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**A long-term temporal comparison of ecological predictors
on relative elephant presence within a forested environment**

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A dissertation submitted for the degree of Master of Science by
Research in the School of Natural Sciences

July 2022

Declaration to include in your thesis

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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Abstract

The plight of forests and the restoration of forests worldwide has gained recent traction, with emphasis being drawn on forests at the 2021 COP26 summit in Glasgow where the United Nations coined this the “Decade of Restoration”. With forests holding much of the world’s biodiversity, they are of key conservation concern, along with playing an important role in climate regulation. Therefore, monitoring the relationships between the forests themselves and the fauna within are key for successful conservation. Within forests, large herbivores have a crucial role and help to maintain ecosystem functioning through seed dispersal, nutrient and carbon cycling, creation of microhabitats and opening previously inaccessible areas for smaller animals. Of the large herbivores, the megaherbivores (weighing in excess of 1000 kg) have the greatest impact, and of particular interest is the African elephant. From conducting a review of previous research from Kibale National Park, Uganda, three questions were developed: (1) How does disturbance history and vegetation cover affect relative elephant abundance? (2) How does rainfall variation across years affect relative elephant abundance in a forested environment? And (3) How has cumulative diameter at breast height (DBH) of trees in Kibale changed and has there been any influence by elephants? These questions were addressed using a combination of long-term elephant abundance data and forest structure with remotely sensed land cover classification. The results showed that relative elephant abundance in Kibale has increased but has been higher than expected from natural recruitment. This has been attributed to elephants migrating from the Democratic Republic of Congo into Kibale. As a result, the ecological predictors used in the mixed model (disturbance history and rainfall) showed minimal slight significant effects on relative elephant abundance. Land classification did not work for mapping earlier years (1996-2008) and therefore was dropped from the models. We suggest that more information is required for land classification of previous years along with substantial knowledge of the study area to interpret such longitudinal data.

Keywords:

Elephant, forest, abundance, ecological predictors, land classification

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Chapter 1: Ecological predictors of elephant presence and habitat use

Abstract

Understanding how large herbivores impact their habitats requires an awareness of predictors that influence population and behaviour. Through population changes, movement and foraging behaviours, large herbivores can completely change habitat types, altering plant diversity, growth and abundance. Such changes in population, movement and foraging can be influenced by both ecological and anthropogenic factors, ranging from availability of forage and water to human disturbance such as logging. Of particular interest from the large herbivores are those that are classed as megaherbivores (> 1000 kg in weight) as these herbivores can have greater impacts on their habitat. This review focuses on the factors that affect the relative abundance of the African elephant as they fulfil multiple roles within their habitat through seed dispersal, nutrient and carbon cycling. This review comes to focus on the elephant population within Kibale National Park, Uganda, because of a gap in the literature in large scale studies that investigate the elephants' impacts on a park wide basis, and how these impacts are facilitated by ecological factors. Three questions are highlighted: (1) How does disturbance history and vegetation cover affect relative elephant abundance? (2) How does rainfall variation across years affect relative elephant abundance in a forested environment? And (3) How has cumulative diameter at breast height (DBH) of trees in Kibale changed and has there been any influence by elephants? These questions reflect the gap in the literature on the Kibale elephants and aim to provide a target for supplementary information to improve understanding of this population of elephants.

Introduction

Large herbivores can alter vegetation diversity and abundance through their foraging and movement behaviour, which can have significant impacts on their habitats (Jorritsma *et al.*, 1999; Liu *et al.*, 2015). They often promote plant diversity by foraging on abundant plant species which can prevent dominance by a few species (Burns *et al.*, 2009; Beguin *et al.*, 2022), growth of plant species through seed dispersal (Iravani *et al.*, 2011; Lum and Min, 2021) and by influencing nutrient cycles through their movements, urine and faeces (van der Waal *et al.*, 2011; Forbes *et al.*, 2019). However, these benefits may be outweighed by the impact of their movement and feeding behaviours on their habitat. This can include suppressing the growth of

vegetation and halting the successional stages of regrowth (Ameztegui and Coll, 2015; Bobrowski *et al.*, 2015). For example, red deer (*Cervus elaphus*) have been shown to impede forest regeneration by slowing down and even inhibiting the succession of shrubs and trees, keeping landscapes open (Müller *et al.*, 2017).

The foraging behaviour of large herbivores and the influence this exerts on ecosystems is also shaped by environmental factors, such as variation in rainfall (Beekman and Prins, 1989; Young *et al.*, 2009). One example is the change in movement patterns to adjust to food availability (Beekman and Prins, 1989; Young *et al.*, 2009). Wildebeest (*Connochaetes taurinus*) are a well-known migratory animal and seasonally move across the savanna landscape, which has been suggested to be driven by the availability of new grass growth to maximise energetic intake (Morrison and Bolger, 2012). Such changes in movement can impact the use of habitat, which is important to understand as animals can play important roles in the structuring and functioning of ecosystems. Those that have particularly influential roles are described as ecosystem engineers (Gilad *et al.*, 2004; Berke, 2010; Chapman *et al.*, 2013). These animals can alter the habitat type (Law *et al.*, 2017; Brazier *et al.*, 2021), the food availability for other species (Desbiez and Kluyber, 2013; Roman *et al.*, 2014), and can be important in habitat creation (Desbiez and Kluyber, 2013; Pike and Mitchell, 2013; Losapio *et al.*, 2021). Identifying these species and managing their populations appropriately is key in conservation practices (Berke, 2010; Chapman *et al.*, 2013) and for understanding how anthropogenic activities may impact them (Losapio *et al.*, 2021; Beirne *et al.*, 2021).

As human populations continue to expand, the impacts caused by human activity becomes an increasing concern as some lead to wide reaching and long lasting impacts (Kleinman *et al.*, 2019). Major threats include illegal trade, disease, habitat loss and fragmentation (Ripple *et al.*, 2015; Torres-Romero *et al.*, 2020). These lead to range contractions and population declines, with about 60% of large herbivores threatened with extinction (Ripple *et al.*, 2016).

One of the most widespread forms of anthropogenic disturbance in forests is logging, which can result in a change of forest composition, altering succession and causing shifts in faunal species richness and composition (Watson *et al.*, 2018; Han *et al.*, 2021; Messina *et al.*, 2021). Logging

also creates canopy gaps that are larger and often more abundant than natural tree fall gaps (Struhsaker, 1997). These gaps provide optimum growth conditions for terrestrial herbaceous vegetation (THV), which can rapidly invade the gap and potentially suppress forest regeneration (Chapman and Chapman, 1999) and can be a preferred forage for some species (Chapman and Chapman, 1997). Animal species use these gaps in different ways and the larger gaps created by logging may lead to more frequent use by larger species (Struhsaker, 1997; Wall *et al.*, 2021). As a result of this, forest edge dynamics can be expanded (Struhsaker, 1997; Wall *et al.*, 2021). For example, when white-tailed deer (*Odocoileus virginianus*) populations are at high densities, their foraging on woody and herbaceous plant species can expand the forest edge, going deeper into the forest (Alverson *et al.*, 1988). Therefore, understanding the impact anthropogenic practices have on large mammals will supply crucial information on how large mammal habitat use may change.

Megaherbivores

Ecosystems often experience the greatest impact from large-bodied herbivores (weighing in excess of 1000 kg) with high absolute energetic demands. These megaherbivores include rhinos, elephants, giraffe, and common hippopotamus. As a result of their size, they have few non-human predators making food availability the primary factor limiting population growth (Owen-Smith, 1988; Pradhan *et al.*, 2008; Cromsigt and te Beest, 2014; Mukherjee *et al.*, 2019; Hyvarinen *et al.* 2021). Megaherbivores need to acquire considerable amounts of forage to fulfil their nutrient requirements, which often means they may need to traverse large ranges (Mukherjee *et al.*, 2019). In addition, when enclosed by boundaries, such as fences or human habitation, populations of megaherbivores can become locally overabundant, increasing pressure on the ecosystem and causing rapid changes to the composition of vegetation (Cromsigt and te Beest, 2014). The impact megaherbivores have on the vegetation can also impact other animal species, through altering availability of forage or changing the vegetation structure (Owen-Smith, 1988; Foster *et al.*, 2014; Guldemond *et al.*, 2017).

Megaherbivores are often considered ‘ecosystem engineers’ and ‘keystone species’ due to their disproportionately large impact on their environment relative to their abundance (Waldram *et al.*, 2008; Cromsigt and te Beest, 2014). They often fill multiple ecological functions, which cannot

be replaced by smaller herbivores (Sandhage-Hofmann *et al.*, 2021). For example, the white rhinoceros (*Ceratotherium simum*) maintains short grass patches in African savannas which results in reduced fuel loads for fire and creates suitable forage for smaller herbivore species, including impala, wildebeest, and zebra (Waldram *et al.*, 2008; Cromsigt and te Beest, 2014). Also in Africa, the foraging of hippopotamuses (*Hippopotamus amphibius*) can engineer surrounding environments from grassy areas to short-grass grazing lawns, and create water channels within rivers (Chritz *et al.*, 2016).

Importance of elephants

Elephants can have profound impacts on the environments they inhabit. There are three species of elephant, the African savanna elephant, *Loxodonta africana*, the African forest elephant, *Loxodonta cyclotis*, and the Asian elephant, *Elephas maximus*. Because of their large ranges, elephants are very important in seed dispersal (Campos-Arceiz and Blake, 2011; Terborgh *et al.*, 2016; Beirne *et al.*, 2021). Elephants have been found to disperse seeds far from the parent tree (Campos-Arceiz and Blake, 2011; Bunney *et al.*, 2017), potentially giving the seedlings higher success rates, as they will not be overshadowed and outcompeted by the parent (Chapman and Chapman, 1995; Cochrane, 2003). In addition, after consumption by elephants, seeds often have improved germination success (Chapman *et al.*, 1992; Babweteera *et al.*, 2007; Blake *et al.*, 2009; Campos-Arceiz and Blake, 2011). The large size of elephants means that they are the sole dispersers of certain tree species and the removal of elephants may lead to a decrease in the abundance of these species (Chapman *et al.*, 1992; Campos-Arceiz and Blake, 2011; Tweheyo *et al.*, 2013). For example, in Kibale National Park, Uganda, elephants are the sole disperser of *Balanites wilsoniana* seeds (Chapman *et al.*, 1992; Cochrane, 2003), with the fruits of *B. wilsoniana* being too large for other species to consume (Chapman *et al.*, 1992; Campos-Arceiz and Blake, 2011). Elephants are also important for nutrient cycling making previously stored nutrients available through feeding on plant material, and excavating termite mounds and salt licks, increasing soil fertility (Poulsen *et al.*, 2018). Additionally, through their mobility and large consumption of vegetation, elephants have considerable throughput of dung and thus, can redistribute nutrients away from nutrient rich areas, creating a relatively homogenous distribution of nutrients (Poulsen *et al.*, 2018; le Roux *et al.*, 2018). From this, it can be determined how elephants are assisting in regeneration and success of plant species.

Elephants use multiple parts of a plant in their foraging, stripping bark, breaking off twigs and leaves, or pushing over small trees (Wing and Buss, 1970; Chapman *et al.*, 1997; Landman *et al.*, 2019). The African Savanna elephant, *L. africana*, has a pronounced impact on the structure and function of the savanna ecosystem because of their tendency to uproot and consume entire plants, as well as toppling and altering the physical structure of trees (Coverdale *et al.*, 2016; Landman *et al.*, 2019). Additionally, savanna elephants increase the understory richness and biomass through inadvertently creating associational refuges, composing of damaged branches that impede other herbivores access (Coverdale *et al.*, 2016). Grazers and browsers can benefit from this alteration of the understory species as it promotes the growth of native grasses (Coverdale *et al.*, 2016; Landman *et al.*, 2019). For example, within Chobe National Park, Botswana, the feeding of elephants upon stems and branches promoted more browse, in areas known as ‘browsing lawns’, providing suitable forage for mesoherbivores, such as impala and greater kudu (Makhabu *et al.*, 2006).

In forested environments elephants can have a limiting effect on the rate of regeneration/succession through their feeding on saplings and small trees (Chapman *et al.*, 1997; Malhi *et al.*, 2016; Terborgh *et al.*, 2016) and can play a large role in changing the structure of forests (Tweheyo *et al.*, 2013). However, the impact of elephants can be exacerbated as a result of previous habitat disturbance, both elephant induced and anthropogenic (Bonnell *et al.*, 2011). In Murchison Falls National Park, Uganda, elephants have been found to limit tree growth in woodland environments (Buechner and Dawkins, 1961; Smart *et al.*, 1985) and with a coupled effect of fire, can suppress growth completely (Smart *et al.*, 1985). During the years of civil unrest in Uganda (1970s and 1980s) poaching rates were high and as a result numbers of elephants, and other wildlife populations plummeted. In the absence of feeding by elephants and other animals, a floristically poor environment was created, dominated by just two species, *Acalypha bipartita* and *Achyranthes aspera* (Smart *et al.*, 1985). Therefore, this provided a basis to study the impact elephants have on the environment and when elephant numbers were low, tree growth ensued, but as elephant populations recovered, there was a dramatic decrease in tree density (Buechner and Dawkins, 1961; Hatton and Smart, 1984; Smart *et al.*, 1985). Therefore,

having longitudinal information on elephant habitat use can help explain their impacts on the landscape.

