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A 40-year Evaluation of Drivers of African Rainforest Change

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Abstract

Background: Tropical forests are repositories of much of the world's biodiversity and are critical for mitigation of climate change. Yet, the drivers of forest dynamics are poorly understood. This is in large part due to the lack of longitudinal data on forest change and changes in drivers.

Methodology: We quantify changes in tree abundance, diversity, and stand structure along transects first enumerated in 1978 and resampled 2019 in Kibale National Park, Uganda. We tested five predictions. First, based on the purported role of seed dispersal and herbivory and our quantification of changes in the abundance of frugivores and herbivores, we tested two predictions of how faunal change could have influenced forest composition. Second, based on an evaluation of life history strategies, we tested two predictions concerning how the forest could have changed following disturbance that happened prior to written history. Finally, based on a 50-year climate record, we test the possible influence of climate change on forest dynamics.

Results: More trees were present on the assessed transects in 2019 (508) than in 1978 (436), species richness remained similar, but diversity declined as the number of dominant species increased. Rainfall increased by only 3 mm over the 50 years but this effect was not significant. Annual average monthly maximum temperature increased significantly by 2.2°C over 50 years. The abundance of frugivorous and folivorous primates and elephants increased over the 50 years of monitoring. The predictions that as the abundance of seed dispersing frugivores increases the abundance of their preferred fruiting tree species would increases and that as the abundance of folivorous would cause a decline in their preferred species were both not supported. Since Kibale was disturbed prior to historical records, we predicted that light-demanding species would decrease in abundance, while shade-tolerant species would increase - this was supported. Finally, while temperature increased over the 50 years, we found no means to predict *a priori* how individual species would respond.

Conclusions: Our study revealed subtle changes in the tree community over 40 years, sizable increases in primate numbers, a substantial increase in the elephant population and an increase in local temperature. Yet, a clear picture of what set of interactions impact the change in the tree community remains elusive. Our data on tree life-history strategies and frugivore/herbivore foraging preferences suggest that trees species are under opposing pressures.

Introduction

Tropical forests are repositories of much of the world's biodiversity. Covering only 7% of the world's land surface, tropical forests account for 60% of the world's biodiversity (Bradshaw, Sodhi and Brook 2009). These forests are critical to successful mitigation of climate change. For example, tropical forests and wetlands are estimated to contribute 23% of the mitigation needed to limit global warming to 2°C by 2030 (Griscom *et al.* 2017; Wolosin and Harris 2018). Yet, these forests are increasingly threatened. Globally, ~60 million ha of tropical primary forest were lost from 2002 to 2019, with most forest loss occurring in Brazil (24.5 Mha), Indonesia (9.5 Mha), and the Democratic Republic of the Congo (4.8 Mha)(Weisse and Gladman 2020). To put this in perspective, an area of old-growth tropical forest larger than Madagascar was lost over

18 years. Restoring tropical forest is a necessary part of mitigating the effects of climate change and requires an understanding of what naturally drives tropical forest dynamics and the ecological processes that are affected (Ma *et al.* 2016). Surprisingly, the drivers of forest dynamics are poorly understood, due in large part to the lack of suitable longitudinal data spanning decades. Many of the species involved in structuring tropical forest ecological systems have generation times stemming from years to many decades (trees Swaine, Lieberman and Putz 1987; birds Sæther *et al.* 2005; mammals Clutton-Brock and Sheldon 2010) and their populations typically respond very slowly to most environmental changes that are anything short of catastrophes (Chapman *et al.* 2013a; Jezkova and Wiens 2016).

Further complicating our understanding of the drivers of tropical forest dynamics is the need to consider the synergistic interaction of multiple drivers. Important interacting processes include pollination, seed dispersal and predation, herbivory, disease, competition, disturbance regimes, and climate. All of these are perturbed by human actions and the legacy effect of human imposed disturbance that occurred decades or centuries earlier has to be considered (Richards 1996). Furthermore, normative ecosystem response is obscured by stochastic events like droughts (Condit *et al.* 2017). Thus, it is hardly surprising that our understanding of driving factors/processes has often been judged by examining the strong signal produced by extreme events. For example, Harrison et al. (2013) provided detailed tree census data 15 years after intensive hunting eliminated most large frugivores. They documented a consistent decline in tree diversity but found no evidence of reduction in above-ground biomass (see also Chapman *et al.* 2003; Poulsen, Clark and Palmer 2013). Their study clearly illustrates the importance of frugivores in maintaining tree diversity but does not contribute to an understanding of the relative importance of drivers of forest composition under less extreme conditions.

Here, we quantify changes in tree abundance, diversity, and stand structure (species rank abundance, and size class structure) and mammal abundance of ten species in Kibale National Park, Uganda (hereafter Kibale) between 1978 and 2019. We consider five drivers of change and how they have affected the forest tree community over 23-50 years.

Mounting evidence suggests bottom-up processes, like seed dispersal and herbivory, are dominant drivers of tropical forest communities (Crawley 1989; Wright and Jones 2006; Wright *et al.* 2007; Chapman *et al.* 2013a). For example, a reduction in populations of large-bodied seed-dispersing primates corresponds with lower seedling densities of large-seeded forest trees species (Chapman and Onderdonk 1998; Pacheco and Simonetti 2000) and higher seedling aggregations around parent trees (Pacheco and Simonetti 2000). Similarly, by foraging on trees, elephants (*Loxodonta africana*) can convert forest ecosystems to grasslands (Laws 1970; Stuart, Hatton and Spencer 1985; Dublin, Sinclair and McGlade 1990; Wright and Jones 2006). Folivorous primates can also shift tree community structure by eating leaves of preferred species to the extent that the trees die, or by eating flowers to the degree that species cannot set fruit (Hladik 1977; Chapman 1995; Jin-Eong 1995; Chapman *et al.* 2013a; Chapman *et al.* 2013b). Based on the purported role of seed dispersal and herbivory in structuring tropical forests, we advance two predictions. First (*Prediction 1*), an increase in the abundance of seed dispersing frugivores is expected to correspond to an increase in the abundance of fruit bearing trees prominent in their diet and *vice versa*. Second (*Prediction 2*), increases

in arboreal herbivore/folivore abundance is expected to correspond to a decrease in the abundance of their preferred foods.

