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Tropical tree community shifts: Implications for wildlife conservation

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ABSTRACT

In tropical forest systems tree community change after initial succession (approximately 50–100 years) is very difficult to detect because of the very slow pace of transformation. Since the mid 1980s, there has been an accumulation of evidence that many forests traditionally considered old growth or mature forests have been disturbed. Using 18 years of data on forest change in Kibale National Park, Uganda, we tested the following hypotheses. Species that frequently recruit only into areas of large-scale disturbance (e.g., conversion to agriculture) (1) have a more strongly negative annualized rate of population change (i.e., recruitment is less than mortality) than trees recruiting into the understory or canopy treefall gaps and (2) these species are declining in their average cumulative diameter at breast height (DBH). Both hypotheses were verified. We then examined relationships between forest change and diets of the five diurnal primates in Kibale. The emergent patterns suggest that forest change will lead to declines in some species, particularly the black-and-white colobus (*Colobus guereza*). We concluded that what was considered mature forest in Kibale has actually been disturbed in the recent past, and we discuss how potential sources of disturbance (dry-periods, elephant population fluctuations, and human disturbance) may affect both forest change and animal populations. We assess how such information might be useful in forest management.

1. Introduction

Over the past 50 years the human population grew by 3.7 billion people (Potts, 2007) and is estimated to grow by another 2–4 billion people over the next 50 years (United Nations, 2005). Between now and 2050, 90% of this growth will occur in developing countries, many of which are tropical and sustain the greatest proportion of the world's biodiversity (Potts, 2007; Bradshaw et al., 2009). This exponential growth in human population has brought many challenges to ecological systems, and continued growth is predicted to exacerbate ever-increasing demands for environmental products and services, particularly in the tropics (Houghton, 1994). While there is continuing debate about the efficacy of fortress conservation versus integrated conservation and development (Redford and Sanderson, 2000; Sunderland et al., 2008), the primary mechanism for protecting the diversity of tropical forests has been through establishment of parks and reserves (Oates, 1999; Terborgh, 1999; Terborgh et al., 2002), particularly in regions with high population densities. Conservation managers in such reserves have thus placed much emphasis on immediate challenging issues such as habitat loss (Brooks et al., 2002), bushmeat hunting (Fa et al., 2002; Laurance et al., 2008), and recently climate change (Chapman et al., 2006; Malcolm et al., 2006; Brook et al., 2008).

An assumption still applied to protected area management in many regions is that protected areas must be managed to preserve their current state, preventing disturbance or successional processes. A classic example of this concern is with respect to fire in North American forest systems (Agee, 1993). Initially fire was suppressed because it was seen as damaging timber; however, it soon became apparent that fire played an important role in the ecosystem and suppressing fire often did more damage than good. Suppressing fires resulted in the accumulation of fuels, thus when a fire did occur, it was often more intense and disastrous. The perspectives that disturbance is a natural part of ecosystem dynamics

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have become central to management of many systems in North America and depends on a thorough understanding of natural successional dynamics.

While the dynamics of North American forest ecosystems have been well-studied, tropical systems are less understood (see Chazdon, 2003). However, what is becoming apparent is that forest change in tropical systems can be difficult to assess after initial stages of succession (approximately 50–100 years), because the pace of change is very slow. Since the mid 1980s there has been an accumulation of evidence that many forests traditionally considered old growth or pristine have actually been disturbed relatively recently (i.e., between 200 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 a 4000 years old history of human disturbance (Bush and Colinvaux, 1994). Thus, what appeared to be undisturbed forest to Neotropical ecologists is regenerating forest as young as 350 years old (Clark, 1996). Similarly, the current Maya forests are as young as 1100 years old, which is when the classic Maya period ended, and the population collapsed and abandoned the cities (Gomez-Pompa, 1987). Similar evidence, particularly from Africa, Central America, and Amazonia has emerged (Tutin and Oslisly, 1995; Haberle and Ledru, 2001; Anchukaitis and Horn, 2005; Bush et al., 2007; Kennedy and Horn, 2008). Like North American land managers of 50 years ago, these findings suggest that tropical forest researchers and managers must consider disturbances that may have occurred in the distant past (distant in terms of scientific documentation, but not in terms of tropical forest dynamics) in the construction of informed management plans for tropical reserves and the fauna they support. Most tropical forest systems likely do not experience large-scale disturbance on the scale of North American fire-affected ecosystems, but they are likely changing slowly in response to past disturbances. If true, it will be necessary to consider such disturbances in terms of future impacts on the forest and its fauna; an aspect that has been prominently absent in the past (Clark, 1996; Lawes et al., 2007b).

