introduction

Trees account for much of the biomass in tropical forest ecosystems and their distribution and abundance profoundly influence the animal communities inhabiting these ecosystems (Davies, 1994; Hart, 2001; Brugiére et al., 2002). Myriad studies of tree community structure

and composition have been conducted throughout the tropics to document and explain the patterns of tree diversity found in the earth's tropical forests (Condit, 1995; Pitman *et al.*, 2001). One outcome of these studies has been the realization that tropical forest tree community structure and composition varies widely not only between forests on different continents (Gentry, 1988a,b; Phillips *et al.*, 1994), but also between forests on the same continent (Terborgh & Andresen, 1998; Ter Steege *et al.*, 2000) and even between different sites within the same forest (Paijmans, 1970; Proctor *et al.*, 1983).

Most studies of intraforest variation in tree structure and composition have compared sites that differ in forest type (e.g. lowland versus montane, undisturbed versus disturbed), and it is therefore not entirely surprising that the identities and densities of tree species generally differ markedly between sites in these studies (Congdon & Herbohn, 1993; Parthasarathy, 1999; Swamy *et al.*, 2000). Comparisons between sites ≥ 5 km apart of similar forest types within the same forest have been less common (Butynski, 1990; Chapman *et al.*, 1997; Pitman *et al.*, 1999). Nevertheless, studies conducted in the Kibale Forest, Uganda suggest that even within the same forest type, considerable spatial heterogeneity in tree community structure and composition can exist (Butynski, 1990; Chapman *et al.*, 1997). For example, in their comparison of four sites at Kibale, Chapman *et al.* (1997) found that densities of many tree species varied widely between sites with certain species among the most abundant at some sites and absent at others. They concluded that the causes of this spatial variability were potentially manifold, ranging from small differences in elevation and rainfall to past differences in habitat alteration by elephants and humans. They also noted that the diets of several primate species differed considerably between sites based at least partly on the abundance of different tree species at these sites (Chapman *et al.*, 1997, 2002a; Chapman, Chapman & Gillespie, 2002b).

In this study, we compared the distribution and density of tree species at two sites, Buyangu and Isecheno, separated by approximately 11 km of continuous forest in the Kakamega Forest, Kenya. We found that differences between the sites are substantial. We discuss the potential ecological and anthropogenic factors that might account for this variation and the implications of this variation for one primate species, *Cercopithecus ascanius*, which has been studied at both sites.

Methods

Study sites

The Kakamega Forest is the easternmost remnant of the Guineo–Congolian rain forest that stretches across much of central and west Africa. Located approximately 40 km NW of Lake Victoria and at elevations ranging from 1400 to 1700 metres above sea level (m.a.s.l.), the Kakamega Forest covers 240 km² though only approximately 100 km² still consists of indigenous forest (Fig. 1). The remaining portion of the reserve consists of plantations, tea fields, and grasslands (Wass, 1995). The indigenous forest has been fragmented into at least two blocks, the largest of which is 86 km² and includes our study sites, Buyangu and Isecheno (Fig. 1; Brooks, Pimm & Oyugi, 1999). Logging occurred in the forest at various intervals from the 1930s to 1982, though most records detailing the exact locations and species targeted for logging are believed to have been destroyed (Tsingalia, 1988).

Much of Buyangu (0°19'N; 34°52'E; elevation approximately 1500 m.a.s.l.) is known to have been logged from 1969 to 1982, with some sections heavily felled and others left relatively undisturbed (Tsingalia, 1988; Kiama & Kiyapi, 2001). The abundance of very large stems (≥ 40 cm d.b.h.) in the central section of Buyangu surveyed in this study relative to other areas suggests that our study area received no more than light selective logging, if any at all. In 1982, Buyangu received protection

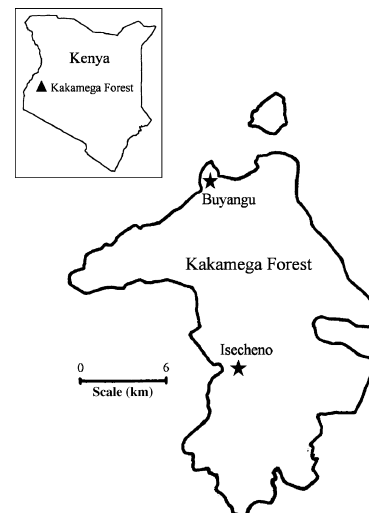


Fig 1 Buyangu and Isecheno study sites in the Kakamega Forest, western Kenya.

via governmental decree and eventually became a National Reserve (Tsingalia, 1988). Today the only disturbance reported to be occurring at the study site is cattle grazing in the glades along its edges (Gathua, 2000).

