

Spatial and temporal variability in the structure of a tropical forest

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Summary

This study examines spatial and temporal variation in the forest structure of the Kibale National Park, Uganda by contrasting tree density, tree size, and forest composition among four areas each separated by less than 15 km, and by quantifying changes in the composition of one of these forests over a 20-year period. Densities of some tree species differed markedly between sites, and some species common at one location were absent at others. Monthly phenological monitoring demonstrated that it was not uncommon for phenological patterns to differ between the forests. To examine temporal variation in the tree composition over a 20-year period, a sampling regime that was carried out in the early 1970s was replicated on the floristic composition of one of these sites, using identical methods in the same sampling areas. While no form of human intervention occurred in this area between the early 1970s and 1992, there were marked changes in the densities of some tree species. Twenty-seven percent of the identified species increased in abundance, 33% decreased, and 40% remained relatively unchanged. The observed spatial and temporal variation in forest composition could be the result of abiotic factors, such as altitude or rainfall, or biotic factors such as elephant and/or human influences on ecosystem dynamics; the implications of this variation for frugivores are discussed.

Key words: ecosystem, elephants, forest, frugivores, Kibale, tree

Résumé

Cette étude examine les variations spatiales et temporelles de la structure forestière du Kibale National Park, en Ouganda, en faisant contraster la densité des arbres, leur taille et la composition forestière de quatre zones situées à moins de 15 km les unes des autres, et en quantifiant les changements survenus dans la composition d'une de ces forêts pendant une période de vingt ans. La densité de certaines espèces d'arbres variait fortement d'un site à l'autre, et certaines espèces, communes à un endroit étaient absentes à d'autres. Un contrôle phénologique mensuel a montré qu'il n'était pas rare que des schémas phénologiques différent entre les forêts. Pour étudier les variations temporelles de la composition des arbres sur une période de vingt ans, on a réitéré un échantillonnage, qui avait été réalisé au début des années 1970, de la composition

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floristique d'une des zones en reprenant les mêmes méthodes aux mêmes endroits. Alors qu'il n'y avait eu aucune forme d'intervention humaine dans cette zone entre le début des années 1970 et 1992, il y avait pourtant des changements marqués dans la densité de certaines espèces d'arbres. Vingt-sept pourcents des espèces identifiées étaient plus abondantes, 33% diminuaient et 40% restaient à peu près inchangées. Les variations spatiales et temporelles de la composition forestière pourraient être le résultat de facteurs abiotiques, tels que l'altitude ou les chutes de pluies, ou de facteurs biotiques, comme l'influence des éléphants ou des hommes sur la dynamique de l'écosystème. On discute les implications de ces variations sur les frugivores.

Introduction

Comparative studies of the structure and composition of tropical forests indicate differences between forests from widely separated geographical regions (Whitmore, 1979; Gentry, 1990), or examine forests that experience markedly different climatic patterns (Frankie, Baker & Opler, 1974). Comparisons of forest structure in neighbouring sites (e.g. separated by between 1 and 100 km) have received much less attention (Butynski, 1990), although this scale of variation is of particular significance to local animal populations, and analysis at this scale may provide a tool to explore adaptations of animals to their environment.

Hypotheses proposed for the functional significance of specific social or behavioural characters of animals are often based on contrasts of independent studies conducted on populations that are often separated by thousands of kilometres (Eisenberg, Muckenhirn & Rudran, 1972; Clutton-Brock & Harvey, 1977; McKey, 1978; Oates *et al.*, 1990). The premise for such contrasts is that sufficient variation will exist in the ecological conditions among widely separated sites to permit us to detect differences in behavioural response variables. However, there is increasing evidence from studies made over a number of years (Goodall, 1986) and from observations on neighbouring communities (1 to 100 kilometres; Butynski, 1990; Chapman & Fedigan, 1990), that large differences in diet and social organization can occur on both a large temporal and a small spatial scale. Given such variation, small-scale contrasts may be more sensitive at detecting ecological determinants of behaviour than comparisons made on larger scales because other unmeasured parameters are less likely to differ between study groups than would be the case if contrasts were made between widely separated populations.

If large differences in the composition of neighbouring forests are common, it raises the question as to why these differences exist: whether the differences are caused by changes in soil conditions or elevation that occur over a short distance, due to differences in past disturbance regimes, or whether they relate to how animals have previously modified their environment (Buechner & Dawkins, 1961; Smart, Hatton & Spence, 1985; McNaughton, Ruess & Seagle, 1988; Naiman, 1988).

This study describes the composition of four neighbouring forests in Kibale National Park, Uganda, known locally as Kanyawara, Dura River (near Kanyanchu), Mainaro, and Ngogo. The first three sites are each approximately 15 km apart along a N-S gradient, while Ngogo is 12 km south-east of Kanyawara (Figure 1). To quantify how forest structure can change over a small

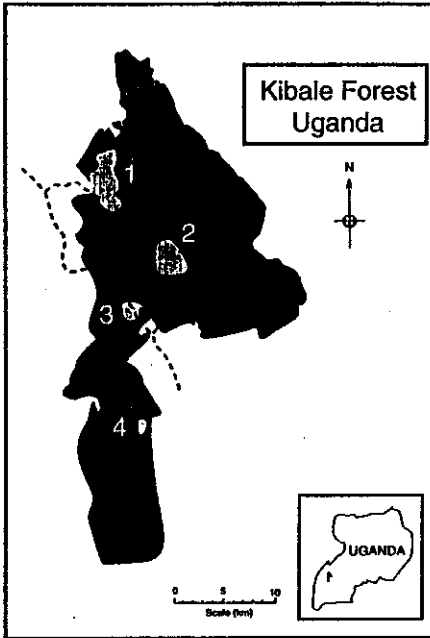


Fig. 1. The location of the four sites within Kibale National Park where forest composition was quantified and the location of Kibale within Uganda (1=Kanyawara, 2=Ngogo, 3=Dura River (near Kanyanchu), 4=Mainaro).

spatial scale, the size and density of tree species at all localities has been investigated in this study. To examine temporal changes in forest composition, data collected in the early 1970s (Struhsaker, 1975; Waser, 1974) have been compared to data collected in 1992 using identical methodology at the same sample plots. The implications of this spatial and temporal variation in forest composition on the behavioural patterns of animals is subsequently discussed and speculation is made as to whether the differences in forest composition may be the result of small differences in abiotic factors, such as elevation or rainfall, or biotic factors, such as elephant and/or human influences on ecosystem dynamics.