Less than 5% of the area covered by tropical forests is legally protected; many are subjected to illegal exploitation (Oates, 1996; Peres, 1990; Redford, 1992); and they often occur in fragmented landscapes that limit dispersal (Lawes et al., 2007a). Thus, it is vital we have the means to evaluate the long-term effectiveness of protected areas for conserving the flora and fauna of most concern. If tree community compositions of protected areas are changing following a disturbance that is not recognized by managers, it is possible that the reserve will not protect the species it was designed to preserve. Furthermore, understanding the significance of past disturbance on tropical forest reserves is critical if we are to understand how current and future disturbances, i.e., climate change, will affect these protected areas (Malhi and Phillips, 2004; Wright, 2005; Lawes et al., 2007a; Phillips et al., 2008).

Our research evaluates changes in tree community structure three times over 18 years in Kibale National Park, Uganda. We combined our long-term record of tree mortality and recruitment with a detailed knowledge of conditions under which tree species recruit, to speculate on which species represent late successional species that are declining in abundance in the main forest and provide conjecture on the future composition of the tree community. Specifically, using 18 years of data on forest change, we tested the following hypotheses. Species that frequently recruit into areas of large-scale disturbance (e.g., conversion to agriculture) (1) have a more strongly negative annualized rate of population change (i.e., recruitment is less than mortality) than trees recruiting into the understory or canopy gaps, and (2) these species are declining in their average cumulative diameter at breast height (DBH). These predictions are based on the following logic. If some tree species can only recruit into large gaps (see also Snook and Negreros-Castillo, 2004) as the stand ages and adults of these species die, they cannot be replaced by seedlings growing up in the understory. As a consequence of large adult trees of these species dying we expect the average cumulative diameter at breast height to decline because it is unlikely that smaller trees of these species will be able to grow rapidly to make up for the loss in DBH. This would represent part of forest dynamics in forests of this nature (Chazdon, 2003). Based on estimates of the rate and compositional change of the forest tree community and detailed information on primate diets, we predict how primate populations will respond to this successional change. There is a large body of literature that indicates that specific taxonomic groups, like birds (Lain et al., 2008; Vallecillo et al., 2009) and primates (Johns, 1992; Chapman et al., 2000) respond rapidly and in species-specific ways to disturbance. Thus, if the patterns we document concur with prior studies of these species, this would lend support to the generality of our findings and predictions. In this way, we provide an example of how managers can incorporate long-term tropical forest change into conservation planning. Finally, we discuss how potential sources of disturbance in the area (dry-periods, elephant population fluctuations, and human disturbance) may affect forest change and the response of forest organisms.

2. Methods

2.1. Study site

Kibale National Park (795 km^2) is located in western Uganda (0°13′–0°41′N and 30°19′–30°32′E) near the foothills of the Ruwenzori Mountains (Struhsaker, 1975, 1997). Kibale is a mid-altitude, moist-evergreen forest receiving an annual average of 1698 mm (1990–2008). Kibale was gazetted as a Forest Reserve in 1932 and became a National Park in 1993. The section of forest examined in this study (locally known as Forestry Compartment K30) has been described as relatively undisturbed mature forest (Struhsaker, 1975; Skorupa, 1988) or relatively undisturbed old forest (Struhsaker, 1997). K30 is a 282-ha area that has not been commercially harvested and is connected to other unlogged areas in the park. Prior to 1970, a few large stems (0.03–0.04 trees/ha) were removed by pitsawyers, but this extremely low level of extraction has had little impact on forest structure (Skorupa, 1988; Struhsaker, 1997). The forest is considered *Parinari* forest by foresters because the spreading crown of *Parinari excelsa* can be distinguished on aerial photographs. The canopy is dominated by trees such as *P. excelsa, Carapa grandiflora, Olea welwitschii, Aningeria altissima, Strombosia scheffleri*, and *Newtonia buchananii* (Osmaston, 1959). An inventory of forest can be found in Chapman et al. (1997).

