



Recovery of tree and mammal communities during large-scale forest regeneration in Kibale National Park, Uganda

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ABSTRACT

Tropical landscapes are changing rapidly as a result of human modifications; however, despite increasing deforestation, human population growth, and the need for more agricultural land, deforestation rates have exceeded the rate at which land is converted to cropland or pasture. For deforested lands to have conservation value requires an understanding of regeneration rates of vegetation, the rates at which animals colonize and grow in regenerating areas, and the nature of interactions between plants and animals in the specific region. Here, we present data on forest regeneration and animal abundance at four regenerating sites that had reached the stage of closed canopy forest where the average dbh of the trees was 17 cm. Overall, 20.3 percent of stems were wind-dispersed species and 79.7 percent were animal-dispersed species, while in the old-growth forest 17.3 percent of the stems were wind-dispersed species. The regenerating forest supported a substantial primate population and encounter rate (groups per km walked) in the regenerating sites was high compared to the neighboring old-growth forests. By monitoring elephant tracks for 10 yr, we demonstrated that elephant numbers increased steadily over time, but they increased dramatically since 2004. In general, the richness of the mammal community detected by sight, tracks, feces, and/or camera traps, was high in regenerating forests compared to that documented for the national park. We conclude that in Africa, a continent that has seen dramatic declines in the area of old-growth forest, there is ample opportunity to reclaim degraded areas and quickly restore substantial animal populations.

Key words: *Acanthus pubescens*, elephants; *Lantana camara*; logged forest; primates; restoration ecology; tropical rain forest.

RECENT GLOBAL ASSESSMENTS REPORT THAT 2.3 MILLION KM² OF FOREST WAS LOST BETWEEN 2000 AND 2012, and in the tropics, forest loss has increased by 2101 km²/yr (Hansen *et al.* 2013). This loss was greatest in South America and Africa, with the latter losing 67 million ha in this 12 yr period (FAO 2010). In East Africa, only 28 percent of the forest remains of what was present in the 1800s, prior to strong European influence (FAO 2005). In Uganda, where this study was conducted, deforestation has reduced tropical forest from the pre-European extent of 20 percent (39,942 km²) cover to 3 percent (5991 km²; Howard *et al.* 2000) and it is estimated that the current rate of forest loss in Uganda is 7 percent/yr (Pomeroy & Tushabe 2004). In sub-Saharan Africa, industrial round wood production (excluding plantation production) increased from 23 to 71 million m³ from 1960 to 2010 (Estrada 2013). In addition to its direct effects,

industrial logging leads to the construction of roads that promotes further deforestation through subsequent agricultural development and cattle ranching (Butler & Laurance 2008), and increased bushmeat hunting (Willkie 2000).

Ultimately, changes in forest cover are driven by increased human population size and natural resource consumption rates. The UN Population Division estimates that the world's population is expected to rise from 7 billion in 2011 to 9 billion by 2050. In African countries with tropical forest, human population density increased from 8 people/km² in 1950 to 35 people/km² in 2010 (Estrada 2013). Today human population density exceeds 400 people/km² in some areas bordering protected forests (Hartter *et al.* 2014). It is not surprising that this increase in human population density corresponds with an increase in the extent of cropland, which globally expanded by 48,000 km²/yr between 1999 and 2008, largely at the expense of forest (Phalan *et al.* 2013).

That many logged forests persist as secondary forests is in part because in 2008, for the first time, more people lived in

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cities than in rural settings (Wright & Muller-Landau 2006, Jacob *et al.* 2008). This urbanization trend is increasing and the UN Population Division estimates that 90 percent of the world's population growth between 2000 and 2030 will occur in cities of the developing world. Approximately 350 million Sub-Saharan Africans currently live in cities, which is almost the population of Canada and the United States combined (Estrada 2013). This movement of people from a rural to urban setting offers great conservation opportunities as abandoned or devalued land can be restored. However, for these lands to have conservation value (*i.e.*, sustain viable plant and animal populations or function as corridors), restoration must be achieved on a landscape scale. Designing effective conservation and management plans at a large scale requires an understanding of vegetation regeneration rates, the rates at which animals colonize regenerating areas, and the nature of interactions between plants and animals for given habitats in different parts of the world and at different phases of the regeneration process. Some of these variables differ dramatically between continents. For example, Sub-Saharan Africa has a rich savanna animal community that often use forests, including elephants, many ungulates, and baboons, while in South America the community of animals that moves between savanna and forest is very species poor. These animals are important dispersers of seeds into regenerating forest or may kill regenerating stems through over-browsing, thus animal management is important in large scale forest restoration projects, as it is for savanna restoration projects.

Given the need to develop a more theoretical understanding of restoration and practical strategies to meet conservation needs, in this study we: (i) briefly describe the tree community in four large regenerating areas with different disturbance histories in Kibale National Park, Uganda; (ii) examine the relative abundance of some mammal taxa (primates, elephants) that are important seed dispersers and/or ecosystem engineers in regenerating and old-growth forest; and finally (iii) discuss the processes and pathways of forest regeneration in Kibale National Park, Uganda and how globally representative they are.

