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Changes in Elephant Abundance Affect Forest Composition or Regeneration?

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ABSTRACT

While overall numbers of African elephant have declined dramatically in recent times, some populations are now confined to protected areas and are locally overabundant—an undesirable situation for both biodiversity conservation and elephants. In forested protected areas, options to manage elephants are limited because it is difficult to safely approach animals, yet it is vital that these populations are managed because browsing by elephants can dramatically alter forest ecosystems. Using data collected over 50 yr in Kibale National Park, Uganda, we examine the prediction that increasing elephant numbers and associated changes in their foraging behavior have caused a shift in tree community composition. Although the relative abundance of elephants increased significantly between 1996 and 2010, the population structure of their preferred tree food species did not change, nor did tree community composition change in favor of species able to re-sprout after elephant damage. Furthermore, over the last 50 yr Kibale elephants have not become more selective foragers, as would be expected if more nutritious tree species were declining. However, elephants are more abundant in disturbed areas dominated by shrubs and grasses and appear to have arrested forest succession in these areas. At their current abundance, elephants have not selectively altered the composition of intact old growth forest, but they do inhibit the regeneration of disturbed areas.

Abstract in Spanish is available in the online version of this article.

Key words: arrested succession; disturbance; elephant conservation; forest tree composition; regeneration; restoration; selective foraging.

PLANT COMMUNITIES CAN BE STRONGLY INFLUENCED OR EVEN RESHAPED BY THE ACTIONS OF animals (Jones *et al.* 1994, Power 1997, Crain & Bertness 2006, Wright & Jones 2006, Chapman *et al.* 2013). Several classic examples illustrate the influence of animals on plant communities, including prairie dogs (*Cynomys* spp. [VanNimwegen *et al.* 2008,]), sea otters (*Enhydra lutris*; [Estes & Palmisano 1974,]), and beavers (*Castor canadensis*; [Naiman 1988,]). Perhaps the most dramatic example of a mammal affecting plant communities is that of changes in African elephant (*Loxodonta africana*) densities causing significant changes in vegetation structure over large areas (Buechner & Dawkins 1961, Laws 1970, Smart *et al.* 1985, Hawthorne & Parren 2000, Lawes & Chapman 2006). Elephants browse on small trees, pushing them over, and often killing them. They also debark large trees, thereby reducing tree survival rates (Laws 1970, White *et al.* 1993, Lwanga 1994, Sheil & Salim 2004). For example, when elephants in Murchison Falls National Park, Uganda, were protected from organized hunting in the 1930s, their population growth was associated with a 55–59 percent reduction in the number of large trees (Buechner & Dawkins 1961). Conversely, illegal hunting during the Ugandan civil war (1970s and 1980s) dramatically reduced elephant numbers in Murchison, followed by a corresponding increase in the park's woodland area (contrast the information presented in these references Brooks & Buss 1962, Buss & Savage 1966, Douglas-Hamilton *et al.* 1980, Eltringham & Maplas 1980). The role elephants played in this woodland increase was verified in experiments excluding elephants and resulting in marked tree regeneration (Hatton & Smart 1984, Smart *et al.* 1985). Given that the elephant culling policy initiated in 1967 was stopped in 1994 (Van Aarde & Pimm 1999, Dickson & Adams 2009), the impact of elephant numbers on large trees is also a concern in Kruger National Park, South Africa (Shannon *et al.* 2008, Smit & Ferreira 2010).

Although elephants can play an important role in structuring the composition of vegetation (Chapman *et al.* 1992, Babweteera *et al.* 2007, Campos-Arceiz & Blake 2011, Bonnell *et al.* 2012), it is clear that at a large spatial scale elephant numbers have

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declined dramatically over the past century (Brooks & Buss 1962, Blake & Hedges 2004, Blanc *et al.* 2007, Burn *et al.* 2011, Maisels *et al.* 2013). Elephants are currently found in 37 African countries and their total population was estimated to be 472,000 animals in 2007 (Blanc *et al.* 2007). The most recent estimate of forest elephant populations indicates a decline of approximately 62 percent between 2002 and 2011 and a 30 percent loss in their geographical range (Maisels *et al.* 2013). Despite their overall decline elephants are locally overabundant in some regions. This results in habitat modification undesirable for both biodiversity conservation and elephants, where management strategies call for forest habitats to be maintained (Cumming *et al.* 1997, Guldemond & Van Aarde 2008, Scheiter & Higgins 2012). For example, high elephant densities in the vicinity of water sources can make mopane woodland habitats susceptible to elephant over-browsing (Ben-Shahar 1996).

