Human Ecology (2019) 47:765–775
https://doi.org/10.1007/s10745-019-00103-w

Evidence and Ecology of Historic Human Settlements in Kibale National Park, Uganda

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Abstract

Ecosystem conservation often focuses on protecting wild places, but many remote forests and expansive savannahs have a deep human history of ecosystem management. Here we document grinding stones in the center of a high conservation-value forest, Kibale National Park, Uganda, indicating a historic human presence. Grinding stones were found at a minimum density of one per 0.57 km^2 and in a range of forest types. Ecological plots around grinding stones were dominated by late successional tree species, although forest structure was comparable to formerly logged areas of Kibale. Building a more comprehensive understanding of human land-use before 1932, when protection policies began, will help explain current habitat heterogeneity. Future work should combine archaeology and ethnography to study the history and lifestyle of people who lived in Kibale. Understanding the role of people in this forest—and the role of the forest in local cultures—may elucidate contemporary ecology.

Keywords Forest structure · Conservation · Anthropogenic · Regeneration · Archaeology · Grinding stones · Kibale national park · Uganda

Introduction

Anthropogenic impacts on ecosystems often focus on the present or recent past, including logging or habitat fragmentation in the last half century (Gourlet-Fleury *et al.* 2013), but humans have also played important roles in deeper history (Chazdon 2003; Morin-Rivat *et al.*. 2017; Roberts *et al.* 2017). For example, in North America, forests that early Euro-American explorers identified as relatively untouched by humans actually reflect a long history of management by indigenous peoples (Denevan 1992). Similarly, the Serengeti, once thought by conservationists to be a "pristine" habitat, is now understood as having been maintained by pastoralists over millennia (Marshall *et al.* 2018). In fact, most tropical ecosystems, including forests, have a deep history of management by humans (Garcin *et al.* 2018; Levis *et al.* 2018). A holistic understanding of the history of human interactions is key for understanding and conserving those ecosystems, especially in tropical forests, where contemporary agricultural and industrial practices contribute to alarming deforestation rates (Curtis *et al.* 2018).

In East Africa, many of the forests have disappeared or become fragmented across landscapes (Aleman *et al.* 2018). Kibale National Park in western Uganda remains one of the last refuges in East Africa for a host of plant and animal species (Chapman *et al.* 2013). Kibale National Park is a tropical, mid-altitude forest with a mix of climax and regenerating forests, grasslands, and swamps, surrounded on all sides by agricultural land (Struhsaker 1997; Hartter and Southworth 2009; Hartter *et al.* 2015). Kibale is home to 13 primate species, and several long-term studies, such as those on red colobus monkeys and chimpanzees, have provided foundational knowledge about primate ecology and conservation, making Kibale one of the most well studied tropical forests, especially for primate behavior and ecology (Struhsaker 1997; Chapman *et al.* 2005b; Struhsaker 2010; Watts 2012).

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Given the scientific and conservation value of Kibale National Park, it is valuable to understand its history. Kibale became a Crown Forest Reserve in 1932 (with official demarcation in 1941), to enable systematic logging by British colonial forces (Osmaston 1959). Some parts of Kibale Forest experienced intensive logging through the 1970s whereas other parts were not logged and were maintained as a "nature reserve" (Struhsaker 1997). In addition, despite being legally protected, some parts of the forest were converted to homes and farms by a population of Ugandan agriculturalists who migrated to the area between the 1950s and 1990s (Van Orsdol 1986; Hartter *et al.* 2015). Several conservation studies have focused on direct human impacts on the forest ecosystem, for example assessing the impact of logging on primates in Kibale (Skorupa 1986; Struhsaker 1997; Chapman and Lambert 2000), or examining the spatial dynamics of illegal forest use (Mackenzie *et al.* 2011). Additional studies have investigated forest dynamics since the cessation of commercial logging. Grasslands that were protected from anthropogenic fires due to researcher presence have become forests (Lwanga 2003). Formerly logged areas have become reforested, although in some areas less rapidly than expected (Chapman *et al.* 1997; Lawes and Chapman 2006; Bonnell *et al.* 2011). Although the aforementioned studies provide insight into the impact of human activity on forest structure in Kibale, they focus on activities occurring over the past 60 years. The areas of the forest that were never part of logging concessions, however, are sometimes framed as "pristine" (Chapman *et al.* 2002), despite likely experiencing human occupation or use in the distant past (Chapman *et al.* 2010).

There is evidence of a long history of human presence in Kibale Forest. An early report on Kibale describes a small church in the center of the forest at a site called Ngogo, which had "been unoccupied for many years" (Osmaston 1959:10). Soil analysis suggests that grasslands within Kibale are anthropogenic (Lang Brown and Harrop 1962). Importantly, some studies have mentioned in passing the existence of several potsherds and grinding stones within the forest (Mitani *et al.* 2000; Isabirye-Basuta and Lwanga 2008; Watts 2012). Grinding stones were a common method for processing flour and other plant materials until quite recently, and to some extent are still used today in East Africa (Nixon-Darcus and D'Andrea 2017), including Uganda (Muhwezi *et al.* 2009). The presence of abandoned grinding stones indicates a history of humans in the landscape before it became a Reserve in 1932, but no study has explicitly documented the extent of settlement or contemporary ecology in formerly settled sites.