Methods

The Kibale National Park, located in western Uganda ($0^{\circ}13'$ to $0^{\circ}41'N$ and $30^{\circ}19'$ to $30^{\circ}32'E$) near the base of the Ruwenzori Mountains, is a moist, evergreen forest, transitional between lowland rain forest and montane forest (Struhsaker, 1975; Skorupa, 1988; Wing & Buss, 1970; Butynski, 1990; Fig. 1). All four study areas consist of a series of moderately undulating valleys with an average slope of 8.7° at Kanyawara, 6.6° at the Dura River, 5.9° at Mainaro, and 6.0° at Ngogo. Kanyawara and Ngogo are sites of on-going long-term research programmes for which extensive phenological and meteorological data are available. Kanyawara is situated at an elevation of 1500 m (main camp), the

River Dura site is at 1250 m, Mainaro is at 1200 m, and Ngogo is at approximately 1350 m. However, within each site there are elevational changes from hill tops to valley bottoms of 150–200 m (measured with a Paulin Micro Surveying Altimeter, APS, Cottonwood, AZ). The Dura River passes through the Mainaro and Dura River sites. Kanyawara exhibits slightly cooler temperatures (annual mean daily minimum 1977 to 1994 = $16.4^{\circ} \pm 0.4^{\circ}\text{C}$; maximum = $23.3^{\circ} \pm 0.6^{\circ}\text{C}$) than Ngogo (annual mean daily minimum 1977 to 1984 = $16.7^{\circ} \pm 0.4^{\circ}\text{C}$; maximum = $24.2^{\circ} \pm 0.6^{\circ}\text{C}$). Mean annual rainfall averaged 167 cm (1977–94; 157 cm 1977–84) at Kanyawara and 149 cm (1977–84) at Ngogo. Temperature and rainfall data are not available for the Dura River and Mainaro sites.

Vegetation transects that were 200 m by 10 m, were established at each study site (26 transects at Kanyawara, 24 at Ngogo, 4 at Mainaro, and 4 at Dura River). At Kanyawara and Ngogo, the location of transects was selected at random within the existing trail systems. The trail system consists of a grid system designed to provide access to the forest, and therefore the trails avoid the very swampy wet valley bottoms. At the Mainaro and Dura River sites there were no pre-existing trails, and transects were established perpendicular to each other at 50-m intervals. The area around Kanyawara has experienced different logging regimes. For the purpose of this comparison only those transects in areas of the forest that have not been logged ($N=12$; forestry compartment K-30) are contrasted with the other sites. This sampling regime produced a total sampling area of 4.8 ha at Ngogo, 2.4 ha at Kanyawara and 0.8 ha at both the Dura River and Mainaro sites. Each tree greater than 10 cm DBH (Diameter at Breast Height) within 5 m of each side of the trail was individually marked with a numbered aluminium tag and measured (DBH). This produced a sample of 2637 trees at Ngogo, 1173 trees at Kanyawara, 338 trees at Dura River, and 293 trees at Mainaro. Since sampling at the Dura River and Mainaro sites covers a smaller area, densities of rare or clumped tree species may be less accurately represented in the sample than for the more extensively studied areas (Fig. 2).

Phenological information had been recorded continuously once a month since January 1990 at Kanyawara ($N=41$ months), April 1990 at Ngogo ($N=37$ months), and July 1995 at both Mainaro and Dura River. The stage of leaf development was documented (leaf bud, young leaves, mature leaves by visual assessment through binoculars) and the presence or absence of flowers and ripe and unripe fruits for all trees was noted.

At Ngogo and Kanyawara, slope, amount of light reaching the ground, and amount of ground vegetation were recorded for all transects at 20-m intervals. Light was ranked by looking directly up into a tube (100 mm diameter) covered with a grid consisting of nine cells and counting the number of grid cells in which light could be seen. A measure of ground vegetation was determined 2 m off the side of the trail by counting all stems less than 2 m in height within a 1-m radius circle.

To quantify temporal variation in tree composition between the early 1970s and 1992, the tree enumeration conducted by Struhsaker (1975) was replicated. In K-30, the forestry compartment relatively undisturbed by recent human activity, 4.2 ha was sampled, compared to 1.6 ha in K-14, a lightly logged forestry compartment. All trees greater than 10 m in height in 5-m wide transects were identified. Since Struhsaker (1975) presented detailed information

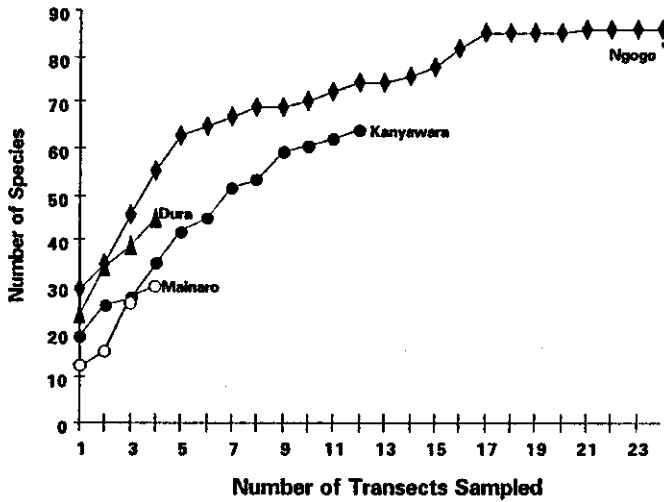


Fig. 2. The cumulative species-area relationship for the four sites sampled in Kibale National Park, Uganda. Each transect samples an area of 0.2 ha.