In some instances, local overabundance has led to elephant culls to maintain ecosystem integrity (Shannon *et al.* 2008, Dickson & Adams 2009, Smit & Ferreira 2010). However, such management programs have only been applied in savanna/woodland systems, where estimates of elephant populations are relatively easy and a variety of management options are possible (Pimm & Van Aarde 2001, Dickson & Adams 2009). In forests, estimating elephant density is more difficult (Walsh & White 1999, Wanyama *et al.* 2009) and management options are limited because the dense forest makes it difficult to approach animals safely. Elephants have become increasingly confined to protected areas, and, in the absence of natural or anthropogenic forces regulating their populations, they will become locally overabundant in both forests and savannas. New and innovative management options may be urgently required to avoid significant disturbance to forest ecosystems by such elephant populations.

Here, we examine five predictions concerning changes in elephant numbers, adjustments in elephant feeding patterns, and subsequent modification in the structure and composition of the plant community in Kibale National Park, Uganda (hereafter Kibale): (1) the relative abundance of elephants has increased since 1996; (2) the more elephants prefer a tree species, the greater its annualized rate of population decline; (3) a tree species' ability to re-sprout after elephant damage is negatively correlated with its population decline; (4) elephants have arrested forest succession by favoring previously disturbed sites with a high proportion of shrubs and grasses; and (5) elephants have become more selective in their diet over time as former preferred tree foods have declined.

METHODS

STUDY AREA.—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 Rwenzori Mountains (Struhsaker 1975, 1997, Chapman & Lambert 2000). Kibale is a mid-altitude, moist-evergreen forest receiving an annual average rainfall of 1696 mm (1990–2012; C.A. Chapman and L.J. Chapman unpubl. data). Kibale was designated a Forest Reserve in 1932 and became a National Park in 1993. This study was conducted in the Kanyawara area of the park, near Makerere University Biological Field Station, in three forestry compartments with different disturbance (logging) histories. Compartment K-30 (282 ha) has not been commercially harvested and is considered a relatively undisturbed mature forest (Struhsaker 1975, Skorupa 1988), a relatively undisturbed old forest (Struhsaker 1997), or an old growth forest (Chapman *et al.* 2010a). Prior to 1970, pitsawyers removed a few large stems (0.03–0.04 trees/ha), but this had little impact on forest structure (Skorupa 1988, Struhsaker 1997). This area is dominated by large *Parinari excelsa* (hence its recognition as a *Parinari* forest by foresters) and other timber species such as *Carapa grandiflora, Olea capensis, Pouteria altissima, Strombosia scheffleri*, and *Newtonia buchananii* (Osmaston 1959, Chapman & Chapman 1997). Compartment K-15 (347 ha) was selectively logged at high intensity from September 1968 through April 1969 with an average 21 m^3/ha or approximately 7.4 stems/ha harvested (Skorupa 1988, Struhsaker 1997). It is estimated that logging and incidental damage destroyed 50 percent of all trees (Skorupa 1988, Chapman & Chapman 1997). Eighteen tree species were harvested, with nine species contributing more than 95 percent of the harvest volume. This area had more flat valley bottoms than the K-30 area (Skorupa 1988, Struhsaker 1997). Compartment K-14 (405 ha), was selectively logged at low intensity from May through December 1969 (averaging 14 m^3/ha or approximately 5.1 stems/ha). Twenty-three tree species were harvested, with nine accounting for 94 percent of the harvest volume; approximately 25 percent of all trees were destroyed by logging and incidental damage (Skorupa 1988, Struhsaker 1997). Logging in this compartment was spatially heterogeneous as some areas were heavily logged (*i.e.*, Mikana), while others were largely untouched (Chapman & Chapman 2004).