Located approximately 11 km south of Buyangu, the site that is now Isecheno Nature Reserve (0°14'N; 34°52'E; elevation 1580 m) was selectively logged for very large trees in the 1940s (Cords, 1987) and even today suffers from some illegal exploitation (tree felling for poles, liana cutting for removal of dead firewood, honey harvesting) by local people, particularly on its periphery (Cords & Tsingalia, 1982; Kokwaro, 1988; Tsingalia, 1988; Fashing *et al.*, 2004). However, with the exception of some small tree harvesting believed to have occurred along our vegetation transects, the tree community in our study area at the center of Isecheno appears to have suffered relatively little anthropogenic disturbance over the past two decades (Fashing *et al.*, 2004).

Rainfall and temperature data are available only for Isecheno. Over a 5-year period (1976–81), rainfall averaged 2215 ± 26 mm year⁻¹ with peaks typically occurring from March to August and October to November (Cords, 1987). Average minimum monthly temperatures ranged from 11 to 21°C while average maximum monthly temperatures ranged from 18 to 29°C (Cords, 1987).

Data collection

Data were collected on tree population structure and composition using identical methods at Buyangu and Isecheno in 1998. Tree species identity and GBH were recorded for all trees ≥ 47 cm g.b.h. (15 cm d.b.h.) whose trunks were located within 5 m on either side of the transect. The g.b.h. measurements were then converted to d.b.h. values. Transects consisted of a series of adjacent 25×10 m segments (quadrats) that followed existing trails through the forest. These trails were established by Gathua in 1996 at Buyangu and by the Forest Department several decades earlier at Isecheno (Zimmerman, 1972). At Buyangu, transects were spaced at regular 50 m intervals and began at locations ranging from along the forest edge to as far as 500 m inside the forest. At Isecheno, transects were spaced at irregular 50–135 m intervals and each began on the forest edge and penetrated as far as 700 m into the forest. The distance of the eastern-most from the western-most transect was 600 m at Buyangu and 525 m at Isecheno. A total of 4.95 ha were censused along fourteen transects at Buyangu and 4.15 ha were censused along nine transects at Isecheno. A similar

percentage of quadrats could be classified as 'forest edge' at each site (Buyangu: 13%; Isecheno: 12%).

Data analysis

Tree species nomenclature based on identifications from the two sites was standardized by following the taxonomic scheme of Beentje (1994). The EstimateS freeware program (Colwell, 2000) was used to create species-area curves for both sites. Data points for these curves were generated by determining the means and standard deviations of 100 randomizations of the pooling order of quadrats (Colwell, 2000). Relative density was calculated as the density of one species as a percent of total tree density. Shannon–Wiener diversity index (H'_s) and evenness index (E) were calculated as in Stiling (2002).

Degree of similarity between Buyangu and Isecheno was assessed in two ways. First, Sorensen's Index of community similarity (C_s) was calculated as in Stiling (2002). Secondly, species-specific overlap in relative density was calculated by taking the lower of the two relative densities for each species at Buyangu and Isecheno and summing them.

Because data were often not normally distributed, all statistical tests in this paper are nonparametric and two tailed. Significance level was set at $P \leq 0.05$ for all tests.

Results

Species-area curves for both Buyangu and Isecheno are approaching asymptotes, suggesting that both censuses detected most of the species in the study areas (Fig. 2). Number of species recorded differed considerably between sites with 69 species recorded at Buyangu and 58 species at Isecheno (Table 1). The trajectories of the two species-area curves clearly show that most of the intersite difference in species richness cannot be attributed to the fact that a larger area was sampled at Buyangu (Fig. 2). In fact, when the mean number of species detected from 100 resamplings of randomly chosen quadrats totalling 4.15 ha at each site is calculated, Buyangu still contains 67 species and Isecheno only 58 species. Despite this disparity in species richness, when again controlling for area sampled, species diversity was virtually identical at the two sites (Buyangu: $H' = 3.38$; Isecheno: $H' = 3.39$). Species evenness was slightly lower at Buyangu ($E = 0.80$) than at Isecheno ($E = 0.84$).