concerning the location of the transects he sampled, it was possible to resample the exact same areas 20 years later. The original transects were established along trails cut along compass bearings and did not follow topographic features (Olupot *et al.*, 1994). The K-14 area was sampled to provide an initial understanding of the extent of temporal variability in forest structure that can occur after disturbance. Forestry compartment K-14 (390 ha of forest) was selectively harvested between May and December 1969 and removal was relatively light (averaging $14 \text{ m}^3 \text{ ha}^{-1}$ or approximately $5.1 \text{ stems ha}^{-1}$). Twenty-three tree species were removed, with only 9 species contributing 94% of the total timber harvest (Kasenene, 1987; Skorupa, 1988).

Results

Densities of some tree species differed markedly between the sites (Table 1). For example, two of the ten most common trees at Ngogo were very rare at Kanyawara (*Pterygota mildbraedii* occurs in K-30 but was not recorded on the transects; Fig. 3). *Baphiopsis parviflora* and *Cynometra alexandri* were the most abundant tree species at the Mainaro site, but were not found at the other three locations (Table 1). Similarly, *Bequaertidendron oblanceolatum* was the third most common species at the Dura River site, but it was not found at any of the other locations. Sampling indicated that very rare species were often absent from one of the two sites (Table 1), although this may have been due to limitations of the transect sampling method. Species-area curves suggest that the number of new species found decreases after approximately nine transects (Fig. 2). The average size (DBH) of each of the common tree species was similar between all locations (Table 1), despite differences in densities.

Table 1. Tree density (individuals ha⁻¹), mean tree size (cm DBH for trees >10 cm DBH) and the standard error of tree size for four locations in Kibale National Park, Uganda

Species	Kanyawara			Ngogo			Dura			Mainaro		
	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE
<i>Uvariopsis congensis</i>	60.4	15.6	0.4	100.6	15.9	0.2	60.0	15.1	0.8	43.8	18.6	0.8
<i>Celtis durandii</i>	47.1	33.3	2.4	57.5	28.6	1.2	63.8	35.4	2.9	33.8	18.5	2.9
<i>Chrysophyllum albidum</i>	1.3	12.7	1.5	64.6	25.9	1.0	47.5	20.2	1.9	21.3	32.0	4.7
<i>Baphiopsis parviflora</i>	-	-	-	-	-	-	-	-	-	116.3	13.2	0.3
<i>Funtumia latifolia</i>	33.8	25.7	1.8	36.3	25.7	1.1	43.8	29.4	2.7	2.5	12.2	2.2
<i>Diospyros abyssinica</i>	40.0	25.2	1.5	69.0	23.6	0.8	1.3	38.8	-	1.3	58.8	-
<i>Markhamia platycalyx</i>	50.0	23.5	1.2	24.8	22.2	1.0	8.8	23.5	6.6	1.3	25.3	-
<i>Bosqueia phoberos</i>	50.0	14.2	0.4	5.6	36.8	3.2	22.5	55.0	7.1	-	-	-
<i>Cynometra alexandri</i>	-	-	-	-	-	-	-	-	-	63.8	63.4	4.2
<i>Bequaertiodendron oblanceolatum</i>	-	-	-	-	-	-	57.5	28.5	2.1	-	-	-
<i>Tabernaemontana</i> sp.	14.4	1.1	4.6	33.8	15.4	0.5	8.8	14.9	2.1	-	-	-
<i>Leptonychia mildbraedii</i>	35.4	14.0	0.4	2.5	13.5	0.8	-	-	-	-	-	-
<i>Celtis mildbraedii</i>	-	-	-	0.2	20.0	-	-	-	-	32.5	30.9	4.7
<i>Chaetacme aristata</i>	17.1	17.7	1.2	4.8	25.7	2.3	3.8	15.3	1.2	1.3	14.0	-
<i>Teclea nobilis</i>	17.1	16.2	0.8	3.8	27.4	3.4	-	-	-	-	-	-
<i>Dictyandra arborescens</i>	0.4	20.8	-	12.1	13.2	0.5	3.8	12.1	0.4	3.8	12.1	0.5
<i>Pleiocarpa pycnantha</i>	1.3	14.1	1.7	1.3	21.4	8.1	13.8	11.9	0.5	2.5	11.1	0.4
<i>Strombosia scheffleri</i>	12.5	42.8	4.5	3.1	51.4	3.2	2.5	55.5	13.5	-	-	-
<i>Mimusops bagshawei</i>	3.3	75.1	10.7	3.1	76.5	7.5	7.5	69.8	18.8	-	-	-
<i>Aphania senegalensis</i>	1.7	17.2	3.3	4.6	26.2	2.4	3.8	19.7	4.6	3.8	17.4	3.3
<i>Dombeya mukou</i>	9.2	26.7	2.4	3.1	23.9	2.8	1.3	26.5	-	-	-	-
<i>Ficus mucoso</i>	-	-	-	0.6	-	-	1.3	154.7	-	11.3	14.3	1.1
<i>Linociera johnsonii</i>	5.4	20.9	2.6	7.5	18.3	1.3	-	-	-	-	-	-
<i>Premna angolensis</i>	4.6	44.2	8.4	4.4	31.3	3.9	2.5	65.7	50.4	1.3	16.5	-
<i>Millettia dura</i>	3.3	21.1	4.4	7.7	14.9	0.7	1.3	13.0	-	-	-	-
<i>Pancovia turbinata</i>	10.8	17.0	1.5	0.2	15.6	-	1.3	12.2	-	-	-	-
<i>Pterygota mildbraedii</i>	-	-	-	10.8	94.4	9.9	1.3	85.0	-	-	-	-
<i>Dasylepis eggelingii</i>	1.3	17.5	3.3	7.9	12.3	0.4	2.5	12.9	0.8	-	-	-