Elephant numbers in the Kibale region have been dynamic and have been shaped by a variety of factors operating at different spatial and temporal scales. As a result, understanding how their numbers are in balance with ecosystem structure and function is difficult. Wing and Buss (1970) estimated that Kibale supported approximately 1770 elephants in the early 1960s, but state that based on a number of sources of error the estimate could be as low as 400 animals. Recent estimates suggest that 390 elephants currently occupy Kibale (Wanyama *et al.* 2009), but again the error associated with this number is recognized as being large. Between 1929 and 1959, Ugandan control workers and trophy hunters killed 40,000 elephants, resulting in a 75 percent decrease in the area used by elephants (Brooks & Buss 1962). As recently as 50 yr ago, elephants migrated between Kibale and Queen Elizabeth National Park to the south, Rwenzori Mountains National Park to the west, and into the Democratic Republic of Congo by both southern and northern routes (Wing & Buss 1970). Thus, it is possible that at the time of Wing and Buss's estimate in the 1960s, elephant numbers were very high because they were in the process of being confined to the national park by hunting, or that the survey's estimates included a large number of transient animals. However, since the 1960s evidence suggests that elephant numbers declined dramatically until the early 1990s when Kibale became a national park and people living illegally in the south of what is now the park were resettled (van Orsdol 1986, Chapman & Lambert 2000, Hartter *et al.* 2011). Since then the elephant population has increased and dispersed throughout the park (*i.e.*, in the 1990s elephants were not found in the south of the park where human encroachment was extensive, but they are present in the south in large numbers today). Currently, elephants are confined within the park boundary or a few hundred meters of it during crop raiding events (Naughton-Treves *et al.* 1998, MacKenzie *et al.* 2011, Naughton *et al.* 2011).

PREDICTION 1: THE RELATIVE ABUNDANCE OF ELEPHANTS HAS INCREASED SINCE 1996.—We conducted censuses to quantify the relative abundance of elephants between July 1996 and June 1997, July 2005 and June 2006, and June 2008 and July 2009 (see Chapman *et al.* 2010b for details of the transects). Census data are comparable across time as the same methods were used in each census; the same observers walked the same census routes and recorded the same types of elephant sign each time. Transects were approximately 4 km long and two observers walked each transect at approximately 1 km/h and counted elephant trails that crossed the transects. In forest with dense undergrowth, such as Kibale, elephants make an unmistakable trail that is relatively easy to identify and follow. In the first two periods, we walked transects every 2 wk to ensure we could tell fresh from old trails; however in the third period, we were confident at aging trails, therefore we walked transects once a month. We combined the biweekly estimates from the first two periods to produce a monthly estimate comparable to the last period. In total, observers walked 184 transects covering 736 km.

PREDICTION 2: THE MORE ELEPHANTS PREFER A TREE SPECIES, THE GREATER ITS ANNUALIZED RATE OF POPULATION DECLINE.—We defined elephant diet preferences with respect to the number of times a tree species was fed on by an elephant divided by the abundance of that tree species in the forest (note: this is different than selectivity used below when contrasting the long-term data). In 2011 and 2012, we determined the preference values for tree species by establishing 77 elephant 'diet plots' measuring 10 m × 50 m (total sample area of 3.85 ha) in areas damaged by elephants; this was done within ~10 days of the damage occurring. As researchers were in the field every day, and the general location of herds in the region was known, we were able to know the approximate date that the elephants were in a particular area and sampled the area soon after to ensure reliable identification of the trees upon which elephants fed (*i.e.*, leaves of killed trees were still on the stem). Within each diet plot, we identified the species of all tree stems >0.5 m tall that had signs of elephant damage, estimated their height and measured their diameter at breast height (dbh; if above 1.2 m tall). We described the extent of elephant damage on a 1–5 scale, where 1 indicated little damage, 4 indicated damage thought to be sufficient to eventually kill the stem, and 5 indicated that elephant damage had killed the stem. Trees were identified using recognized taxonomic keys (Polhill 1952, Hamilton 1991, Katende *et al.* 1995, Lwanga 1996). To calculate the abundance of tree species in the forest, we used data from 26 permanent vegetation plots established in the Kanyawara area in 1989. Each plot was 200 m × 10 m, providing a total sample area of 5.2 ha. These plots were in the same general area as the diet plots, but it is possible that slight differences in location introduced some bias in the determination of preference. Given the number of plots, however, the bias is assumed to be small. We identified the species of each tree with dbh >10 cm (measured at 1.2 m from the ground on the uphill side; note 1.3 m from the ground is a more traditional standard) within 5 m of each side of the transect, individually marked it with a uniquely numbered aluminum tag, and measured its dbh. This provided an initial sample of 2096 trees (67 species). We resurveyed these plots in May 2000, September–November 2006, and January–April 2013. During each resurvey, we relocated all previously tagged trees to assess survival, remeasured them to quantify growth, and identified, tagged, and measured new trees recruiting into the >10 cm dbh size class. We noted mortality and ascertained the cause of death when possible. To assess if preferred tree species had greater population declines as a consequence of elephant foraging, we determined the population changes for each tree species in the 26 plots between 1989 and 2013 and correlated the annualized rate of population change with elephant diet preferences.