The size class distributions of stems at both sites exhibit the roughly negative exponential, or 'inverse J', curves typical of 'natural' rain forests (Fig. 3; Richards, 1996). When trees

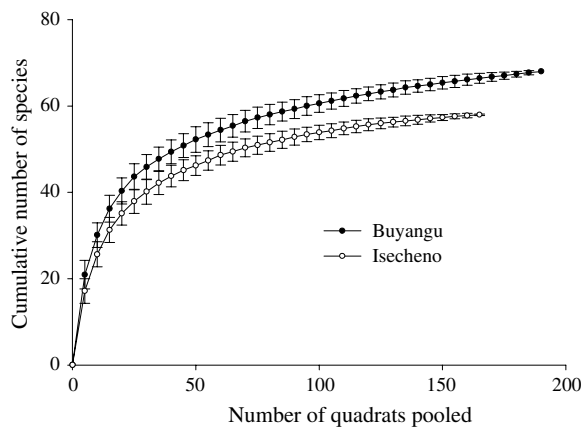


Fig 2 Cumulative species–area relationships for the study transects at Buyangu and Isecheno. Data points plotted on the graph are the mean values resulting from 100 randomizations of the pooling order of quadrats. The corresponding standard deviations are plotted as error bars. To improve legibility, only every fifth data point is plotted. Each quadrat represents an area of 0.025 ha.

are divided into 10 cm d.b.h. categories (15–24, 25–34, 35–44, 45–54, 55–64, 65–74, 75–84, 85–94, 95–104 and 105+ cm), size class distributions do not differ between the two study areas (Kolmogorov–Smirnov test: $\chi^2 = 1.85$, $P > 0.30$). Furthermore, mean d.b.h. is similar at Buyangu (38.5 ± 0.7) and Isecheno (39.8 ± 0.9).

Stem density was markedly higher at Buyangu ($353.9 \text{ stems ha}^{-1}$) than at Isecheno ($271.6 \text{ stems ha}^{-1}$). This pattern of Buyangu featuring a greater abundance of stems holds for all 10 cm d.b.h. size class categories examined in this study. When 4.15 ha of 0.025-ha quadrats are selected at random from each site, stem density per quadrat is significantly higher at Buyangu than at Isecheno (Wilcoxon signed ranks test: $Z = -5.67$, $P < 0.0001$).

Forty-five of the 86 species (52%) described in this study were found at one site but not the other (Fig. 4). Forty-one percent ($n = 28$) of the species that were detected at Buyangu were not detected at Isecheno, while 29% ($n = 17$) of the species identified at Isecheno were not identified at Buyangu. Similarity in species composition between the two sites as measured by Sorensen's Index is 66.7%. Similarity between the two sites as measured by species-specific overlap in relative density is 61.2%. Several tree species are among the most abundant at one site, but rare or absent at the other (Fig. 4). Most striking is *Strychnos usambarensis* Gilg which is the second most common tree species at Buyangu but is represented by only one stem at Isecheno. Other species that are among the

fifteen most abundant at Buyangu but whose densities are $\geq 35\%$ lower at Isecheno are *Celtis gomphophylla* Bak., *Polyscias fulva* (Hiern) Harms, *Ficus sur* Forssk., *Bridelia micrantha* (Hochst.) Baill., *Diospyros abyssinica* (Hiern) F. White, *Markhamia lutea* (Benth.) K. Schum., and *Heinsenia diervillioides* K. Schum. Species that are among the fifteen most abundant at Isecheno but whose densities are $\geq 35\%$ lower at Buyangu are *Ficus exasperata* Vahl, *Teclea nobilis* Del., *Cordia africana* Lam., *Albizia gummifera* (JF Gmel.) C.A. Sm., and *Bequaertiodendron oblanceolatum* (S. Moore) Heine & J.H. Hemsl.