Movement Behaviour

Predicting an animals' impact on the environment requires understanding their movement behaviour (Beirne *et al.*, 2021). Elephants can travel long distances to acquire the forage they need and can use many habitat types, each one potentially fulfilling a different requirement of their reproductive, nutritional and energetic needs (Beirne *et al.*, 2020). It is important to understand drivers of movement, with savanna elephants often being constrained by water availability, which is a key factor driving their distribution and abundance (Chamaillé-Jammes *et al.*, 2007; Boulton *et al.*, 2019). However, for African forest elephants (*L. cyclotis*) the seasonal variation in rainfall in forests is not as pronounced as that in savannas, and thus, permanent water sources are likely to be more easily accessible to them. The movement of forest elephants, instead, tends to be more influenced by forage availability, in particular, tree fruiting seasons due to the forest elephants' frugivorous nature (Blake and Inkamba-Nkulu, 2004; Beirne *et al.*, 2020).

Movements can be constrained with the creation of national parks, as animals may be fenced within a protected area, or, their natural habitat within the park's boundaries may be completely surrounded by human settlements and arable land (Loarie *et al.*, 2009; Grandos *et al.*, 2012; Gubbi *et al.*, 2012; Wadley *et al.*, 2018). This can create locally overabundant populations that can exacerbate their impact on the environment and be detrimental to the functioning of the ecosystem (Blake *et al.*, 2008; Chapman *et al.*, 2010a; Vanak *et al.*, 2010; Shaffer *et al.*, 2019). Through increased foraging this may alter the structure of vegetation by promoting the growth of certain species and suppressing the growth of others, changing the landscape (Vanak *et al.*, 2010). For example, at high densities elephants have been seen to alter woodland into shrubland environments through their foraging and suppress tree regeneration in forested environments (Bonnell *et al.*, 2011; Guldmond *et al.*, 2017). Additionally, in southern Africa, elephants were found to "bunch-up" along fences, causing them to revisit the same foraging locations, increasing the pressure on the vegetation (Loarie *et al.*, 2009). This intensification of resource use can degrade the ecosystem and alter the structure and diversity of vegetation, promoting

growth of a few dominant species that are resistant to herbivory (Guldemon *et al.*, 2017; Beirne *et al.*, 2021).

Elephants often move along pathways that link resources (Beirne *et al.*, 2020), with some being used for decades (von Gerhardt *et al.*, 2014). For example, in some forest elephant (*L. cyclotis*) populations in Africa pathways have been seen to connect fruiting trees, allowing the elephants to move more efficiently when the trees come into fruit, as well as between mineral deposit sites (Blake and Inkamba-Nkulu, 2004; Campos-Arceiz and Blake, 2011; Beirne *et al.*, 2020).

Elephant pathways can have different uses, and these can be distinguished (Vanleeuwe and Gautier-Hion, 1998). For example, one study in the Congo found that elephants used particular pathways for travelling long distances and connecting favourite sites which they named as “boulevards”. Boulevards were found to be long, straight paths that had an East-West orientation, crossing through all vegetation types. In contrast, distinct “foraging paths” were described which were shorter and more meandering, also providing the elephants with herbaceous foods and tree fruits (Vanleeuwe and Gautier-Hion, 1998). Studying the way pathways are laid out in the environment will provide a means into understanding how an animal interacts with its environment and whether there are any changes in behaviour.

Feeding behaviour

Elephants can be selective in their feeding (Field, 1971; Terborgh *et al.*, 2016). However, due to their large size, lower relative energy demands, large gut and therefore longer post-gut fermentation, elephants can consume low-quality forage, avoided by other small herbivores, to fulfil their considerable dietary requirements (Shannon *et al.*, 2006; O’Kane *et al.*, 2011). This has led to elephants being deemed as non-selective bulk feeders, with a tendency to forage on grasses, leaves, branches, fruits, and bark. Fruit is seen to be an important part of a forest elephant’s diet and, when it is available, both savanna and forest elephants will seek it out (Merz, 1981; Short, 1981; White *et al.*, 1993; Vanleeuwe and Gautier-Hion, 1998; Blake *et al.*, 2009; Campos-Arceiz and Blake, 2011; Beirne *et al.*, 2020). The African forest elephant (*L. cyclotis*) may consume more fruit than the other elephant species (Campos-Arceiz and Blake, 2011). For example, in Bia National Park, Ghana, elephant density varied seasonally and was strongly correlated with the fruiting of particular tree species (*Tieghemella heckii* and *Parinari excelsa*)

(Short, 1983). In Lopé Reserve, Gabon, elephant densities sharply increased when *Sacoglottis gabonensis* were fruiting (White, 1994; Campos-Arceiz and Blake, 2011).

Elephants tend to target a range of tree parts as forage, this can vary between the species and sexes (Shannon *et al.*, 2006; Terborgh *et al.*, 2016). Savanna elephant males will tend to use their weight to push over and break open trees, however, females are more likely to use smaller branches, leaves and fruit (Stokke and du Toit, 2000; Shannon *et al.*, 2006). Forest dwelling elephants also tend to target smaller, younger trees, which may increase the mortality rate of preferred species (Chapman *et al.*, 2010a; Terborgh *et al.*, 2016). When trees have fallen, elephants will forage on the canopy leaves as these tend to be more nutritious, and they will also strip branches (Coverdale *et al.*, 2016; Terborgh *et al.*, 2016). In doing this, it provides previously inaccessible parts of the tree to smaller herbivores (Coverdale *et al.*, 2016; Landman *et al.*, 2019). Additionally, through feeding on bark, the elephants may inadvertently kill trees by exposing them to fire, disease and infection (Chapman *et al.*, 2010a; Shannon *et al.*, 2011). The consequences of tree loss and knowing what species are being lost is important for conservation efforts and ensuring the environment is not being substantially altered and even degraded.

As human settlements and agriculture expand and further disturb habitats, instances of human-elephant conflict increases (Shaffer *et al.*, 2019; Sintayehu and Kassaw, 2019). Elephants leave protected areas to eat crops - a high-risk, high-gain foraging strategy that seems to be more common in males (Sukumar and Gadgil, 1988; Chiyo *et al.*, 2011; Srinivasaiah *et al.*, 2019). Both African and Asian elephants benefit from crop-foraging as it provides highly nutritional foods (Chiyo and Cochrane, 2005; Rode *et al.*, 2006; Chiyo *et al.*, 2011). These higher nutrient levels enable male elephants to have faster growth rates and longer musth periods, which ultimately makes them stronger competitively (Chiyo and Cochrane, 2005; Srinivasaiah *et al.*, 2019). However, elephants are very destructive when feeding on crops and can completely wipe out a farmer's crop in one raid (Sakar *et al.*, 2016), subsequently being targeted for punishment, being wounded or killed, as farmers try to protect their crops. Understanding if other ecological factors impact why elephants crop-forage is important in mitigating the effects, protecting both animals and humans.

Ecological predictors of elephant abundance

Movement and foraging behaviour can be shaped by both ecological or anthropogenic factors (Barnes *et al.*, 1991; Guisan and Thuiller, 2005; de Boer *et al.*, 2013). Examples include food abundance and distribution (e.g. Caillaud *et al.*, 2010; Boulton *et al.*, 2019), proximity to water (Chamaillé-Jammes *et al.*, 2007; Boulton *et al.*, 2019) and, the presence of predators (e.g. Karanth *et al.*, 2004; de la Torre *et al.*, 2017). As stated previously, savanna elephants tend to be driven by water (e.g. Chamaillé-Jammes *et al.*, 2007; Boulton *et al.*, 2019) but forest elephants have been said to be driven by forage acquisition (Blake and Inkamba-Nkulu, 2004; Beirne *et al.*, 2020). However, studying forest elephants and making observations of their behaviours is more difficult than that of savanna elephants (Molina-Vacas *et al.*, 2019). Therefore, having long-term data on their activities is key to improving the understanding of forest elephant behaviours. Kibale National Park, Uganda, is an ideal study site to study forest elephant movement and impact. This park supports both African savanna and African forest elephants (Mondol *et al.*, 2015; Keigwin *et al.*, 2016; Kalbitzer *et al.*, 2019) and records of their population and activities have been maintained for two decades (1996-2019), providing a substantial background and understanding (Wing and Buss, 1970; Struhsaker *et al.*, 1996, Omeja *et al.*, 2014; Omeja *et al.*, 2016).

Previous studies in Kibale National Park

Kibale National Park (hereafter Kibale) is a 795 km² tropical rain forest located in Western Uganda at the foothills of the Ruwenzori Mountains (Wing and Buss, 1970; Chapman *et al.*, 2018). It is composed mostly of tall forest with a canopy of 25-30 m and the remainder of the park is a mosaic of swamp, grassland, former pine plantations and colonising forest (Wing and Buss, 1970, Chapman and Chapman, 1997). Prior to being a national park, Kibale was a forest reserve with a history of logging (Struhsaker, 1997; Chapman *et al.*, 2010b; Chapman *et al.*, 2018). Sites of previous logging disturbances can provide ideal locations to study animal impact on forest regeneration.

Elephant abundance in Kibale has varied greatly over time (Chiyo and Cochrane, 2005; Chapman *et al.*, 2010a), with the most recent estimates predicting that the population is increasing and is dispersed throughout the park (Chapman *et al.*, 2010a; Omeja *et al.*, 2014; Sarkar *et al.*, 2016). However, in the 1990s there was an exponential increase in the elephant

population that was far too high for it to be natural recruitment alone (Sakar *et al.*, 2016). It has been suggested that this was due to migration of elephants into the park from surrounding regions (Keigwin *et al.*, 2016; Sakar *et al.*, 2016; Chapman *et al.*, 2018), which has also meant that Kibale is now recording hybrid individuals that are the offspring of forest and savanna elephants (Mondol *et al.*, 2015; Kalbitzer *et al.*, 2019).

Most studies within Kibale have focussed on the elephant impact around the Makerere University Biological Field Station (known as the Kanyawara region e.g., Struhsaker *et al.*, 1996; Omeja *et al.* 2014) and crop-foraging behaviour (e.g., Chiyo and Cochrane, 2005; Chiyo *et al.*, 2005). These studies indicate that elephants prefer disturbed areas, where there is a high abundance of herbaceous growth, in particular the species *Acanthus pubescens* (Struhsaker *et al.*, 1996; Lawes and Chapman, 2006; Bonnell *et al.*, 2011; Omeja *et al.*, 2014). *A. pubescens* (hereafter *Acanthus*) is a sub-woody shrub that can dominate areas of open canopy and previously disturbed sites (Paul *et al.*, 2004; Lawes and Chapman, 2006). Logged areas provide optimal growth conditions for *Acanthus* and they suppress the growth of seedlings from other species, outcompeting them (Chapman and Chapman, 1999; Paul *et al.*, 2004; Bonnell *et al.*, 2011). Elephants frequent these areas to feed on *Acanthus*. Through their foraging, elephants also suppress forest regeneration by inadvertently trampling seedlings whilst they feed upon *Acanthus* (Struhsaker, 1997; Chapman *et al.*, 2010a; Bonnell *et al.*, 2011; Omeja *et al.*, 2014). Understanding the relationship between *Acanthus* and elephants in Kibale will help to mitigate potential degradation caused by elephants and will provide key information in determining whether *Acanthus* is a true driver of elephant abundance and habitat use.

Many studies on elephants in forested environments have been conducted over relatively short periods of time. Studies that last over longer time periods are becoming more common, but still lacking. However, the data available for Kibale has been collected over the course of multiple decades (since 1989 [Chapman *et al.*, 2010b]), with focus on the same study sites, allowing temporal comparisons to be made. Therefore, using this longitudinal data this study will aim to explore the impact elephants have on the forest and to determine drivers of their distribution and relative abundance.

Therefore, questions such as: (1) How do patterns of vegetation cover affect elephant abundance? (2) How does rainfall variation across years affect elephant abundance in a forested environment? (3) How has cumulative diameter at breast height (DBH) in Kibale changed and has there been any influence by elephants? can be asked. A combination of these questions with the longitudinal data and full-scale study of Kibale will provide insights into any temporal changes that may occur within the population and additional insight that small-scale studies won't show, such as fluctuations in abundance due to external effects. Through monitoring the DBH of the Kibale forest will also enable any impacts to be noted on tree growth and regeneration which will be particularly beneficial for management of Kibale and ensuring there are no long-term negative effects from the elephants.