2.2. Vegetation plots

We established 11 permanent vegetation plots in K30 in December 1989, placed randomly within the existing trail system. Each plot was 200 m × 10 m, providing a total sampling area of 2.2 ha. A great deal of thought and empirical research has been directed into the most rigorous criteria for establishing plot size, shape, and number for a variety of research questions (reviewed by Dengler et al., 2009). We wished to monitor the phenology of trees over a large area in a repeatable way; and the size and shape of the plots seemed appropriate for this at the time. Since we are making comparisons over time and not singling out rare species, many of the concerns about plot size and number are not critical to the questions we are asking (Dengler et al., 2009). Each tree with diameter at breast height (DBH) >10 cm within 5 m of each side of the trail was identified, individually marked with a numbered aluminum tag, and measured (DBH). This provided an initial sample of 1321 trees. The initial mean number of trees with >10 cm DBH per plot was 97 + 6.3 SE. Plots were resurveyed in May 2000 and September–November 2006. All tagged trees were re-located and measured to assess growth, and new trees recruiting into the >10 DBH size class were identified, tagged, and measured. Mortality was noted and the cause of death was ascertained where possible. In a study of growth it is essential that DBH be measured accurately and using the same criteria during each period. To ensure accuracy, we always measured the place to quantify DBH from 1.2 m above the ground, and if the tree was on a hill we measured this from the downhill side. If the tree had large buttresses (e.g., large *Olea capensis*), DBH was measured from above the buttresses. To do this we mounted a meter stick on a pole and extended it to the top of the buttress and read the diameter directly. The measurement of DBH was made by the same person using the same rules in each of the three time periods (Tusiime Lawrence).

2.3. Evaluation of recruitment strategies

To determine what tree species recruit in situations representative of a large human disturbance (e.g., agricultural clearing); we quantified recruitment into a harvested pine plantation immediately adjacent to the forest. Pine plantations (*Pinus caribaea*, *P. patula*, *Cupressus lusitanica*) were established in Kibale between 1953 and 1977 when it was a forest reserve. These plantations were established on grasslands created when the original forest was cleared and cultivated. The land was used for subsistence agriculture and grazing until 1900 when the local livestock were devastated by rinderpest and the area was abandoned (Osmaston, 1959; Kingston, 1967; Wing and Buss, 1970). The exotic plantations were harvested and left to naturally regenerate to native forest after Kibale became a national park in 1993. We quantified recruitment into a plantation that was harvested in 1998. Timber was non-directionally felled using chain saws and rolled to saw mills, which severely damaged indigenous trees that had recruited into the pine plantation. There was no regeneration of softwood pine species following harvest. The clear-felled plantation was allowed to regenerate naturally from the few remaining indigenous trees, resprouts from trees that were damaged by the harvest (often cut at ground level), seeds in the soil seed bank, or newly arrived seeds deposited by wind or animal dispersal (Duncan and Chapman, 2003). The plantation was adjacent to natural forest, and the interior was less than 250 m from natural forest with an abundance of avian and mammalian seed dispersers.

In May 2002, two 200 × 100 m (2 ha) plots were established in the harvested pine plantation and each plot was divided into fifty 20 × 20 m sub-plots. The plots were adjacent to one another and separated by approximately 20 m. At this time, the area was dominated by grasses such as *Pennisetum purpureum* and *Hyparrhenia* spp. No saplings could be seen emerging from the grass, and we search among the tall grass stems to find seedlings and young saplings. The plots were monitored for new recruits at approximately 4 month intervals until May 2006, and any new woody recruit was tagged (Table 1).

It is possible that some common species that recruited in large numbers in this disturbed area could also recruit well in the forest or in forest gaps, and thus would not be representative of species specialized to recruit in large disturbed areas. To evaluate this we checked species against data presented in Zanne and Chapman (2005), which examined gap and understory species. Zanne and Chapman (2005) quantified tree species richness and individual density in 24 plots (5 × 5 m) in closed canopy forest that was undisturbed. All plots were in closed canopy forest and at least 5 m from any gap edges (with gap edge defined as cleared of vegetation to within 2 m of the forest floor; Brokaw, 1982). For gap plots, treefall gaps were examined where fallen trees had no remaining fine branches or leaves but little decay had occurred on the main bole. Approximately 60 such gaps were found. We then randomly selected a subset of these gaps, placing plots in the center of the gap. Gap size was determined by measuring the longest axis and the second longest axis perpendicular to the first. Gaps averaged 300 m^2 (range: 39–636 m^2). Only stems <2 m tall were selected as these plants would likely have recruited under gap conditions.

Of the 40 species that recruited into the large disturbed area (Table 1), 13 species each contributed >1% of the total recruits. However, *Diospyros abyssinica*, also recruited well in the understory and in gaps, as did *Funtumia latifolia* to some degree, so these species were excluded. This left 11 species that together comprised 89% of all recruits that we classified as specialist species of large disturbed areas.

2.4. Analytical approach

We contrasted two indices of tree community structure between species that recruited frequently into areas with large disturbances and those that did not: (1) annualized rate of population change and (2) change in cumulative DBH in the plots. DBH is a reliable predictor of both fruit crop size and leaf biomass, is practical and easy to measure, and has low inter-observer error (Brown, 1978; Harrington, 1979; Catchpole and Wheeler, 1992; Chapman et al., 1992, 1994). We calculated the annualized rate of population change = r for the two recruitment types, using a standard model of exponential population growth:

$$r = \ln N_t - \ln N_0$$

where N_t and N_0 are population sizes or cumulative DBH at time t and time 0 and ln is the natural logarithm.