PREDICTION 3: A TREE SPECIES' ABILITY TO RE-SPROUT AFTER ELEPHANT DAMAGE IS NEGATIVELY CORRELATED WITH ITS POPULATION DECLINE.—We resampled the 26 vegetation plots between February and July 2012 to specifically document tree death or damage (*e.g.*, the main stem snapped) and whether it was likely to be caused by elephants. We noted if the tree had resprouted and yielded a new stem. We compared these survey results with those from 2000 to determine the proportion of stems per tree species killed or damaged by elephants in each time period. These surveys underestimated elephant damage, as we could not relocate some tagged trees (4%), possibly because they died early in the period between 2000 and 2012 and decayed. We determined species-specific mortality rates between 1989 and 2013 and related it to the proportion of trees that were damaged by elephants and resprouted. A significant correlation between these two variables would suggest that elephant damage has driven a shift in the composition of the forest toward species in that resprouted.

PREDICTION 4: ELEPHANTS HAVE ARRESTED FOREST SUCCESSION BY FAVORING PREVIOUSLY DISTURBED SITES WITH A HIGH PROPORTION OF SHRUBS AND GRASSES.—We assessed the relative abundance of elephants in each of the three compartments in 1996–1997, 2005–2006, and 2008–2009 using the methods described in Prediction 1. We evaluated vegetation ground cover in each of the 26 vegetation plots when we inventoried the resprouting trees in 2012. Every 5 m along the 200 m vegetation plot, we estimated the proportion of ground covered by three broad ground vegetation types: shrubs, grasses, or ferns. We used a one-way analysis of variance (ANOVA) on arcsine-square root transformed data to examine differences in ground cover between compartments. In conducting this analysis, we tested to ensure the assumptions of the model were met.

PREDICTION 5: ELEPHANTS HAVE BECOME MORE SELECTIVE IN THEIR DIET OVER TIME AS THEIR PREFERRED TREE FOODS HAVE DECLINED.—If elephant numbers have increased, and given that their feeding often causes the death of the stems they eat, we predicted that elephants would feed more selectively than they did 20 yr ago, *i.e.*, they would continue to seek out species that for some reason were particularly beneficial, but since the density of those species had declined they would be more selective. The study by Wing and Buss (1970) clearly demonstrated that the elephant population in Kibale were very selective foragers—in their study they enumerated 250 woody species, 108 were browsed significantly more than expected, 91 as expected, and 51 less than expected. We evaluated dietary preference for a set of 13 tree species for which there were comparable data in 1962–1963 (Wing & Buss 1970), 1978–1979 (Kasenene 1980, 1984, 1987), 1993 (Lwanga 1994, Struhsaker *et al.* 1996), and 2012–2013 (this study). Wing and Buss (1970) studied elephant habitat use and foraging patterns over the entire park. Almost 15 yr later, Kasenene (Kasenene 1980, 1984, 1987) quantified elephant damage in eleven 0.81 ha plots in the logged (N = 5) and unlogged (N = 6) forestry compartments. In 1992 and 1993, Lwanga (1994) recorded elephant damage to trees along fresh elephant trails in all forestry compartments near the Makerere University Biological Field Station (Kanyawara); much of this information is reported in Struhsaker *et al.* (1996). A species selection ratio was calculated as the quotient of the proportional contribution of that species to the total number of browsed trees divided by its proportional contribution to the total number of trees enumerated. A ratio greater than one indicates the species was selectively browsed (Crawley 1983, Struhsaker *et al.* 1996). We assessed differences among years using Kruskal–Wallis test.

RESULTS

PREDICTION 1: THE RELATIVE DENSITY OF ELEPHANTS HAS INCREASED SINCE 1996.—In general, the number of elephant trails recorded per km of transect walked increased over time, and at each time period we observed more elephant trails in the heavily logged area (with more ground vegetation—see Prediction 4) than in the unlogged or lightly logged areas (Fig. 1).