Chapter 2: Ecological predictors of elephant abundance and habitat use in a forest environment

Abstract

Recent attention has been directed to the plight of forests worldwide and the impacts humans are having on these vital environments. This has consequently led to further need in understanding the role of large herbivores within forests and how their behaviours can be predicted. Of particular interest is the African elephant, a species that has been shown to have substantial impacts on forests in both promoting and limiting growth. Using a combination of long-term relative elephant abundance data and forest composition, with land cover classification from Kibale National Park, Uganda, mixed models were used to address three questions: (1) How does disturbance history and vegetation cover affect relative elephant abundance? (2) How does rainfall variation across years affect relative elephant abundance in a forested environment? And (3) How has cumulative diameter at breast height (DBH) of trees in Kibale changed and has there been any influence by elephants? Results found that although relative abundance has increased, which is higher than what would be expected of natural recruitment, this has little to do with ecological predictors within Kibale. Study duration had the strongest impact which has been attributed to migration of elephants into Kibale leading to the greater increase in relative abundance. Results also showed that rainfall seems to influence relative elephant abundance, but more is needed to understand the true effects. Forest structure does not appear to have been affected by elephant foraging, but this does not account for trees recruiting into the larger size classes and any after a time-lag effects may be evident. The land cover metrics from the remote sensing were unable to be used due to error in the classifying ability of older maps and therefore, land cover was not included in the final model. This study revealed a substantial awareness of background information is needed to interpret results of long-term datasets and further highlights the complicated relationship between elephants and their habitats. Additionally, that more information is required for successful land classification, especially for historical comparisons which can provide false information if there is insufficient knowledge of the study area.

Introduction

Restoring forests worldwide to aid in curbing carbon emissions was set as a priority at the recent COP26 summit in Glasgow, and the United Nations coined this decade the “Decade of Restoration” (UN, 2021). Forests hold much of the world’s biodiversity and play an important role in climate regulation (Ma *et al.*, 2016; Matos *et al.*, 2020; Bowd *et al.*, 2021). However, many of the world’s forests are under increasing anthropogenic pressure, with around 1.5 million km² of forest worldwide experiencing degradation between 1980 and 2012 (Gibbs *et al.*, 2010; Hansen *et al.*, 2013; Matos *et al.*, 2020), with less than 50% of the world’s tropical forests remaining, and those still intact at risk from logging, fires, fragmentation, mining, and hunting (Brancalion *et al.*, 2019). Therefore, understanding the ecological processes involved in regulating growth and functioning of these systems are fundamental to restoration.

Large herbivore foraging and movement can alter plant biomass and structure and play key roles in nutrient transport, including carbon cycling (Laws, 1970; Smart, 1985; McNaughton *et al.*, 1997; Ramirez *et al.*, 2018; Malhi *et al.*, 2022). As a result, these species can significantly alter forest regeneration pathways (Laws 1970, Smart 1985; Beguin *et al.*, 2016; Omeja *et al.*, 2016), and understanding the determinants of large herbivore habitat use and abundance is key to meeting restoration goals (Malhi *et al.*, 2022). Such factors that influence animal behaviour include forage availability and quality (van Beest *et al.*, 2013), proximity to water (Shannon *et al.*, 2009), presence of predators (Gallagher *et al.*, 2017), and proximity to and disturbance by anthropogenic practices (Karanth *et al.*, 2009; Shaffer *et al.*, 2019). These factors therefore provide a baseline for studying large herbivore impact under different conditions.

Large herbivores are important seed dispersers, playing significant roles in seed transport in savanna, woodland, and forest environments (Campos-Arceiz and Blake, 2011; Iravani *et al.*, 2011; Ramirez *et al.*, 2018). They move across large ranges and multiple habitat types, where seeds can be dispersed over a great distance and among habitats (Iravani *et al.*, 2011; Harich *et al.*, 2016). This aids seed survival through transporting seeds away from high levels of competition under parent trees (Connell, 1971; Janzen, 1971; O’Farrill *et al.*, 2013; Boissier *et al.*, 2020), to areas which are potentially more open and provide beneficial conditions for growth.

Large herbivores can have detrimental impacts on their environment, particularly when occurring in high local abundance. In many woodland and forest environments when large herbivores are at high densities, they can limit and stop tree regeneration (Månsson and Jarnemo, 2013; Omeja *et al.*, 2014; Arnold *et al.*, 2018; Poulsen *et al.*, 2018). This consequently can result in negative effects upon other faunal abundance, because of a reduction in biomass and structure of vegetation (Foster *et al.*, 2014). This is not limited to woodland and forest environments. For example within African savannas, exclusion plots have been used to determine the impact impala (*Aepyceros melampus*) browsing has on seedling survival of woody species. These plots found that impala can inhibit the seedling survival by approximately 50% (Moe *et al.*, 2009; O’Kane *et al.*, 2012). This could potentially affect the long-term dynamics of savanna woodlands (O’Kane *et al.*, 2013), especially when impala occur at high densities (Moe *et al.*, 2009; O’Kane *et al.*, 2012).

Similarly, when elephants in Murchison Falls National Park, Uganda were protected in the 1930s, their population growth corresponded with a 55–59 % reduction in the number of large trees (Buechner and Dawkins, 1961). Conversely, illegal hunting during the Ugandan civil war (1970s and 1980s) dramatically reduced their numbers in this park and this was followed by a dramatic increase in the park’s woodland area (Brooks and Buss, 1962; Douglas-Hamilton *et al.*, 1980; Eltringham and Maplas, 1980; Buss and Savage, 1966). The role elephants played in this woodland increase was verified in experiments that documented a marked tree regeneration where elephants were excluded (Hatton and Smart, 1984; Smart *et al.*, 1985). These trends match observations across Africa (Stevens *et al.*, 2017), including Kruger National Park, South Africa associated with changes in elephant culling policy (Shannon *et al.*, 2008, Smit and Ferreira, 2010). This has led to an increase in the elephant abundance, resulting in elevated levels of treefall within Kruger, with elephants reaching, and in some instances, exceeding 100 times the rate of treefall compared to treefall rates measured in 2012 (Asner and Levick, 2012; Asner *et al.*, 2016).

In many areas of the world, restoration efforts are occurring in previously degraded areas that are now protected and habitats degraded by logging are receiving a great deal of attention (Chapman and Chapman, 2004; Romero *et al.*, 2013). The recovery time of forest regeneration following

logging is highly variable (Bonnell *et al.*, 2011). Typically, the tropical tree community gradually regenerates, so that the stand structure is similar to the pre-logging structure within 60 or so years (Plumptre, 1996; Bonnell *et al.*, 2011; Felton, 2013). However, in some circumstances, the gaps that are created by logging become dominated by vegetation that prohibits tree establishment or growth and regeneration is arrested. (Putz, 1985; Chapman and Chapman, 2004; Paul *et al.*, 2004; Duclos *et al.*, 2013). The forest gaps provide optimal conditions for fast-growing terrestrial herbaceous vegetation (THV) (Paul *et al.*, 2004; Chapman and Lawes, 2006) which becomes dominant, limiting the resources for tree seedlings. THV is subsequently foraged on by large herbivores and their disturbance does not kill the THV, but it can further suppress tree regeneration. (Lawes and Chapman, 2006; Berzaghi *et al.*, 2019; Kalbitzer *et al.*, 2019). In the Bia-Goaso Forest Block, western Ghana, secondary forests created by logging disturbances were the most significant predictors of elephant densities. The secondary forest provided more palatable forage and additional protection from poachers with dense thickets of thorny vegetation (Danquah, 2016). Therefore, forest gaps can be maintained through the interaction between elephants and THV inhibiting tree regeneration (Omeja *et al.*, 2014; Berzaghi *et al.*, 2019).

Longitudinal studies are key to detect changes in distribution and identify the predictors of foraging and movement behaviours. Kibale National Park, Uganda provides a unique opportunity to determine how elephant abundance has changed and the factors that influence their abundance. Indirect counts of relative elephant abundance have been collected using the same methods for 23 years, with 11 years of data for some sites in the national park. Several studies have focused on the localised impact of elephants within specific areas of Kibale (Struhsaker *et al.*, 1996; Lawes and Chapman, 2006; Omeja *et al.* 2014); however, a long-term, whole park study has not been conducted. Therefore, this will aid in determining temporal change in relative abundance and provide understanding of the ecological predictors influencing abundance. Additionally, through long-term forest monitoring, any impacts the elephants may have will also be seen.

Using indirect measures of elephant presence (dung and track counts) from across Kibale, this study aims to provide a park-wide analysis on the factors influencing temporal change of

elephant presence and temporal change. Combining long-term records of elephant presence and forest structure with satellite imagery we focus on three questions: (1) How does disturbance history and vegetation cover affect relative elephant abundance? The Kibale elephants have been documented to be more abundant within the regenerating sites of the park (Chapman and Chapman, 1997; Omeja *et al.*, 2016), drawn to these areas by the presence of THV (Lawes and Chapman, 2006; Bonnell *et al.*, 2011), and thus, our first prediction is (P1) there will be a higher abundance of elephants within sites categorised as regenerating forest and areas that have a higher cover of THV. (2) How does rainfall variation across years affect relative elephant abundance in a forested environment? Elephants are known as a water-dependent species and within African savannas, elephants often base their movements on water acquisition (Chamaillé-Jammes *et al.*, 2007; Dunkin *et al.*, 2013). However, within forested environments water is more easily accessible with higher rainfall and permanent forage supply compared to that of the savanna. For this reason, our second prediction is (P2) that in Kibale, a tropical forest, rainfall will not have an impact on elephant abundance. (3) How has cumulative diameter at breast height (DBH) of trees in Kibale changed and has there been any influence by elephants? Due to the elephant's large size, they can have a pronounced impact when foraging, knocking over and killing young trees, potentially reducing forest regeneration (Chapman *et al.*, 2010a; Terborgh *et al.*, 2016). However, elephants are also important in seed dispersal and can improve the success rate of seedling germination (Babweteera *et al.*, 2007; Campos-Arceiz and Blake, 2011). While the species they feed on intensively are not always those that they disperse the seeds of, our third prediction (P3) that there will be no significant change in cumulative DBH of elephant preferred tree species, nor forest structure, due to the mixed impact elephants can have.

Methods:

Study Area:

Kibale National Park (hereafter Kibale, *Figure 1*) is a 795 km² mid altitude (920-1590m), moist-evergreen forest located in western Uganda (0° 13' – 0° 41' N and 30° 19' – 30° 32' E; Wing and Buss, 1970; Chapman *et al.*, 2021). The area has two wet seasons with a mean annual rainfall at Makerere University Biological Field Station (MUBFS) of 1655 mm (1970-2020, Chapman *et*

al., 2021). There is an elevational gradient, decreasing from the north to the south (Chapman *et al.*, 2018). Kibale was gazetted as a forest reserve in 1932 with the aim to provide sustained hardwood timber production (Struhsaker, 1997; Chapman *et al.*, 2005) and became a national park in 1993 (Chapman *et al.*, 2010a). The logging to the north and agricultural encroachment to the south, coupled with its natural features, has resulted in a mosaic of landscapes throughout the park, including swamp, secondary forest, and grasslands. (Wing and Buss, 1970; Chapman and Lambert, 2000; Lawes and Chapman, 2006).

We used eight sites selected because of the variation in the level and timing of disturbance (Chapman *et al.* 2018). Sebitoli is the most northern site and was logged during the 1960s, but extraction rates are not known. The next three sites surround MUBFS and have the longest records of monitoring; these are K30, K15 and K14. K30 (282 ha) is considered as old-growth

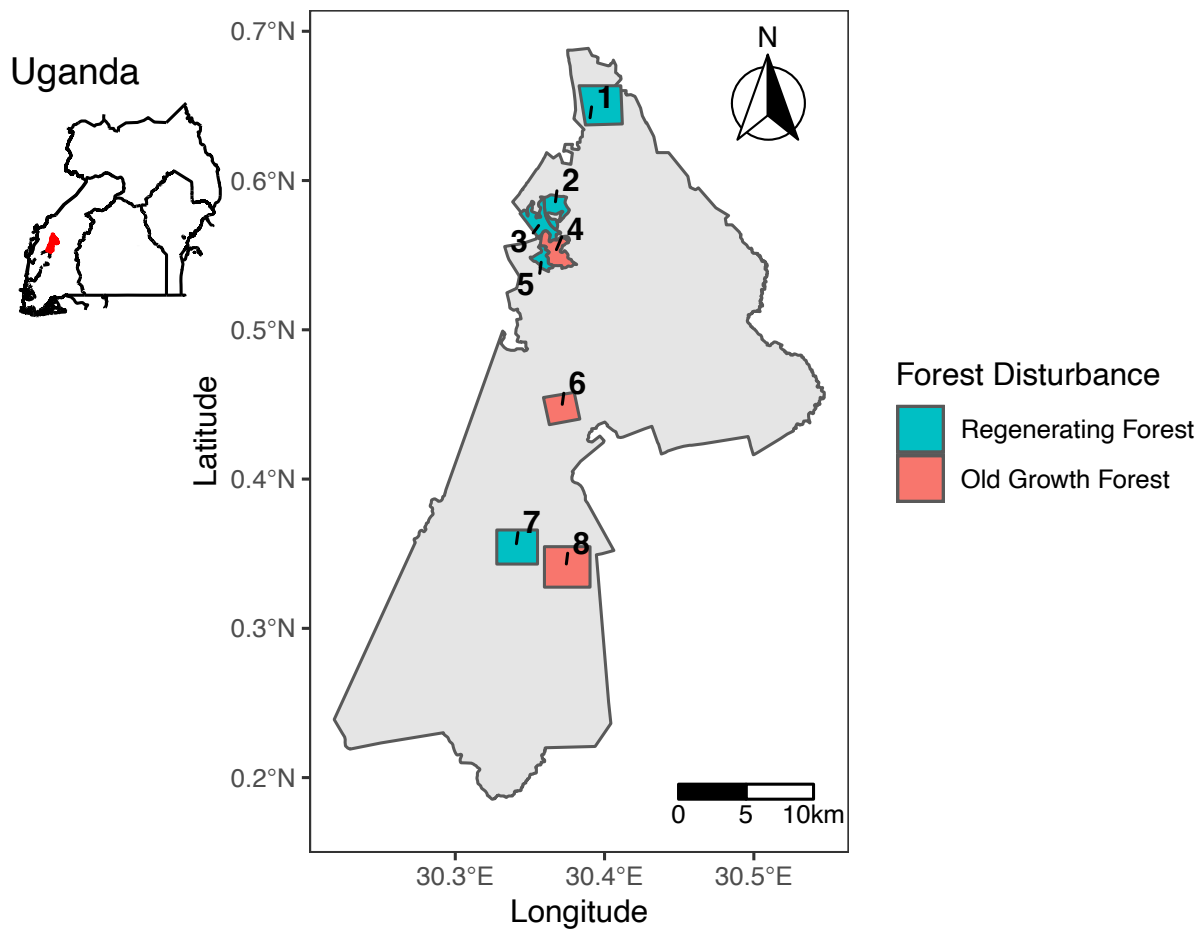


Figure 1. Location of Kibale National Park, Uganda, with the sites used in this study numbered. 1) Sebitoli, 2) K15, 3) K14, 4) K30, 5) Nyakatojo, 6) Dura, 7) P1, 8) Mainaro. Scale in kilometres.