Research since the 1980s has shown that many forests traditionally considered “pristine” were disturbed by people relatively recently (i.e., between 100 and 4000 years ago (Clark 1996)). For example, the first paleoecological studies from the Darien of Panama, an area previously described as one of the last untouched Neotropical forests, revealed an extensive 4000 year old history of human disturbance (Bush and Colinvaux 1994). Similar evidence has accumulated for many other regions, including Africa, Central America, and Amazonia (Gomez-Pompa 1987; Tutin and Oslisly 1995; Richards 1996; Bush *et al.* 2007). Disturbance influences what resource allocation (Grubb 1977; Bloor and Grubb 2003; Zanne and Chapman 2005; Zanne, Chapman and Kitajima 2005; Kitajima and Poorter 2008) and recruitment strategies of trees (Coley 1983; Hubbell *et al.* 1999; Dalling *et al.* 2012) are most adapted for a particular location and time following the disturbance. For example, light-demanding species are better adapted to recruit in gaps following disturbances and use new resources for growth, while shade-tolerant species tend to recruit into the system slowly over decades and invest more in their wood density, roots, and defensive mechanisms (e.g., plant toxins) so that they are not disrupted by herbivory during their establishment (Grubb 1977; Richards 1996; Wright 2002; Chave *et al.* 2009). In addition, some species are adapted to recruit after catastrophic disturbances that create extremely large clearings and these large clearings can be made naturally or through human actions (Chazdon 2003). For example, mahogany (*Swietenia macrophylla*) recruits in areas dramatically disturbed by hurricanes (Snook 1996) or in areas of erosion or in forests killed by flooding (Gullison *et al.* 1996). With respect to Kibale, the rainforest was disturbed by people prior to written or oral history, thus we make the following predictions. First (*Prediction 3*), we predict that light-demanding species should decrease in abundance between 1978 and 2019, while shade tolerant species increase. Second, (*Prediction 4*) tree species that recruit in areas typically disturbed by human clearance (i.e., larger than a single tree fall gap) should decline in abundance over the 40 years.

Plants respond to slight shifts in temperature and rainfall associated with climate change (van Vliet and Schwartz 2002; Walther *et al.* 2002). For example, the average first flowering date of 385 British plant species has advanced by 4.5 days over the past decade compared to the previous four decades (Fitter and Fitter 2002; Wolkovich *et al.* 2012). In Panama, flower and seed production increased during El Niño years (Wright and Calderón 2006). In Kibale, annual fruiting varied over 3.8-fold between 1998 and 2013 and fruiting was positively influenced by temperature, rainfall, and solar radiation. As we have documented such relationships among climate and phenology patterns in Kibale (Chapman *et al.* 2005; Chapman *et al.* 2018b), we propose the following prediction, *Prediction 5* shifts in the composition of the tree community correspond to directional change in the climate at Kibale. We develop scenarios of tree community response to climate change based on habitat preferences (e.g., trees that typically occur in wet valley bottoms will increase in abundance if the climate gets wetter).

Methods

Study Site and Vegetation

Our longitudinal study of vegetation was conducted in Kibale National Park, Uganda spanning the period from the first assessment of forest composition conducted in December 1978 to the resampling of the same plots completed in May 2019 – 40 years and 5 months apart. The 795 km^2 park is in western Uganda (0° 13' - 0° 41' N and 30° 19' - 30° 32' E) near the foothills of the Rwenzori Mountains (Struhsaker 1997; Chapman and Lambert 2000). Kibale is dominated by mid-altitude (920 - 1590 m), moist-evergreen forest that receives a mean annual rainfall of 1655 mm (1970 – 2020).

Rainfall data were collected immediately adjacent to the study area. The daily rainfall data were summarized per month. The collection of these meteorological data was maintained through rebel intrusions into the park and the COVID19 pandemic and data for only 8 of a total 612 months were incomplete and thus not included. For the missing 8 months, we fitted an ARIMA time series model with Fourier terms for seasonality to interpolate these values using all other values. Temperature data (daily minimum and maximum) were collected over the same period. However, thermometers had to be replaced several times, and they were relocated twice (first by a distance of ~ 1 km, and then by only 30 m). An analysis of the temperature data from 1970 until 2020 indicated that these changes in thermometer and location (hereafter sources) had impacts on measured temperature that were challenging to control for. For example, the magnitude of the difference between minimum and maximum temperature appears to vary with the source (i.e., some thermometers show higher max. temperature, hereafter T_{max}, and lower min. temperature, hereafter T_{min}). Therefore, we used the TerraClimate dataset (http://www.climatologylab.org/terraclimate.html; (Abatzoglou *et al.* 2018). Temperature from this dataset was correlated with the different monthly temperature sources measured on the ground (Pearson's correlation coefficient for T_{max}: 0.46 – 0.80; for T_{min}: 0.14 – 0.40).

There has been a long history of human presence in the Kibale region. Pollen analyses and archeological studies indicate that there was widespread deforestation throughout much of Uganda between 2000 and 5000 years ago associated with the spread of Bantu-speaking agriculturalists (Langdale-Brown, Osmaston and Wilson 1964; Hamilton 1974; Hamilton 1984; Hamilton, Taylor and Vogel 1986; Taylor, Marchant and Robertshaw 1999). Sediment cores near the study site indicate a second period of forest clearing at approximately 400 years ago (Taylor, Marchant and Robertshaw 1999). Potsherds and grinding stones have been found in the forest (Struhsaker 1975; Mitani, Struhsaker and Lwanga 2000; Isabirye-Basuta and Lwanga 2008; Chesterman *et al.* 2019) and the decorations on the pottery are typical of the period between 200 to 400 years ago (Isabirye-Basuta and Lwanga 2008). In the 1950s, Osmaston (1959) described a small long-abandoned church in the center of the forest and soil analysis indicates that the grasslands enclosed within Kibale are of anthropogenic origin (Lang Brown and Harrop 1962). Kibale forest was established as a Crown Reserve between 1926 and 1932 for sustained hardwood timber production and became a National Park in 1993 (Struhsaker 1997; Naughton-Treves 1999; Chapman, Struhsaker and Lambert 2005). The study area in Kibale (K-30, 282 ha) was not logged and there was no timber harvest before 1970 (Struhsaker 1975) and none has occurred since. Kibale is now well protected from poaching, timber harvesting, and agricultural encroachment. The Uganda Wildlife Authority (UWA) regularly (9.2 days a month; data from 2005 to 2017) sends out patrols to prevent encroachment (Hou *et al.* 2021) and poaching by snaring game is limited by find-and-remove programs (Hartell *et al.* 2020).

Botanical Sampling and Species Categorization

In August 1971, transects were established along compass bearings and all woody plants greater than 10 m in height within 2.5 m of the center of the transect were identified. The set of transects were 2833 m in length in an area of approximately 2 km^2. The transects were resampled in December 1978, at which time the Diameter at Breast Height (DBH) of the trees was measured. We used these 1978 data (436 trees) to ensure that the same trees were sampled at different times. These transects have been maintained over the decades. The transects were resampled in May and June 2018 and 2019 and differences in the presence or absence of trees were investigated and clarified and 2019 measurements were used in analyses (Table 1).

We categorized species as light-demanding or shade-tolerant from a statistical assessment of stem distribution among habitats described in Zanne and Chapman (2005) (see also Zanne, Chapman and Kitajima 2005). Briefly, over two years Zanne and Chapman (2005) quantified tree density (newly germinated seedlings to adults) in each of four canopy types (closed canopy forest, treefall gaps, forest/ grassland edge, and grassland) for 63 species. For rare species not found in these habitat plots, categorization is based on descriptions in Eggling and Dale (Eggeling and Dale 1952), Polhill (1952-), Hamilton (1991), Katende et al. (1995), Lwanga (1996), and an independent assessment made by Peter Grubb, based on his observations of seedlings and saplings in Kibale and elsewhere (Grubb, P. pers. comm.). Since the disturbance that occurred in Kibale happened a few hundred years ago, we are not considering pioneer species that rapidly colonise after disturbance and die out 20-40 years later (e.g., *Cecropia, Muntingia, Trema*).