Here we report the presence of grinding stones in the center of Kibale National Park at the Ngogo site and describe their spatial distribution. In addition to describing the number and location of grinding stones, we examine the forest structure where grinding stones are present. If grinding stones are prevalent, it suggests a historic human presence in an area that has been considered to have minimal human disturbance. If grinding stones are associated with predominantly colonizing tree species and areas that resemble recently logged forests, it may indicate that human settlements were relatively recent and that there are long-term impacts to forest regeneration. Alternatively, if grinding stones are associated with late successional species and the forest is mature in these areas, it suggests a deeper history of human settlement and that the forest has since recovered. We consider this a first step in a multidisciplinary effort to document the relationship and dynamics of people in this ecosystem. Studying human-forest interactions before protectionist conservation policies were adopted nearly 90 years ago is key for understanding the state of ecology and biodiversity conservation today (Chapman *et al.* 2010).

Methods

Study Area

The study was conducted in the Ngogo area of Kibale National Park. Kibale National Park is a moist evergreen forest, approximately 795 km^2 in size, located between the coordinates 0.18–0.69° N and 30.22–30.55° E. Elevation ranges between 924 and 1623 m, and the Ngogo area falls between 1254 and 1515 m. Kibale Forest was gazetted as a Crown Forest in 1932, a Central Forest Reserve in 1948, and established as a national park in 1993 (Struhsaker 1997; Hartter and Southworth 2009). There are two rainy seasons annually, occurring in March through May and September through November, and two dry seasons, which occur

Fig. 1 Stones, worn by grinding, remain as subtle markers of historic human presence. Example of grinding stone found in Kibale National Park (**a**) with 3 × 5 in. notebook for scale, and (**b**) another grinding stone amidst saplings and small trees

December through February and June through August. Mean annual rainfall in Kibale National Park is 1749 mm (Chapman *et al.* 2005b). We recorded spatial locations for grinding stones between December 2017 and May 2018, and conducted ecological sampling between February and May 2018.

Grinding Stone Identification and Spatial Analysis

Grinding stones were encountered over the course of long-term research on chimpanzees at Ngogo by field staff from the region who were familiar with grinding stones, including one of the co-authors who has expertise in traditional practices of the local Batooro people. Another co-author identified additional grinding stones while studying chimpanzees from October 2017 to June 2018, which were confirmed by Ugandan co-authors. Grinding stones were found on an existing trail grid created by researchers to facilitate studying monkeys and chimpanzees, or were encountered in off-trail areas while following or searching for chimpanzees. The trails are generally oriented north-south and east-west, and are separated by approximately 50 to 100 m.

We conducted several analyses to understand the spatial distribution of grinding stones using a Geographic Information System (GIS) framework. To calculate the density of grinding stones, we determined the size of the minimum convex polygon in km^2 that contained all grinding stones, and divided that by the number of grinding stones. In addition, we calculated the minimum distance from each grinding stone to the next nearest grinding stone.

We used a 1-arc sec (30.87 m) spatial resolution SRTM digital elevation model (DEM), acquired from the US Geological Survey Earth Explorer portal, to test whether grinding stone locations were associated with patterns in terrain. To test whether grinding stones are found in relatively high elevation areas, we compared grinding stone elevation to the average elevation in a 170 m-radius zone around each grinding stone using a paired t-test. We determined 170 m as the radius because the closest grinding stone sites found were approximately 170 m apart from one another. To determine if grinding stones are situated on the highest ground in a given area, we compared elevation of grinding stones to the maximum elevation in the 170 m zone surrounding each grinding stone using a paired t-test. We also used the DEM to calculate a layer for slope in degrees. To determine if grinding stones are more likely to be found on flatter land, we compared slope at grinding stone locations to the mean slope in the 170 m-radius surrounding area using a paired t-test. We also tested whether grinding stones were located on the flattest possible area by comparing slope at grinding stone locations to the minimum slope in the 170 m-radius surrounding area using a paired-test. DEM processing, zonal statistic calculations, and statistical analysis were carried out in R (R Core Team 2018).

Ecological Plots

We determined plant diversity and forest structure in areas surrounding grinding stones through a stratified sampling method. For each grinding stone, we constructed a 20 × 20 m square plot orthogonal to magnetic north with the grinding stone in the center. We identified the species and measured diameter at breast height (DBH) of adult trees (>10 cm DBH) within this plot. We then selected a corner of the 20 × 20 m plot in which to construct a 10 × 10 m subplot, and we ensured that subplots did not contain research trails. We identified and measured DBH for saplings (between 2.5 and 10 cm DBH) within subplots. DBH was measured at a height of 1.30 m on the up-hill side of the tree for all specimens. For trees with stems diverging lower than 1.30 m from the ground, we measured and summed the DBH of the three largest stems. Species were identified at the time of sampling by two co-authors who both have extensive ecological experience in Kibale Forest. In addition, we recorded the forest type in which each plot was situated, based on classifications delineated by the Max Planck Institute's Pan African Programme (Arandjelovic *et al.* 2012). These plots allowed us to create a species inventory and calculate several ecological indices described below.