Discussion

Our comparison of two sites at Kakamega, Buyangu and Isecheno, separated by approximately 11 km of contiguous forest, revealed that there are several similarities and many differences between their tree communities (Table 2). Some of these differences between sites are difficult to explain. For example, although the forest at Isecheno is of a similar overall size class structure to the forest at Buyangu, the forest at Isecheno contains a significantly lower density of trees. The hypothesis that recent anthropogenic disturbance at Isecheno accounts for this stem density disparity between sites is not supported by the available evidence. While humans do appear to have harvested some trees of the smallest stem size class along the transects at central Isecheno in recent years (Fashing *et al.*, 2004), this limited recent exploitation of small trees cannot explain why Buyangu has higher stem densities at all 10 cm d.b.h. size classes. For intersite differences in stem density to have arisen among trees of all size categories, a factor operating over the long-term is likely to be responsible.

A more plausible hypothesis for the tree stem density disparity between sites is that tree seedling survival has long been lower at Isecheno where there is a superabundance of *Brillantaisia nitens* (Acanthaceae), a light-gap-invading semi-woody undergrowth species that probably became common at Isecheno after the selective logging of the 1940s or some other long ago disturbance event. Though quantitative data on undergrowth species density at Kakamega are not available, it is readily apparent to scientists who have visited both sites that *B. nitens* is far less abundant at Buyangu (M. Cords, pers. comm.). The notion that *B. nitens* may be responsible for the lower tree density at Isecheno is supported by long-term research at Kibale Forest, Uganda where Struhsaker (1997) noted that once *B. nitens* and other fast-growing monocarpic semi-woody species invade an

Table 1 Tree density (stems, ha⁻¹), relative density (%), mean d.b.h. (cm, for trees ≥15 cm d.b.h.), and the standard error of d.b.h. for two sites in Kakamega Forest