Large canopy-level trees were assigned as large-gap specialists if they preferentially recruited into gaps that were larger than those created by tree falls (Langdale-Brown, Osmaston and Wilson 1964; Chapman *et al.* 1999; Chapman *et al.* 2008; Isabirye-Basuta and Lwanga 2008). Building on habitat associations of trees in Kibale (Zanne and Chapman 2005), Chapman et al. (2010a) identified four large-gap species that were not early successional (pioneer) species (i.e., species that die within 20-40 years after they colonize a disturbance). These four species often become canopy level trees in old-growth forest: – *Celtis africana, Celtis durandii, Diospyros abyssinica*, and *Funtumia latifolia*. The lifespan of these trees is unknown, but it is likely that they live at least a few hundred years. To further verify if these species typically recruit after large anthropogenic disturbances, we established seven 200 by 10 m plots in the study area and seven similar plots in a large disturbed area immediately adjacent to the study area (Nyakatojo 86.2 ha). This disturbed area was an anthropogenically derived grassland, dominated by elephant grass (*Pennisetum purpurem*), but between 1967 and 1968 the area was converted to a pine plantation (Kingston 1967; Struhsaker 1975). The pines were harvested in 1998 and the natural forest was left to regenerate (Zanne *et al.* 2001; Duncan and Chapman 2003; Omeja *et al.* 2016). We expected that the four species that usually recruit into large disturbed areas would dominate this recently disturbed area. This proved to be true and thus these four species were used to test *Prediction 4;* that they would decline in abundance over the 40 years as they were expected to recruit fewer trees than other species.

Changes in Seed Disperser and Herbivore Populations

To evaluate if changes in the abundance of the seed dispersing frugivores (*F*) or herbivores (*H*) have driven species shifts in the tree community (*Predictions 1* and *2*), we monitored changes in the relative abundance of the following mammal species; primates - redtail monkeys (*Cercopithecus ascanius - F*), blue monkeys (*C. mitis - F*), and mangabeys (*Lophocebus albigena - F*), red colobus (*Piliocolobus tephrosceles – H*) and black-and-white colobus (*Colobus guereza - H*); ungulates - red duiker (*Cephalophusharveyi – H)*, blue duiker (*Cephalophusmoniticola - H*), and bushbuck (*Tragelaphusscriptus - H)*; pigs bushpig (*Potamochoerus larvatus - H*); and elephants - forest elephants (*Loxodonta cyclotis - H*), savanna elephants (*Loxodonta africana - H*), and their hybrids.

A single species may have multiple ecological roles, such as sometimes being a folivore, but also eating fruits and dispersing seeds. The classification of predominantly *F* or *H* was based on published descriptions of animal species' diets ((Oates 1977; Rudran 1978; Olupot 1998; Chapman, Chapman and Gillespie 2002; Stickler 2004; Rode *et al.* 2006; Struhsaker 2017) and extensive observation and sampling of dung (CAC unpublished data). The potential effects of elephants and the primates on forest dynamics are clearly documented (Wing and Buss 1970; Oates 1977; Rudran 1978; Olupot 1998; Chapman, Chapman and Gillespie 2002; Stickler 2004; Rode *et al.* 2006; Omeja *et al.* 2014). However, these effects are not so clear for less well-known duikers, bushbuck, and bushpigs. While, duikers are largely frugivorous, acting as seed dispersers (Gautier-Hion, Emmons and Dubost 1980; McCoy 1995; Brugiere *et al.* 2002; Molloy and Hart 2002), their effect on seedling dynamics is only partially understood (Lwanga 1994). Bushbuck are browsers (Gautier-Hion, Emmons and Dubost 1980) but their influence on forest dynamics is not known. Bushpigs forage on the forest floor often eating tubers and are known to prey on seeds of several prominent canopy tree species, including: *Balanites wilsoniana, Chrysophyllum albidum, Cordia millenii, Mimusops bagshawei,* and *Parinari excelsa.* While some seeds pass through their gut intact, this is uncommon (Rafael Reyna-Hurtado unpublished data, Ghiglieri *et al.* 1982). Their role in forest dynamics is poorly understood.

We assessed primate abundance (groups/km walked) in six censuses, each of a year's duration, between 1970 and 2019 (1970 (Struhsaker 1975), 1980 (Skorupa 1988), 1996, 2005, 2014, 2019 (Chapman *et al.* 2010b; Chapman *et al.* 2018a, Chapman 2019 unpublished data). We conducted 165 transect walks and covered 660 km. To minimize sources of error, we used the same methods each year and walked the same 4 km transect once per month for 12 months. Censuses were conducted between 0700 hours and 1400 hours at a speed of approximately 1 km/hr. The census team comprised experienced observers. With these methods, we estimated the number of groups/km walked. It is impossible to obtain accurate group counts during these censuses because some species occurred in groups of over 150 animals, while the cryptic behaviour of others make it difficult to detect all individuals. Thus, we separately evaluated group size in three periods (July 1996–May 1998, July 2010–May 2011; May 2017-May 2018, N = 220 group counts; (see Gogarten *et al.* 2015 for an analysis of the first two periods). Three observers spent approximately eight days each month with the sole aim of accurately estimating group sizes.

For duiker, bushbuck, bushpig and elephants, we evaluated changes in abundance through track and dung counts made in 1996, 2005, 2014, and 2019 along the same 4 km transect used to determine the abundance of the primates. A single set of tracks in a line was counted as one sighting. Both dung and tracks were removed after they were counted to ensure that they were not repeatedly counted. The tracks and dung of

the two duiker species can be distinguished when the sign is of good quality, but quality declines over time and depends on the season and environment. Thus, it was not always possible to distinguish the species, so we report a combined duiker value. Censuses of duiker, bushbuck, and bushpigs in Kibale are available from prior to 1996 (Nummelin 1990; McCoy 1995; Struhsaker 1997; Lwanga 2006); however, there are methodological differences among studies (Struhsaker 1997) that make comparisons problematic.

To examine *Prediction #1* that changes in the abundance of seed dispersing frugivores results in a corresponding change in the abundance of fruit-bearing tree species, we determined the 10 most frequently used fruiting tree species for blue monkeys (Rudran 1978), redtail monkeys (Stickler 2004 only in the K30 area), and mangabeys (Olupot 1998 data from 1992 and 1993). These species often eat fruits from the same species and this comparison produced 17 tree species that were examined for changes in their abundance (Table 2). *Prediction #2* was evaluated for folivorous primates and the tree species most likely to be killed by colobine foraging (2013a) were monitored for their change in abundance from 1978 to 2019 (Table 3). In addition, for *Prediction #2* we expected that tree species preferred by elephants would change in abundance with changes in elephant numbers. The species preferred by elephants were determined from several studies (Kasenene 1980; Kasenene 1984; Kasenene 1987; Lwanga 1994; Struhsaker, Lwanga and Kasenene 1996; Omeja *et al.* 2014) (Table 4). To quantify elephant feeding preferences their tree species selection ratio was calculated (for details of the calculation see Omeja *et al.* 2014). A ratio greater than one indicates the species was selectively browsed. The foraging preferences of bushpigs, duiker, or bushbuck are insufficiently known to permit predictions of how they may affect forest composition change. However, we report on changes in the abundance of these species so that evaluations may be made in the future.