It is likely that primate populations are more strongly influenced by changes in the abundance of tree species that produce food items than by the overall abundance of all trees. Kibale is an unrivaled location for primate research because a large number of long-term studies have been conducted on the primate foraging behavior, and since the area has a high richness and biomass of primates. To determine important primate food trees, we accessed detailed diet data for the five diurnal primate species through published accounts or raw data available to CAC. We included foods (i.e., a specific part from a particular species) that constituted $\geqslant$4% of the time spent feeding as reported by Rudran (1978) and Butynski (1990) for blue monkeys (*Cercopithecus mitis*), Waser (1975) and Olupot (1994) for mangabeys (*Lophocebus albigena*), Harris and Chapman (2007) and Oates (1977) for black-and-white colobus (*Colobus guereza*), Rode et al. (2006, unpublished data) and Stickler (2004, unpublished data) for redtails (*Cercopithecus ascanius*), and Chapman and Chapman (2002, unpublished data) and Struhsaker (Struhsaker, 1975) for red colobus (*Procolobus rufomitratus*). We chose a 4% cutoff because it included specific food items that were consistently considered important by previous researchers studying these species at Kibale and our team, while avoiding incorporating large numbers of rarely used species (Chapman et al., in press). We used the vegetation plot data for each of the three time periods to estimate the cumulative DBH of food trees.

We calculated the annualized rate of population change and % change in cumulative DBH for species assigned to each recruitment category for each of the three monitoring periods. To test the significance of temporal variation in these parameters, we compared repeat samples of plots across years. Repeated measures analysis of variance was used to test the significance of temporal (among years) and between recruitment categories (between-subject effect) and their interaction. The advantage of using a repeated measures analysis of variance is that it tests for significant differences

Table 1
Mean stand density (stems/ha) of tree species in a former pine plantation in Kibale National Park, Uganda, the % of the total recruits that each species in the plantation comprised, and the % of recruits found in the understory of forest compartment K30 based on an enumeration of small plots in the understory (all stems <2 m) and gaps. Authorities follow Hamilton (1991).

Family	Species	Stems/ha	% Recruits	% Understory Gap recruits
Myrsinaceae	*Maesa lanceolata* (Forsk.)	216	27.41	0.00
Fabaceae	*Albizia grandibracteata* (Taub.)	144	18.27	0.05
Euphorbiaceae	*Bridelia micrantha* (Baill.)	77	9.77	0.00
Ulmaceae	*Trema orientalis* (Bl.)	70	8.88	0.00
Ulmaceae	*Celtis durandii* (Engl.)	53	6.73	0.87
Ulmaceae	*Celtis africana* (Brum.)	46	5.84	0.26
Papilionaceae	*Milletia dura* (Dunn.)	39	4.95	0.00
Apocynaceae	*Funtumia latifolia* (Stapf)	31	3.93	1.43
Rutaceae	*Fagara angolensis* (Engl.)	23	2.92	0.00
Bignoniaceae	*Spathodia campanulata (P. Beauv)*	11	1.40	0.00
Papilionaceae	*Erythrina abyssinica* (Lam.)	10	1.27	0.00
Rosaceae	*Prunus africana* (Kalkman)	10	1.27	0.00
Ebenaceae	*Diospyros abyssinica* (White)	10	1.27	41.51
Boraginaceae	*Ehretia cymosa* (Thonn.)	7	0.89	0.00
Oleaceae	*Olea capensis* (Gilg and Schellenb.)	5	0.63	0.00
Rutaceae	*Clausena anistata* (Benth.)	5	0.63	1.05
Moraceae	*Ficus natalensis* (Hochst.)	3	0.38	0.00
Verbenaceae	*Premna angolensis* (Guerke)	3	0.38	0.00
Euphorbiaceae	*Croton macrostachyus* (Hochst.)	3	0.38	0.00
Euphorbiaceae	*Macaranga schweinfurthii* (Pax)	2	0.25	0.00
Rubiaceae	*Vangueria apiculata* (K. Schum.)	1	0.13	0.02
Euphorbiaceae	*Sapium ellipticum* (Pax)	1	0.13	0.00
Melianthaceae	*Bersama abyssinica* (Fresen.)	1	0.13	0.00
Fabaceae	*Acacia* sp.	1	0.13	0.00
Sapindaceae	*Blighia unijugata* (Baill.)	1	0.13	1.66
Sterculiaceae	*Dombeya mukole* (Sprague)	1	0.13	0.00
Flacourtiaceae	*Casearia battiscombei* (R.E.Fr.)	1	0.13	0.00
Fabaceae	*Dichrostachys* glomerata (Chiov.)	1	0.13	0.00
Pittosporaceae	*Pittosporum spathicalyx* (DeWild.)	1	0.13	0.00
Alangiaceae	*Alangium chinense* (Harms)	1	0.13	0.00
Araliaceae	*Polyscias fulva* (Harms)	1	0.13	0.00
Flacourtiaceae	*Scolopia rhamnophylla* (Gilg)	1	0.13	0.26
Borganinaceae	*Cordia africana* (Lam.)	1	0.13	0.00
Rutaceae	*Teclea nobilis* (Del.)	1	0.13	6.76
Moraceae	*Myrianthus holstii* (Beauv)	1	0.13	0.23
Bignoniaceae	*Kigelia moosa* (Sprague)	1	0.13	0.17
Ulmaceae	*Chaetacme aristata* (Planch.)	1	0.13	0.45
Euphorbiaceae	*Neoboutonia macrocalyx* (Pax)	1	0.13	0.00
Meliaceae	*Guarea cedrata* (Pellegr.)	1	0.13	0.00
Rubiaceae	*Hallea stipulosa*(DC.) J.-F. Leroy	1	0.13	0.00