METHODS

STUDY SITE.—The study was conducted between May 2014 and July 2015 in Kibale National Park (hereafter referred to as Kibale), Uganda, but draws on data collected since 1989 in the area. The park (795 km²) is located in western Uganda (0°13'–0°41' N and 30°19'–30°32' E) near the foothills of the Rwenzori Mountains (Fig. 1; Table 1). Kibale is a mid-altitude (920–1590 m), moist-evergreen forest. Mean annual rainfall is 1689 mm (1990–2014), falling during two rainy seasons (measured at Makerere University Biological Field Station, Chapman CA & Lambert 2000, Stampone *et al.* 2011; Chapman unpubl. data).

REGENERATING FORESTS.—We quantified forest regeneration at four sites (Table 2). All of these sites were larger than a square kilometer and at least 100 m from the forest edge, with the

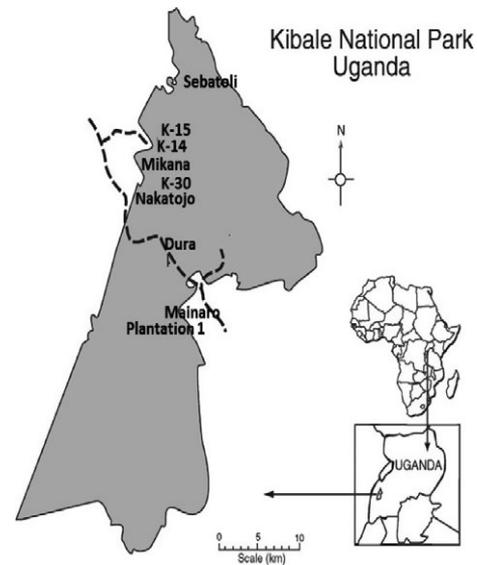


FIGURE 1. Map of Kibale National Park, Uganda, showing the location of the 10 study sites examined in this study.

plantation 1 site being well over 10 km² and approximately 5 km from the forest edge. Three of these regenerating sites (Kanyawara, Mikana, and Nyakatojo) in northern Kibale were formerly tree plantations, planted with *Pinus caribaea*, *P. patula*, and *Cupressus lusitanica* between 1953 and 1977, on grasslands that had been forested in the 18th century (Kingston 1967). According to oral history, these lands were originally forested areas that were cleared for agriculture (Struhsaker 1997). The oral history is supported by three lines of evidence; the grasslands were typically centered around the crest of a high, which was the preferred location to defend homes (Peterson 2012), recent fossil tree leaves on areas now dominated by grassland indicates that these areas once supported high forest (Osmaston 1959, Wing & Buss 1970), and these areas are regenerating when fire is removed (Lwanga 2003). These lands were abandoned when a rinderpest epidemic devastated livestock shortly after 1900 (Osmaston 1959, Kingston 1967, Wing & Buss 1970). Native tree species invaded once the plantations matured and were not removed (Zanne & Chapman 2001, Omeja *et al.* 2009). Two of these three sites (Mikana, Nyakatojo) were harvested in 1998. Commercial timber was felled with chainsaws and either rolled or winched to nearby portable sawmills, pit-sawing stations, or roadsides. These activities resulted in many native stems being killed or damaged. Although few stems >1 m tall persisted, many native individuals survived and root-sprouting and coppicing by native species were common. There was no regeneration of plantation species (Duncan & Chapman 2003). The Kanyawara Plantation was logged by chainsaw in 1993 as part of the expansion of Makerere University Biological Field Station (MUBFS). Unlike the other two pine plantations, only a few trees were cut for timber and most stems were left where they fell. Following harvest all of these areas were left to regenerate and not subject to any significant human activity.

TABLE 1. Description of field sites, forest types, and sampling details at Kibale National Park, Uganda. Sites are labeled by the year when sampling took place. The location of each site is given in Fig. 1.

Study sites	Size (ha)	History	Animal abundance	Vegetation plots	Camera traps
Dura River		Old-growth	1995; 2014	–	–
K-14	405	Lightly logged	1995; 2004–05; 2007–08; 2014	–	–
K-15	347	Heavily logged	1995; 2004–05; 2007–08; 2014	–	–
K-30	282	Old-growth	1995; 2004–05; 2007–08; 2014	–	–
Kanyawara Plantation	~20	Formerly pines	–	2014	2015
Mainaro		Old-growth	1995; 2014	2014	–
Mikana Plantation	~30	Formerly pines	–	–	–
Nyakatojo Plantation	~60	Formerly pines	2014	2014	–
Plantation 1	~120 km ²	Planted natives	2014	2014	–
Sebatoli		Heavily logged	1995; 2014	–	–

TABLE 2. A description of the tree community in four regenerating areas in Kibale National Park, Uganda. Only genus names are listed in the table unless there are more than one species from the same genera. Species recorded include: *Bridelia micrantha*, *Sapium ellipticum*, *Funtumia latifolia*, *Diospyros abyssinica*, *Milletia dura*, *Neoboutonia macrocalyx*, *Celtis africana*, and *Celtis durandii*.