Species (Family)	Buyangu				Isecheno			
	Density	Rel. density	d.b.h.	SE	Density	Rel. density	d.b.h.	SE
<i>Acacia abyssinica</i> Benth. (Mimosaceae)	2.0	0.6	41.7	3.0	–	–	–	–
<i>Alangium chinense</i> (Lour.) Harms (Alangiaceae)	0.4	0.1	17.5	2.5	–	–	–	–
<i>Albizia gummifera</i> (J.F. Gmel.) C.A. Sm. (Mimosaceae)	1.0	0.3	*	*	6.7	2.5	52.3	5.4
<i>Albizia</i> sp. (Mimosaceae)	0.6	0.2	*	*	–	–	–	–
<i>Aningeria altissima</i> (A. Chév.) Aubrév. & Pellegr. (Sapotaceae)	4.0	1.1	69.9	9.3	6.0	2.2	47.0	6.6
<i>Antiaris toxicaria</i> (Pers.) Lesch. (Moraceae)	31.9	9.0	39.0	1.9	29.6	10.9	35.3	1.6
<i>Bequaertiodendron oblancoatum</i> (S. Moore) Heine & J.H. Hemsl. (Sapotaceae)	0.6	0.2	22.7	2.4	6.5	2.4	22.6	1.7
<i>Bersama abyssinica</i> Fres. (Melianthaceae)	–	–	–	–	1.0	0.4	23.3	2.7
<i>Bischofia javanica</i> Blume (Euphorbiaceae)	–	–	–	–	2.2	0.8	32.9	4.4
<i>Blighia unijugata</i> Bak. (Sapindaceae)	6.9	1.9	38.7	4.5	6.3	2.3	25.8	2.2
<i>Bridelia micrantha</i> (Hochst.) Baill. (Euphorbiaceae)	10.9	3.1	28.2	1.5	2.2	0.8	48.2	8.0
<i>Canthium keniense</i> Bullock (Rubiaceae)	–	–	–	–	0.7	0.3	21.3	2.7
<i>Casaeria battiscombei</i> R.E. Fries (Flacourtiaceae)	1.2	0.3	34.2	12.4	0.7	0.3	18.7	2.2
<i>Cassipourea ruwensorensis</i> (Engl.) Alston (Rhizophoraceae)	3.4	1.0	19.6	0.9	2.2	0.8	29.8	6.0
<i>Celtis africana</i> Burm.f. (Ulmaceae)	13.3	3.8	42.6	3.1	15.9	5.9	46.6	2.6
<i>Celtis gomphophylla</i> Bak. (Ulmaceae)	26.9	7.6	32.7	1.6	14.5	5.3	23.6	1.3
<i>Celtis mildbraedii</i> Engl. (Ulmaceae)	6.5	1.8	30.2	3.6	–	–	–	–
<i>Chaetacme aristata</i> Planch. (Ulmaceae)	3.6	1.0	19.0	0.8	3.9	1.4	25.9	2.1
<i>Chrysophyllum albidum</i> G. Don (Sapotaceae)	1.2	0.3	92.0	23.6	0.7	0.3	54.3	20.3
<i>Cordia africana</i> Lam. (Boraginaceae)	1.0	0.3	20.6	1.5	7.0	2.6	30.5	2.1
<i>Cordia millenii</i> Baker (Boraginaceae)	0.2	0.1	41.0	–	–	–	–	–
<i>Craibia brownii</i> Dunn (Papilionaceae)	2.0	0.6	24.7	1.6	0.2	0.1	29.0	–
<i>Croton macrostachyus</i> Del. (Euphorbiaceae)	1.2	0.3	32.7	5.1	–	–	–	–
<i>Croton megalocarpus</i> Hutch. (Euphorbiaceae)	10.9	3.1	34.3	2.3	14.5	5.3	54.6	2.8
<i>Croton sylvaticus</i> Hochst. (Euphorbiaceae)	7.7	2.2	39.4	3.1	6.7	2.5	39.2	2.5
<i>Cupressus</i> sp. (Cupressaceae)	–	–	–	–	1.0	0.4	19.8	2.0
<i>Diospyros abyssinica</i> (Hiern) F. White (Ebenaceae)	10.3	2.9	49.8	7.2	2.4	0.9	35.3	4.2
<i>Dovyalis macrocalyx</i> (A. Rich.) Warb. (Flacourtiaceae)	–	–	–	–	0.2	0.1	18.0	–
<i>Ehretia cymosa</i> Thonn. (Boraginaceae)	–	–	–	–	0.7	0.3	18.3	2.3
<i>Entada abyssinica</i> A. Rich. (Mimosaceae)	0.2	0.1	29.0	–	–	–	–	–
<i>Erythrina abyssinica</i> DC (Papilionaceae)	0.4	0.1	25.0	2.0	–	–	–	–
<i>Fagaropsis angolensis</i> (Engl.) Dale (Rutaceae)	0.2	0.1	31.0	–	0.5	0.2	23.0	7.0
<i>Ficus</i> sp. (Moraceae)	0.2	0.1	15.0	–	–	–	–	–
<i>Ficus cyathistipula</i> Warb. (Moraceae)	0.2	0.1	33.0	–	–	–	–	–
<i>Ficus exasperata</i> Vahl (Moraceae)	5.9	1.7	36.0	4.0	21.0	7.7	47.6	5.4
<i>Ficus lutea</i> Vahl (Moraceae)	2.0	0.6	71.9	25.3	0.2	0.1	23.0	–
<i>Ficus natalensis</i> Hochst. (Moraceae)	–	–	–	–	0.2	0.1	207.0	–
<i>Ficus sansibarica</i> Warb. (Moraceae)	0.8	0.2	135.5	17.2	–	–	–	–
<i>Ficus sur</i> Forssk. (Moraceae)	11.3	3.2	41.0	4.7	7.0	2.6	35.5	5.2
<i>Ficus sycomorus</i> L. (Moraceae)	0.4	0.1	45.0	5.0	–	–	–	–
<i>Ficus thonningii</i> Bl. (Moraceae)	1.6	0.5	123.3	23.0	1.9	0.7	136.3	29.5
<i>Ficus vallis-choudae</i> Del. (Moraceae)	0.8	0.2	101.0	42.5	–	–	–	–
<i>Funtumia africana</i> (Benth.) Stapf (Apocynaceae)	37.4	10.6	34.6	1.0	25.8	9.5	38.5	1.5
<i>Harungana madagascariensis</i> Poir. (Guttiferae)	4.6	1.3	26.5	1.5	1.7	0.6	32.7	3.6
<i>Heinsenia diervillioides</i> K. Schum. (Rubiaceae)	7.5	2.1	17.7	0.4	–	–	–	–