PREDICTION 2: THE MORE ELEPHANTS PREFER A TREE SPECIES, THE GREATER ITS ANNUALIZED RATE OF POPULATION DECLINE.—There was no evidence that the abundance of more preferred elephant foods declined between 1989 and 2013 (damage rank = 1 Spearman rank coefficient $r_{sp} = 0.1543$, damage rank ≥2 $r_{sp} = 0.2159$, damage rank ≥4 $r_{sp} = -0.0551$). This was the case for all species and only for the species listed by Struhsaker *et al.* (2006) as preferred foods. All tree species (N = 16) identified by Struhsaker *et al.* (Table 6 in Struhsaker *et al.* 1996) as significantly preferred species (Table 1) were also identified as preferred species in our study (N = 68), with the exception of *Dasylepis eggelingi* and *Blighia unijugata* (considering all rankings of damage). This suggests

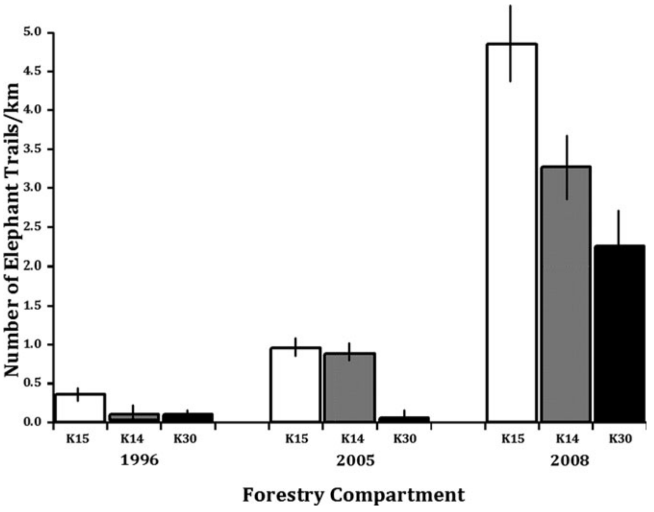

FIGURE 1. Elephant sign (trails ± SE) recorded in areas with different logging history (unlogged (K30), lightly logged (K14), and heavily logged (K15)) in Kibale National Park during three periods (July 1996 to June 1997, July 2005 to June 2006, and June 2008 to July 2009).

TABLE 1. *Elephant selection ratios reported from four different studies in Kibale National Park, Uganda between 1962 and 2013.*

Tree species	1962–64*	1978–79†	1993‡	2012–13§
Antiaris toxicaria	2.85	2.08	3.47	6.61
Blighia unijugata	2.80	n/a	3.00	1.06
Celtis africana	3.42	3.27	1.22	0.68
Ficus exasperata	0.96	n/a	3.94	2.50
Funtumia latifolia	1.65	0.93	0.26	0.10
Lovoa swynnertonii	2.85	0.82	3.56	1.00
Mimusops bagshawei	3.21	0.63	4.32	2.33
Monodora myristica	1.69	1.75	0.00	5.06
Newtonia buchananii	2.12	1.60	4.66	5.22
Parinari excelsa	1.17	0.19	5.75	0.61
Strombosia scheffleri	2.66	0.66	4.06	0.28
Trichilia splendida	2.20	1.90	0.71	2.02
Trilepsium madagascariense	2.95	2.29	2.72	0.38
Average	2.35	1.46	2.90	2.14

*Data from Wing & Buss (1970), sampling done in 1962 between 1964 and included the whole park.

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

‡Data from Lwanga (1996), sampling done in 1993, and includes forestry compartments K30 and K15 (average of compartments presented).

§This study, sampling done in 2012 and 2013, and includes forestry compartments K30, K14, and K15 (average of compartments presented).

consistency in dietary preferences across years, potentially based on the nutritional value of the food species (Rode *et al.* 2006).