Analysis

We estimated sampling saturation or completeness and species richness of the tree community using the estimator of sample coverage in the R package ‘iNEXT’ (Hsieh, Ma and Chao 2013). Because species richness is not sensitive to species abundances and gives disproportionate weight to rare species, we measured tree species diversity with Hill’s numbers (Jost 2006), using the ‘entropart’ package (Marcon and Hérault 2013) for R version 4.0.2 (R-Core-Team 2020). We used the following Hill’s numbers (Gotelli and Chao 2013): species richness (0D); the number of ‘common’ species in the community (1D) measured as the exponential of Shannon’s entropy; and the number of ‘very abundant’ or ‘dominant’ species in the community (2D), measured as the inverse of the Simpson index (Chao, Chiu and Hsieh 2012).

Climate change influences forest plant community composition and structure, either directly (e.g., causing tree or seedling death) or indirectly (e.g., causing the disruption of processes such as pollination). We investigated changes in several descriptors of climate over the period 1970-2019. For rainfall, we examined annual totals and monthly averages calculated over the entire period. For both maximum and minimum temperature (T_{max} and T_{min}), we examined mean annual monthly temperatures, and monthly means over the period 1970-2019. In addition to general summaries, including mean values, and the range of values, we examined the variation (Coefficient of Variation; CV) in annual trends from 1970 to 2019 using a time series decomposition. For rainfall, T_{min}, and T_{max}, we applied a “Seasonal and Trend decomposition using Loess”

(STL) in the 'fabletools' package for R. We applied linear models to the trend component from these decompositions as the outcome variable and date as the predictor variable.

Results

The Forest in 1978 and 2019

More trees were present on the sampled transects in 2019 (508) than in 1978 (436), but species richness remained similar, decreasing by only two species (Table 5). Diversity (H') declined as the number of dominant species (2D) increased, suggesting the community assemblage became more even over the 40 years, particularly with respect to the common species.

Change in Kibale's Climate

The average annual rainfall from 1970 until 2020 was 1655 mm and ranged from 1197 mm in 1993 to 2214 mm in 1996 (Figure 1), however time series analysis showed no significant variation or change in rainfall over the long-term. Rainfall increased by 0.06 mm/year and by 3 mm over the 50 years but this effect was not significant (P = 0.16).

There are two distinct rain seasons in Kibale, with a first peak in April and a second peak in October. On average, the wettest month of the year (October) received 253 mm rainfall, whereas the driest month (January) received 59.6 mm. The annual average monthly T_{max} from 1970 until 2019 was 26 °C and ranged from 24.8 °C in 1975 to 27.6 °C in 2019. The annual average T_{min} was 13.8 °C, ranging from 12.7 °C in 1971 to 15.3 °C in 2009. Both the annual average monthly T_{max} and T_{min} increased over time. T_{max} increased by 0.043 °C/ year and by 2.16 °C over 50 years, while Tmin increased by 0.036 °C / year and by 1.78 °C over 50 years. In contrast to rainfall, there are single annual peaks for T_{max} and T_{min}. Maximum monthly temperatures are usually recorded in February with an average of 27.7 °C, and the lowest T_{min} of 13.1 °C in January.

Changes in Animal Abundance

While the number of groups of frugivorous seed-dispersing monkeys detected per km walked fluctuated slightly over time, there was no significant change in the relative abundance of groups over the last 50 years (Table 6). The only exception to this trend was a decrease in abundance of blue monkeys. This decrease has been monitored and is occurring park-wide (Butynski 1990; Chapman *et al.* 2000; Chapman *et al.* 2010b). However, mean group size increased for all frugivorous primate species between 1996 and 2018 (Table 6) and thus primate density in the area actually increased.

Similarly, the abundance of folivorous primates - red colobus and black-and-white colobus - groups in the area varied slightly between 1970 and 2019, but with no overall change in group density. However, again group sizes increased and thus population density (number of individuals per km walked) increased (Table 6).

In general, the abundance of elephants, duiker, and bushbuck increased between 1996 and 2005 and has remained relatively stable since. In contrast, bushpig abundance increased from 1996 until 2008 and declined thereafter (Table 6).

Evaluation of the Predictions

Prediction 1: *as the abundance of seed dispersing frugivores increases, the abundance of their preferred fruiting tree species increases*. Of the 17 preferred species in the diet of the frugivorous primates, seven increased in abundance as predicted, three declined, and for seven there was no change in abundance (Table 2). Given that greater rates of seed dispersal with increasing frugivore numbers would take time to be represented as fruit-bearing trees, we examined if there was an increase in the abundance only in the smallest size classes. Considering only those stems between 10 and 15 cm DBH, four species increased as predicted, five decreased, and for the remainder there was no change in abundance. Thus, *Prediction 1* was not supported.

Prediction 2: as the abundance of folivorous primates increases, the abundance of heavily defoliated tree species declines. Of the 13 tree species frequently used by colobus, seven occurred in the sample area. Of these (90 trees across both sampling years, 6.9 individuals per species, range 1-40), four species support the prediction, two species increased contrary to the prediction, and for one species there was no change (Table 3). Considering only the two species with ≥10 individuals (*Dombeya mukole, Markhamia lutea*), both species declined in abundance in accordance with the prediction.

Also, with respect to *Prediction 2*, we expected that *as elephants increased in abundance, the tree species that elephants preferentially fed on would decline.* There were twelve highly preferred elephant food species (Table 4). Of those in the area, 56% increased in abundance, the opposite to what was expected, 33% decreased as expected, 11% remained the same (Table 4). Considering only those species with ≥10 individuals, all three increased in abundance. Thus, *Prediction 2* as it applies to elephants was not supported.

Prediction 3: as the forest was disturbed by humans prior to written history, we predicted that light-demanding species would decrease in abundance between 1978 and 2019, while shade-tolerant species would increase. As predicted, light-demanding species decreased in abundance (1978 - 65.4%, 2019 – 50.8%), while the abundance of shade-tolerant species increased (1978 – 34.5%, 2019 – 49.2%) (Table 5). Consistent trends were observed for all species and the ten most abundant species (Table 5). Comparing rank abundance curves there was a decrease in the dominance of light demanding species and an increase for shade-tolerant species (Figure 2). Comparing the size-frequency distributions of light-demanding and shade-tolerant species, they follow the expected J-shaped curve (Figure 3). The increase in shade-tolerant species was particularly marked in the smaller DBH size classes (<40 cm DBH) and shade-tolerant species dominated the 10-19.9 cm DBH size class (Figure 3). Thus, *Prediction 3* was supported.