between three or more related or matched samples (in this case plots that might not be independent) for a specific measure (in this case year). Following Potvin et al. (1990), Mauchly's criterion was used to test for the compound symmetry of the variance–covariance matrix. If the criterion was rejected, the Greenhouse-Geisser test, which relaxes the symmetry assumption, was used to obtain corrected significance levels (Potvin et al., 1990). We also considered trends for single species using a one-way repeated measures ANOVA.

3. Results

As predicted, the rate of population change for forest trees was more strongly negative for those species that recruited into the understory or large gaps (mean 1989–2000 $r = -0.143$; 2000–2006, $r = -0.209$) than species that recruited into the main forest (mean 1989–2000 $r = -0.007$; 2000–2006, $r = 0.009$; between-subject effects $F = 24.874$, $P < 0.001$). There was no significant time effect ($P = 0.404$), but there was a marginal interaction effect ($P = 0.055$) suggesting that the difference between the tree recruitment classes varied among time periods.

As predicted, the % change in the cumulative DBH in the vegetation plots was more negative for species that recruited into large gaps (mean % change 1989–2000 = −13.069; 2000–2006 = −13.047) compared to species that recruited into the main forest (mean 1989–2000 = −5.417; 2000–2006, 5.731; between-subject effects $F = 10.446$, $P = 0.004$). There was no significant time ($P = 0.392$) or interaction effect ($P = 0.394$).

Repeated measures analysis of variance was used to detect effects of time, species, and their interaction on the cumulative DBH of primate foods. DBH was log transformed to improve normality and stabilize the variance. There was a significant effect of species ($F = 3.317$, $P = 0.017$), but also a marginal year by species effect ($F = 1.945$, $P = 0.081$). To explore this further, we examined changes in cumulative DBH of the food trees for each species separately. For mangabeys ($F = 0.001$, $P = 0.998$), redtail monkeys ($F = 1.166$, $P = 0.332$), blue monkeys ($F = 2.356$, $P = 0.136$), and red colobus ($F = 1.181$, $P = 0.312$) there was no significant change in the cumulative DBH of food trees over time. However, for black-and-white colobus, the cumulative DBH of food trees declined ($F = 4.011$, $P = 0.034$). Note that this analysis does not consider the possibility that there has been a change in the amount of food items provided per cm change in DBH.

Using a repeated measures analysis of variance on logged data of the cumulative DBH of each primates food on each transect and with species as a between-subject factor produced a marginally significant year by species effect ($F = 1.945$, $P = 0.081$). To explore this further we examined the changes in cumulative DBH of the food trees for each primate separately, and we found differences among species. For mangabeys ($F = 0.001$, $P = 0.998$), redtail monkeys ($F = 1.166$, $P = 0.332$), blue monkeys ($F = 2.356$, $P = 0.121$), and red colobus ($F = 1.181$, $P = 0.312$) there was no significant change in the cumulative DBH of food trees over time. However, for black-and-white colobus the cumulative DBH of available food trees declined ($F = 4.011$, $P = 0.034$). Note (as above) that this analysis does not consider the possibility that there has been a change in the amount of food items provided per cm change in DBH.