Prediction 3: a tree species' ability to resprout after elephant damage is negatively correlated with its population decline.—We considered 33 trees (1.4% of the 2358 trees sampled in 2013) to have been killed by elephants within the last year. A further 27 trees (1.2%) had been pushed over or damaged by elephants to the extent that the main stem was no longer present, but the tree was still alive and resprouting. Forty-six trees (2.0%) had resprouted from damage that could not be conclusively attributed to elephants. The stems of eight trees (0.34%) had been snapped by a falling larger tree, but were resprouting. The change in the population size for each tree species was independent of the proportion of trees damaged by elephants and able to resprout ($r_{sp} = 0.015$, $P = 0.587$).

Prediction 4: elephants have arrested forest succession by favoring previously disturbed sites with a high proportion of shrubs and grasses.—The number of elephant trails was greater in the logged than the unlogged areas, which was consistent among years (Fig. 1). As predicted, the heavily logged area had more ground vegetation than the old growth forest ($F_{2,17} = 6.63$, $P = 0.007$; Scheffe *post hoc* test $P = 0.008$), but ground vegetation did not differ between the lightly logged and old growth areas (Scheffe post-hoc test $P = 0.187$).

Prediction 5: elephants have become more selective in their diet over time.—The average selection ratio of the 13 species for which there are comparable data between 1962 and 2013 did not change over time (Kruskal–Wallis$_{3/45}$, $P = 0.058$, Table 1). Selectivity during the 1978/1979 period was low, which is what resulted in this test being marginally significant; however, comparing the last two periods when elephant density data are availability there was no significant change (Mann–Whitney $P = 0.243$).

DISCUSSION

Interactions between elephants and the tree community are dynamic and dependent on elephant density, the ability of the tree community to recover from elephant damage, and the time scale over which damage occurs. We tested five predictions concerning how changes in elephant numbers and feeding behavior might affect the tree community of Kibale National Park, Uganda. While we documented a dramatic increase in the relative abundance of elephants, this increase did not lead to a decline in the annualized rate of population change in their preferred food species. Furthermore, we found no evidence to support the prediction that elephant feeding preferences changed as their abundance increased, which we expected as their preferred food species became less abundant. However, an important caveat is that present elephant abundance is possibly one quarter that documented in the early 1960s (Wing & Buss 1970).

Evaluating these predictions assumes that changes in elephant trails counts reflect actual changes in density. In Kibale, where the herbaceous vegetation is often extensive (Malenky *et al.* 1993), elephant trails are readily apparent regardless of the area or nature of the ground vegetation. Thus, it is unlikely that the increase in relative density is indicative of changes in the ground vegetation; furthermore, there is no evidence of a large change in the extent or nature of the ground vegetation. However, increases in elephant trail numbers could be caused by elephants increasing their movement rate; a hypothesis for which we have no data with which to evaluate. Yet, we have no reason to expect elephants move more in the later census relative to the first; furthermore, since the first census the elephant population has dispersed throughout the park while prior they were restricted to the more northern areas (*i.e.*, in the 1990s elephants were not found in the south of the park where human encroachment was extensive, but they are present in the south in large numbers today). We therefore view the increase in elephant trail number to reflect a true change in density.

The lack of an effect by elephants on the composition of the old growth tree community in Kibale may reflect: (1) a nonlinear interaction between elephants and preferred food tree species; (2) shifts in tree abundance are caused by other factors, masking the influence of elephants; (3) the degree and scale to which elephants are selective is sustainable under current elephant abundance and food tree species densities; or (4) elephant numbers are still recovering from culling and poaching in the 1960s and probably still below the level that their food resources can sustain.

It is possible that elephant damage will not have an effect on old growth tree community composition until a threshold abundance of elephants is reached. As elephant numbers increase, their effect on the tree community may not be initially apparent because tree recruitment might depend on other environmental factors, such as the nature of gap formation (Hubbell *et al.* 1999, Zanne & Chapman 2005) or seed dispersal (Wright *et al.* 2000, Jordano *et al.* 2011). However, after such thresholds are passed, elephants may quickly start playing a structuring role in forest composition.

Elephant may affect the composition of the forest, but their influence may not be as great as other factors. Working in the same area, Chapman *et al.* (2010a) documented that the abundance of tree species frequently recruiting into large disturbed areas has declined, relative to species that can recruit into the understory or canopy gaps. Other Kibale research showed that changes in folivorous primate density influence forest composition; over 17 yr, 78 percent of tree species known to be killed by excessive red colobus (*Procolobus rufomitratus*) foraging declined in abundance (Chapman *et al.* 2013). If a number of processes simultaneously influence forest composition, identifying the impact of a single process, such as elephant foraging, will be difficult.