Study sites	Years of recovery	# of trees	Mean # of species	Mean DBH plot	SD DBH plot	Three most common trees (number)
Mikana	16	109	6.1	12.75	2.98	<i>Celtis durandii</i> (23), <i>Funtumia</i> (17), <i>Diospyros</i> (10)
Nyakatojo	16	51	3.44	22.48	15.63	<i>Diospyros</i> (9), <i>Milletia</i> (8), <i>Funtumia</i> (7), <i>Neoboutonia</i> (7)
Kanyawara	21	137	6	14.76	5.1	<i>Diospyros</i> (41), <i>Funtumia</i> (18), <i>Celtis africana</i> (14)
Plantation 1	21	40	2.9	19.76	11.18	<i>Bridelia</i> (9), <i>Sapium</i> (11), <i>Funtumia</i> (5)

The fourth regenerating site (Plantation 1) has a more intense history of land use. The general area of Plantation 1 extends from the center of Kibale to the far south of Kibale. It was illegally occupied by subsistence farmers from the 1970s until their eviction in 1992 (van Orsdol 1986, Baranga 1991). Encroachment by these farmers adversely affected approximately 120 km² of forest. After their eviction, fire-maintained grasslands dominated the area (elephant grass; *Pennisetum purpurea*). Frequent fires spread into the park from neighboring agricultural lands, 1996 aba, and fires set by poachers to drive game (Struhsaker, 2003; Omeja et al. 2011). At this site, the Forest Absorbing Carbon Emission (FACE) Foundation set up a carbon offset reforestation program in collaboration with the Uganda Wildlife Authority (UWA) in 1993. This program aimed to restore 10,000 ha of formerly settled and degraded lands within the park, through planting several native tree species in areas that had been cleared of grass, weeding these areas, and maintaining fire breaks (Omeja et al. 2011). We sampled this area 21 yr after the initial planting of native species.

The spatial distribution of sites and land use in adjacent sites may influence the outcome of the comparison. For example, one site is to the far south, and since Kibale covers a north-south elevational gradient, the southern site receives less rain and is hotter (Chapman et al. 2010a). The habitats adjacent to each of the regenerating areas supports different mammal and bird communities, thus influencing the type and number of seed dispersers

coming to the site and the likelihood that specific animals will use or permanently colonize a study site (C. A. Chapman, S. Bortolamiol, P. A. Omeja, F. P. Paim, R. Sengupta, J. P. Skorupa, and K. Valenta, submitted). Adjacent to Kanyawara and Mikana were agricultural land outside of the park, logged forest, and old-growth forest, while Nyakatojo just had logged forest and old-growth forest next to it (Chapman & Chapman 1997, Chapman et al. 1997). Adjacent to the southern site was areas of old-growth (often *Cynometra*-dominated forest), planted-regenerating forest, and anthropogenic grasslands (Chapman et al. 1997). Rates of regeneration of the tree community and carbon sequestrations are presented in Omeja et al. (2012) and Wheeler et al. (in press).

VEGETATION SURVEYS.—We surveyed vegetation diversity and structure at the four regenerating sites (Kanyawara, Mikana, Nyakatojo, Plantation 1) using a 4 km transect and ten 10 × 10 m plots. Plots were established 20 m off of one randomly selected side of the transect line and were spaced 50 m apart. We identified all species above 5 cm dbh and measured their dbh. Here, we report the mean number of tree species and mean dbh (both with standard deviation) for each of these sites.

MAMMALIAN ABUNDANCE.—We assessed mammalian relative abundance at these four regenerating sites by: (i) qualitatively reporting different species encountered either through field observations, tracks/dung identification, or camera traps; and (ii) comparing

encounter rates with primates in two of these regenerating sites (Nyakatojo, Plantation 1), and immediately adjacent old-growth forest in forestry compartment K-30 and at Mainaro (Struhsaker 1997, Chapman *et al.* 2010b). Nyakatojo and Plantation 1 had different histories of disturbance and recovery, but both were dominated by tall grasses (mainly *Pennisetum purpurea*) at the time that restoration began (Chapman *et al.* 2010b). We also present data on relative abundance of elephants (*Loxodonta africana*) for additional sites for which we have long-term data; these sites are K-14 (lightly logged), K-15 (heavily logged), Sebatoli (heavily logged), and old-growth forests K-30, Dura River, and Mainaro.

Forest compartment K-15 at Kanyawara is a 347-ha section of forest that experienced high-intensity selective felling of native trees from September 1968 through April 1969. Harvest averaged 21 m³/ha or approximately 7.4 stems/ha (Skorupa 1988, Struhsaker 1997); however, collateral damage was much higher. It is estimated that approximately 50 percent of all trees in K-15 were destroyed by logging and incidental damage (Skorupa 1988, Chapman & Chapman 1997). For Sebatoli at the far north of the park, we were unable to obtain information on the level of extraction. However, detailed quantification of stand structure suggests that the level of extraction was similar to, or slightly lower than that in K-15. In each of these regenerating areas we used camera traps to capture the cryptic and/or nocturnal terrestrial mammal community (Table 3).