4. Discussion

We predicted that if the forest at Kibale was recovering from large-scale disturbances in its distant past, then trees that colonize large-scale disturbances should show more strongly negative annualized rates of population change and cumulative DBH than trees typically recruiting in the forest understory or treefall gaps. Our results support these predictions. This represents a successional process where late successional species are being replaced by more mature forest species. It has long been recognized that disturbance is an important feature structuring forest communities (Gleeson, 1926; Ewel, 1980; Clark, 1996), and forest structure is thought to represent a complex interplay between disturbance events and regeneration processes (Chazdon et al., 2007). Yet, in many forests where disturbance has occurred in the distant past, disturbance is not given the consideration that it deserves (Clark, 1996). Liesch et al. (2009) studied forests that ranged in time since disturbance from 4 to 120 years and concluded that it would take between 1000 and 4000 years to reach the endemism levels that exist in mature forest. Some forest types may be adapted to catastrophic disturbance. For example, Snook and Negreros-Castillo (2004) documented that establishment of natural strands of mahogany (*Swietenia macrophylla*) may have resulted from major disturbance occurring hundreds to thousands of years ago, because seedlings establish and grow well in such large disturbances, but not in the forest understory. For a review of tropical forest dynamics see Chazdon (2003).

The disturbance that occurred long ago in what had been considered Kibale's mature forest likely accounts for the decline in the black-and-white colobus food trees. The black-and-white colobus are known to do very well in disturbed areas (Struhsaker, 1975; Oates, 1977; Harris, 2005), and this species routinely colonizes large-scale disturbances dominated by the tree species our study found to show a strongly negative annualized rate of population change and a decline in cumulative DBH. To evaluate the long-term effectiveness of protected areas for conserving the flora and fauna, it is important to understand the potential impact of the disturbance-dependent changes on the forest tree community. If tree community compositions of protected areas are changing because of disturbance events in the past that are not detected or easily detectable by managers, it is possible that the reserve may not protect the flora and fauna it was designed to conserve.

If conservation biologists are to effectively respond to slow forest changes such as we have quantified, they must do two things. First, it is necessary to explore the environmental history and any disturbances leading to changes in community structure and composition at a site. To do this an analysis such as we have conducted here would identify the nature of the change and allow predictions to be made of which species might be negatively affected in the future. Unfortunately, conservation biologists rarely have the luxury of such lengthy periods of study prior to making decisions. An alternative, more rapid means of assessing if forests are changing after a disturbance is to locate a large-scale disturbance, determine the tree species recruiting into the disturbed area and determine if these species are common in what is thought to be mature forest. If disturbances are very large, coring lakes and analyzing the cores for periods where grass pollen dominates the lake sediments provides another means of identifying if and when large disturbances have occurred that resulted in the ecosystem shifting from one dominated by forest to one dominated by grasses (Taylor et al., 1999). This technique has been used extensively in Central America lakes to determine the periods of human occupation by searching for corn (*Zea mays)* pollen in lakes sediments (Mueller et al., 2009). Other rapid methods, for example using wood density to document forest disturbance and conservation priority, may also be considered (Slik et al., 2008). The second issue that is important in evaluating response to slow forest change is identifying the cause of the disturbance. In the region of Kibale National Park, Uganda, there are at least three possible processes that could create such large-scale disturbances: (1) a period of aridity that caused a mortality event among rainforest trees, (2) the destructive activities of elephants (*Loxodonta africana;* Lawes and Chapman, 2005), and (3) human-caused disturbance in the distant past.

4.1. A period of aridity

Kibale receives 1698 mm annually at the Kanyawara field station located in the northern third of the park. To the south, the park is drier, and rainforest is replaced by open *Acacia* woodland. This woodland assumes dominance when rainfall is just less than 1350 mm of rain per year (Chapman and Lambert, 2000). A prolonged period of aridity with the annual rainfall was <1300 mm a year could account for the death of rainforest trees and the formation of large disturbed areas. However, rainfall records for the last century indicate that the area has become wetter not drier (Fig. 1) (Struhsaker, 1997; Chapman et al., 2005). Kibale currently receives ~300 mm more rainfall/year than it did at the start of the 20th century. This shift into a wetter precipitation regime is consistent with expected climatic changes in many areas of the tropics (Hulme et al., 2001; Seager et al., 2007). Other climatic changes include: less frequent droughts, an earlier onset of the wet season rains, and an increase of just over 4 °C in average maximum monthly temperature over 33 years (Fig. 1; Chapman et al., 2005). Rainfall projections are comparatively less consistent than temperature predictions (Unmüβig and Cramer, 2008), but in tropical and East Africa, a 7% increase in rainfall is anticipated (Boko et al., 2007). These changes are much higher than global averages (but see Altmann et al., 2002 for a similar example from East Africa; IPCC, 2001). This provides strong evidence that there was not a period of aridity during the last century. However, the picture becomes less clear if we consider a longer time scale. Accumulating palaeolimnological evidence indicates that there was a prolonged and ex-