Ecological Data Analysis

We assessed the structure and successional stage of the forest in areas where grinding stones were found. We determined the successional stage of each tree species identified in the current study based on previous research on Ugandan and Kenyan forest succession (Lwanga 2003; Kirika *et al.* 2010). We then calculated plot-level measures for basal area, stem density, and Shannon's diversity index for life stage and successional stage ecological guilds. We calculated basal area as the circular area occupied by trees, using DBH measurements to obtain the radius of trees. We aggregated basal area calculations for each ecological guild within each plot and divided by the area sampled to get the $\mathrm{cm}^2/\mathrm{m}^2$ rate of area occupied by trees in the ecological guild. We calculated stem density by dividing the number of trees measured by the area sampled for each ecological guild within each plot. We also calculated Shannon's diversity index for adult and sapling trees for each plot using the 'vegan' community ecology package (Oksanen *et al.* 2018) in R.

To assess the successional stage of each plot, we calculated indices comparing basal area and stem density between early and late successional species for adult and sapling trees in each plot. We used the formula

$$\frac{x-y}{x+y}$$

where x is the structural measure (basal area or stem density) for late successional species, and y is the same measure for early successional species. This formula provided us with a value between −1 and 1 indicating the degree to which basal area or stem density for adults or saplings in each plot was dominated by early or late successional species. For a given structural measure, a value closer to −1 would indicate domination by early successional species, while a value closer to 1 would indicate domination by late successional species, and a value of 0 would indicate no bias between early and late successional species. We used paired t-tests to compare indices of successional domination between adult and sapling trees at the plot level to test whether the sapling guild contained more early or late successional stage species in comparison with the adult guild across grinding stone locations.

We contextualized the forest structure in this study by qualitatively comparing our basal area results for adult trees, differentiated by size class and forest type, to a previous study of forest structure in areas of Kibale National Park that had experienced varying degrees of logging intensity (Chapman *et al.* 1997). All data manipulations and statistical tests were carried out in R (R Core Team 2018).

Results

Grinding Stones

We recorded 21 grinding stones in the Ngogo area of Kibale National Park (example shown in Fig. 1). Three sites contained two grinding stones within 10 m of each other, whereas the remaining sites contained only one grinding stone. Grinding stones were distributed across an area of 11.95 km^2 at a density of one stone per 0.57 km^2 (Fig. 2). Grinding stones were found at a median distance of 195.26 m apart from one another, with a minimum distance of approximately 10 m, a maximum distance of 1.80 km, and a standard error of 110.18 m. Excluding grinding stones found within the same 20 × 20 m ecological plot, the minimum distance between independent sites with grinding stones was 168.57 m. For the statistical analysis on grinding stone elevation and slope, we excluded the three grinding stones found within the same ecological plot, leaving us with 18 stones.

Grinding stones ($N = 18$) were situated at high elevations relative to the surrounding area (mean difference = 3.42 m; paired t-test: $t = 3.07$, $p = 0.007$), but not at the highest-lying points in those areas (mean difference = −9.32 m, $t = -6.92$, $p < 0.001$). Grinding stones appeared to be on somewhat flatter surfaces than the average surrounding terrain (mean difference = −1.086 degrees, $t = -1.76$, $p = 0.097$), but were not found on the flattest parts of those areas (mean difference = 4.62 degrees, $t = 6.90$, $p < 0.001$).

Forest Structure and Ecology

We constructed ecological plots to measure forest structure and diversity for 17 of the 21 grinding stones. We excluded three grinding stones that were within 10 m of another grinding stone, selecting only one for the plot. We excluded one additional grinding stone that was discovered within the Ngogo Research Camp.

Grinding stones were present in a range of forest types, including savannah-bushy ($N = 1$), colonising forest ($N = 5$), open canopy forest ($N = 5$), and closed canopy forest ($N = 6$). Overall, we sampled a total area of 0.68 ha for adult trees and 0.17 ha for sapling trees. Across plots, we identified and measured 52 individual tree species in adult and sapling plots, and identified an additional 14 species within 20 × 20 m plots that were too small to measure as adults (Table 1). Across all adult plots, we found 45 unique tree species, an average (± SE) Shannon's diversity index of 1.92 ± 0.13, an average basal area of 45.80 ± 4.15 cm^2/m^2, and an average stem density of 598.44 ± 39.16 stems/ha. Across all sapling plots, we found 33 unique species, an average Shannon's diversity index of 1.64 ± 0.11, an average basal area of 4.38 ± 0.47 cm^2/m^2, and an average stem density of 2262.5 ± 198.72 stems/ha.

Structural Indices of Ecological Succession

We used plot-level indices to assess whether the forest composition in areas with grinding stones was trending towards later ecological succession. As described earlier, a value of −1 indicates complete domination by early successional species, a value of 1 indicates domination by late successional species, and a value of 0 indicates no bias between early and late successional species. Among adult trees, the average basal area successional index was 0.92 ± 0.03, and the average stem density successional index was 0.82 ± 0.05. Among sapling trees, the average basal area successional index value was 0.99 ± 0.01, and the average stem density successional index was 0.947 ± 0.02. Although both adult and sapling tree species were biased toward late successional trees, sapling plots compared to adult tree plots were more dominated by late successional species based on basal area (mean difference = −0.073; paired t-test: $t = -2.08$, $p = 0.055$) and stem density (mean difference = −0.124, $t = -2.16$, $p = 0.047$).