Species	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE
<i>Xymalos monospora</i>	8.8	15.3	1.1	1.5	13.8	1.4	-	-	-	-	-	-
<i>Neoboutania</i> sp.	1.3	26.6	7.2	7.9	22.6	1.7	-	-	-	-	-	-
<i>Cassipourea ruwensorensis</i>	7.1	18.0	5.4	1.1	14.3	0.8	-	-	-	-	-	-
<i>Olea welwitschii</i>	3.3	43.6	13.4	3.1	50.7	14.8	1.3	108.1	-	-	-	-
<i>Rothmannia urcelliformis</i>	1.3	13.5	1.8	5.2	12.7	0.4	1.3	10.3	-	-	-	-
<i>Strychnos mitis</i>	7.5	28.7	3.6	0.2	11.6	-	-	-	-	-	-	-
<i>Harrisonia abyssinica</i>	-	-	-	2.5	18.6	2.3	2.5	19.3	5.2	2.5	12.8	2.8
<i>Oxyanthus speciosus</i>	2.5	11.3	0.6	4.8	13.7	0.8	-	-	-	-	-	-
<i>Lovoa swynnertonii</i>	0.8	88.0	29.4	2.7	70.6	12.7	3.8	15.5	4.3	-	-	-
<i>Cola gigantea</i>	-	-	-	0.4	66.8	18.8	6.3	95.3	27.1	-	-	-
<i>Pseudospondius microcarpa</i>	1.7	130.0	23.1	1.3	104.1	32.8	3.8	114.3	58.8	-	-	-
<i>Celtis africana</i>	4.2	26.5	8.0	1.0	40.4	8.8	-	-	-	1.3	10.2	-
<i>Turraea floribunda</i>	-	-	-	-	-	-	-	-	-	6.3	20.4	3.4
<i>Monodora myristica</i>	0.4	53.5	-	0.4	58.3	1.0	3.8	64.3	12.4	1.3	74.5	-
<i>Ficus exasperata</i>	3.8	47.3	21.1	0.4	130.5	19.5	-	-	-	8.3	11.0	-
<i>Lychnodiscus cerospermus</i>	-	-	-	-	-	-	5.0	21.2	2.5	-	-	-
<i>Balanites wilsoniana</i>	1.7	43.8	28.1	1.7	29.0	11.0	1.3	84.7	-	-	-	-
<i>Kigelia moosa</i>	3.3	13.8	0.8	0.8	13.5	1.4	-	-	-	-	-	-
<i>Newtonia buchananii</i>	-	-	-	0.2	129.0	-	3.8	45.1	27.7	-	-	-
<i>Ficus sansibarica</i>	1.7	-	-	2.1	-	-	-	-	-	-	-	-
<i>Polyscias fulva</i>	0.8	17.6	5.6	0.2	14.9	-	-	-	-	2.5	12.6	1.4
<i>Fagaropsis angolensis</i>	2.5	43.5	15.4	0.6	41.0	12.4	-	-	-	-	-	-
<i>Parinari excelsa</i>	2.9	101.1	22.2	0.2	61.8	-	-	-	-	-	-	-
<i>Spathodea campanulata</i>	0.8	66.2	27.9	2.3	36.4	4.7	-	-	-	-	-	-
<i>Elaeodendron buchananii</i>	-	-	-	2.7	17.5	1.7	-	-	-	-	-	-
<i>Schrebera arborea</i>	-	-	-	1.5	22.1	3.9	1.3	77.0	-	-	-	-
<i>Vitex amboniensis</i>	-	-	-	0.2	29.3	-	2.5	14.5	2.7	-	-	-
<i>Albizia glaberrima</i>	-	-	-	-	-	-	2.5	62.5	49.6	-	-	-
<i>Albizia grandibracteata</i>	1.3	26.9	8.0	-	-	-	1.3	18.6	-	-	-	-

Table 1. Continued.