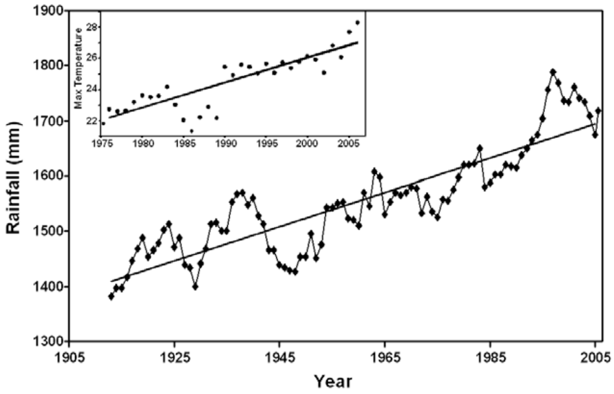

Fig. 1. The 10-year running average of the annual rainfall in the area of Kibale National Park, Uganda from 1900 to 2006, and an inlay of the average monthly temperature since 1975.

treme drought in East Africa approximately 200 years ago, which is also reflected in oral histories of the region (Bessems et al., 2008). Similarly, evidence based on salinity of cores suggests a severe drought that lasted over 200 years occurred about 3000 years ago. The impact of these drying events on the tree community of Kibale is unknown, but it is possible that they could have caused large-scale tree mortality, opening up the forest and facilitating the establishment of species requiring large-scale disturbances to recruit.

4.2. Elephants

Based on what we know about savanna/woodland dynamics (Laws, 1970; Laws et al., 1975; Naiman, 1988; Dublin et al., 1990), it is reasonable to suggest that the spatial and temporal differences in forest composition between areas of Kibale are the result of large mammals (particularly elephants) impacting the ecosystem. Evidence suggests that changes in elephant numbers can cause major floristic and structural changes in vegetation (Buechner and Dawkins, 1961; Laws, 1970; Smart et al., 1985). Elephants browse on small trees, and push them over, increasing the mortality rate of their preferred species (Lwanga, 1994; Struhsaker et al., 1996). In addition, by foraging on bark and exposing the functional tissues, elephants can also kill very large trees (Wing and Buss, 1970; White et al., 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. When elephants were protected from organized hunting, their population growth was associated with a dramatic decrease in tree density (Buechner and Dawkins, 1961). Comparison of aerial photographs taken in 1932 and in 1956 illustrated a 55–59% reduction in the number of large trees in 24 years (Buechner and Dawkins, 1961). The increase in hunting activity in the park during periods of civil unrest in the 1970s and 1980s decreased the elephant population correlating with an increase in the area covered by trees (Brooks and Buss, 1962; Buss and Savage, 1966; Wing and Buss, 1970; Douglas-Hamilton et al., 1980; Eltringham and Maplas, 1980). This effect was quantified in experimental areas with long-term exclusion of grazing and browsing pressure and marked tree regeneration (Smart et al., 1985).

Evidence suggests that elephants have also affected forest structural dynamics in Kibale National Park. Lwanga (1994) provided information on tree preference of elephants in Kibale. Using these values, we discovered that all of the common tree species (>2 individuals/ha) that were selected by elephants showed an increase in abundance from the early 1970s to 1992 (Chapman et al., 1997). During this period, elephant numbers were low in Kibale; and this likely permitted these tree species to recruit into adult size classes. Evidence from stand curves in Kibale (Osmaston, 1959) and Budongo Forest Reserve (Laws et al., 1975) and examination of previous damage to felled trees (Laws et al., 1975; Sheil and Salim, 2004) all suggest that stand regeneration in these forests is not continuous and implicate concentrated elephant activity as the cause of periodic slowed regeneration.

In Kibale it is currently estimated that there are approximately 393 elephants (Wanyama et al., in press). In contrast, between October 1962 and June 1964, Wing and Buss (1970) estimated that Kibale supported 1773 elephants indicating a much higher density of elephants in the 1960s (Wing and Buss, 1970). Brooks and Buss (1962) documented that the total area used by elephants in Uganda was reduced by 75% between 1929 and 1959 corresponding to the 40,000 elephants killed by Ugandan control workers and trophy hunters. Wing and Buss (1970) stated that the elephants of Kibale migrated to and from Queen Elizabeth National Park to the south, Rwenzori National Park to the east, and the Democratic Republic of Congo by southern and northern routes. Today, elephants rarely leave Kibale other than to raid crops in fields up to 3 km from the park boundary (Hartter, in press; Naughton-Treves et al., 1998) and until very recently were not seen in the southern third of the park because of human activities (Chapman and Chapman, unpublished data). As a result, elephant numbers have been reduced, but because the elephants are confined and concentrated, their impact on local areas of the forest may be acute.