forest and has not been commercially logged. K15 (347 ha) witnessed the highest levels of disturbance (around 50% of all trees logged or secondarily damaged) out of the three compartments around MUBFS and a 1km-by-1km surveying grid has been mapped out within it. K14 (405 ha) is found south of K15 and had a lower amount of disturbance in comparison (around 25% of all trees logged). Adjacent to K30 is a former pine plantation called Nyakatojo (86.2 ha) that was harvested in the mid-1990s and allowed to regenerate. South of Nyakatojo is a site on the Dura River and further south of this is Mainaro. Both sites have had little to no disturbance. Just west of Mainaro is a 4 km trail through an area of replanted forest called P1. P1 was an area that was disturbed by agricultural encroachment in the 1970s and 1980s, but forest regeneration has been facilitated by enrichment planting starting in the mid-1990s (Omeja *et al.*, 2016) (Figure 1). Further information on the sites and extraction rates can be found in Chapman *et al.*, (2018).

Study species:

African elephants (*Loxodonta* spp.) inhabit a wide range of habitats across Africa and many studies have highlighted the varied impacts resulting from their foraging and movement (Blake and Inkamba-Nkulu, 2004; Coverdale *et al.*, 2016; Tsalyuk *et al.*, 2019). The IUCN has now recognised African elephants as two separate species, savanna (*L. africana*) and forest (*L. cyclotis*) and they are listed as endangered and critically endangered respectively (Roca *et al.*, 2001; Rohland *et al.*, 2010; Gobush *et al.*, 2021a; Gobush *et al.*, 2021b). Much research has focused on the savanna elephant, but in recent years the forest elephant has been receiving increased attention due to population declines, poaching and continued development of their key role within forests (Blake *et al.*, 2007; Campos-Arceiz and Blake, 2011; Mills *et al.*, 2018; Poulsen *et al.*, 2018; Laguardia *et al.*, 2021). Elephants are considered non-selective bulk feeders, feeding on a range of vegetation, particularly grass and browse. However, forest elephants may consume more fruit than the other elephant species, including Asian elephants (*Elephas* spp.) (Campos-Arceiz and Blake, 2011).

In Kibale there are both forest and savanna elephants and their hybrids (Mondol *et al.*, 2015; Kalbitzer *et al.*, 2019; Bonnald *et al.*, 2021). The elephant population of Kibale decreased from initial surveys in the late 1960s (Wing and Buss, 1970), however, it increased rapidly during the

early 2000s at a rate that was too steep for it to be the result of natural recruitment alone. This increase has been attributed to immigration of elephants from the Democratic Republic of Congo into Uganda at a boundary crossing near to Queen Elizabeth National Park (QENP) (Keigwin *et al.*, 2016; Daniel *et al.*, 2021). This migration likely involved forest elephants, as prior to this the population was believed to be savanna elephants contiguous with those in QENP. Elephants used to range outside of the park (Omeja *et al.*, 2014); however, due to the expansion of rural settlements, this has limited movement beyond the park boundaries. It is not possible to distinguish between the two species in the data we collected; hereon they are referred to as elephants.

Acanthus pubescens (prickly acanthus), hereafter *Acanthus*, is a sub-woody shrub native to East Africa that often occurs in the previously disturbed open areas of Kibale (Duclos *et al.*, 2013). *Acanthus* can grow up to 3m tall and form dense thickets that limit tree seedling growth and regeneration (Paul *et al.*, 2004; Lawes and Chapman, 2006). *Acanthus* is a preferred forage for elephants within Kibale, with frequent visits to patches of the shrub and these foraging visits seem to negatively impact the regeneration (Paul *et al.*, 2004), so much so that elephants have been deemed to keep the sites in a permanently disturbed state (Struhsaker, 1997; Lawes and Chapman, 2006; Omeja *et al.*, 2014). However, this has only been documented by studies at sites near MUBFS. Elephants also use grassland areas, and their trampling inhibits forest tree regeneration similar to that in areas of *Acanthus*, but in the grasslands, fire also plays a role. We will determine if a combination of *Acanthus* and grassland areas, which we will refer to as THV, is a predictor for elephant habitat use across Kibale.

Data Collection:

Elephant censuses

Teams of experienced observers sampled transects between 3.6 and 4.45 km in length at each site (Table 1). These typically were conducted monthly for one year, spanning the years 1996-1997, 2005-2006, 2008-2009, 2014-2015, 2018-2019 (Omeja *et al.*, 2014; Omeja *et al.*, 2016; Sarkar *et al.*, 2021). A total of 1594.8 km was walked. These surveys recorded dung and track (footprints) counts, any direct elephant observations, sounds, or other indications of elephant presence (i.e., broken vegetation). Dung and tracks were removed during each census walk by

clearing vegetation and covering footprints, after they were recorded, so that they would not be counted the following month. The sum of all signs was subsequently used to determine relative elephant habitat use through division by the length of the transect to standardise across all sites for comparison. This provided the relative elephant abundance to address questions 1 and 2. The sites around MUBFS (K14, K15, K30) have the longest recording spanning 1996 – 2019. Dura, Mainaro, Nyakatojo, and Sebitoli recordings were started in the 2008 survey year and P1 was recorded from 2014 till – 2019. For further details see Omeja *et al.* (2014), Omeja *et al.* (2016), Chapman *et al.* (2018), and Sarkar *et al.* (2021).

Table 1: Number of transects walked per site per year.

Site	Number of transects walked						Transect length (km)	Total distance (km)
	1996	2006	2008	2014	2019	Total		
Sebitoli	0	0	14	13	4	31	4.2	130.2
K15	25	24	13	13	19	94	4	376
K14	25	23	13	11	18	90	3.6	324
K30	25	22	13	11	17	88	4	352
Nyakatojo	0	0	12	10	9	31	4	124
Dura	0	0	12	11	5	28	4.45	124.6
P1	0	0	0	12	2	14	4	56
Mainaro	0	0	12	10	5	27	4	108
						403		1594.8

Land-use land-cover mapping

To address how land-cover patterns impact relative elephant abundance (question 1), a ground-truthing dataset was obtained from the K15 site (347 ha), just north of MUBFS. K15 was selected because of a 1 km² transect grid that has been set up and due to K15's logging history, which has a higher coverage of THV than other sites around MUBFS thus creating a good truthing dataset. To survey the grid, hand drawn land cover maps were made within each 100 m by 100 m cells of the 1 km² grid between 19th July 2021 and the 6th August 2021. Each trail was walked, and the vegetation cover was mapped on paper representing one of the grid cells (1-101). If an area in the interior of the 100 m by 100 m cell was inaccessible either a path was cut, or a tree climbed for observation. These highlighted the vegetation cover pattern and included four vegetation types: (1) *Acanthus*, (2) forest canopy, (3) grass, and (4) swamp. These maps were georeferenced with coordinates taken for each corner of the grid cell. Using Google Earth Pro (7.3.4.8248, 64-bit) the coordinates were plotted and were used to create shape files

containing the proportions of each grid cell. A shape file containing the park boundaries (UNEP-WCMC, 2021) was used to clip the generated maps so areas surrounding the park were excluded.

Land cover maps were generated of the whole park using Google Earth Engine (GEE, Gorelick *et al.*, 2017). The satellites used were Sentinel-2 MSI: Level-2A surface reflectance for 2019 (10-20 metres), USGS Landsat 8 Surface Reflectance (SR) Tier 1 for 2014 (30 metres), USGS Landsat 7 SR Tier 1 for 2008 and 2006 (30 metres), and USGS Landsat 5 SR Tier 1 for 1996 (30 metres). The image generated for 1996 was given a date range of the 15th June 1994 to 31st December 1997 as there were no images for the elephant survey date range in 1996 (6th July 1996 to 7th June 1997). Cloud masked image composites were created for Sentinel-2A and Landsat 8 satellite images dated between the 19th July 2021 and the 6th August 2021 of the study area. This date range was selected as it corresponded to the collection of the ground-truthing data (hand-drawn cover maps of K15). The composites of the Sentinel-2A and Landsat 8 images were combined using data fusion of the median pixel values to improve the image quality (Phiri and Morgenroth, 2017). The enhanced vegetation index (EVI) was calculated and added as an extra band to the satellite because of its propensity to distinguish between vegetation types in high biomass regions, such as forests (Matsushita *et al.*, 2007; Valtonen *et al.*, 2021). EVI was calculated using the following equation:

$$\text{Equation 1) } 2.5 * ((\text{NIR} - \text{RED}) / (\text{NIR} + 6 * \text{RED} - 7.5 * \text{BLUE} + 1))$$

Where NIR is the near-infrared band, RED is the red band and BLUE is the blue band of the satellite in use.

Images generated for the 2021 year were then used to test an unsupervised classification model for land cover types. The year 2021 was selected as validation data were available. The image was cross validated with the land cover maps made for K15 of the same date range to determine how accurate the coverage patterns were. The unsupervised classification used 10,000 random pixels to ensure the variety of land-cover types across the park were included in the model. Class sizes, which are the specified number of classifying categories to be used by the unsupervised model, of 4 through to 7 were used in a k-means algorithm to generate classified maps (Wu *et*

al., 2019). From the unsupervised classified maps, land cover was reliably confirmed by a combination of the hand-drawn cover maps and knowledge of the park. These were then used to derive a supervised classification model (Phiri and Morgenroth, 2017). The supervised model used a random forest algorithm set to 50 decision trees (Talukdar *et al.*, 2020). These were validated through a confusion matrix (Şatir and Berberoğlu, 2012) before being applied to calculate the land cover from the image composite of the corresponding elephant census year. The total land cover was calculated in kilometre squared (km²) for each of the eight study sites. The locations of the study sites were obtained from shape files containing their proportions.

Through a combination of the hand-drawn cover maps of K15, unsupervised classification and knowledge of Kibale, generated 730 reference points which were split into training and validation points. The land cover classes included: water, forest, THV, swamp, and human/other (other including any other unclassified cover type); five in total. Of these, a random selection of ~75% were used for training and ~25% were used as validation points.

Rainfall

Rainfall was collected at MUBFS and a site 20 km east to Kibale, the city of Fort Portal (obtained from the Government of Uganda), and daily rainfall values were summarised to gain average monthly values (Chapman *et al.* 2021). Rainfall was collected from 1970 to 2020; this study uses values from 1996 to 2019 as these correspond with the elephant survey years.

Forest structure and composition

Twenty-six permanent vegetation plots (200 by 10 m) were set up in K14, K15, and K30 in 1989 to monitor forest structure and tree recruitment (Chapman *et al.*, 2010a; Chapman *et al.*, 2010b). Surveys of the diameter at breast height (DBH, 1.2 m above ground level) were taken in 1989, 1999, 2006, 2013, and 2017. These three sites around MUBFS have the longest record of data, from 1989-2017. If DBH was greater than 10 cm, the tree was tagged, species name was recorded along with its DBH measurement. Trees were measured each survey and if a new tree recruited into the > 10 cm DBH size class, it was added. If a tree died this was noted and the cause of death described if possible (Chapman *et al.*, 2010a; Chapman *et al.*, 2010b).

The tree enumeration was refined using data on elephant preferred feeding trees gathered from Omeja *et al.* (2014) with some additions from Cochrane (2001). Further details on the methods for calculation of a species selection ratio can be found in Omeja *et al.* (2014). These feeding data resulted in us considering 17 species (Table 1) as elephant preferred foraging trees. Data from the forest plots were categorised as either a preferred or non-preferred species. This provides the data used for addressing question 3.

Table 2: Elephant preferred feeding trees collated from Omeja *et al.* (2014) and Cochrane (2003) with part use from Rode *et al.* (2006).