Comparison to Logged Sites in Kibale

We compared our findings with Chapman and Chapman's (1997) study of forest structure in Kibale National Park in sites that varied in the intensity of former logging activities. We found that overall, and across two of three forest types, larger trees represented the greatest share of basal area (Fig. 3a). This matches the size-class basal area distribution pattern found in unlogged and lightly logged forest areas (Fig. 3b). However,

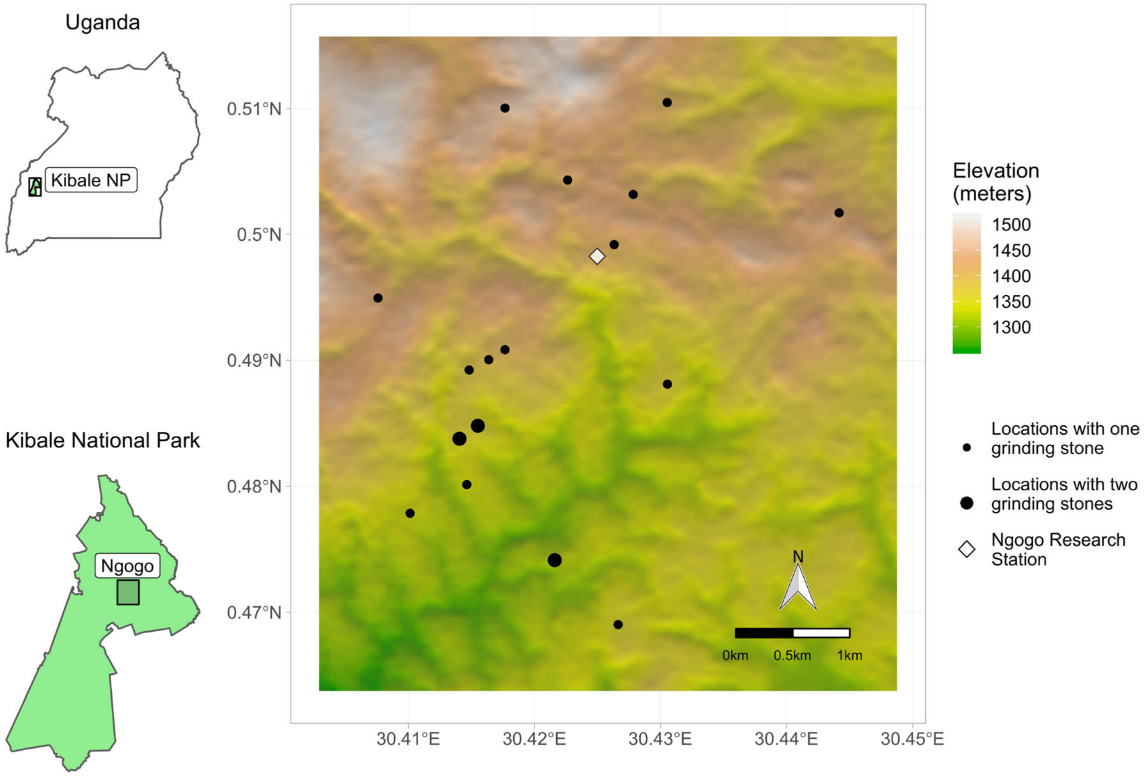


Fig. 2 Map of grinding stones found in the Ngogo area of Kibale National Park in western Uganda. A total of 21 grinding stones were found and included in this study. Points indicate grinding stone sites with one stone (small dot) or two stones (large dot); one grinding stone was found at the Ngogo Research Station (white diamond)

the average basal area across our ecological plots was less than half the basal area recorded for unlogged sites at Ngogo, and is more similar to basal area found in sites that had previously been subject to logging disturbance (Fig. 4) (Chapman and Chapman 1997).

Discussion

We documented 21 grinding stones–nearly two per square kilometer–scattered throughout the center of Kibale Forest in western Uganda. Previous studies have mentioned the presence of several grinding stones in Kibale Forest (Mitani *et al.* 2000; Isabirye-Basuta and Lwanga 2008), but this is the first report of their prevalence and distribution. Grinding stones were often at higher elevations than the surrounding areas, corresponding to reports that people lived on hills (Lang Brown and Harrop 1962). Three pairs of grinding stones were within the same site, approximately 10 m from each other. Other grinding stones were up to 1.8 km apart. Grinding stones found nearby one another suggest that multiple grinding stones originated within a single household or compound, whereas those at distances separated by over one kilometer likely indicate different settlements. Although the current study cannot assess the type and size of settlements, their distribution suggests that a network of former human settlements once existed in the forest that is now Kibale National Park.

Whether humans settled throughout what is now Kibale National Park, or only in the Ngogo area, is an open question. We report grinding stones in the limited area of Ngogo because that is where we have been conducting other research activities. It is possible that humans only lived in Ngogo, although we do not find this likely. Some grinding stones have been reported in other parts of the forest, including north (coauthor's observation) and south (Gerald Kirungi, pers. comm. 2018) of Ngogo. Importantly, 14 of the 21 grinding stones were found along trails forming a grid for use by researchers. Thus, it is likely that the number of stones documented in this study is an underestimate, and that additional surveys will uncover more grinding stones.