PRIMATE ABUNDANCE.—The primate species surveyed were redbtail monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), mangabeys (*Lophocebus albigena*), baboons (*Papio anubis*), red colobus (*Procolobus rufomitratus*), and black-and-white colobus (*Colobus guereza*). A variety of methods have been proposed for estimating animal density or abundance and considerable controversy exists regarding their accuracy for forest dwelling mammals (see also National Research Council 1981, Defler & Pinto 1985, Chapman *et al.* 1988, Whitesides *et al.* 1988, Struhsaker 1997, Fashing & Cords 2000, Teelen 2007, Hassel-Finnegan *et al.* 2008, reviewed by Chapman *et al.* 2010b, Struhsaker 2010). The DISTANCE program is often advocated as an accurate means of estimating primate population densities (Buckland *et al.* 2010); however, following Lwanga *et al.* (2011) we elected not to use this approach as this method has been demonstrated to overestimate densities of forest primate groups, often by more than double, when compared with the most accurate estimates of density that are based on studies of specific social groups with identifiable individuals (reviewed by Chapman *et al.* 2010b). Group density can also be calculated using sighting distances (estimated distance to the first animal seen), plotted at set intervals or bins (*e.g.*, 10 m intervals) to set a cut-off rule to evaluate transect width (National Research Council 1981, Chapman *et al.* 2000, 2010b). However, with this approach sighting distance of different species or habitats often have to be lumped to obtain a sufficiently robust sample to identify a clear cut-off distance (Teelen 2007, Chapman *et al.* 2010b). Also, determining strip width may be subject to error when sample sizes are small and different observers estimating distance is a potential source of error.

TABLE 3. An account of mammal species recorded in the regenerating sites (Kanyawara, Mikana, Nyakatojo and Plantation 1) in Kibale National Park, Uganda. Principal means of identification is reported.

Species	Common name	Reported from
Artiodactyla		
<i>Cephalophus barveyi</i>	Red duiker	Field observation
<i>Cephalophus monticola</i>	Blue duiker	Field observation
<i>Hylocoerus meinertzhageni</i>	Giant forest hog	Tracks/dung
<i>Potamochoerus porcus</i>	Bush pig	Field observation
<i>Syncerus caffer</i>	Buffalo	Field observation
<i>Tragelaphus scriptus</i>	Bushbuck	Field observation
<i>Tragelaphus spekei</i>	Sitatunga	Field observation
Carnivora		
<i>Canis domesticus</i>	Hunting dog	Camera traps
<i>Genetta</i> sp.	Genet sp.	Camera traps
<i>Nandinia binotata</i>	African palm civet	Tracks/dung
Primates		
<i>Cercopithecus ascanius</i>	Redtail monkey	Field observation
<i>Cercopithecus lhoesti</i>	L'hoesti monkey	Field observation
<i>Cercopithecus mitis</i>	Blue monkey	Field observation
<i>Colobus guereza</i>	Black and white colobus	Field observation
<i>Pan troglodytes</i>	Chimpanzee	Field observation
<i>Papio anubis</i>	Baboon	Field observation
<i>Procolobus rufomitratus</i>	Red colobus	Field observation
Proboscidea		
<i>Loxodonta africana</i>	Elephant	Field observation
Rodentia		
<i>Hystrix</i> sp.	Porcupine	Field observation
<i>Thryonomys</i> sp.	Cane rat	Camera traps

As a result of these considerations, we calculate encounter rate as a measure of relative abundance, which is the number of groups seen per kilometer of census trail walked (Chapman *et al.* 2000, Mitani *et al.* 2000, Teelen 2007). This method does not take into account differences in detection probability among periods or differences in the ability of the observers to detect animals (although variance in observer's ability to spot groups have previously been quantified to be low (Lwanga *et al.* 2011) and the same observers conducted the last three censuses), nor does it correct for visibility differences due to logging or regeneration. One might think encounter rate would not be appropriate to examine changes in primate populations in the logged area because the forest is regenerating. However, we have previously shown that there is no difference among areas in the magnitude of the change of tree basal area (identical basal areas can be achieved by either high densities of very small trees or low densities of very large trees, which may influence frugivores if many small trees are too small to bear fruit) and it appears that the logged area in Kibale is in a state of arrested succession (Chapman & Chapman 2004, Lawes & Chapman 2005). It is important to note that this analysis does not investigate the possibility that group size might have changed over time (Gogarten *et al.* 2014).