Prediction 4: large-gap tree species were predicted to generally decline in abundance as they represent senescing individuals that recruited into disturbed areas 200-400 years ago. Four tree species are known to recruit into large disturbed areas (Chapman *et al.* 2010a). The density of these four species was greater in

the recently disturbed area (Nyakatojo) adjacent to our study site (*Celtis africana* – Nyakatojo proportion 5.4 individuals/ha, old-growth 4.4; *Celtis durandii* – 19.8, 12.8; *Diospyros abyssinica* – 15.6, 10.0; *Funtumia latifolia* 11.7, 2.5), thus these species are undoubtedly large-gap specialists. *C. durandii* and *D. abyssinica* declined in abundance in the old-growth forest between 1978 and 2019; however, *C. africana* and *F. latifolia* did not. Thus, *Prediction 4* was not upheld.

Finally, in *Prediction 5:we argued that a directional change in the climate in Kibale should be associated with a species shift in the composition of the tree community.* If rainfall had changed and temperature remained constant, we expected species common in valley bottoms to increase over time. If temperature and rainfall had changed, we could have used the elevational gradient in Kibale with its cooler wetter conditions in the north and hotter and drier conditions in the south to test predictions on how the abundance of specific tree species would change. However, these patterns were not found. Thus, while T_{max} and T_{min} have both increased significantly over the 50 years, we have no means to predict *apriori* how individual species would respond.

Discussion

There were no major disturbances in the study forest in recorded history and correspondingly the changes in the forest structure that we documented between 1978 and 2019 were subtle. We recorded slightly more trees in the second enumeration, but species richness was similar and the tree community assemblage became more evenly distributed. To gain further insights to what might be driving changes in tree community composition, we examined changes in seed dispersal, herbivory, human induced disturbance, and climate on putative changes to the tree community over the last 40 years.

Animal populations increased in density, which we predicted would affect the tree community. Folivorous and frugivorous primates have steadily increased in abundance. The reasons for this increase or the general increase in group size in not yet known (Gogarten *et al.* 2015; Chapman *et al.* 2018a). Similarly, the elephant population in Kibale increased substantially between our two sampling times, likely a combined result of both births and immigration of forest elephants and effective recent anti-poaching efforts (Keigwin *et al.* 2016). However, hunting and habitat degradation dramatically impacted elephant populations in Uganda over the last 100 years. Brooks and Buss (1962) reported that the area used by elephants in Uganda was reduced by 75% between 1929 and 1959 partially in association with the 40,000 elephants killed by Ugandan control workers and trophy hunters. In the early 1960s, Kibale was thought to support 1773 elephants (Wing and Buss 1970), in 1996 the population was estimated at 300 animals (Cochrane 2003), while in 2005 an extensive transect census of the park estimate the number of elephants to be 393 (95% confidence limits 230-675, Wanyama *et al.* 2009). These studies indicate that elephant numbers have been reduced but are recovering. Elephants prefer the logged areas of Kibale where terrestrial vegetation is more abundant (Lawes and Chapman 2006), and our results suggest that given their current density, their trampling of seedlings and foraging has not impacted the old-growth forest.

We found no evidence that observed increases in the abundance of frugivores led to an increase in the trees whose seeds they disperse. Similarly, despite five decades of observation to determine which tree species the

folivorous primates damage and kill through overuse, only slightly more than half of the tree species examined followed the predicted pattern. For elephants, we found that only 33% of preferred tree species in the diet of elephants decreased in abundance. The effects of frugivory and herbivory do not appear to be strong enough to affect forest composition over the time period and spatial scale evaluated.

It is possible that other biotic factors obscured the effect of herbivory and frugivory. For example, the increase in the number of frugivores may have resulted in more seeds being dispersed, but seed predators increased during this same period, masking recruitment trends such as observed for *Monodora myristica* in Kibale (Balcomb and Chapman 2003). A site with greater frugivore density had more seeds dispersed, but this did not result in more saplings. Alternatively, it is possible that 40 years of monitoring is insufficient to detect change as tropical trees have slow growth. For example, *Chrysophyllum* sp. seedlings and saplings grow extremely slowly in the shaded understory, with their mean height doubling only every 27 years (Connell and Green 2000). Thus, a 20 cm seedling could take almost 60 years to reach a meter in height, if it survived that long in the understory and did not have the growth advantage of a light gap (see also Kalbitzer, McInnis and Chapman 2019). Clearly a long-term perspective is needed to examine the cascading effects of one change, such as the gradual decline in seed disperser abundance in a forest.

With respect to anthropogenic changes - century old human-induced disturbance and climate change - our findings are mixed. Forest disturbance that occurred prior to written history was still affecting changes in the forest tree species composition, but no consistent pattern is revealed. As *Prediction 3* suggests, light-demanding species decreased in abundance over time, while the abundance of shade tolerant species increased. Presumably, the light demanding species became abundant in the forest following a historical disturbance and these trees are now senescing, dying, and not being replaced. However, we also predicted that species that typically recruit into large disturbed areas should decline between 1978 and 2019 and this was not supported by our data. We could not make *apriori* predictions of the effect of temperature change on specific tree species independently of changes in rainfall. Thus, we were unable to test how specific tree species are affected by the observed increase in temperature.

We present a 40-year record of change in a tropical tree community, and some of the longest and most detailed records of tropical forest mammal populations dynamics ever accumulated, and site-specific information on tree life-history strategies, climate change, and on forest disturbance that occurred prior to written history. With respect to primates and elephants, we have decades of observational data and ecological studies upon which to examine the influence of foraging on plant species sorting. Our study revealed subtle changes in the tree community between 1978 and 2019, sizable increases in primate numbers, and a substantial increase in the elephant population. Yet, a clear picture of what set of interactions impact the change in the tree community remains elusive. Our data on tree life-history strategies and frugivore/herbivore foraging preferences suggest that species are under opposing pressures. For example, both *C. durandii* and *D. abyssinica* were predicted to decrease because they have been senescing after an anthropogenic disturbance 200-400 years ago. However, since the frugivores that disperse seeds of these tree species have increased in abundance, any influence from the prior anthropogenic disturbance may have been obscured.

Our exploration illustrates the challenges that must be faced to understand and predict change in terrestrial plant community dynamics. Of critical importance to addressing forest dynamics are longitudinal data and the interactions among important variables/processes over long time frames (Franklin *et al.* 2016). To understand the nature of the interactions, emphasis should be given to forests that have not recently experienced major disturbances, both in terms of the forest structure and animal populations. Disturbance to these interactors may have cascading effects on the forest community that take decades to return to a typical state – if there is a typical state at all (Pickett 1980). However, such studies can act as a comparison point to build a framework for future efforts. Within such a framework the scientific community can address whether and when forests will be influenced by novel biogeochemical conditions (e.g., CO_2 enrichment or N deposition) and novel assemblages of plants and animals, including invasive species or where diseases or human actions cause dramatic declines in populations (Franklin *et al.* 2016). Given the current global conditions it will be important to explore how interactions between climate and disturbance regimes lead to shifts among vegetation types, with special attention given to thresholds. Modeling efforts will be required to integrate plant physiology, demography, and biogeography, past forest history, and future climate and land use change (Franklin *et al.* 2016). A significant challenge will be to predict how forest communities have been influenced by past human impacts and how they will respond to future policy changes. By meeting these challenges researchers will have the information to convince policy makers of the appropriate actions that must be made to most effectively conserve the rich biodiversity of tropical forests.