Species	Kanyawara			Ngogo			Dura			Mainaro		
	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE
<i>Bombax buonopozense</i>	-	-	-	-	-	-	-	-	-	2.5	13.1	0.1
<i>Craibia brownii</i>	-	-	-	-	-	-	-	-	-	2.5	16.7	4.2
<i>Suregada procera</i>	-	-	-	-	-	-	-	-	-	2.5	19.8	2.6
<i>Ficus saussureana</i>	0.4	-	-	0.6	-	-	-	-	-	1.3	-	-
<i>Myrianthus</i> sp.	2.1	20.2	4.3	-	-	-	-	-	-	-	-	-
<i>Blighia unjugata</i>	0.8	50.4	31.0	1.0	55.2	10.2	-	-	-	-	-	-
<i>Piptadeniastrum africanum</i>	-	-	-	1.9	129.0	9.2	-	-	-	-	-	-
<i>Aningeria altissima</i>	1.7	156.8	61.1	-	-	-	-	-	-	-	-	-
<i>Carterispermum laurinum</i>	1.7	71.5	36.4	-	-	-	-	-	-	-	-	-
<i>Cassine buchananii</i>	0.4	10.1	-	-	-	-	1.3	11.8	-	-	-	-
<i>Ficus sur</i>	-	-	-	0.4	-	-	-	-	-	1.3	22.6	-
<i>Lovoa (trichilodea?)</i>	-	-	-	1.7	16.9	3.0	-	-	-	-	-	-
<i>Maeria duchesnei</i>	1.3	22.8	4.8	0.4	16.9	5.4	-	-	-	-	-	-
<i>Turrea robusta</i>	-	-	-	1.5	24.7	3.6	-	-	-	-	-	-
<i>Treculia africana</i>	-	-	-	0.2	20.5	-	1.3	73.0	-	-	-	-
<i>Vangueria</i> sp.	-	-	-	0.2	30.2	-	1.3	10.2	-	-	-	-
<i>Allophylus</i> sp.	-	-	-	-	-	-	-	-	-	1.3	16.0	-
<i>Alstonia boonei</i>	-	-	-	-	-	-	-	-	-	1.3	27.0	-
<i>Casseearia battisombel</i>	1.3	11.5	0.5	-	-	-	-	-	-	-	-	-
<i>Chrysophyllum gorungosamum</i>	1.3	91.9	37.0	-	-	-	-	-	-	-	-	-
<i>Croton macrostachyus</i>	-	-	-	-	-	-	-	-	-	1.3	29.5	-
<i>Croton sylvaticus</i>	0.8	16.7	0.7	0.4	12.6	-	-	-	-	-	-	-
<i>Ficus vallis-choudae</i>	-	-	-	-	-	-	1.3	-	-	-	-	-
<i>Lindackeria</i> sp.	-	-	-	1.3	11.1	0.5	-	-	-	-	-	-
<i>Phyllanthus discoideus</i>	-	-	-	1.3	18.4	3.0	-	-	-	-	-	-
<i>Rauwolfia oxyphylla</i>	-	-	-	1.3	19.8	4.6	-	-	-	-	-	-
<i>Thecacoris lucida</i>	1.3	57.1	5.9	-	-	-	-	-	-	-	-	-
<i>Warbugia stuhlmanni</i>	-	-	-	1.3	21.2	6.6	-	-	-	-	-	-
<i>Fagara angolensis</i>	0.8	13.4	0.3	0.2	15.6	-	-	-	-	-	-	-

Species	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE	Density	DBH	SE
<i>Ficus natalensis</i>	0.4	-	-	0.6	-	-	-	-	-	-	-	-
<i>Apodytes dimidiata</i>	0.8	16.5	3.5	-	-	-	-	-	-	-	-	-
<i>Euclina longiflora</i>	0.8	11.3	0.5	-	-	-	-	-	-	-	-	-
<i>Ficus</i> spp.	-	-	-	0.8	-	-	-	-	-	-	-	-
<i>Margaritaria discoidea</i>	-	-	-	0.8	18.7	2.2	-	-	-	-	-	-
<i>Rauvolfia vomitaria</i>	-	-	-	0.8	23.7	3.5	-	-	-	-	-	-
<i>Cordia abyssinica</i>	0.4	20.2	-	0.2	12.0	-	-	-	-	-	-	-
<i>Cordia millenii</i>	0.4	16.9	-	0.2	142.0	-	-	-	-	-	-	-
<i>Cordia</i> spp.	0.4	18.7	-	0.2	41.8	-	-	-	-	-	-	-
<i>Ficus trichopoda</i>	-	-	-	0.6	-	-	-	-	-	-	-	-
<i>Ficus conraui</i>	0.4	-	-	0.2	-	-	-	-	-	-	-	-
<i>Antiaris toxicaria</i>	0.4	14.8	-	-	-	-	-	-	-	-	-	-
<i>Reischniedia ugandensis</i>	0.4	24.7	-	-	-	-	-	-	-	-	-	-
<i>Bersama abyssinica</i>	0.4	27.4	-	-	-	-	-	-	-	-	-	-
<i>Coffea eugenoides</i>	0.4	18.0	-	-	-	-	-	-	-	-	-	-
<i>Dasylepis racemosa</i>	0.4	10.0	-	-	-	-	-	-	-	-	-	-
<i>Macaranga schweinfurthii</i>	-	-	-	0.4	13.2	1.2	-	-	-	-	-	-
<i>Mitragyna rubrostipulata</i>	-	-	-	0.4	23.3	11.3	-	-	-	-	-	-
<i>Prunus africana</i>	-	-	-	0.4	16.3	1.3	-	-	-	-	-	-
<i>Symphonia globulifera</i>	0.4	41.4	-	-	-	-	-	-	-	-	-	-
<i>Turraeanthus africanus</i>	-	-	-	0.4	12.3	-	-	-	-	-	-	-
<i>Cusearia engleri</i>	-	-	-	0.2	11.2	-	-	-	-	-	-	-
<i>Entandrophragma angolense</i>	-	-	-	0.2	11.2	-	-	-	-	-	-	-
<i>Euadenia eminens</i>	-	-	-	0.2	26.0	-	-	-	-	-	-	-
<i>Ficus ovata</i>	-	-	-	0.2	-	-	-	-	-	-	-	-
<i>Ficus cyathistipula</i>	-	-	-	0.2	-	-	-	-	-	-	-	-
<i>Morus lactea</i>	-	-	-	0.2	11.1	-	-	-	-	-	-	-
<i>Oncoba routedgei</i>	-	-	-	0.2	19.3	-	-	-	-	-	-	-
<i>Oncoba spinosa</i>	-	-	-	0.2	21.9	-	-	-	-	-	-	-
<i>Psychotria megistosticta</i>	-	-	-	0.2	12.0	-	-	-	-	-	-	-
<i>Rimorea oblongifolia</i>	-	-	-	0.2	10.2	-	-	-	-	-	-	-