ELEPHANT ABUNDANCE.—We determined elephant relative abundance by counting the number of times elephant tracks crossed transects. Direct elephant counts are not possible in dense forest as elephants avoid humans and charge when feeling threatened. In all seasons, elephant tracks are very easy to detect in comparison to smaller mammals. In 2004–2005 and 2007–2008, these censuses were only done at sites neighboring Makerere University Biological Field Station due to logistical constraints. A total of 1850 km was walked along transects over the four time periods. From June to August 2015, ten camera traps (Reconyx—PC800 HyperFire Professional Semi-Covert IR) were set at 50 m intervals along a transect through the regenerating forest in Kanyawara plantation.

RESULTS

In all four regenerating sites for which we collected vegetation data (16–21 yr; Table 2), a closed tree canopy was established. Mean number of trees per plot (4000 m², *N* = 40 plots) varied from 40 to 137 (mean = 84 ± 46 SD; Table 2). In comparison there were on average 486 trees in this area (4000 m²) in the old-growth forest. Trees in regenerating forest were from only a few species (mean = 4.6 ± 1.7 SD tree species per plot). In all regenerating areas there were 35 species in 0.4 ha, while in the old-growth forest 85 species were found in 2.6 ha. The dbh of trees in regenerating forest ranged from 12.8 to 22.5 cm and averaged 17 cm (±4.5 SD; Table 2). In comparison, the dbh in old-growth forest ranged from 10 (minimum evaluated) to 297 cm, with an average of 24.7 (median = 18.0). Species richness and stem density in the regenerating areas were not a function of time since regeneration began (Omeja *et al.* 2012), and likely were a result of other environmental features of the plots (*e.g.*, soil type and moisture), disturbance prior to regeneration, and treatment received since. Overall, in regenerating forest 20.3 percent of stems were wind-dispersed species and 79.7 percent were animal-dispersed species, while in the old-growth forest 17.3 percent of the stems were wind dispersed. Although most tree species were animal-dispersed, one wind-dispersed species (*Funtumia latifolia*) was among the three most common species at the Mikana site (Table 2). Throughout all regenerating areas the native *Acanthus pubescens* and the introduced *Lantana camara* were common in the understory and in areas with large canopy openings *A. pubescens* often formed what was nearly monodominant stands.

In general, the richness of mammals detected by sight, tracks, feces and/or camera traps (Table 3), was relatively high in regenerating forests compared to the total mammal richness documented for the national park (Struhsaker 1997). This includes all diurnal primates, elephants, seven Artiodactyl species, and three of the 16 carnivores known to occur in Kibale (Struhsaker 1997). Many of the carnivores that were not sighted are either extremely shy, rare, transients (*e.g.*, *Panthera leo*), or very small and often nocturnal (*e.g.*, *Viverra* spp.). We did not encounter hippopotamus (*Hippopotamus amphibius*) as they are only found in one lake in southern Kibale, an area that was not sampled, and

warthogs (*Phacochoerus aethiopicus*) that are also in the far south region of the park, which we did not sample.

Primate encounter rate (groups per km walked) in two regenerating sites (Nyakatojo, Plantation 1) was high compared to the neighboring old-growth forests (K-30, Mainaro), but varied among species and sites (Fig. 2). For example, the encounter rate of red colobus was almost twice that in the old-growth forest than in the neighboring regenerating forest, but black and white colobus encounter rate was similar between the two areas. In contrast in the north, baboon encounter rate in the old-growth forest was approximately ten times less than in the regenerating forest (Fig. 2). An intriguing exception is the blue monkey. Blue monkey abundance gradually declines from the north of Kibale to the south (Struhsaker & Leland 1979, Chapman & Lambert 2000, Chapman *et al.* 2005), which corresponds with a decline in elevation and rainfall. The reasons for these patterns of decline are currently unknown. Baboon abundance is also puzzling; it appears to be dramatically increasing at the more northern sites, which corresponds to long-term researcher accounts (Chapman 1989, 1995, Chapman *et al.* 2010b). By contrast, redtail monkey populations established quickly in all type of regenerating habitats.