Declarations

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Author's Contributions

CC conceived of the research and initiated the project, CC, JG, ML, AS, UK formalized they hypotheses, CC, PO collected the data, CC, CG-A, JG, RH, ML, DS, AS, and UK analysed the data and all authors wrote the manuscript and approved the final version.

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Ethics approval and consent to participate

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Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Tables

Table 1:

The density (trees per ha) of the ten most common tree species >10 cm DBH in an old-growth section of forest in Kibale National Park, Uganda that was enumerated in 1978 and 2019.

	1978		2019	
Family	Species	Density	Species	Density
Ebenaeae	*Diospyros abyssinica*	78.36	*Diospyros abyssinica*	63.54
Ulmaceae	*Celtis durandii*	40.95	*Celtis durandii*	34.59
Annonaceae	*Uvariopsis congensis*	33.18	*Uvariopsis congensis*	40.24
Bignoniaceae	*Markhamia lutea*	29.65	*Funtumia latifolia*	33.89
Apocynceae	*Funtumia latifolia*	26.12	*Trilepisium madagascariense*	29.65
Olacaceae	*Strombosia scheffleri*	8.47	*Markhamia lutea*	19.77
Rutaceae	*Vepris nobilis*	8.47	*Strombosia scheffleri*	17.65
Sterculiaceae	*Dombeya kirkii*	7.06	*Vepris nobilis*	16.24
Leguminosae	*Millettia dura*	6.35	*Celtis africana*	12.00
Ulmaceae	*Chaetacme aristata*	5.65	*Chaetacme aristata*	10.59
Ulmaceae	*Celtis africana*	4.94	*Aphania senegalensis*	8.47

Table 2:

The density (trees per ha) of fruiting tree species in an old-growth section of forest in Kibale National Park, Uganda that was enumerated in 1978 and 2019 and the percentage of time three common frugivorous primates spent feeding on their fruit. The species listed are those that were the ten most eaten trees for any of these primates.

Family	Species	Density 1978	Density 2019	Redtail diet (%)	Blue diet (%)	Mangabey diet (%)
Sapotaceae	*Blighia unijugata*	0	1.41			3.93
Ulmacaea	*Celtis africana*	4.94	12.00		8.2	2.37
Ulmacaea	*Celtis durandii*	40.95	34.59	20.5	5.07	16.98
Ulmacaea	*Chaetchme aristata*	5.65	10.59		1.4	
Euphorbiaceae	*Croton macrostachys*	0	0			5.84
Ebenaeae	*Diospyros abyssinica*	78.36	63.54	5.4	3.29	8.5
Moraceae	*Ficus brachylepis*	1.41	0			5.79
Moraceae	*Ficus capensis*	0	0			0.16
Moraceae	*Ficus congensis*	0	0			0.61
Moraceae	*Ficus exasperata*	1.41	0.71	1.7	4.49	6.29
Oleaceae	*Linociera johnsonii*	0	0			
Euphorbiaceae	*Macaranga schweinfurthii*	0	0	3.4		
Sapotaceae	*Mimusops bagshawei*	0	7.06	3.8	3.05	
Sapotaceae	*Pancovia turbinata*	0.71	5.65		8.17	
Rosaceae	*Parinari excelsa*	0	2.82		2.13	
Rutaceae	*Teclea nobilis*	8.47	14.83		6.53	
Annonaceae	*Uvariopsis congensis*	33.18	40.24		6.53	5.11

Table 3:

The species documented to have been killed by extensive red colobus foraging based on long-term observation in Kibale National Park, Uganda (Chapman *et al.* 2013a) and their density (per ha) in 1978 and 2019 in the surveyed forest. Rare and edge species known to be killed by the red colobus were not found along the surveyed areas.

Family	Tree species	Descriptor	Density 1978	Density 2019	Trend
Fabaceae	*Albizia grandibracteata*	Forest	0	4.24	Up
Sterculiaceae	*Dombeya mukole*	Forest	7.06	0	Down
Moraceae	*Ficus exasperata*	Forest	1.41	0.71	Down
Bignoniaceae	*Markhamia lutea*	Forest	28.24	19.77	Down
Euphorbiaceae	*Neoboutonia macrocalyx*	Forest	3.53	0	Down
Rosaceae	*Prunus africana*	Forest	0.71	0.71	Same
Euphorbiaceae	*Sapium ellipticum*	Forest	0	2.12	Up
Rutaceae	*Fagara angolensis*	Rare	0	0	—
Fabaceae	*Newtonia buchananii*	Rare	0	0	—
Guttiferae	*Harungana madagascarensis*	Edge	0	0	—
Myrtaceae	*Eucalyptus grandis*	Edge	0	0	—
Lauraceae	*Persea americana*	Edge	0	0	—
Fabaceae	*Sesbania sp.*	Edge	0	0	—

Table 4:

Elephant selection ratios reported from four different studies in Kibale National Park, Uganda between 1962 and 2013 and the density (per ha) of stems of these species found during our sampling in 1978 and 2019.

Family	Tree species	1962-64[1]	1978-79[2]	1993[3]	2012-13[4]	Average	1978	2019
Moraceae	*Antiaris toxicaria*	2.85	2.08	3.47	6.61	3.75	0	0
Fabaceae	*Newtonia buchananii*	2.12	1.6	4.66	5.22	3.40	0	0
Sapotaceae	*Mimusops bagshawei*	3.21	0.63	4.32	2.33	2.62	1.41	7.06
Moraceae	*Ficus exasperata*	0.96	n/a	3.94	2.5	2.47	1.41	0.71
Sapindaceae	*Blighia unijugata*	2.8	n/a	3	1.06	2.29	0	1.41
Ulmacaea	*Celtis africana*	3.42	3.27	1.22	0.68	2.15	4.94	9.88
Annonaceae	*Monodora myristica*	1.69	1.75	0	5.06	2.13	2.12	1.41
Moraceae	*Trilepsium madagascariense*	2.95	2.29	2.72	0.38	2.09	4.94	29.65
Meliaceae	*Lovoa swynnertonii*	2.85	0.82	3.56	1	2.06	2.12	1.41
Rosaceae	*Parinari excelsa*	1.17	0.19	5.75	0.61	1.93	2.82	2.82
Olacaceae	*Strombosia scheffleri*	2.66	0.66	4.06	0.28	1.92	8.47	17.65
Meliaceae	*Trichilia splendida*	2.2	1.9	0.71	2.02	1.71	0	0
	Average	2.35	1.46	2.9	2.14	2.38		

1 Data from Wing and Buss 1970, sampling done between 1962 and 1964 and included the whole park.

2 Data from Kasenene (1980; 1984; 1987) sampling done in 1978 and 1979 and included forestry compartments K30 and K14 (average of compartments presented).