Grinding stones occurred in a variety of forest types. Most grinding stones were found in forests, including mature open or closed canopy forests, as well as colonizing forests. One was found in an area that is currently grassland. The variability in tree biodiversity and density across grinding stone sites indicates that settlements may have been occupied and/or abandoned at different time periods or that these sites have undergone divergent ecological processes since. For example, the grassland where one grinding stone was found has been

Table 1 Inventory of species found in 10 × 10 m and 20 × 20 m plots. Type denotes the successional stage of forest in which this species most frequently occurs. Succession type was derived from previous literature on Ugandan forest vegetation (Lwanga 2003; Kirika *et al.* 2010). Basal area is calculated as the area occupied by all individuals of that species using DBH measured at breast height relative to the area sampled per forest type. Stem density is calculated as the number of stems for an individual species in each forest type, divided by the area sampled per forest type. N indicates the number of 20 × 20 m plots for measuring adults and 10 × 10 m plots for recording saplings

			Overall		Colonising forest ($N = 5$)				Open Canopy ($N = 5$)				Closed Canopy ($N = 6$)			
					Adult		Sapling		Adult		Sapling		Adult		Sapling	
	Species	Type	Adult stems	Sapling stems	Basal Area	Stem Density	Basal Area	Stem Density	Basal Area	Stem Density	Basal Area	Stem Density	Basal Area	Stem Density	Basal Area	Stem Density
1	*Aeglopsis eggelingii*	late	4	2	0.0936	0.0005	0.0144	0.0020	–	–	–	–	0.7175	0.0012	0.0085	0.0017
2	*Albizia coriaria*	early	1	–	0.7978	0.0005	–	–	–	–	–	–	–	–	–	–
3	*Albizia gummifera*	late	1	–	0.4788	0.0005	–	–	–	–	–	–	–	–	–	–
4	*Allophylus dummeri*†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	*Aningeria altissima*†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	*Antiaris toxicaria*	late	–	1	–	–	–	–	–	–	0.0299	0.0020	–	–	–	–
7	*Aphania senegalensis**	unknown	7	5	0.9229	0.0015	0.0857	0.0020	1.8103	0.0015	0.0368	0.0020	0.0897	0.0004	0.2734	0.0050
8	*Balanites wilsoniana*	late	3	1	2.7063	0.0015	0.0799	0.0020	–	–	–	–	–	–	–	–
9	*Bequaertiodendron oblancelatum*	late	–	1	–	–	0.0153	0.0020	–	–	–	–	–	–	–	–
10	*Bersama abyssinica*†	early	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	*Blighia unijugata* †	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
12	*Cassipourea ruwensorensis*	late	2	2	–	–	0.3081	0.0040	–	–	–	–	0.1940	0.0008	–	–
13	*Celtis africana*	late	2	6	0.3659	0.0010	0.7866	0.0100	–	–	–	–	–	–	0.0267	0.0017
14	*Celtis durandii*	late	30	–	21.2325	0.0050	–	–	13.2882	0.0020	–	–	116.060	0.0067	–	–
15	*Celtis zenkeri*	late	1	–	–	–	–	–	–	–	–	–	0.0726	0.0004	–	–
16	*Chaetacme aristata*	late	5	2	–	–	0.0321	0.0020	0.1139	0.0005	0.0175	0.0020	2.9544	0.0017	–	–
17	*Chrysophyllum albidum*	late	37	16	3.3972	0.0025	0.2396	0.0080	89.3458	0.0075	3.2092	0.0180	106.824	0.0071	0.4743	0.0050
18	*Citropsis articulata*	late	–	4	–	–	–	–	–	–	–	–	–	–	0.3250	0.0067
19	*Coffea arabica**†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20	*Coffea spp.**†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
21	*Dasylepis eggelingii*	late	8	39	0.7754	0.0010	0.1177	0.0040	0.5253	0.0015	9.2669	0.0320	0.6629	0.0012	15.3139	0.0350
22	*Dictyandra arborescens**†	unknown	–	–	–	–	–	–	–	–	–	–	–	–	–	–
23	*Diospyros abyssinica*	late	39	22	26.8324	0.0060	0.9241	0.0100	18.4959	0.0045	2.0072	0.0120	79.8971	0.0075	4.4125	0.0183
24	*Diospyros congensis**	late	2	–	0.2097	0.0005	–	–	–	–	–	–	0.3349	0.0004	–	–
25	*Dombeya mukole*	early	6	–	0.9326	0.0010	–	–	2.1361	0.0015	–	–	0.1341	0.0004	–	–
26	*Dovyalis macrocalyx*	late	–	2	–	–	–	–	–	–	–	–	–	–	0.0642	0.0033
27	*Elaeodendron buchananii*	late	8	4	21.6062	0.0040	0.1204	0.0020	–	–	0.3591	0.0040	–	–	0.0981	0.0017
28	*Erythrina abyssinica*†	early	–	–	–	–	–	–	–	–	–	–	–	–	–	–
29	*Fagaropsis angolensis*	early	1	4	0.2821	0.0005	0.0813	0.0020	–	–	0.1589	0.0040	–	–	0.0107	0.0017
30	*Funtumia africana*	early	16	5	10.0110	0.0030	–	–	–	–	0.9314	0.0080	12.4148	0.0042	0.0207	0.0017
31	*Harrisonia abyssinica*	late	4	–	2.0018	0.0020	–	–	–	–	–	–	–	–	–	–
32	*Kigelia moosa*	late	1	–	–	–	–	–	0.0444	0.0005	–	–	–	–	–	–
33	*Leptonychia mildbraedii**	unknown	1	3	–	–	0.0368	0.0020	–	–	–	–	0.0471	0.0004	0.1210	0.0033
34	*Lindackeria bukobensis*†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35	*Lindackeria schweinfurthii**	late	3	1	–	–	–	–	0.0643	0.0005	–	–	0.9901	0.0008	0.0155	0.0017
36	*Lovoa swynnertonii*	late	1	1	–	–	–	–	–	–	0.0407	0.0020	2.7885	0.0004	–	–
37	*Markhamia platycalyx*	early	7	–	–	–	–	–	29.5168	0.0025	–	–	1.6607	0.0008	–	–
38	*Millettia dura*	late	12	–	9.2017	0.0040	–	–	–	–	–	–	1.5772	0.0017	–	–
39	*Mimusops bagshawei*	late	–	4	–	–	0.0229	0.0020	–	–	–	–	–	–	0.1003	0.0050