Alternatively, elephant foraging may not affect old growth tree community composition because elephants forage in a relatively unselective manner at a small spatial scale. At large spatial scales, elephants have been shown to be selective with respect to the habitat they choose. De Knegt *et al.* (2011) demonstrated that elephants select areas based on large-scale characteristics, such as the proximity to water or a habitat's herbaceous biomass. Holdo (2003) documented that elephants selected foraging areas with high soil quality, rather than the availability of particular plant species. Similarly, our data indicate selection on large spatial scales as elephants had high relative abundance in areas with thicker herbaceous layer (Fig. 1). At smaller spatial scales, elephants may be forced to be relatively unselective to merely obtain sufficient food intake (Shrader *et al.* 2012). Given their large body size (males 5500–6000 kg, females 2500–2800 kg [Owen-Smith 1988]), elephants are expected to be less selective than smaller species because they have lower nutrient requirements per unit of body mass (Jarman 1974). Furthermore, they can afford to be less selective because, as hind-gut fermenters, their rapid digestive passage compensates for lower digestive efficiency in breaking down fiber (Bell 1971). These observations have led elephants to be classified as non-selective bulk feeders (Van Soest 1994, Pretorius *et al.* 2012). As a result, elephants may not be selecting specific tree species on which to feed. In Chobe National Park, Botswana, Owen-Smith and Chafota (2012) documented that at times more than 50 percent of the trees in this ecosystem were moderately or highly acceptable to elephants, but that 40–70 percent of the food elephants consumed was from just one or two favored and abundant shrubs.

It is difficult to know the level of elephant abundance that would represent a 'natural' or equilibrium state, if this state even exists. Elephant numbers in Uganda may be still recovering from culling in the 1960s and poaching in the 1970s and 1980s. If so, it is not surprising that most of our predictions of food selection and elephant influence on the tree community were unsupported. Alternatively, elephant numbers may already be elevated because high human population density has confined them within the boundary of the park. A longer term understanding of elephant population change and tree community dynamics is needed to distinguish between these alternatives and this is underway.

The effect of elephant foraging at large spatial scales may significantly affect the future of Kibale and other forested ecosystems. Our results support previous research indicating the importance of the interaction between herb cover and elephant damage on tree regeneration in Kibale (Osmaston 1959, Struhsaker *et al.* 1996, Chapman & Chapman 1997, 2004, Lawes & Chapman 2006). By feeding on the herbs and grasses that often colonize disturbed areas, elephants prevent forests from recovering after disturbance. Without continued elephant disturbance, advanced regeneration by tree species would likely penetrate the herb canopy and eventually recover disturbed forest (Paul *et al.* 2004, Lawes & Chapman 2006). Thus, elephants may be influencing Kibale at the habitat level, maintaining areas in a state of arrested succession by favoring herbaceous vegetation capable of resprouting after elephant foraging. Given the large areas of regenerating forest in the south of Kibale and in the logged areas to the north (Chapman & Chapman 1997, Omeja *et al.* 2011, Tweheyo *et al.* 2013), elephant foraging likely plays a significant role in forest dynamics on a park-wide scale. In addition, elephants are important seed dispersers and thus in the future as elephant numbers increase, they will be dispersing more of the seeds of fruits they ingest. This will likely promote these species over others (Chapman *et al.* 1992, Babweteera *et al.* 2007, Campos-Arceiz & Blake 2011). The large-scale impact of elephant seed dispersal on forest composition is an interesting area for further study, particularly in the regenerating forests in southern Kibale.

In summary, the elephants of Kibale are increasing in number, yet they have not become more selective foragers as would be expected if the more nutritious tree species were declining. However, elephants are more abundant in disturbed areas dominated by shrubs and grasses and appear to have arrested forest succession in these areas. At their current abundance, elephants appear not to be altering the composition of intact old growth forest, but they are playing a very significant role in inhibiting tree regeneration in disturbed areas and in Kibale these are extensive. Particular, attention should be made to their impact in the regenerating forest in the south of Kibale, where their interaction with *Lantana camara*—an aggressive invasive herb capable of suppressing regeneration— may change forest dynamics. It would also be interesting to elucidate if their numbers are increasing from natural recruitment or the movement of herds from Queen Elizabeth.

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