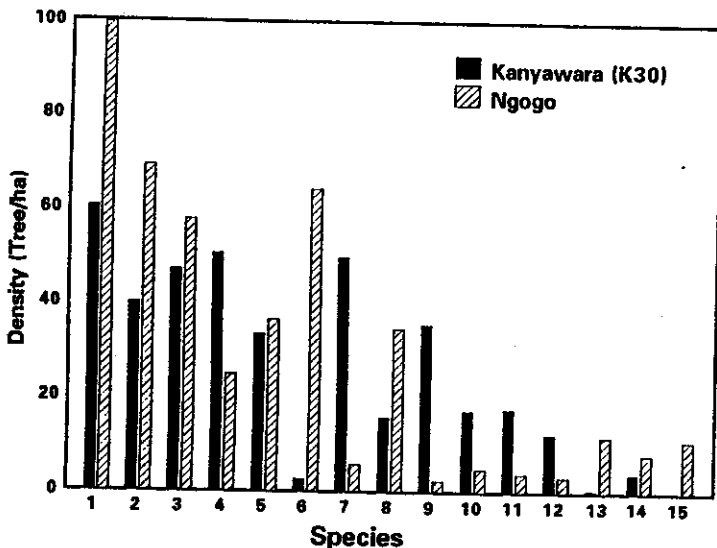


Fig. 3. The density of the most common trees (greater than 10 cm DBH) at each of two neighbouring forest blocks (Kanyawara and Ngogo) of the Kibale National Park, Uganda. The tree species presented are: 1) *Uvariopsis congensis*, 2) *Diospyros abyssinica*, 3) *Celtis durandii*, 4) *Markhamia platycalyx*, 5) *Funtumia latifolia*, 6) *Chrysophyllum albidum*, 7) *Boxqecia phoberos*, 8) *Tabernaemontana* sp., 9) *Leptonychia mildbraedii*, 10) *Chaetacme aristata*, 11) *Teclea nobilis*, 12) *Strombosia scheffleri*, 13) *Dictyandra arborescens*, 14) *Milletia dura*, 15) *Pterygota mildbraedi*.

There were also notable differences in the average monthly density of trees bearing ripe fruit at the Kanyawara and Ngogo study sites (overall mean Kanyawara—878 fruiting tree km^{-2} ; Ngogo—1748 fruiting tree km^{-2} ; Fig. 4). It was not uncommon for fruit to be abundant at one location, but scarce at another. For example, in June and July 1990, ripe fruit was abundant in Kanyawara as a result of the fruiting of *Uvariopsis congensis*. However, *U. congensis* did not fruit at Ngogo at this time, and fruit was generally scarce in the forest. Conversely, the density of trees bearing ripe fruit was high at Ngogo in December 1990, but low at Kanyawara. Frequently, tree species fruited at Ngogo a month or so prior to Kanyawara (e.g. Dec 1991 to Jan 1992 or June to July 1993).

An analysis of each year separately illustrates that there is considerable spatial variability in annual fruiting patterns. For example, in 1992 Ngogo had more fruit than Kanyawara (average monthly fruiting trees km^{-2} : Ngogo=1878, Kanyawara=576), but this situation was reversed in 1993 (average monthly fruiting trees km^{-2} : Ngogo=929, Kanyawara=1424).

At Ngogo, there were fewer stems of ground vegetation than at Kanyawara (1-m radius sampling plots: Ngogo mean=6.5 stems plot^{-1} , $N=260$; Kanyawara mean=10.01 stems plot^{-1} , $N=240$; $F=77.80$, $P<0.0001$). At Ngogo, the amount of light reaching the ground was less than at Kanyawara (Ngogo mean rank=1.71, Kanyawara mean=2.53; Mann-Whitney, $P<0.0001$). There was a

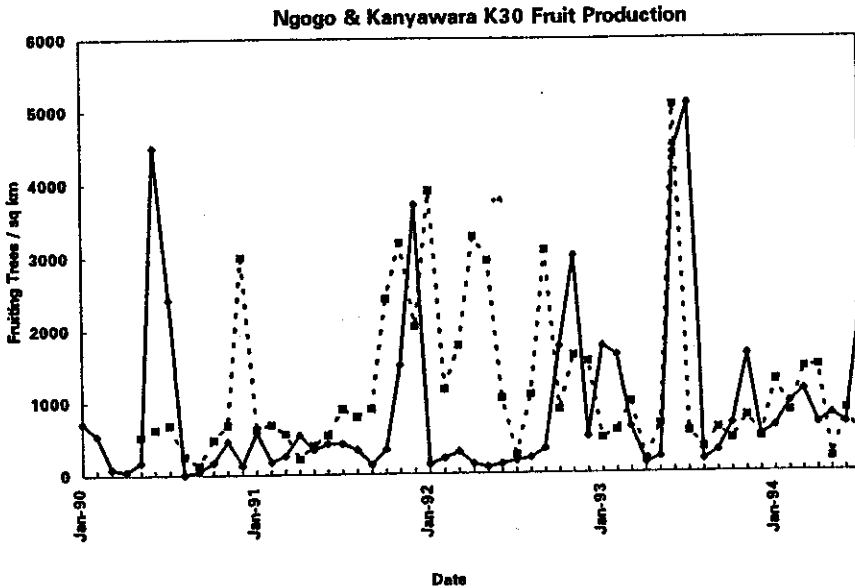


Fig. 4. The number of trees per square kilometre bearing ripe fruit at the Ngogo and Kanyawara study sites in the Kibale National Park, Uganda quantified on a monthly basis. The square symbols represent the Ngogo values, and the diamond shaped symbols represent the Kanyawara values.

correlation between the amount of light at a sampling site and the number of stems of ground vegetation ($r=0.155$, $P=0.0011$).

While no significant form of human intervention occurred in the K-30 area between the early 1970s and 1992, there were a number of marked changes in the densities of some tree species (Table 2). For example, *Funtumia latifolia* was almost three times more abundant in 1993 than it was in 1972, while *Dombeya mukole* decreased in abundance by 50% over this time. Overall, tree density in K-30 increased by 27% from 315 trees ha^{-1} in 1972 to 400 trees ha^{-1} in 1992. Twenty-seven percent of the identified species increased in abundance, 33% decreased, and 40% remained relatively unchanged (Table 2). In the forestry compartment that had been lightly logged (K-14) in 1969, tree density increased by 88%, from 256 tree ha^{-1} in 1972 to 481 tree ha^{-1} in 1992. Sixty-seven percent of the tree species increased in abundance, 15% decreased, and 18% remained unchanged.