3 Data from Lwanga (1994), sampling done in 1993, and includes forestry compartments K30 and K15 (average of compartments presented).

4 Data from Omeja et al. (2014) done in 2012 and 2013, and includes forestry compartments K30, K14, and K15 (average of compartments presented).

Table 5:

Descriptions of the tree community in 1978 and 2019 in an old-growth section of forest in Kibale National Park, Uganda. 1D is the exponential of Shannon's entropy and is interpreted as the number of 'common' species in the community, which weights each species according to its frequency in the community, and 2D is the inverse Simpson concentration, which favors abundant species and is therefore interpreted as the number of 'very abundant' or 'dominant' species in the community.

	All Species		Top Ten Species	
	1978	2019	1978	2019
Abundance	436	508	345	391
Completeness	0.97	0.98	—	—
Richness	45	43	—	—
1D	15.5	18.8	—	—
2D	8.7	12.4	—	—
Diversity	71.8	78.1	84.6	93.5
Mean DBH	23.7	28.0	21.3	26.4
% of Light demanding Species (n)	65.4%(279)	50.8%(253)	68.7%(237)	50.1% (196)
% of Shade-tolerant species (n)	34.5% (147)	49.2% (245)	31.3% (108)	49.9% (195)

Table 6:

The relative abundance of herbivorous/folivorous mammals that can often suppress regeneration and the abundance of seed-dispersing frugivorous primates that promote regeneration in an old-growth forest in Kibale National Park, Uganda. For the primate species we also include data on group sizes estimated, from which we calculated individuals / km walked in the final survey.

Year	Elephant	Duiker	Bushbuck	Pig	Red Colobus	B&W Colobus	Redtail Monkey	Blue Monkey	Mangabey
Tracks or Groups/km walked									
1970					0.97	0.22	0.70	0.45	0.09
1980					1.14	0.12	0.64	0.39	0.16
1996	0.05	1.11	0.09	0.13	0.64	0.17	0.35	0.09	0.40

2005	7.00	8.71	1.25	1.75	0.47	0.21	0.41	0.17	0.19
2008	3.19	6.87	1.62	4.63	0.67	0.33	0.73	0.14	0.32
2014	6.66	10.16	1.23	2.14	0.56	0.27	0.56	0.15	0.27
2019	6.68	8.12	1.68	0.91	0.62	0.29	0.42	0.1	0.23
Group Sizes									
1996					35.26	8.89	20.50	9.74	12.05
2010					47.47	7.89	13.99	10.60	17.31
2018					71.90	15.14	23.30	15.10	25.60
# of Individuals / km walked									
1996					22.57	1.51	7.18	0.88	4.82
2010					31.80	2.60	10.21	1.48	5.54
2019					44.58	4.39	9.79	1.51	5.89

Figures

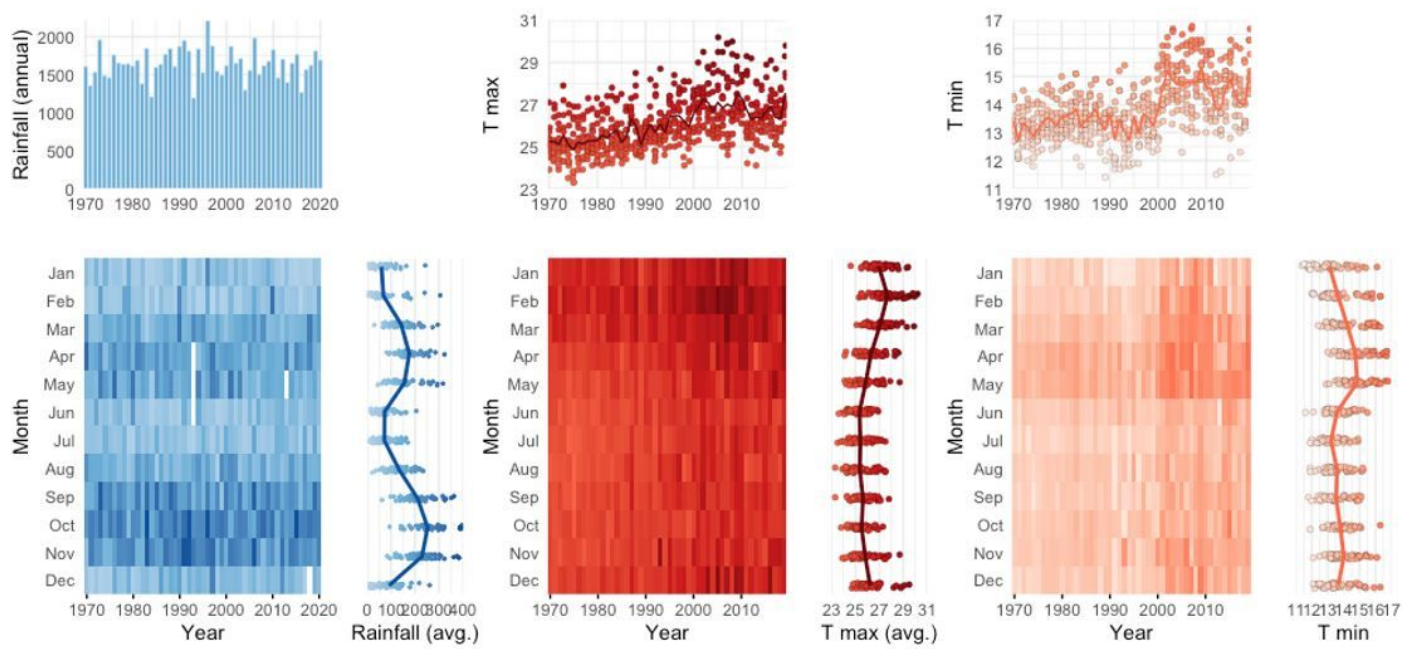

Figure 1

Patterns of rainfall, maximum temperature (°C, Tmax) and minimum temperature (°C, Tmin) between 1970 and 2020 for the area near Makerere University Biological Field Station in Kibale National Park, Uganda. For details, see text.