Table 1 Continued

Species (Family)	Buyangu				Isecheno			
	Density	Rel. density	d.b.h.	SE	Density	Rel. density	d.b.h.	SE
<i>Khaya anthotheca</i> C.DC. (Meliaceae)	0.2	0.1	18.0	–	–	–	–	–
<i>Kigelia moosa</i> Sprague (Bignoniaceae)	1.0	0.3	22.2	3.0	0.5	0.2	17.0	2.0
<i>Lepidotrichilia volkensii</i> (Gurke) Leroy (Meliaceae)	0.4	0.1	20.5	2.5	–	–	–	–
<i>Lepisanthes senegalensis</i> (Poir.) Leenh. (Sapindaceae)	1.8	0.5	42.1	4.0	–	–	–	–
<i>Maesa lanceolata</i> Forssk. (Myrsinaceae)	3.2	0.9	18.3	0.8	0.2	0.1	23.0	–
<i>Maesopsis eminii</i> Engl. (Rhamnaceae)	–	–	–	–	1.0	0.4	44.0	9.3
<i>Manilkara butugi</i> Chiov. (Sapotaceae)	3.2	0.9	53.8	5.2	2.2	0.8	42.1	5.7
<i>Margaritaria discoidea</i> (Baill.) Webster (Euphorbiaceae)	–	–	–	–	1.7	0.6	39.3	7.4
<i>Markhamia lutea</i> (Benth.) K. Schum. (Bignoniaceae)	9.9	2.8	43.8	4.3	3.9	1.4	27.3	3.7
<i>Maytenus senegalensis</i> (Lam.) Exell (Celastraceae)	0.2	0.1	27.0	–	–	–	–	–
<i>Milicia excelsa</i> (Welw.) C.C. Berg (Moraceae)	–	–	–	–	4.8	1.8	29.6	1.9
<i>Monodora myristica</i> (Gaertn.) Dunal (Annonaceae)	1.2	0.3	24.2	4.5	–	–	–	–
<i>Morus mesozygia</i> Stapf. (Moraceae)	6.1	1.7	43.6	5.4	3.1	1.2	36.0	5.1
<i>Nuxia congesta</i> Fres. (Loganiaceae)	0.8	0.2	31.3	4.1	–	–	–	–
<i>Olea capensis</i> L. (Oleaceae)	2.4	0.7	95.2	20.6	5.8	2.1	54.2	10.9
<i>Phyllanthus inflatus</i> Hutch. (Euphorbiaceae)	1.0	0.3	23.0	5.8	–	–	–	–
<i>Polyscias fulva</i> (Hiern) Harms (Araliaceae)	22.8	6.4	33.8	1.6	5.1	1.9	34.5	3.3
<i>Premna angolensis</i> Gurke (Verbenaceae)	2.4	0.7	57.3	6.4	1.0	0.4	22.3	4.6
<i>Prunus africana</i> (Hook.f.) Kalkm. (Rosaceae)	2.2	0.6	46.5	6.8	2.9	1.1	94.3	9.0
<i>Psidium guajava</i> (Myrtaceae)	1.8	0.5	17.2	1.1	–	–	–	–
<i>Rinorea brachyptala</i> (Turcz.) O. Ktze. (Violaceae)	–	–	–	–	0.7	0.3	27.3	4.7
<i>Rothmannia urcelliformis</i> (Hiern) Robyns (Rubiaceae)	0.2	0.1	22.0	–	–	–	–	–
<i>Sapium ellipticum</i> (Krauss) Pax (Euphorbiaceae)	0.8	0.2	27.0	4.4	2.9	1.1	55.8	8.8
<i>Schrebera arborea</i> A. Chevalier & A. Chevalier (Oleaceae)	0.6	0.2	66.3	13.9	–	–	–	–
<i>Spathodea campanulata</i> P. Beauv. (Bignoniaceae)	0.2	0.1	18.0	–	0.5	0.2	34.5	19.5
<i>Strombosia scheffleri</i> Engl. (Olacaceae)	2.6	0.7	26.2	3.3	5.8	2.1	30.3	2.0
<i>Strychnos usambarensis</i> Gilg (Loganiaceae)	35.4	10.0	40.9	1.2	0.2	0.1	33.0	–
<i>Suregada procera</i> (Prain) Croizat (Euphorbiaceae)	0.6	0.2	17.7	1.7	–	–	–	–
<i>Teclea nobilis</i> Del. (Rutaceae)	5.7	1.6	21.7	0.9	9.2	3.4	21.0	0.8
<i>Teclea</i> sp. (Rutaceae)	–	–	–	–	0.7	0.3	24.3	5.6
<i>Terminalia brownii</i> Fresen. (Combretaceae)	0.8	0.2	20.8	1.5	–	–	–	–
<i>Toona ciliata</i> (Meliaceae)	–	–	–	–	3.6	1.3	40.5	6.1
<i>Trema orientalis</i> (L.) Bl. (Ulmaceae)	5.7	1.6	31.8	1.4	–	–	–	–
<i>Trichilia emetica</i> Vahl. (Meliaceae)	4.0	1.1	32.0	6.7	2.2	0.8	29.7	5.0
<i>Trilepisium madagascariense</i> DC. (Moraceae)	14.7	4.2	59.3	3.9	17.1	6.3	52.0	4.0
<i>Vangueria volkensii</i> K. Schum. var. <i>volkensii</i> (Rubiaceae)	–	–	–	–	0.5	0.2	17.0	1.0
<i>Vitex doniana</i> Sweet (Verbenaceae)	0.2	0.1	25.0	–	–	–	–	–
<i>Vitex keniensis</i> Turrill (Verbenaceae)	–	–	–	–	0.7	0.3	23.7	1.8
<i>Zanthoxylum gillettii</i> (De Wild.) Waterm. (Rutaceae)	0.2	0.1	18.0	–	4.3	1.6	42.1	10.3
<i>Zanthoxylum mildbraedii</i> (Engl.) Waterm. (Rutaceae)	–	–	–	–	0.5	0.2	17.5	0.5
unidentified	–	–	–	–	0.5	0.2	19.0	1.0