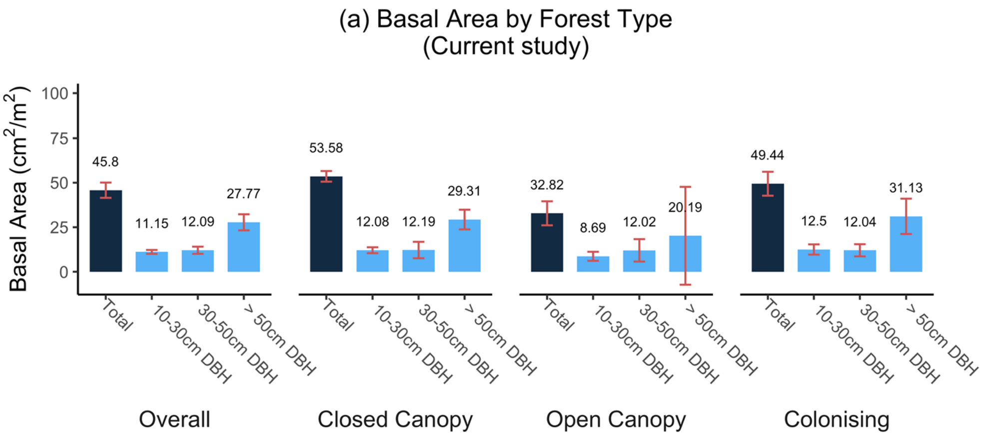
Table 1 (continued)

			Overall		Colonising forest ($N = 5$)				Open Canopy ($N = 5$)				Closed Canopy ($N = 6$)			
					Adult		Sapling		Adult		Sapling		Adult		Sapling	
40	*Monodora myristica*	late	–	1	–	–	–	–	–	–	–	–	–	–	0.0924	0.0017
41	*Morus lactea*	late	2	1	–	–	–	–	–	–	–	–	0.3049	0.0008	0.0197	0.0017
42	*Ochna spp.**	late	–	3	–	–	–	–	–	–	0.0575	0.0040	–	–	0.0464	0.0017
43	*Olea capensis welwitschii*	late	7	–	60.0693	0.0035	–	–	–	–	–	–	–	–	–	–
44	*Oncoba spp.**	late	1	–	1.1203	0.0005	–	–	–	–	–	–	–	–	–	–
45	*Pancovia spp.**	late	2	–	–	–	–	–	–	–	–	–	0.7391	0.0008	–	–
46	*Parinari excelsa**	unknown	2	–	–	–	–	–	–	–	–	–	11.9366	0.0008	–	–
47	*Piptadeniastrum africanum*†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
48	*Pleiocarpa pycnantha**	unknown	1	–	–	–	–	–	–	–	–	–	0.0770	0.0004	–	–
49	*Premna angolensis*	late	3	–	0.0868	0.0005	–	–	–	–	–	–	2.1781	0.0008	–	–
50	*Pterygota mildbraedii*	late	11	59	6.8923	0.0030	0.6891	0.0100	–	–	4.8909	0.0280	23.8323	0.0021	36.8630	0.0667
51	*Randia urcelliformis*	late	1	4	–	–	–	–	0.0788	0.0005	0.0799	0.0040	–	–	0.1671	0.0033
52	*Rauvolfia oxyphylla**	early	2	–	1.2213	0.0010	–	–	–	–	–	–	–	–	–	–
53	*Rothmannia whitfieldii**	late	1	5	–	–	–	–	–	–	0.1559	0.0060	0.0777	0.0004	0.0917	0.0033
54	*Sapium ellipticum*	late	3	–	6.9754	0.0015	–	–	–	–	–	–	–	–	–	–
55	*Spathodea campanulata*	early	1	–	0.9996	0.0005	–	–	–	–	–	–	–	–	–	–
56	*Strombosia scheffleri*	late	1	1	–	–	–	–	0.0465	0.0005	0.0269	0.0020	–	–	–	–
57	*Tabernaemontana holstii**	late	17	15	0.2034	0.0005	1.3151	0.0080	0.7017	0.0015	0.4991	0.0080	9.9355	0.0054	1.5015	0.0117
58	*Tabernaemontana odoratissima**†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
59	*Tabernaemontana spp.**†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
60	*Tarenna pavettoides*	late	1	3	–	–	–	–	–	–	–	–	0.0574	0.0004	0.2917	0.0050
61	*Teclea nobilis*	late	27	43	49.2980	0.0085	12.6118	0.0440	0.5437	0.0010	1.6139	0.0160	4.2829	0.0033	7.1202	0.0217
62	*Trichilia dregeana**	late	1	3	0.0788	0.0005	0.0107	0.0020	–	–	0.0277	0.0020	–	–	0.0091	0.0017
63	*Trichilia prieureana**†	late	–	–	–	–	–	–	–	–	–	–	–	–	–	–
64	*Uvariopsis congensis*	late	86	98	40.3718	0.0105	27.5825	0.0720	245.586	0.0200	62.2297	0.0800	56.5197	0.0104	15.0626	0.0367
65	*Vangueria apiculata*†	early	–	–	–	–	–	–	–	–	–	–	–	–	–	–
66	*Warburgia ugandensis*	late	11	1	41.4694	0.0055	0.1204	0.0020	–	–	–	–	–	–	–	–