The dynamic nature of elephant numbers over the last hundred years makes it difficult to evaluate their impact on forest regeneration. However, it is clear that elephants can impact the structure of the forest and convert forested areas to open grass and herb dominated areas and that these herbs can inhibit tree regeneration (Lawes and Chapman, 2005; Gooden et al., 2009). How elephants might have influenced forest competition 200 or more years ago is difficult to evaluate, but it will be important to monitor their impact on forest structure in the future (e.g., via excluding elephants from forested areas and examining changes in the composition of the sapling community).

4.3. Anthropogenic forest clearing in the distant past

Although much of Kibale is considered to be old-growth forest, there is evidence of human disturbance occurring in the distant past. Kibale National Park obtained its first legal status in 1932 as a Crown Reserve. The first detailed descriptions of the area were made in the late 1950s (Osmaston, 1959), and document migration of people from the area as a result of a rinderpest outbreak. Pollen diagrams from the Rwenzori Mountain Lakes (Livingstone, 1967) and Kigezi in south western Uganda (Hamilton, 1974; Hamilton et al., 1986), suggest extensive forest clearance by humans dating back beyond 4800 years ago. A 6 m long core from the Kabata Swamp approximately 10 km from Kibale found similar evidence of clearing (Taylor et al., 1999) approximately 2500 years ago that could have been associated with the arrival of the Bantu-speaking people. A second episode of forest clearing about 400 years ago is associated with shifts in settlement patterns from grassland areas to wetter, more forested regions (Taylor et al., 1999). In addition, a number of pits for storing grain and an array of potsherds have been discovered in what has traditionally been considered undisturbed forest within Kibale (Langdale-Brown et al., 1964; Mitani et al., 2000). It seems likely that in many African forests, such as Kibale, human activities have altered forest composition for centuries. Differences in forest composition between areas may reflect the period of time that the forest has had to recover from human induced disturbance.

Beyond western Uganda, there is also accumulating evidence that areas traditionally considered old growth or pristine forests have experienced large-scale clearing or disturbances in relatively recent times (recent in terms of forest regeneration i.e., between 200 and 4000 years ago, Clark, 1996; Haberle and Ledru, 2001; Anchukaitis and Horn, 2005; Bush et al., 2007; Kennedy and Horn, 2008; Lejju, 2009). For example, the current Maya forests of Northern Guatemala and Southern Mexico were once very highly populated areas. Mayans built cities, planted crops, and used and modified the forest by extracting and planting certain tree species, such as *Brosimum alicastrum*, which is now a common canopy level tree in the Maya forest, especially around archeological sites (Gomez-Pompa, 1987). Palynological evidence from lakes in the region provide evidence that extensive forested areas that currently comprise Maya forest were crop fields, as pollen of *Z. mays* has been found in several samples (Domínguez-Vázquez and Islebe, 2008).

With knowledge of the timing and cause of the disturbance and the approximate speed with which the plant community passes from one successional stage to another, managers could make predictions as to how the animal community will change, and modify the successional pathway to favour species of particular interest.

For example, the red colobus is an endangered primate species, and Kibale supports the only viable population of this species (Struhsaker, 1997). Previous research has shown that availability of leaves rich in protein and low in fiber positively correlates with the abundance of arboreal folivores like the red colobus (Oates et al., 1990; Ganzhorn, 1992; Chapman and Chapman, 2002; Chapman et al., 2002, 2004). Thus, if managers wanted to promote red colobus populations, they could plant trees with leaves high in protein and low in fiber. Based on existing knowledge of nutritional requirements similar management plans could be made for a number of species of interest (Balcomb et al., 2000). Evidence suggests that the small-scale disturbance in protected areas has potential benefits for the preservation of a diverse environmental matrix with high levels of local biological productivity. Many conservation policies have started disturbance programs to maintain habitat heterogeneity (e.g., Aggtelekk National Park, Hungary; Cadí-Moixeró Natural Park, Spain; Kakadu National Park, Australia; Grasslands National Park, Canada). Landscape managers and policy makers must consider both local and regional conservation goals when deciding to remove or maintain disturbance regimes that curtail ecological homogenization (Jacob et al., 2008). Such decisions may be dependent on the stage of succession that produces the management goals of particular sites.

We strongly concur with Clark (1996) – an understanding of the structure and function of a wide variety of tropical forest is urgently needed. In this study, we demonstrated that food tree availability for black-and-white colobus may have been reduced in recent times. If this trend continues, we expect a reduction in the black-and-white colobus populations, and/or behavioral or dietary adjustments. This is a specific example of how information on forest change can be used to inform conservation plans.

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