Tree species	Elephant part use
<i>Antiaris toxicaria</i>	Leaves
<i>Blighia unijugata</i>	Leaves
<i>Celtis africana</i>	Undetermined
<i>Ficus exasperata</i>	Undetermined
<i>Funtumia latifolia</i>	Ripe fruit
<i>Lovoa swynnertonii</i>	Young leaves
<i>Mimusops bagshawei</i>	Leaves
<i>Monodora myristica</i>	Undetermined
<i>Newtonia buchananii</i>	Undetermined
<i>Parinari excelsa</i>	Undetermined
<i>Strombosia scheffleri</i>	Undetermined
<i>Trichilia splendida</i>	Leaves
<i>Trilepsium madagascariense</i>	Leaves
<i>Balanites wilsoniana</i>	Fruit
<i>Tetrapluera tetraptera</i>	Undetermined
<i>Dovyalis macrocarpa</i>	Undetermined
<i>Kigelia moosa</i>	Ripe fruit

Data analysis

Relative elephant abundance

All statistical modelling was conducted in RStudio (R version 4.0.5 (2021-03-31) [R Core Team, 2021]). A generalised linear mixed model (GLMM) approach was taken to evaluate how elephant abundance may be influenced by multiple ecological factors. The models were conducted with the glmmTMB package (Brooks *et al.*, 2017). The response variable was number of signs per kilometre (dung, track, other including visual/acoustic) and six independent explanatory factors were initially considered: duration of study, disturbance history, average monthly rainfall, season, and THV. Duration is a continuous variable with the first month of survey (July 1996) recorded as 1 and each subsequent month as 2, 3, 4 ... 275 months. This included periods where no surveys took place. Categorical variables of disturbance history and season, either old growth or regenerating or wet or dry respectively, with season being determined from the month (Wet = Mar, Apr, May, Sept, Oct, Nov and Dry = Jan, Feb, Jun, Jul, Aug, Dec). THV was defined as a combination of *Acanthus* and grassland cover and was acquired from the land cover calculations corresponding to each survey year for THV (km²). Site was used as a random variable due to repeated measurements across the same transects. Due to the structure of the model, it was used to test the hypotheses for questions 1 and 2.

Poisson and negative binomial (NB) error distributions were selected for the analysis as the dependent variable was based on count data. This also included the zero-inflated counterparts, zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB). After conducting initial data checks with histograms, the data seemed to be zero-inflated and had potential for overdispersion, therefore, NB and ZINB were selected for further use as they perform better than Poisson when zero-inflation and overdispersion are present. Multicollinearity tests were conducted with the performance package (Lüdtke *et al.*, 2021) with high correlation between rainfall and season (rainfall VIF = 33.6, season VIF = 21.7), which subsequently meant that these variables could not be included in the same model. Additionally, there was high multicollinearity between THV (VIF = 21.1) and duration (VIF = 24.7). This led to each independent term being subsequently dropped from a model with all the explanatory terms to find the best model fit with no multicollinearity and the lowest AIC value. From this, two models went forward:

Model 1) Elephant abundance ~ duration + disturbance history + rainfall + (site)

Model 2) Elephant abundance ~ duration + disturbance history + rainfall + THV + (site)

Table 2: Model evaluations of the tested models to find the best fit. Model 1 and Model 2 labelled in brackets.

Model Explanatory terms	Degrees of Freedom	AIC
Duration + Disturbance history + Rainfall (Model1)	6	1845.4
Duration + Disturbance history + Rainfall + THV (Model2)	7	1845.6
Duration + Disturbance history + THV	6	1847.5
Duration + Disturbance history + Rainfall + Season + THV	8	1847.5
Duration + Disturbance history + Season + THV	7	1848.5
Disturbance history + Rainfall + THV	6	1969.7
Null	3	1997.7

These were also tested against a null model including no explanatory variables and both models performed better than the null (Table 2). Overdispersion and zero-inflation tests were conducted using the DHARMA package (Hartig, 2021) which found there to be no overdispersion and no zero-inflation. Model performance was compared using Akaike information criterion (AIC). Due to the AIC scores being within 2 AIC units (AIC = 1845.4, Model 2 AIC = 1845.6) both models were used in the analyses. For a comparison of all the models and the AIC values see Table 2.

Forest structure

Model 3 used the Gamma error family due to the continuous nature of the response variable, forest structure. To meet the assumption of normality in Model 3 and improve model fit the response variable forest structure was log-transformed. The response variable was cumulative DBH (cDBH), calculated through taking the DBH of all trees and dividing by the area sampled for standardisation. The independent variable was the year of sample. Site was included as a random variable to account for the repeated sampling of each site. Comparison of Model 3 to a null can be found in Table 3. The final model took the formula of:

Model 3) Cumulative DBH ~ year + (site)

Table 3: Model evaluations of the tested models to find the best fit. Model 3 labelled in brackets.

Model Explanatory terms	Degrees of Freedom	AIC
Cumulative DBH + Year (Model 3)	7	17150.86
Null	3	17152.46

Results:

Question 1 & Question 2: How does disturbance history and vegetation cover affect relative elephant abundance? How does rainfall variation across years affect relative elephant abundance in a forested environment?

Unfortunately, we were unable to include with confidence the land classification cover values in our model and thus, Model 2 was dropped. This we believe is a result of a change in satellite technology over the time scale we were intending for (two decades, 1996-2021), with better resolution images in later years (Figure 2) and the classifiers power to distinguish between cover classes in a tropical environment. As seen in Figure 2a, horizontal lines appear across the image that have the potential to obscure details when being used for further analyses.

The land classification model had a total of 730 reference points that were obtained from a combination of the hand-drawn land cover maps and knowledge of Kibale. We were able to achieve an accuracy of 84.5% for a mosaiced map of 2021 using both Landsat 8 and Sentinel-2 surface reflectance satellites (Figure 3). However, when using earlier satellites for a composite of 2006 for example, errors arose in the classification with the classifier identifying forest as water and the persistence of horizontal bands that potentially obscure further detail (Figure 3a).

Additionally, when using a smaller scale, focusing on the Kanyawara region (K14, K15, K30, and Nyakatojo), errors occurred in the estimation of cover of forest. The maps were suggesting that forest cover had decreased over the years, however, we knew this not to be the case (Figure 4). We were able to determine this because of the historic knowledge of the park and monitoring

of the forest growth showing that canopy forest is stable and not decreasing (C. Chapman and D. Sarkar, 2022, personal communication).

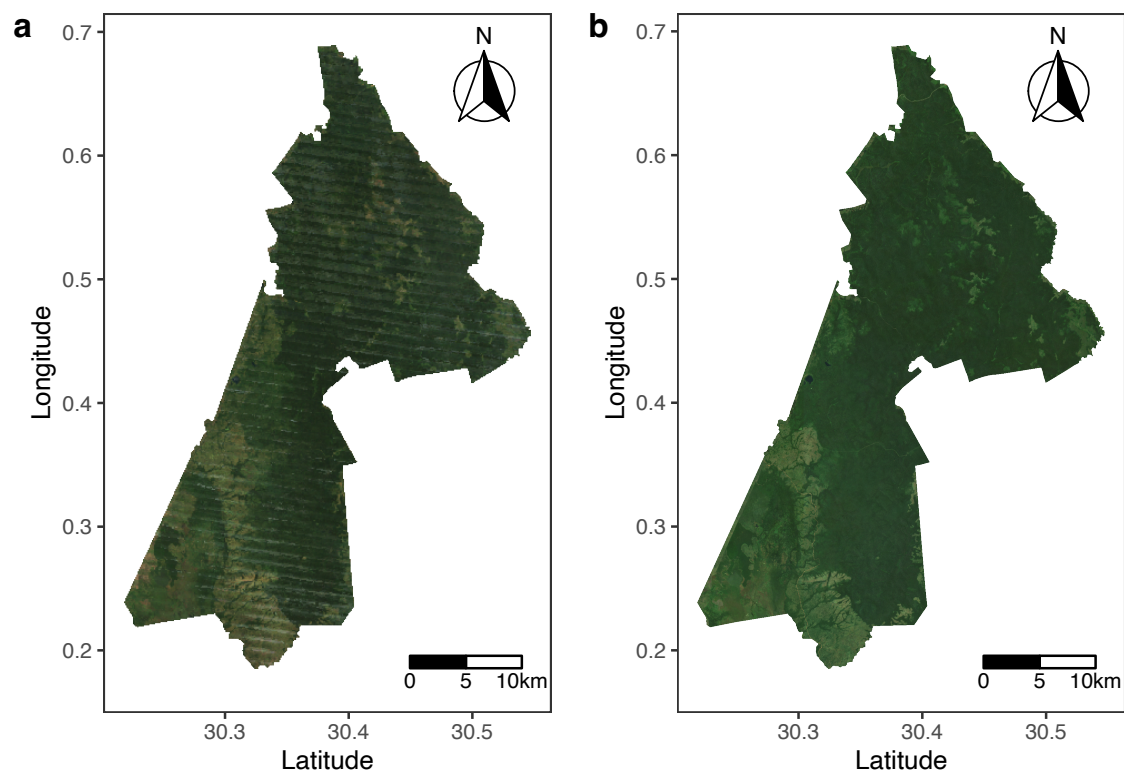


Figure 2: Satellite images of Kibale National Park from a) 2006, b) 2021. Scale in kilometres.

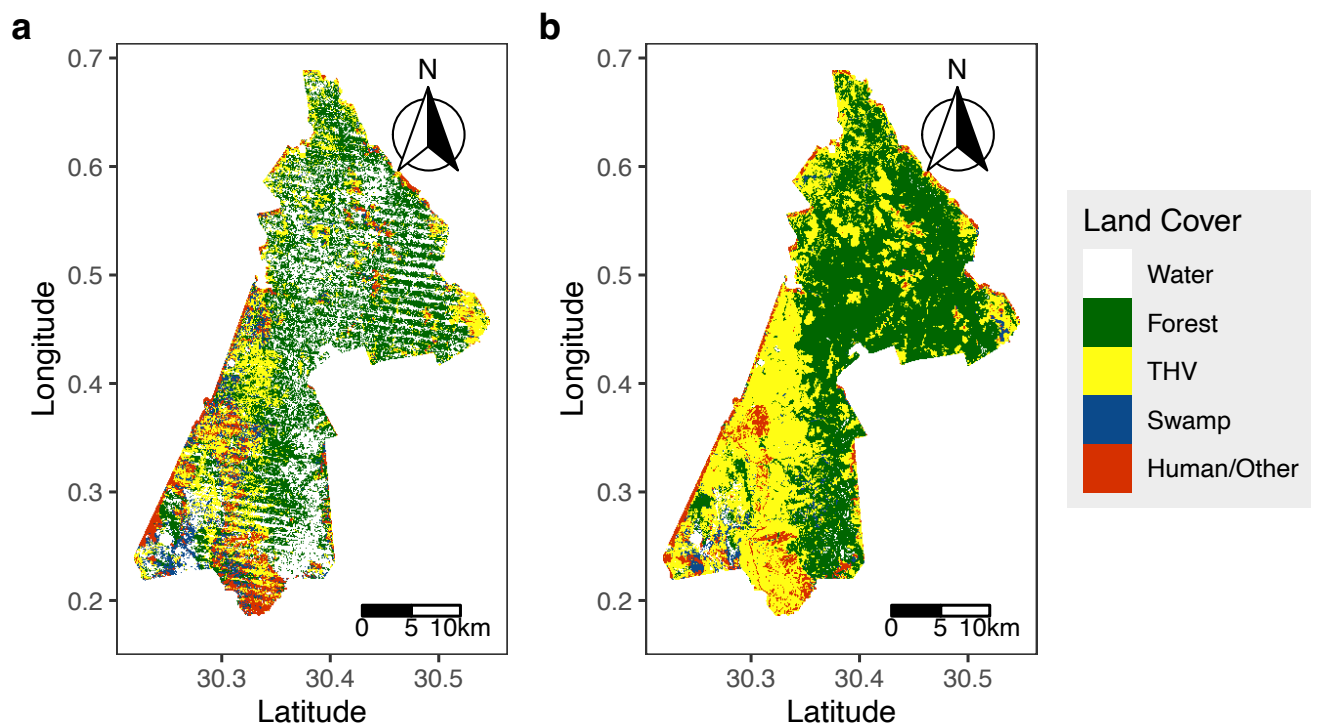


Figure 3: Land classification maps of Kibale National Park from a) 2006, b) 2021. Scale in kilometres.