*Notes relating to the distinction between *Albizia gummifera* and *Albizia* sp. d.b.h. records were lost. However, mean d.b.h. (\pm SE) for both *Albizia* species combined is 106.3 ± 28.7 cm.

area, they inhibit seedlings of other species from invading. Experiments comparing tree seedling survival in areas of Isecheno regularly cleared of *B. nitens* with those where *B. nitens* is allowed to grow would yield further insight into

whether this species might be responsible for the disparity in stem density between our study sites at Kakamega.

The floristic composition of our study sites also proved to be quite different, with species richness differing substan-

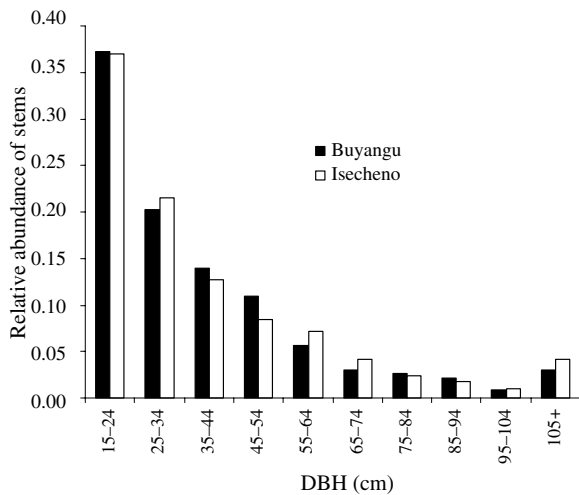


Fig 3 Size class distribution of stems ≥ 15 cm d.b.h. at Buyangu and Isecheno.

tially between sites and 52% of the species identified in our study occurring only at one site. In addition, densities of those species actually present at both sites often differed markedly between sites. Because of a paucity of data on

several key variables, we can only speculate as to the potential sources of these differences in floristic composition between sites. They include small intersite variation in rainfall, soil composition, elevation, and temperature, differences in logging history, and historical differences in the distribution and abundance of large mammals (Tsingalia, 1988; Struhsaker, Lwanga & Kasenene, 1996; Chapman *et al.*, 1997). For example, primates and ungulates are known to influence the floristic composition of tropical forests via their roles as seed dispersers (Struhsaker, 1997; Lambert & Garber, 1998; Nchanji & Plumptre, 2003). Preliminary surveys suggest that the densities of primates and ungulates differ substantially between Buyangu and Isecheno (Gathua, 1995, 2000; Fashing & Cords, 2000) and if these apparent differences in seed disperser density have existed for several decades or more, it is conceivable they might be at least partly responsible for the differences in floristic composition between sites.