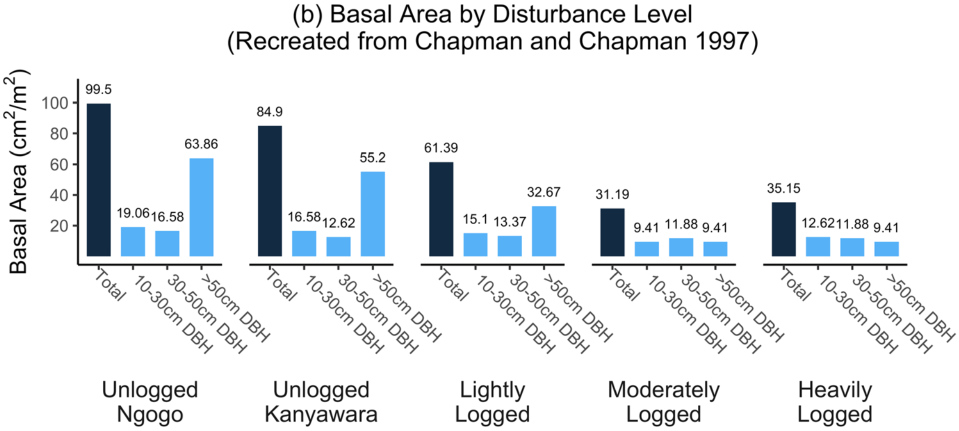
Markings next to species name:

*Successional type determined at the genus level

† Saplings found in 20 m plot, but not the randomly selected 10 m sub-plot for recording saplings



(a) Basal Area by Forest Type
(Current study)



(b) Basal Area by Disturbance Level
(Recreated from Chapman and Chapman 1997)

Fig. 3 Basal area for adult trees across tree size classes, differentiated between forest type, compared to basal area in unlogged (Ngogo and Kanyawara) and logged (Kanyawara) sites in Kibale National Park (Chapman and Chapman 1997)

maintained as grassland by anthropogenic fires, including as recently as 2018 (Lwanga 2003; authors' observations). On the other hand, the fact that some grinding stones were found in mature forest that would otherwise seem unaffected by humans suggests that some grinding stone sites are quite old. For example, one grinding stone occurred in a closed canopy forest with numerous *Chrysophyllum* trees, a tree characteristic of this altitude within Kibale Forest (Kingston 1967; Mucunguzi *et al.* 2007). Our finding that grinding stones occurred in different forest types is not surprising, as Kibale is quite a heterogeneous forest (Chapman *et al.* 1997; Potts *et al.* 2009; Potts and Lwanga 2014).

The prevalence of grinding stones in different forest types suggests that people may have played a role in shaping Kibale's ecological heterogeneity. Kibale National Park is a mosaic landscape of mature and secondary forest, as well as grassland and colonizing forest. There appears to be a trend towards reforestation and forest succession, as grasslands are colonized by forest and secondary forest matures (Chapman and Chapman 1997; Lwanga 2003; Omeja *et al.* 2016). These dynamics have far-reaching implications on primate population dynamics, fruiting patterns, nutritional composition of leaves, and forest conservation (Lwanga *et al.* 2000; Chapman *et al.* 2005a, 2010; Rothman *et al.* 2015). Studies on the causes of Kibale's patchiness have focused on logging activities in the 1970s (Struhsaker *et al.* 1996; Chapman *et al.* 1997), or illegal access and agricultural encroachment by communities living around the park (Van Orsdol 1986; Chapman and Lambert 2000; Mackenzie *et al.* 2011). However, a network of human settlements dating back to before the 1930s may have set the stage for the ecological dynamics seen today. Many forest-dwelling communities across the tropics practice shifting cultivation and subsistence hunting, which create a matrix of old-growth forest, secondary forest, and grassland (Finegan and Nasi 2004; Robinson and Bennett 2004; Padoch and Pinedo-Vasquez 2010). If communities that once lived in Kibale Forest practiced similar forms of agriculture and forest management, this may help explain the mosaic nature of the forest today.

In this study, we limited our analysis of forest structure to areas around grinding stones. By comparing our study to that of Chapman and Chapman (1997), we found that the distribution of trees across size classes is similar to unlogged or lightly logged forest, but the overall area occupied by trees more closely resembles sites that underwent moderate or heavy logging in the last half century. This may indicate that while low levels of disturbance have enabled large trees to grow uninhibited, these