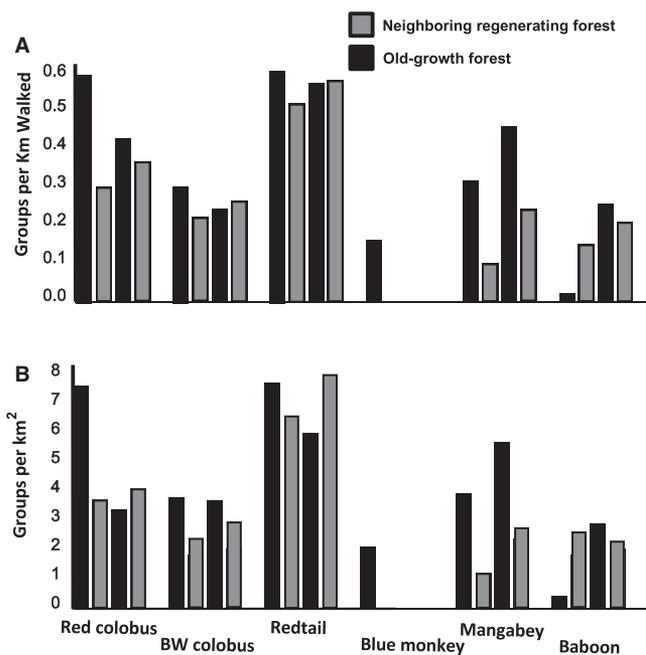


FIGURE 2. Encounter rate (groups per km walked) of the common primates in two old-growth and two neighboring regenerating areas in Kibale National Park, Uganda (the northern sites precede the southern sites). Primate density (groups per km²) is not reported due to high similarity of the results. Comparison between: (A) paired sites K-30 (old-growth) and Nyakatojo (16 yr recovery; formerly pines); and (B) paired sites Mainaro (old-growth) and Plantation 1 (21 yr recovery; reforested with native species). The species represented follow a phylogenetic order that corresponds to dietary strategies (red colobus—folivore, black and white colobus—folivore, redtail monkey—insectivore/frugivore, blue monkey—frugivore, mangabey—frugivore, baboon—frugivore).

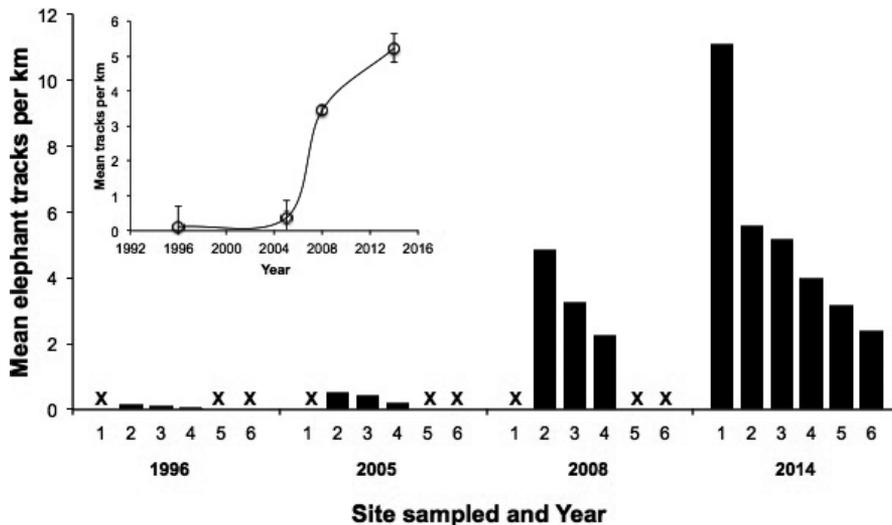


FIGURE 3. Relative abundance of elephants as indicated by tracks crossing transects in old-growth and neighboring regenerating areas in Kibale National Park, Uganda. The areas shown here are those where long-term data are available 1—Sebatoli (logged), 2—K-15 (logged), 3—K-14 (moderately logged), 4—K-30 (old-growth), 5—Dura River (old-growth), and 6—Mainaro (old-growth). Nyakatojo and Plantation 1 are not portrayed because for these areas we do not have long-term data. X marks periods where particular areas were not surveyed in that year. Top inlay represents the mean relative abundance (based on tracks) across all sites for all four sampling periods (1995–1996, 2004–2005, 2007–2008, and 2014–2015).

Elephant relative abundance increased steadily over time in all areas and was highest in logged forests (particularly Sebatoli; Fig. 3). Casual observations and discussions with Uganda Wildlife Authority staff suggest that elephant numbers increased dramatically between 2004–05 and 2007–08, and they continued to increase markedly thereafter.

DISCUSSION

Our data indicate that the plant and animal communities in Kibale National Park, Uganda established substantial populations

in large regenerating areas in less than two decades. The rapid recovery of the animal community is likely the result of the fast regeneration of the tree community to a closed canopy forest, and possibly because the food resources in these regenerating forests are of high quality (Fig 4). For example in Central America, leaves of early pioneer tree species have higher protein-to-fiber ratios (Coley 1983), which is beneficial to folivores, like the colobines in Kibale (Ganzhorn 1992, Chapman & Chapman 2002, but see DeGabriel *et al.* 2014), and lower levels of secondary compounds than old-growth forest trees (see Gogarten *et al.* 2012 for similar results from Kibale). The regenerating trees