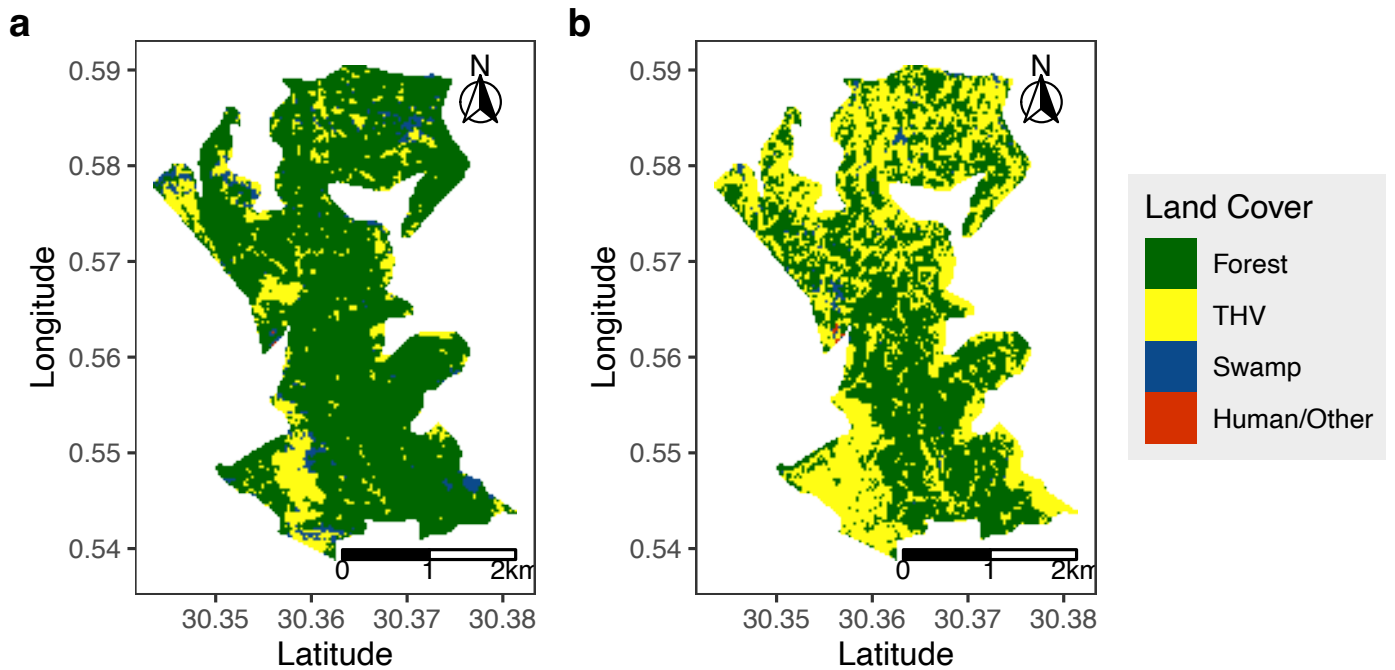


Figure 4: Land classification maps of the Kanyawara region (K14, K15, K30 and Nyakatojo) a) 2006, b) 2021. Scale in kilometres.

Four hundred and three observations of elephant signs were recorded across the eight sites over the duration of the study. Elephant abundance increased rapidly across the park between 1996 and 2008, but then levelled off and is now increasing steadily in more recent surveys (Figure 5). Elephant abundance in Sebitoli and Nyakatojo was high in 2014, however decreased in the latest 2019 survey (Figure 6). Results from Model 1 suggest that study duration and rainfall have a significant effect on elephant abundance (duration, $p = < 2e-16$, rainfall, $p = 0.0427$, see Table 4 for model outputs). Study duration had the most significant effect on elephant abundance, with elephant abundance increasing over time with study duration ($p = < 2e-16$, see Table 4). Contrary to the hypothesis of question 1, the disturbance history seemed to have no impact on elephant abundance as this was not significant ($p = 0.233$, see Table 4). On the other hand,

rainfall is shown to have a slight impact, contrary to our hypothesis for question 2 ($p = 0.0427$, see Table 4).

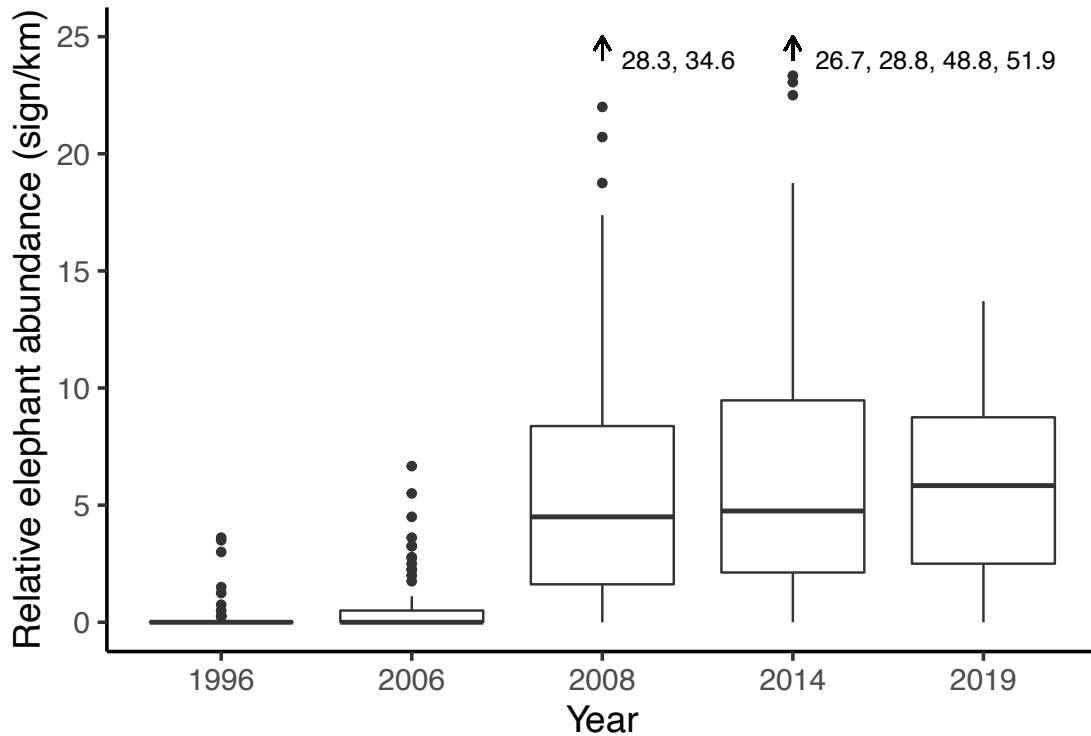


Figure 5: Change in the relative abundance of elephants (sign per kilometre) in Kibale National Park. Arrows represent the outliers outside greater than 25 signs/km.

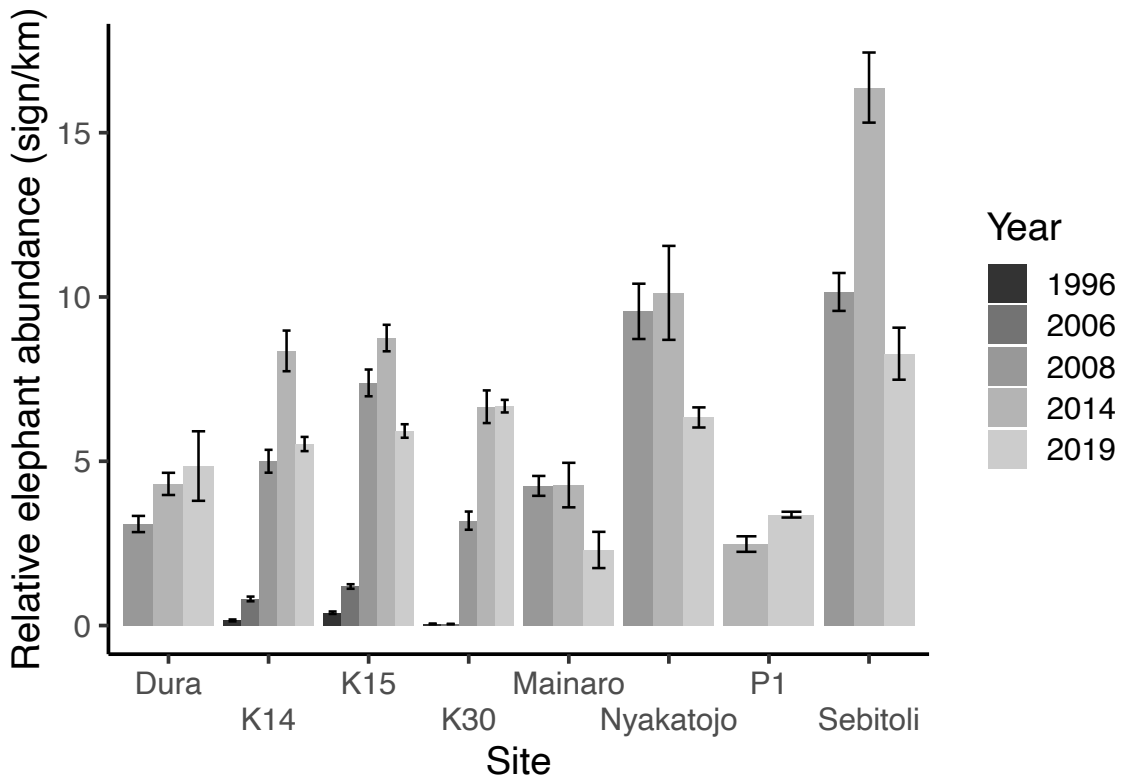


Figure 6: Relative abundance of elephants (sign per kilometre \pm SE) in Kibale National Park recorded in across the different sites.

Table 4: Output summary for Model 1 – Elephant abundance ~ duration + growth + rainfall + (site)

Model 1	Estimate	Std. Error	z value	P value
Intercept	-1.323	0.382	-3.462	0.000535 ***
Duration	0.012	0.000948	12.648	< 2e-16 ***
Disturbance history – regenerating forest	0.4631886	0.3881348	1.193	0.233
Rainfall	0.00167	0.000823	2.026	0.0427 *
			AIC	1845.4

Question 3: How has cumulative diameter at breast height (DBH) of trees in Kibale changed and has there been any influence by elephants?

Over the three sites and 28 years since the first recording, there was a total of 11,218 tree DBH measurements. Results from the Gamma GLMM (Table 5) show that there is a significant difference between the tree density of the survey year 1989 and years 1999, 2006 and 2013 ($p = < 0.05$), showing that density is increasing. There was no difference between 1989 and 2017 ($p = > 0.05$, see Table 5). This is also represented within Figure 7, with very little change within the sites over those years. There appears to be a slight positive change in the cumulative DBH of preferred feeding trees of elephants in K14 and K30 (Figure 7). However, in K15 the cumulative DBH has gradually increased since 1989 and that there are larger preferred feeding trees of elephants within K15 (Figure 7).

Table 5: Output summary for Model 3 – Cumulative DBH ~ year + (site)

Model 3	Estimate	Std. Error	z value	P value
Intercept	0.911718	0.093698	9.730	< 2e-16 ***
Year 1999	0.019388	0.006989	2.774	0.00553 **
Year 2006	0.014645	0.006808	2.151	0.03147 *
Year 2013	0.015602	0.006740	2.315	0.02063 *
Year 2017	0.008683	0.006695	1.297	0.19467
			AIC	17150.9

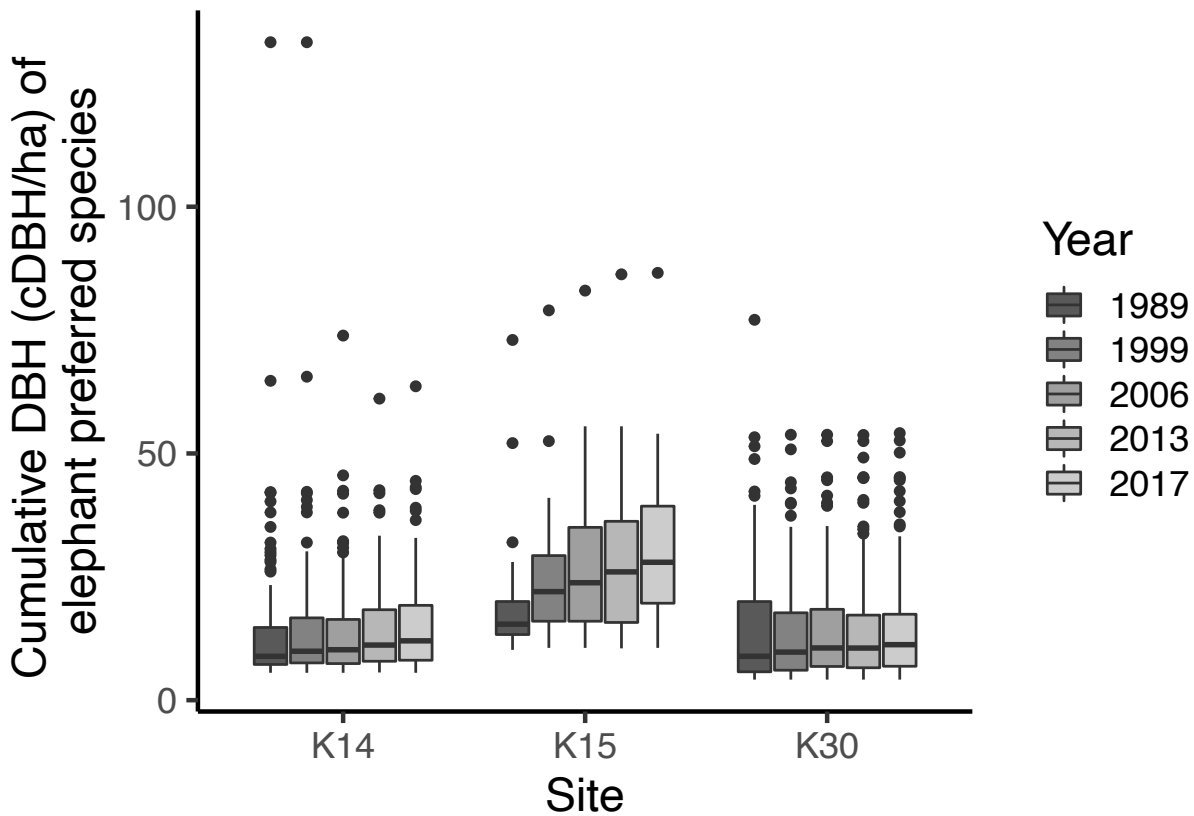


Figure 7: Cumulative DBH of elephant preferred feeding trees in the Kanyawara region (K14, K15, K30) of Kibale National Park.