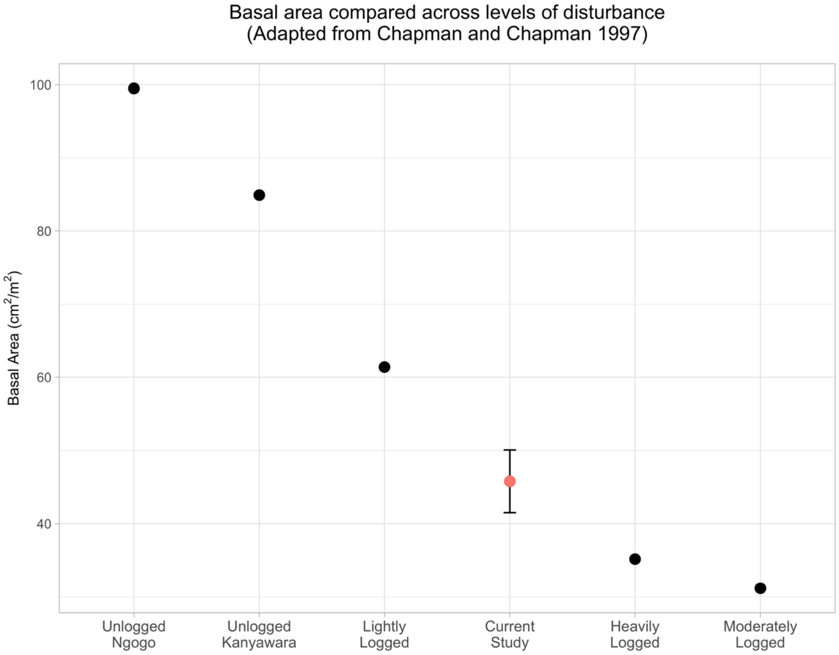


Fig. 4 Basal area of trees at grinding stone sites at Ngogo (red points with error bars) compared to unlogged (Ngogo and Kanyawara) and logged (Kanyawara) sites from Chapman *et al.* (1997) (black points)

areas of the forest are still regenerating. There are two other factors that may have contributed to this result. Most grinding stones were found near research trails, which represented 1.5 m–wide paths bisecting ecological plots. Such trails could represent a persistent disruption in forest regeneration, which may have minor ecological edge effects on nearby forest. Other grinding stones were found while following or searching for chimpanzees using trails blazed by elephants and other wildlife. In Kibale National Park, elephant habitat use is associated with slower forest regeneration (Struhsaker *et al.* 1996; Lawes and Chapman 2006).

It will be fruitful to determine to what extent former areas of historic human settlement have returned to mature forests. Several grinding stones were found in relatively mature forest, such as areas dominated by towering *Pterygota* trees and groves of *Chrysophyllum* trees. Both these species, it may be worth noting, are key foods for chimpanzees (Watts *et al.* 2012). However, there were some trees that are common in Kibale that did not appear in our plots. For example, we found no adult or sapling fig (*Ficus* spp.) trees near grinding stones. Future studies should compare forest structure in areas of former human settlements to those that did not have human settlements. We did not attempt this given the difficulty in determining areas of the forest lacking historic human habitation. As we have demonstrated here, forest areas that superficially appear to be mature and lacking human impact may in fact have experienced human management in the past. Determining areas with absent or lower historic human use would require a more detailed archaeological study identifying additional grinding stones and artifacts, employing participatory mapping with elders who have deep knowledge of the forest, and other methods.

A proper study of contemporary forest ecology needs to incorporate archaeology and anthropology (Briggs *et al.* 2006; Scharf 2014). To understand how people shaped the forest, future studies should (1) quantify forest structure in additional formerly settled areas, (2) determine the years of inhabitation at each grinding stone site, and size of the group living there through archaeological assessments, and (3) interview community elders and review archival records to collect narratives about forest use prior to National Park establishment. Humans are known to have lived in Kibale Forest, and these narratives are still known by people living around the park. The hills and grasslands have names. The Ngogo research site, for example, lies near Ngogo Hill. The origins of the word “Ngogo” and its meaning remain unknown. Ethnographic work may help answer such questions. It also remains unknown how long people have lived in the forest. Archaeological studies, including the dating of potsherds, would provide a chronology of human settlement in this forest (Robertshaw and Collett 1983; Robertshaw 1995).

What role did the forest occupy in people’s culture in the past? How has its role changed in the present day, considering demographic and socio-economic shifts in the area in the last 70 years (Hartter *et al.* 2015), and how have these shifts influenced patterns in resource use and forest regeneration? The answers to these questions carry implications for forest conservation. In the case of Kibale, people living around the Park today continue to rely on the forest for timber, animal protein, and grazing of cattle, most of which occurs illegally (Mackenzie *et al.* 2011). Beyond wood and meat, the forest may represent a cultural resource whose value cannot be replaced by revenue sharing alone (Bortolamiol *et al.* 2018). By the same token, local people whose histories and livelihoods are intertwined with the health of the forest may carry traditional ecological knowledge that should be considered an important piece of the puzzle for any lasting conservation outcomes in Kibale National Park. For durable partnerships between communities and conservationists, policy-makers should fully understand the relationship between local people and the ecosystem, and consider the forest as a coupled human-natural system.

Acknowledgements We thank the Uganda National Council for Science and Technology and the Uganda Wildlife Authority for permission to conduct research. We also thank the Makerere University Biological Field Station. For assistance identifying and documenting grinding stones, thanks to James Zahura, Alfred Tumusiime, Lawrence Ndangizi, Ambrose Twineomujuni, Brian Kamugyisha, and Braise Mugyisha. For additional advice and assistance, thanks to Isabelle Clark and Alinaitwe Izidol. For comments on an earlier version of the manuscript, we thank two anonymous reviewers. This project was inspired by the late Jerry Lwanga.

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