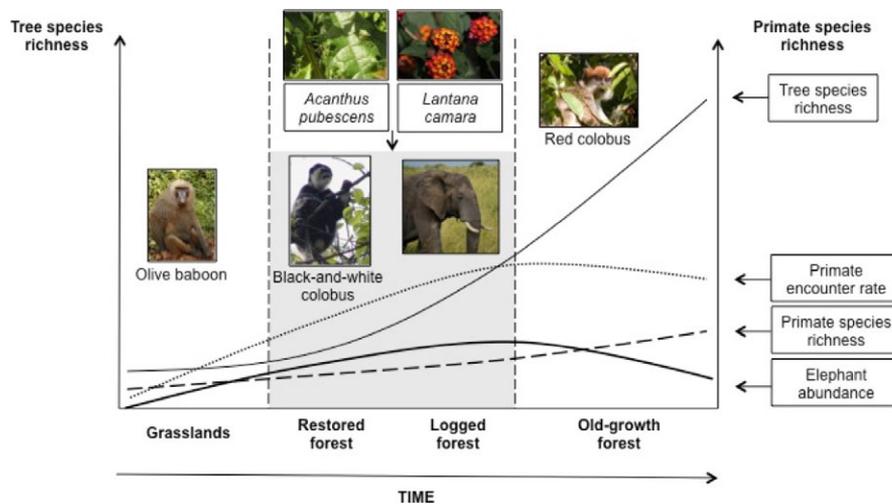


FIGURE 4. Trends of relative tree species richness, primate and elephant abundance illustrating the relation between plant and animal species richness and the invasion of recovering forests by woody weeds.

tended to be from only a few species and although on average there were 4.6 tree species in a 10 × 10 m plot, the tree richness averaged 20 species in each of the regenerating areas, which appears to be sufficient to support a substantial animal population. Most tree species found in the plots were early successional species and were animal-dispersed (~80%), demonstrating the importance of frugivores in regeneration. The possibility that the increase in primate numbers in the regenerating areas is a result of immigration from areas outside the park is very unlikely, because the landscape outside the park is dominated by agricultural and pasture land with a few very small forest fragments that support very few primates of only some species (*i.e.*, less than 1 ha; [Onderdonk & Chapman 2000]). Furthermore, the abundance of primates in the old-growth forest just adjacent to these regenerating forests did not decline, suggesting that while the primates that colonized these regenerating forest may have originated from within the park, their increase in number did not come at the expense of existing park populations (C. A. Chapman, S. Bortolamiol, P. A. Omeja, F. P. Paim, R. Sengupta, J. P. Skorupa, and K. Valenta, submitted).

The roles that primates and other wide-ranging fruit eating species (*e.g.*, elephants, hornbills) play in increasing the diversity of the tree community of the regenerating forest should not be underestimated (Terborgh *et al.* 2015). For example, elephants can move up to 10 km in the time it takes for ingested seeds to be defecated (Chapman *et al.* 1992) and frequently move among old-growth forest, regenerating forest, and grasslands. In doing so they can disperse seeds from old growth forest to the regenerating forest, increasing the diversity and functional capacity of new regrowth. While the establishment and survival of dispersed seeds needs to be quantified (Balcomb & Chapman 2003), the species richness observed in regenerating forest plots suggest that many seeds survive, establish, and grow in regenerating areas (Chapman *et al.* 1992, Chapman 1995, Omeja *et al.* 2011) (but see Lawes & Chapman 2006). A study in Costa Rica showed successful recruitment of seedlings, saplings, and young trees of mature forest species in secondary forests of 12 to 29 yr of age (Norden *et al.* 2009). This was attributed to the high abundance of generalist species in the regional flora, high levels of seed dispersal by these generalists, and local presence of a tree species pool in old-growth forest remnants (Norden *et al.* 2009). Similarly, Lwanga (2003) showed the importance of seed dispersers and fire protection in the protection of regenerating forest along a grassland-savanna boundary. Such studies suggest that given the right conditions, passive forest regeneration offers even heavily disturbed lands the potential to recover to a functioning forest ecosystem.

Floral and faunal regeneration potential may not be the same for all communities and ecosystem services. For instance, a study of butterfly assemblages at Kibale demonstrated long-term impacts of different forest disturbances on species composition (Nyafwono *et al.* 2014). Butterfly assemblages differed in successional and primary forests, and some specialist fruit-feeding species were only found in primary forests (Nyafwono *et al.* 2014). Thus, the success of community reassembly should be evaluated

for different disturbance effects and stages of forest recovery. Predicting rates of recovery requires that environmental variables are taken into account, such as climate and soil conditions, flowering and fruiting phenology, availability of species-specific requirements (*e.g.*, hollow nesting species), and land use history (*e.g.*, swidden agriculture). Nonetheless, our findings emphasize the conservation value of old-growth forest fragments within protected areas for maximizing long-term recovery of protected degraded lands.

In Kibale, other factors appear to be critical to the future state of large regenerating areas of forest. In general, African elephant populations are being decimated, declining by 62 percent between 2002 and 2011 in Central Africa (Maisels *et al.* 2013). Hunting has driven elephants to seek refuge in some protected areas like Kibale, and in many such areas they are locally overabundant, creating extreme tension between parks and local communities. In Kibale, increases in elephant numbers appear to be exponential (Fig. 3) and have been associated with a rise in crop raiding and dramatic consequences for park-people relations. Beyond potential migrations from surrounding areas (*e.g.*, Queen Elizabeth Park, Congo), elephant population growth can also be explained by the prominence of the invasive native understory species *Acanthus pubescens*. Elephants appear to favor regenerating forests where *A. pubescens* is abundant, returning frequently to these sites, with dire consequences for forest recovery. Increases in elephant numbers can cause major floristic changes (Buechner & Dawkins 1961, Laws 1970, Smart *et al.* 1985), and their foraging behavior on *A. pubescens* at Kibale has been demonstrated to damage and arrest the succession process in regenerating forests (Lawes & Chapman 2006). Thus, while elephants may disperse seeds and promote regeneration, they can also cause substantial damage to the existing recruits and impede regeneration. Which role elephants predominantly play will depend on how frequently they revisit a specific area, a parameter likely dependent on elephant density.