Discussion:

This study aimed to determine how elephant abundance in Kibale was affected by (1) disturbance history and (2) rainfall, and (3) whether there has been any change in the cumulative DBH of elephant preferred trees and to infer if the elephants have had any impact on any change in DBH. We found that for questions 1 (how does disturbance history and vegetation cover affect relative elephant abundance?) and 2 (how does rainfall variation across years affect relative elephant abundance in a forested environment?) elephant abundance was not affected by vegetation growth, but was impacted by rainfall, contrary to our hypotheses that elephant abundance would be affected by vegetation growth but not rainfall. Additionally, our results for question 3 indicate that there has been no/very little change in the cumulative DBH of trees within Kibale and there appears to be no visible inferred impact by the elephants at this current time. However, elephant preferred trees do seem to have increased over time, with a greater

change in K15, but this is attributed to forest growth, with the existing trees getting larger. Our hypothesis that there will be no significant change in cumulative DBH of elephant preferred tree species nor forest structure (question 3) has been supported.

A recent study conducted by Daniel *et al.* (2021) found that the elephant population in Kibale has increased from 393 ± 107 in 2005 to 566 ± 236 in 2019 (Wanyama *et al.*, 2010; Daniel *et al.*, 2021). The data here reflect this increase, with duration having a significant impact on elephant abundance. This may be a result of better park management by the Uganda Wildlife Authority (UWA), which enabled better protection of the elephants and forest regeneration, particularly in the south (Sarkar *et al.*, 2021). The occurrence of forest elephants within Kibale has been attributed to migratory crossings from nearby Queen Elizabeth National Park and the Democratic Republic of Congo (Keigwin *et al.*, 2016; Daniel *et al.*, 2021). This migration was likely far greater than any change that could have been driven solely by ecological factors (disturbance history and rainfall, Model 1). The migration into Kibale was thought to be a result of elephants trying to escape poaching threats from the Democratic Republic of Congo (Keigwin *et al.*, 2016). Continued monitoring of the elephant population in Kibale will provide further insight into this movement and if there could be seasonality to it as proposed by Daniel *et al.* (2021). This further highlights the need for long-term data as historical knowledge of systems can provide crucial insights into factors affecting large herbivore ecology and elimination of factors that do not have an impact. It could be argued that the population growth may have been a rare rapid natural increase, as has been seen in Kenya in the Amboseli elephant population (Moss, 2001). However, the population histories of both Kibale and Amboseli are very different. Amboseli is a savanna landscape that allows for direct observations to be made of each individual, therefore, the Amboseli population is one of the few long-term continuous datasets on individually known elephants. This has enabled the life histories to be determined and known for each individual, so ages, group dynamics and birth rates to be estimated. Additionally, savanna landscapes are more prone to drought periods than tropical forests and therefore a quick population recovery may be more likely to be witnessed within elephant populations that are used to such events that could kill large portions of the demographic. Due to the regular rainfall seen within forested environments, droughts are unlikely to occur and populations within will not be exposed to the

same need to recover after a dramatic population drop. Therefore, it is unlikely that the sudden changes in population seen in Kibale can be a result of natural population increase.

Our results show that although there may be an increase in the abundance of elephants, the disturbance history does not appear to have an impact on their relative abundance, contrary to what is suggested in the literature and our hypothesis for question 1 (Barnes *et al.*, 1991; Struhsaker *et al.*, 1996; Chapman and Chapman, 1997; Omeja *et al.*, 2016; Amaya *et al.*, 2021). We would have expected there to be a highly significant positive relationship between elephants and disturbance history, with higher relative abundances recorded within sites of previous disturbance, such as Sebitoli, K15 and K14. However, migration masks any impact of preference for secondary forest in the Kibale elephants. As stated previously, this migration is likely due to elephants escaping poaching threats in the Democratic Republic of Congo (Keigwin *et al.*, 2016), an external factor that was not accounted for in the model. Therefore, these movements were not a result of ecological drivers, but of finding a place of refuge from danger. This highlights the need for additional data to supplement the coarse nature of our data to determine more subtle inferences. This is particularly important if there are other untested factors that are influencing relative abundance as they may provide answers that are currently masked and provide further management strategies that can be more targeted. Additionally, future research may benefit from a longer-term monitoring of exclusion plots with and without elephants, as well as *Acanthus*, to further understand the impact elephants have, combined with *Acanthus* in limiting tree recruitment to build upon work started by Lawes and Chapman (2006). Lawes and Chapman (2006) focused on the area of K15 over a two-and-a-half-year period and found that the elephants had the greatest limiting effect on tree recruitment. Expanding this work to the rest of the park, and at different disturbance histories, will also enable determination of any regional differences in forest recruitment and if there is a greater impact by elephants/*Acanthus* in a particular region and providing further information to be considered in management planning for the park.

Contrary to our hypothesis for question 2, rainfall had a slight positive influence on elephant abundance (Table 5). This result is surprising as elephants are likely only a water-dependent species in drier savanna environments (Chamaillé-Jammes *et al.*, 2007; Boulton *et al.*, 2019). In

forests like Kibale, there are no harsh dry periods and water is reliably available. Historically elephants were recorded to have possibly traversed outside the park as seasons changed (Wing and Buss, 1970); however, this is no longer possible given the human expansion in surrounding regions (Chapman *et al.*, 2010a; Omeja *et al.*, 2014). The slight positive impact of rainfall on abundance may suggest that there could be some remnant seasonal behaviour in the elephants (Daniel *et al.*, 2021). Additional finer rainfall measurements would also provide understanding on how variation of rainfall in different regions of the park effect finer scale movements and habitat use, especially with the decreasing elevational gradient from north to south corresponding to a decrease in rainfall (Chapman *et al.*, 2018). Further analyses into the boundary edge movements of the elephants, especially in the south of Kibale, would enable any seasonal movements to be identified and may provide insights if there is any increase in human-elephant conflict during a particular season. Additionally, knowing elephant movements will enable the already successful human-elephant management strategies (Kolinski and Miliich, 2021) to be implemented in more specific areas that may be more prone to crop-foraging as well as the development of new strategies, such as the removal of *Acanthus* from the forest edge by local communities (C. Chapman, 2022, personal communication). Alternatively, the slight positive influence of rainfall on elephant abundance may be a result of detectability of elephant signs, such as tracks. In the rain, the ground would be more malleable and footprints may have been more easily identified than during drier months when the ground is harder. However, to attempt to reduce this error, the surveys were conducted across a year period that included all seasonal changes.

Cumulative tree size in Kanyawara has marginally grown over time, however, our results show that it has stabilised within the more recent surveys (Table 6). These results agree with previous findings that in the Kanyawara region the growth of the forest has remained stable, with little change from when recordings first began in 1989 (Bonnell *et al.*, 2011). Additionally, cumulative DBH of the elephant preferred species has also seen little change, possibly signifying that any impact by the elephants has not been seen yet. However, K15, does appear to have had an increase in cumulative DBH of the preferred species, possible result of elephants feeding on smaller tree sizes and allowing larger trees to grow (Lawes and Chapman, 2006; Omeja *et al.*, 2016). This continues to highlight the need for longitudinal data to monitor change, especially in

regard to a large herbivore such as elephants, as they could have significant detrimental impacts to their environments.

Following our attempt on land classification of Kibale, future studies will benefit from additional ground-truthing data, such as temperature and elevation, to better distinguish between cover types. They will also benefit from a wider range of ground-truthing points from a greater variety of landcover types, spanning more of the National Park. Due to logistical constraints, we were limited to the areas we could sample. This type of ground-truthing data is vital in getting land classification right in a tropical environment, along with an understanding of the history and current land cover patterns. Additionally, creation of accurate land classification maps will enable areas to be targeted for monitoring of human-wildlife conflict. Areas that are known to be predominately used by the study species, in our case elephants and secondary forest, can be pinpointed in areas of higher human populations and strategies can be implemented to deter the animals from those regions or try to reduce human presence. For example, in India suggestions have been put forward for land use zonation and the designation of a “No Development Zone” around wildlife corridors to prevent conversion of the habitat and reduce human-wildlife conflict (Areendran *et al.*, 2020).

Satellite technology has improved greatly over the years with multiple satellites now available, targeting different data (temperature, land and ocean cover, air quality, etc.). However, trying to compare data from the newer satellites to that recorded from older satellites proves difficult because of the stark change in the resolution of the images produced (Zaki and Latif, 2017; Talukdar *et al.*, 2020). This creates confusion as the lower quality images can be classified as the wrong land cover classes. To alleviate this, numerous reference points from across the park in different land covers are needed, as well as additional information on temperature and elevational differences between cover types (Richardson *et al.*, 2009; Liu *et al.*, 2016; Tang *et al.*, 2016). This is particularly important as the heterogenous nature of tropical environments make it particularly difficult for classifiers to distinguish between cover types compared to the relative ease in boreal environments (Richardson *et al.*, 2009; Zaki and Latif, 2017). Therefore, the heterogenous nature of Kibale, along with its large size and elevational gradient creates difficulty in classifying Kibale with the detail we would have liked.

Therefore, from our research it can be seen that studies cannot take satellite imagery for granted without prior in-depth knowledge of tropical forests and expect the results to be accurate. It is vital to have reliable reference points that represent the study area in full, especially for hard-to-reach locations as points in one region are not comparable for the whole because of heterogeneity. It is advised for future studies classifying tropical systems to use a wider range of validation points that cover the study site, and to take additional ground truthing metrics, such as temperature and elevational recordings between cover types, to use as a spectral signature for more accurate classification. It is crucial for any longitudinal study that uses remote sensing data to understand the history of land cover and what is occurring in the here and now to avoid, as we have, any conclusions that are wrong and do not represent the study area. Studies, such as ours, may then be able to start new longitudinal datasets that within a decade would provide a more accurate study of land cover change.

To conclude, elephants are a long-lived species whose interactions with their environment are complex and cover spatial scales larger than a single park. Longitudinal data and historic knowledge of these sites and surrounding regions will prove invaluable in explaining surprising results, and a combination of camera traps and GPS collars will help to provide insights on fine scale movements that coarse metrics cannot show. As habitat restoration has become of prime concern, understanding the interactions between such large herbivores and their environment has never been more important for establishing meaningful restoration strategies.

References:

- Alverson, W.S., Waller, D.M., Solheim, S.L. (1988). Forests too deer: edge effects in northern Wisconsin. *Conservation Biology*. **2**, pp. 348-58.
- Amaya, P.C., Nourtier, M., Montfort, F., Fusari, A., Randrianary, T., Richard, E., Prin, T., Valls-Fox, H. (2021). Are elephants attracted by deforested areas in miombo woodlands? *African Journal of Ecology*. DOI: 10.1111/aje.12882.
- Ameztegui, A., Coll, L. (2015). Herbivory and seedling establishment in Pyrenean forests: influence of micro- and meso- habitat factors on browsing pressure. *Forest Ecology and Management*. **342**, pp. 103-11.
- Areendran, G., Raj, K., Sharma, A., Bora, P.J., Sarmah, A., Sahana, M., Ranjan, K. (2020). Documenting the land use pattern in the corridor complexes of Kaziranga National Park using high resolution satellite imagery. *Trees, Forests and People*. **2**, p. 100039.
- Arnold, J.M., Gerhardt, P., Steyaert, S.M.J.G., Hochbichler, E., Hackländer, K. (2018). Diversionary feeding can reduce red deer habitat selection pressure on vulnerable forest stands, but is not a *panacea* for red deer damage. *Forest Ecology and Management*. **407**, pp. 166-73.
- Asner, G.P., Levick, S.R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters*. **15**, pp. 1211-7.
- Asner, G.P., Vaughn, N., Smit, I.P.J., Levick, S. (2016). Ecosystem-scale effects of megafauna in African savannas. *Ecography*. **39**, pp. 240-52.
- Babweteera, F., Savill, P., Brown, N. (2007). *Balanites wilsoniana*: regeneration with and without elephants. *Biological Conservation*. **134**, pp. 40-7.

Barnes, R.F.W., Barnes, K.L., Alers, M.P.T., Blom, A. (1991). Man determines the distribution of elephants in the rain forests of northeastern Gabon. *African Journal of Ecology*. **29**, pp. 54-63.

Beekman, J.H., Prins, H.H.T. (1989). Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus caffer*. *African Journal of Ecology*. **27**, pp. 129-47.

Van Beest, F.M., Wal, E.V., Stronen, A.V., Paquet, P.C., Brook, R.K. (2013). Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. *Oecologia*. **173**, pp. 409-20.

Beguin, J., Côté, S.D., Vellend, M. (2022). Large herbivores trigger spatiotemporal changes in forest plant diversity. *Ecology*. p.e3739.