Lastly, just as animals have probably had some influence on the composition of the Kakamega Forest, the variation in floristic composition at Kakamega has probably had a major influence on the socioecology of the animals that

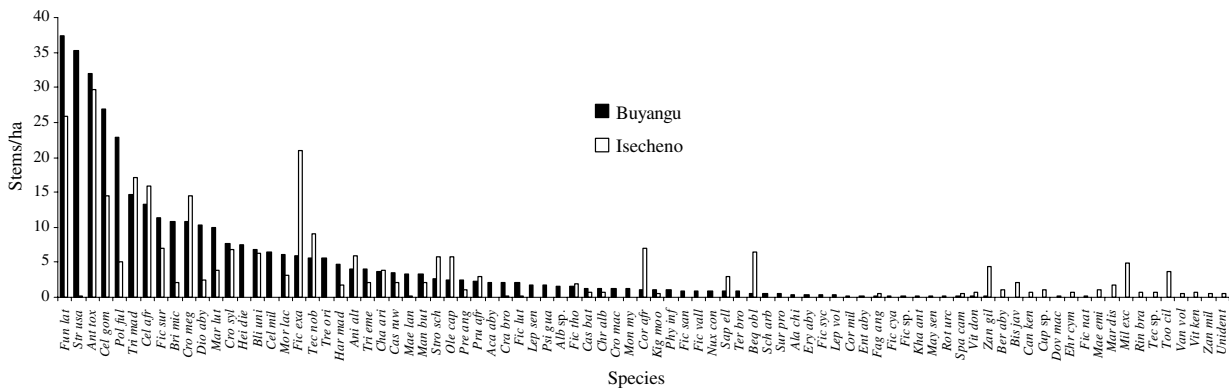


Fig 4 Densities of the 86 tree species (≥ 15 cm d.b.h.) at Buyangu and Isecheno. Species appear in descending order of density for Buyangu. The seventeen species not found at Buyangu appear in alphabetical order at the end. Abbreviations correspond to the first three letters of the genus and species from the taxa listed in Table 1.

Table 2 Summary of the similarities and differences between the tree communities at Buyangu and Isecheno

Similarities	Differences
<ul style="list-style-type: none"> • Species–area curve shape • Species diversity and evenness • Mean d.b.h. • Stem size class distributions 	<ul style="list-style-type: none"> • More species at Buyangu • Stem density higher at Buyangu • 52% of species found at one site but not the other • Sorensen’s Index only 66.7% • Species-specific overlap in relative density only 61.2% • Many tree species among the most abundant at one site but $\geq 35\%$ rarer at the other

inhabit it. Primates, in particular, often exhibit considerable ecological plasticity in response to spatial variation in forest structure and composition (Kool, 1989; Brown & Zunino, 1990; Chapman *et al.*, 2002a,b), and it is therefore not surprising that the diet of one primate species, the redbtail monkey (*C. ascanius*), that has been studied at both Buyangu and Isecheno differs in ways that reflect the different abundance of plant food species at these sites (Cords, 1987; Gathua, 2000). Although the relative proportion of food items (e.g. fruit, invertebrates, etc.) in redbtail diets is similar at the two sites, species-specific dietary overlap in plant food is quite low (35–42%; Chapman *et al.*, 2002a), a phenomenon that can be partly attributed to differences between the tree communities at the two sites. For example, at Buyangu, where *S. usambarensis* is the second most abundant tree species, it is the second- and fourth-ranking species, respectively, in the annual diets of two groups of redbtails (Gathua, 2000). Conversely, at Isecheno, where *S. usambarensis* is extremely rare, redbtails rarely consume it (Cords, 1987; Chapman *et al.*, 2002a). Similar dietary flexibility has also been reported for redbtails, mangabeys (*Lophocebus albigena* Gray), and red colobus monkeys (*Procolobus badius* Kerr) in the Kibale Forest, Uganda where diet also varies considerably over short geographic distances at least partly in response to intersite variation in floristic composition (Chapman *et al.*, 1997, 2002a,b).

In summary, this study highlights the striking extent to which two areas of forest in relatively close proximity and of similar structure can differ in tree species composition and abundance. We hypothesize that differences in stem density between our study sites are because of the greater abundance at Isecheno of *B. nitens*, an undergrowth species believed to inhibit tree regeneration. Differences in species richness and floristic composition are harder to explain and are likely the result of many factors. Redtail monkey dietary choices at the two sites appear to be strongly influenced by the intersite differences in floristic composition. Comparative studies of tree and animal populations at additional sites in the Kakamega Forest would help determine the extent to which the patterns revealed by this study hold over larger spatial scales (e.g. Chapman *et al.*, 1997; Pitman *et al.*, 1999).

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