Elephants browse on small trees and push them over, increasing the mortality rate of their preferred species (Struhsaker *et al.* 1996, Lawes & Chapman 2006). By foraging on bark and exposing functional tissues, elephants can also kill large trees (Wing & Buss 1970, Laws *et al.* 1975, White *et al.* 1993). The history of elephant population dynamics in Murchison National Park, Uganda clearly illustrates how elephants affect habitat structure and ecosystem dynamics. Establishment of the park in 1912 and protection of elephants led to important changes in vegetation and tree density (Buechner & Dawkins 1961). Comparison of aerial photographs taken in 1932 and 1956 documented a ~55–59 percent reduction in large trees (Buechner & Dawkins 1961). The increase in hunting activity in the park during periods of civil unrest in the 1970s resulted in a decline in the elephant population (Brooks & Buss 1962, Buss & Savage 1966, Wing & Buss 1970, Douglas-Hamilton *et al.* 1980, Eltringham & Maplas 1980), which in turn resulted in an increase in tree cover (Smart *et al.* 1985). This effect was quantified and confirmed by long-term exclusion of grazing and browsing pressure and subsequent tree regeneration (Smart *et al.* 1985). At their current abundance in Kibale, elephants appear not to be altering the composition of

intact old-growth forests, but they are playing a very significant role in inhibiting tree regeneration in disturbed areas, and potentially affecting the regeneration trajectory (Lawes & Chapman 2006).

In addition to elephants, our observations revealed that particular attention should be paid to the impact of *Lantana camara*, an aggressive invasive herb capable of suppressing native tree regeneration (Omeja *et al.* in press). *L. camara* shrubs suppress tree seedlings, and may even suppress growth of, or kill, established young trees. *L. camara* has harmful effects on ecosystems in many regions. For example, it was ranked as the most significant weed in non-agricultural areas in Queensland, Australia (Zalucki *et al.* 2007). In Kenya, *L. camara* is threatening the habitat of the sable antelope (*Hippotragus niger*). If *L. camara* continues to form a dense shrub layer then the regeneration pathway to forest recovery may be arrested. This highlights the pressing need to investigate the long-term impacts of this invasive species.

In conclusion, on a continent that has recently seen dramatic declines in forest area, there appears to be opportunity to reclaim secondary forests and abandoned agricultural lands as human populations become more urbanized. Our study demonstrates that fallow land dominated by grassland and disturbed by fire (14.6% of Kibale, [Chapman & Lambert 2000]), can recover to closed canopy forest within 20 yr over large spatial scales. Despite low tree species richness in these initial regenerating forests they nevertheless support a high mammalian diversity. Given the increased number of national parks, increase in areas receiving protection, more extensive law enforcement, and reforestation associated with carbon storage associated with efforts to reduce climate change (Chapman *et al.* in press), the time is right to consider how best to enhance forest rehabilitation and restoration at Kibale and other forest sites across eastern Africa. However, with changes in land use, hunting pressure, and a trend toward urbanization come new challenges. For example, large mammals such as elephants may seek sanctuary from hunting pressure in large forest blocks with areas of regenerating forest and have a disproportionate effect on the trajectory of regenerating forest than other forest animals. While elephants act as seed dispersers, in some large scale incidences they are also significant agents of disturbance. Our work (Lawes & Chapman 2006) demonstrates that disturbance by elephants can and does have perverse outcomes. In Kibale, elephants target understory shrubs and woody herbs that typically inhabit regenerating secondary forest. In doing so, elephants arrest forest succession. By creating disturbances in the forest, they also provide habitat for introduced weedy species, such as *L. camara*, that further affect the pathway of vegetation recovery and can arrest regeneration of secondary forest. Thus, while forest recovery may be occurring at the regional scale in countries like Uganda, there are many attendant processes that need to be considered to ensure that regeneration converges on natural forest conditions and ecosystem functions. Finally, our study emphasizes the tension between restoration and protection in conservation strategies (Possingham *et al.* 2015). With rapid urbanization of human populations an opportunity has been

created to restore degraded forest ecosystems and fallow farmlands to tropical forest. In general, successful restoration projects recover 80–86 percent of reference-level biodiversity and ecosystem services (Benayas *et al.* 2009, Murcia *et al.* 2014). Successful restoration is thus dependent in part on protecting old-growth forests from disturbance to ensure there is a species pool to support secondary succession on disturbed lands. However, protection should not always be prioritized over restoration (Possingham *et al.* 2015).

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