Discussion

Marked differences in the tree species composition between forested sites separated by less than 15 km, variation in the temporal availability of fruit at the different sites, and a high degree of temporal variation in the composition of one forest between the early 1970s and 1992 have been documented in this

Table 2. Density (individuals ha⁻¹) for tree species in the K-30 and K-14 forestry compartments of the Kibale National Park, Uganda. Data are based on trees greater than 14 cm DBH (1992) and >10 m high (1972) which have been demonstrated to be roughly equivalent. The data from 1972 were provided by Peter Waser and Tom Struhsaker

Species	K-14		K-30	
	Density 1972	Density 1992	Density 1972	Density 1992
<i>Markhamia platycalyx</i>	56.6	66.6	58.0	65.0
<i>Diospyros abyssinica</i>	44.3	46.2	65.7	91.7
<i>Celtis durandii</i>	38.8	69.5	34.3	46.2
<i>Funtumia latifolia</i>	11.7	69.5	14.7	41.3
<i>Teclea nobilis</i>	14.8	24.0	21.0	14.7
<i>Uvariopsis congensis</i>	18.5	28.3	25.2	54.5
<i>Bosqueia phoberos</i>	3.7	33.2	2.8	0.2
<i>Strombosia scheffleri</i>	4.9	12.9	14.7	19.6
<i>Millettia dura</i>	4.9	11.1	7.6	4.2
<i>Styrcinos mitis</i>	1.9	2.5	2.1	2.8
<i>Celtis africana</i>	8.6	19.1	2.1	2.1
<i>Chaetacme aristata</i>	1.2	7.1	8.4	5.6
<i>Dombeya mukole</i>	3.7	8.6	4.2	2.1
<i>Parinari excelsa</i>	0.0	2.5	10.5	11.2
<i>Olea welwitschii</i>	5.5	4.9	2.8	4.9
<i>Linociera johnsonii</i>	5.5	10.5	2.8	0.0
<i>Premna angolensis</i>	1.9	1.2	1.4	2.1
<i>Lavoa swymertanii</i>	0.0	0.0	2.8	0.0
<i>Pancovia turbinata</i>	0.0	0.0	6.3	5.6
<i>Minusops bagshawei</i>	0.6	0.6	2.1	3.5
<i>Chrysophyllum</i>	0.6	0.6	2.1	1.4
<i>Aningeria altissima</i>	1.9	1.2	0.7	0.7
<i>Cassipaurea ruwensorensis</i>	1.2	1.9	3.5	2.1
<i>Trema orientalis</i>	6.8	0.0	0.7	0.0
<i>Neobantonia</i> sp.	1.2	6.8	3.5	2.1
<i>Figaropsis angolensis</i>	1.9	3.1	2.1	2.1
<i>Ficus sansibarica</i>	1.2	3.7	0.0	1.4
<i>Aphania scucgulensis</i>	1.2	4.9	2.1	2.1
<i>Cordia millenii</i>	0.0	1.4	1.4	0.0
<i>Ficus exasperata</i>	3.7	6.8	0.0	0.0
<i>Leptonychia mildbraedii</i>	0.6	2.5	2.1	1.4
<i>Monodora myristica</i>	0.0	0.0	1.4	3.5
<i>Newtonia buchananii</i>	1.9	0.6	1.4	0.0
<i>Balanites wilsoniana</i>	0.0	0.0	1.4	1.4
<i>Spathodea campanulata</i>	0.0	0.0	1.4	2.8
<i>Pseudospondias microcarpa</i>	0.0	0.0	1.4	1.4
<i>Rauvolfia venitoria</i>	0.6	1.2	0.0	0.0
<i>Macaranga schweinfurthii</i>	1.2	1.2	0.0	0.0
<i>Mitragyna rubrostipulata</i>	1.2	0.6	0.0	0.0
<i>Sapium</i> sp.	1.2	0.0	0.0	0.0
<i>Apodytes dimidiata</i>	1.2	0.0	0.0	0.0
<i>Blighia unijugata</i>	1.2	3.1	0.0	0.0
<i>Myrianthus</i> sp.	0.0	6.2	0.0	0.0
<i>Kigelia africana</i>	0.0	1.9	0.0	0.0
<i>Linkackeria</i> sp.	0.0	1.2	0.0	0.0
<i>Hex mitis</i>	0.0	1.9	0.0	0.0
<i>Croton</i> sp.	0.0	1.2	0.0	0.0
<i>Cordia abyssinica</i>	0.0	2.5	0.0	0.0

*Known at the time of the 1991 survey but not found on the transect.
Total trees 1991=969 in 3.4 ha of transects.

study. Thus, animal populations inhabiting these different areas will experience different forest compositions, different phenological cycles, and changes in the composition of the forest.

The consequences of changes in forest composition on the behavioural patterns of animals may be small if animals are not responding to forest composition, but to less specific parameters, such as the density and distribution of food resources. Thus, if a specific tree species does not occur at one site, its functional role may simply be replaced by another tree species, or by a cohort of other tree species at another site. Alternatively, differences between the abundance of specific tree species may have dramatic effects. For example, at Mainaro, mangabeys (*Lophocebus albigena*) feed extensively on the fruits of *Cynometra alexandri*, which is absent from all other areas. At Mainaro, *Cynometra alexandri* is very abundant and bears fruit for a number of months. It is difficult to imagine how this difference would not have dramatic impacts not only on the density of these animals, but also on their behavioural patterns (e.g. range use).