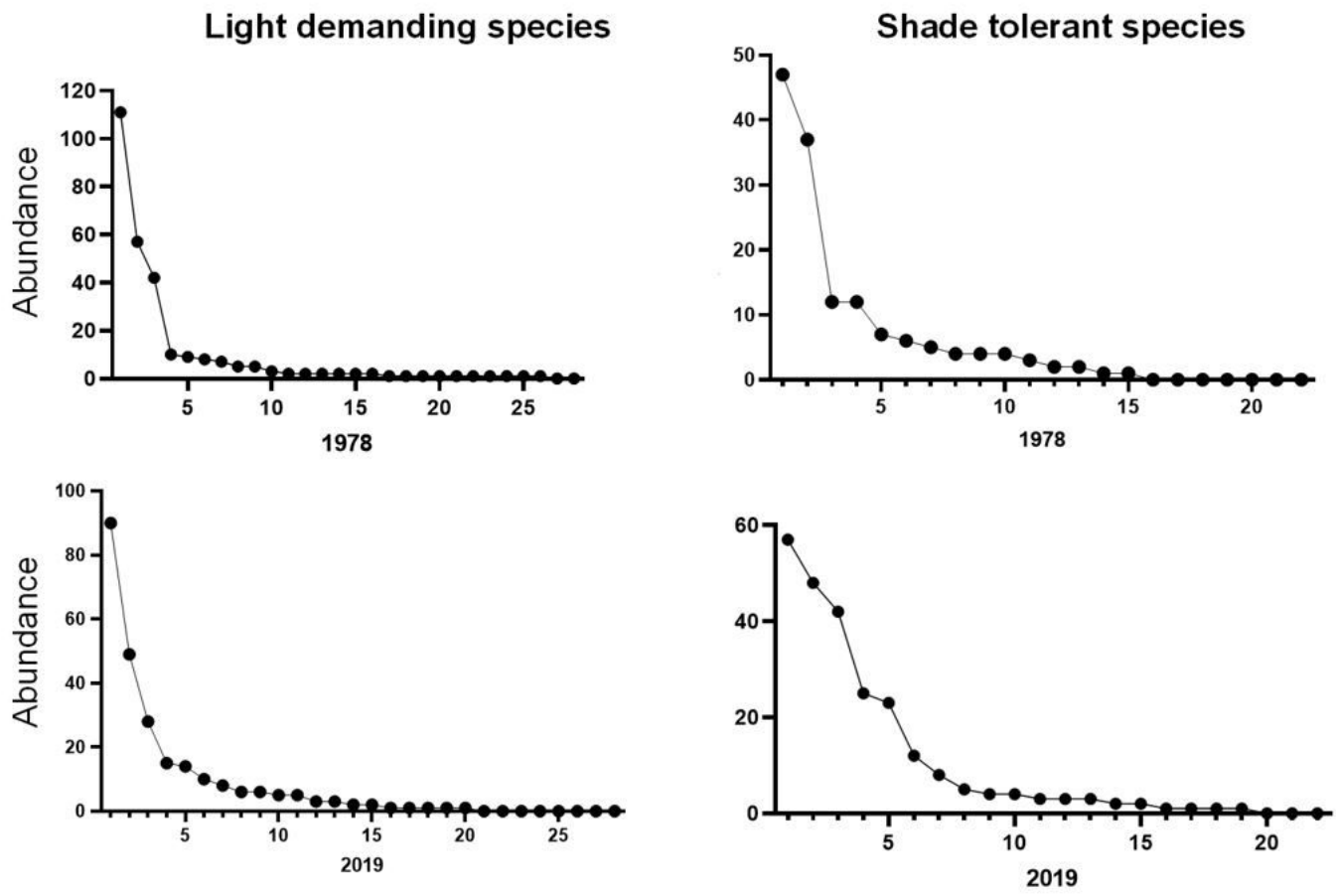

Figure 2

The shade-tolerant and light-demanding species enumerated in plots ranked in order of abundance. Sampling was conducted approximately 40 years apart (1978 and 2019) in an old-growth area of Kibale National Park, Uganda.

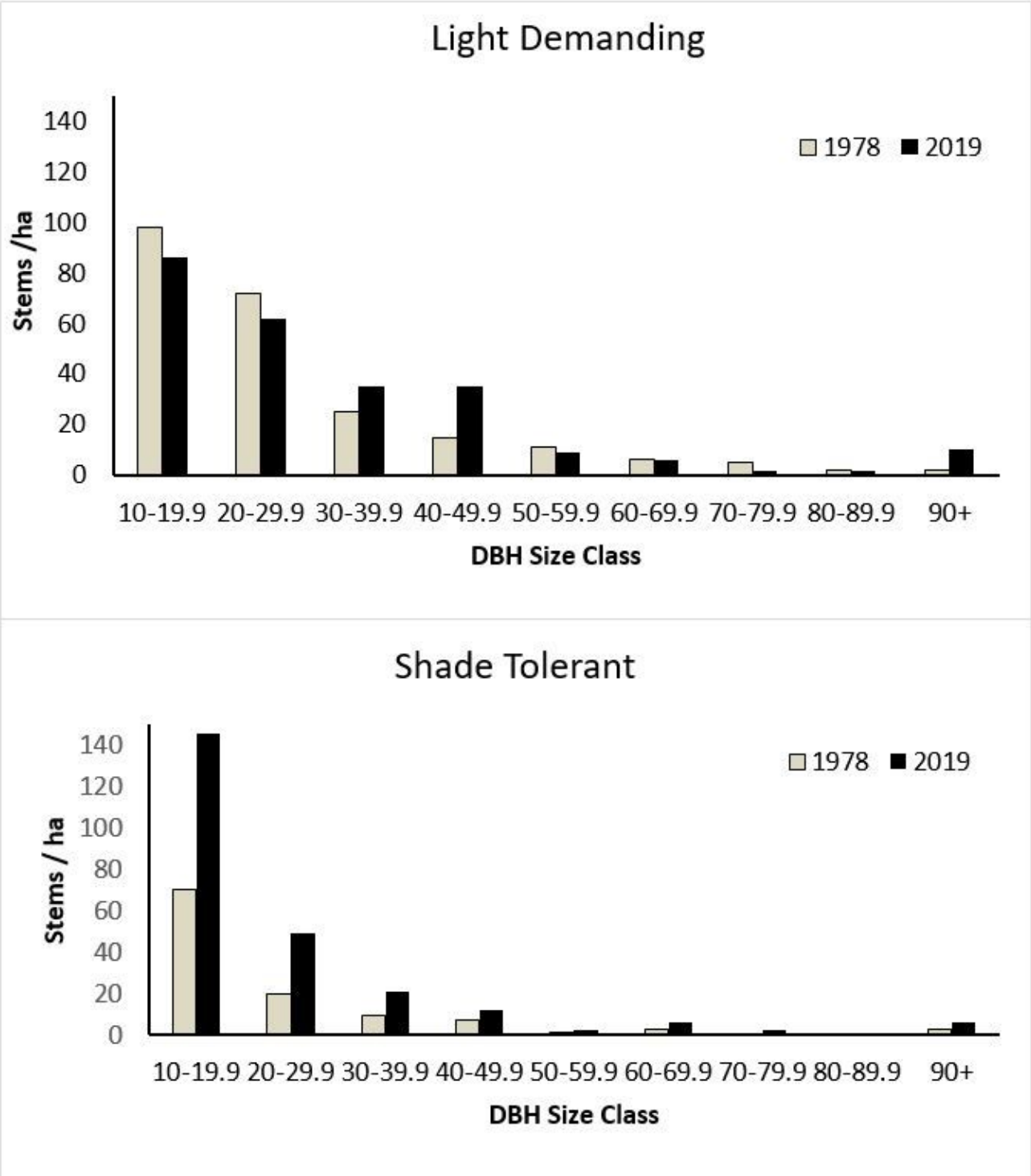

Figure 3

The stand structure (plotted at 10 cm size class intervals) for light demanding and shade tolerant species. Sampling was conducted approximately 40 years apart (1978 and 2019) in an old-growth area of Kibale National Park, Uganda.