To explore the processes that produced the documented differences between forest blocks it would be useful to record long-term changes in the composition of the forest at a location after parameters thought to be important determinants of forest composition had changed, either experimentally or through a natural process. Unfortunately, it is often difficult to perform large-scale manipulations, or to discover natural experiments, and the timescale over which forests change largely prohibits the necessary quantification. Thus, it is necessary to rely on more inferential data. The rainfall and temperature of the two areas for which long-term data are available are very similar, and there is no evidence of dramatic changes in climate over the last 20 years (Chapman & Chapman, unpubl.). The topography of the areas is similar, as are the soils (Lang Brown & Harrop, 1962), and the difference in elevation between the sites is small (two of the sites are less than 50 m apart in elevation). However, it is still possible that slight changes in soil composition, elevation, rainfall, and temperature contribute to the spatial differences in forest composition that have been indicated. Within Kibale, there is an elevational gradient from north to south, which corresponds to a north to south increase in temperature and decrease in rainfall. In addition, a number of species found in northern areas are not found to the south (e.g. *Parinari excelsa*, *Chrysophyllum albidum*; Osmaston, 1959). However, when seedlings of species found in the Ngogo area and not at Kanyawara are transplanted to Kanyawara they appear to do well (transplanted seedlings of *Warburgia stuhlmannii*, *Ficus mucoso*, *Cola gigantea* have survived over 5 years at Kanyawara). These conflicting pieces of evidence suggest that the effects of temperature, rainfall, and altitude need further investigation.

Based on what is known about savanna/woodland dynamics (Laws, 1970; Laws, Parker & Johnstone, 1975; Naiman, 1988; McNaughton *et al.*, 1988), it is reasonable to suggest that the spatial and temporal differences in forest composition between areas of Kibale National Park are the result of animals (particularly elephants) impacting the ecosystem. Evidence suggests that changes in elephant numbers can cause major floristic and structural changes in vegetation (Buechner & Dawkins, 1961; Laws, 1970; Smart *et al.*, 1985). Elephants browse on small trees and push them over, increasing the mortality rate of the

preferred species (Struhsaker, Lwanga & Kasenene, 1996). By foraging on bark and exposing the functional tissues, elephants can also kill very large trees (Wing & Buss, 1970; Laws *et al.*, 1975; White, Tutin & Fernandez, 1993). The history of elephant population dynamics in Murchison National Park, Uganda provides a dramatic illustration of how elephants can affect habitat structure and ecosystem dynamics. Following the establishment of the park in 1912, and the protection of elephants from organized hunting, the tree density decreased dramatically (Buechner & Dawkins, 1961). Comparison of aerial photographs taken in 1932 and in 1956 illustrated a 55–59% reduction in the number of large trees (Buechner & Dawkins, 1961). The increase in hunting activity in the park during periods of civil unrest in the 1970s resulted in a decline in the elephant population (Brooks & Buss, 1962; Buss & Savage, 1966; Wing & Buss, 1970; Douglas-Hamilton *et al.*, 1980; Eltringham & Malpas, 1980). The decrease in elephant numbers resulted in an increase in the area covered by trees (Smart *et al.*, 1985). This effect was quantified in experimental areas where there was long-term exclusion of grazing and browsing pressure and a marked tree regeneration (Smart *et al.*, 1985). Such studies illustrate the extent of major floristic and structural changes that correspond to changes in elephant numbers in savanna/woodland systems.

In Kibale National Park there are no good estimates of current elephant numbers available, but it is clear that their numbers have decreased dramatically since the time when they were surveyed in the mid-1960s (Wing & Buss, 1970). Lwanga (1994) provided information on tree preference of elephants in Kibale (the proportion of each species eaten or damaged by elephants divided by the proportion of the species in the sample area). Using these values, it was found that all of the common tree species (>2 individual ha^{-1}) which were selected by elephants showed an increase in abundance from the early 1970s to 1992. During this period elephant numbers were low in Kibale. It seems reasonable to speculate that the absence of elephants allowed these tree species to be recruited into the adult size classes.

Spatial variation in vegetation structure in Kibale may also relate to elephant activities. For example, if elephants concentrate their activity in particular areas for extended periods, they could create long-term changes in the abundance of their preferred tree species. Subsequently, it may take several decades for the abundance of these preferred tree species to reach previous levels, as they must rely on seedling growth and seeds arriving from outside the affected areas. Present evidence on elephant crop raiding in Kibale suggests that the elephants are using specific areas of the forest for extended periods of time (Naughton-Treves, 1996). This pattern of habitat use would create a landscape composed of patches of elephant degraded–elephant recovering lands. Evidence from stand curves in Budongo (Laws *et al.*, 1975) and Kibale (Osmaston, 1959) and examination of previous damage to felled trees (Laws *et al.*, 1975) all suggest that regeneration of the stand in these forests is not continuous and implicate concentrated elephant activity as the cause of periodic slowed regeneration. The distribution pattern of elephant activity is likely to be a function of their density, and the periodicity of their use of areas as a function of density warrants further consideration.

Finally, the window of time with which these forests have been studied is very short compared to the life span of the trees that make up the forests. Although

the Kibale National Park obtained its first legal status in 1932 when it was gazetted a crown forest, the first descriptions of the area were made in the late 1950s (Osmaston, 1959). Pollen diagrams from the Ruwenzori Mountain Lakes (Livingstone, 1967) and Kigezi in south-western Uganda (Hamilton, 1974; Hamilton, Taylor & Vogel, 1986), suggest extensive forest clearance by man approximately 1000 years ago. Within Kibale, a number of pits for storing grain and an array of potsherds have been discovered in what has traditionally been considered undisturbed forest (Lang Brown & Harrop, 1962). It seems likely that in many African forests, such as Kibale, human activities have altered forest composition for a considerable period of time. Differences in forest composition between areas may reflect the period of time that the area has had to recover from human induced disturbance. Based on what is known about the life history of the canopy trees in Kibale, identifying an area that has been disturbed 1000 years ago from one that had been disturbed 400 years ago, would be a very difficult task.

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