Beguin, J., Tremblay, J.P., Thiffault, N., Pothier, D., Côté, S.D. (2016) Management of forest regeneration in boreal and temperate deer-forest systems: challenges, guidelines, and research gaps. *Ecosphere*. **7**, e01488.

Beirne, C., Meier, A.C., Brumagin, G., Jasperse-Sjolander, L., Lewis, M., Masseloux, J., Myers, K., Fay, M., Okouyi, J., White, L.J.T., Poulsen, J.R. (2020). Climatic and resource determinants of forest elephant movements. *Frontiers in Ecology and Evolution*. **8**, doi:10.3389/fevo.2020.00096.

Beirne, C., Houslay, T.M., Morkel, P., Clark, C.J., Fay, M., Okouyi, J., White, L.J.T., Poulsen, J.R. (2021). African forest elephant movements depend on time scale and individual behaviour. *Scientific Reports*. **11**, pp. 1-11.

Benitez, L., Queenborough, S.A. (2021). Fruit trees drive small-scale movement of elephants in Kibale National Park, Uganda. *Biotropica*. <https://doi.org/10.1111/btp.13010>.

Berke, S.K. (2010). Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integrative and Comparative Biology*. **50**, pp. 147-57.

Berzaghi, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., Scaranello, M., Scarascia-Mugnozza, G., Doughty, C.E. (2019). Carbon stocks in central African forests enhanced by elephant disturbance. *Nature Geoscience*. **12**, pp. 725-9.

Blake, S., Deem, S.L., Mossimbo, E., Maisels, F., Walsh, P. (2009). Forest elephants: tree planters of the Congo. *Biotropica*. **41**, 459-68.

Blake, S., Deem, S.L., Strindberg, S., Maisels, F., Momont, L., Isia, I.B., Douglas-Hamilton, I., Karesh, W.B., Kock, M.D. (2008). Roadless wilderness area determines forest elephant movements in the Congo Basin. *PloS ONE*. **3**, e3546.

Blake, S., Inkamba-Nkulu, C. (2004). Fruit, minerals, and forest elephant trails: do all roads lead to Rome? *Biotropica*. **36**, pp. 392-401.

Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossman, F., Bene-Bene, L., de Semboli, B., Mbenzo, V., S'hwa, D., Bayogo, R., Williamson, L., Fay, M., Hart, J., Maisels, F. (2007). Forest elephant crisis in the Congo basin. *PloS Biology*. **5**, e111.

Blake, S., Deem, S.L., Mossimbo, E., Maisels, F., Walsh, P. (2009). Forest elephants: tree planters of the Congo. *Biotropica*. **41**, 459-68.

Bobrowski, M., Gillich, B., Stolter, C. (2015). Modelling browsing of deer on beech and birch in northern Germany. *Forest Ecology and Management*. **358**, pp. 212-21.

De Boer, W.F., van Langevelde, F., Prins, H.H.T., de Ruiter, P.C., Blanc, J., Vis, M.J.P., Gaston, K.J., Douglas Hamilton, I. (2013). Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. *Biological Conservation*. **159**, pp. 468-76.

- Boissier, O., Feer, F., Henry, P.Y., Forget, P.M. (2020). Modifications of the rain forest frugivore community are associated with reduced seed removal at the community level. *Ecological Applications*. **30**, e02086.
- Bonnald, J., Utge, J., Kuhner, M.K., Wasser, S.K., Asalu, E., Okimat, J.P., Krief, S. (2021). Who are the elephants living in the hybridization zone? How genetics may guide conservation to better protect endangered elephants. *Global Ecology and Conservation*. **32**, e01917.
- Bonnell, T.R., Reyna-Hurtado, R., Chapman, C.A. (2011). Post-logging recovery time is longer than expected in an East African tropical forest. *Forest Ecology and Management*. **261**, pp. 855-64.
- Boult, V.L., Sibly, R.M., Quaife, T., Fishlock, V., Moss, C., Lee, P.C. (2019). Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns. *African Journal of Ecology*. **57**, pp. 10-9.
- Bowd, E.J., Banks, S.C., Bissett, A., May, T.W., Lindenmayer, D.B. (2021). Direct and indirect disturbance impacts in forests. *Ecology Letters*. **24**, pp. 1225-36.
- Brancalion, P.H.S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F.S.M., Zambrano, A.M.A., Baccini, A., Aronson, J., Goetz, S., Reid, J.L., Strassburg, B.B.N., Wilson, S., Chazdon, R.L. (2019). Global restoration opportunities in tropical rainforest landscapes. *Science Advances*. **5**, eaav3223.
- Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., Brown, C.M.L. (2021). Beaver: nature's ecosystem engineers. *Wiley Interdisciplinary Reviews: Water*. **8**, e1494.
- Brooks, A.C., Buss, I.O. (1962). Past and present status of the elephant in Uganda. *Journal of Wildlife Management*. **26**, pp. 38-50.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*. **9**, pp. 378-400.

Buechner, H.K., Dawkins, H.C. (1961). Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Journal of Ecology*. **42**, pp. 752-66.

Bunney, K., Bond, W.J., Henley, M. (2017). Seed dispersal kernel of the largest surviving megaherbivore – the African savanna elephant. *Biotropica*. **49**, pp. 395-401.

Burns, C.E., Collins, S.L., Smith, M.D. (2009). Plant community response to loss of large herbivores: comparing consequences in a South African and a North American grassland. *Biodiversity Conservation*. **18**, pp. 2327-42

Caillaud, D., Crofoot, M.C., Scarpino, S.V., Jansen, P.A., Garzon-Lopez, C.X., Winkelhagen, A.J.S., Bohlman, S.A., Walsh, P.D. (2010). Modelling the spatial distribution and fruiting pattern of a key tree species in a neotropical forest: methodology and potential applications. *PloS ONE*. **5**, e15002.

Campos-Arceiz, A., Blake, S. (2011). Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecologica*. **37**, pp. 542-53.

Cardoso, A.W., Malhi, Y., Oliveras, I., Lehmann, D., Ndong, J.E., Dimoto, E., Bush, E., Jeffery, K., Labriere, N., Lewis, S.L., White, L.T.J., Bond, W., Abernethy, K. (2020). The role of forest elephants in shaping tropical forest-savanna coexistence. *Ecosystems*. **23**, pp. 602-16.

Chamaillé-Jammes, S., Valeix, M., Fritz, H. (2007). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*. **44**, pp. 625-33.

Chapman, C.A., Bonnell, T.R., Gogarten, J.F., Lamber, J.E., Omeja, P.A., Twinomugisha, D., Wasserman, M.D., Rothman, J.M. (2013). Are primates ecosystem engineers? *Int J Primatol.* **34**, pp. 1-14.

Chapman, C.A., Bortolamiol, S., Matsuda, I., Omeja, P.A., Paim, F.P., Reyna-Hurtado, R., Sengupta, R., Valenta, K. (2018). Primate population dynamics: variation in abundance over space and time. *Biodivers Conserv.* **27**, pp. 1221-38.

Chapman, C.A., Chapman, L.J. (1995). Survival without dispersers: seedling recruitment under parents. *Conservation Biology.* **9**, pp. 675-8.

Chapman, C.A., Chapman, L.J. (1997). Forest Regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica.* **29**, pp. 396-412.

Chapman, C.A., Chapman, L.J. (1999). Forest restoration in abandoned agricultural land: a case study from East Africa. *Conservation Biology.* **13**, pp. 1301-11.

Chapman, C.A., Chapman, L.J. (2004). Unfavorable successional pathways and the conservation value of logged tropical forest. *Biodiversity and Conservation.* **13**, pp. 2089-105.

Chapman, C.A., Chapman, L.J., Jacob, A.L., Rothman, J.M., Omeja, P., Reyna-Hurtado, R., Hartter, J., Lawes, M.J. (2010a). Tropical tree community shifts: implications for wildlife conservation. *Biological Conservation.* **143**, pp. 366-374.

Chapman, L.J., Chapman, C.A., Wrangham, R.W. (1992). *Balanites wilsoniana*: elephant dependent dispersal? *Journal of Tropical Ecology.* **8**, pp. 275-83.

Chapman, C.A., Chapman, L.J., Wrangham, R., Isabirye-Basuta, G., Ben-David, K. (1997). Spatial and temporal variability in the structure of a tropical forest. *Afr. J. Ecol.* **35**, pp. 287-302.

Chapman, C., Galán-Acedo, C., Gogarten, J.F., Hou, R., Lawes, M.J., Omeja, P.A., Sarkar, D., Sugiyama, A., Kalbitzer, U. (2021). A 40-year evaluation of drivers of African rainforest change. *Forest Ecosystems*. **8**, pp. 1-16.

Chapman, C.A., Lambert, J.E. (2000). Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *American Journal of Primatology*. **50**, pp. 169-85.

Chapman, C.A., Struhsaker, T.T., Lambert, J.E. (2005). Thirty years of research in Kibale National Park, Uganda, reveals a complex picture for conservation. *International Journal of Primatology*. **26**, pp. 539-55.

Chapman, C.A., Struhsaker, T.T., Skorupa, J.P., Snaith, T.V., Rothman, J.M. (2010b). Understanding long-term primate community dynamics: implications of forest change. *Ecological Applications*. **20**, pp. 179-91.

Chiyo, P.I., Lee, P.C., Moss, C.J., Archie, E.A., Hollister-Smith, J.A., Alberts, S.C. (2011). No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants. *Behavioural Ecology*. **22**, pp. 552-8.

Chiyo, P.I., Cochrane, E.P. (2005). Population structure and behaviour of crop-raiding elephants in Kibale National Park, Uganda. *Afr. J. Ecol.* **43**, pp. 233-41.

Chritz, K.L., Blumenthal, S.A., Cerling, T.E., Klingel, H. (2016). Hippopotamus (*H. amphibius*) diet change indicates herbaceous plant encroachment following megaherbivore population collapse. *Scientific Reports*. **6**, doi: 10.1038/srep32807.

Clark, C.J., Poulsen, J.R., Malonga, R., Elkan Jr, P.W. (2009). Logging concessions can extend the conservation estate for central African tropical forests. *Conservation Biology*. **23**, pp. 1281-93.

- Cochrane, E.P. (2001). *Elephants as seed dispersal agents for tropical forest tree species in Kibale National Park, Uganda*. The University of Wisconsin-Madison.
- Cochrane, E.P. (2003). The need to be eaten: *Balanites wilsoniana* with and without elephant seed-dispersal. *Journal of Tropical Ecology*. **19**, pp. 579-89.
- Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*. Pp. 298-312.
- Coverdale, T.C., Kartzinel, T.R., Grabowski, K.L., Shriver, R.K., Hassan, A.A., Goheen, J.R., Palmer, T.M., Pringle, R.M. (2016). Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering. *Ecology*. **97**, pp. 3219-30.
- Cromsigt, J.P.G.M., te Beest, M. (2014). Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. *Journal of Ecology*. **102**, pp. 566-75.
- Daniel, A., Edward, A., Kennedy, A. (2021). Elephant population status, distribution and conservation threats in Kibale National Park, Uganda. *East African Journal of Environment and Natural Resources*. **4**, pp. 68-78.
- Danquah, E. (2016). Spatial distribution of elephants versus human and ecological variables in western Ghana. *Advances in Ecology*.
- Desbiez, A.L.J., Kluyber, D. (2013). The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. **45**, pp. 537-40.
- Duclos, V., Boudreau, S., Chapman, C.A. (2013). Shrub cover influence on seedling growth and survival following logging of a tropical forest. *Biotropica*. **45**, pp. 419-26.

Dunkin, R.C., Wilson, D., Way, N., Johnson, K., Williams, T.M. (2013). Climate influences thermal balance and water use in African and Asian elephants: physiology can predict drivers of elephant distribution. *Journal of Experimental Biology*. **216**, pp. 2939-52.

Eltringham, S.K., Maplas, R.C. (1980). The decline in elephant numbers in Rwenzori and Kabalega Falls National Parks, Uganda. *Afr. J. Ecol.* **18**, pp. 73-86.

Field, C.R. (1971). Elephant ecology in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.* **9**, pp. 99-123.

Felton, A.M., Felton, A., Rumiz, D.I., Pena-Claros, M., Villaroel, N., Chapman, C.A., Lindenmayer, D.B. (2013). Commercial harvesting of *Ficus* timber – an emerging threat to frugivorous wildlife and sustainable forestry. *Biological Conservation*. **159**, pp. 96-100.

Flint, B.F., Hawley, D.M., Alexander, K.A (2016). Do not feed the wildlife: associations between garbage use, aggression, and disease in banded mongooses (*Mungos mungo*). *Ecology and Evolution*. **6**, pp. 5932-9.

Forbes, E.S., Cushman, J.H., Burkepile, D.E., Young, T.P., Klope, M., Young, H.S. (2019). Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*. **33**, pp. 1597-610.

Foster, C.N., Barton, P.S., Lindenmayer, D.B. (2014). Effects of large native herbivores on other animals. *Journal of Applied Ecology*. **51**, pp. 929-38.

Gallagher, A.J., Creel, S., Wilson, R.P., Cooke, S.J. (2017). Energy landscapes and the landscape of fear. *Trends in Ecology and Evolution*. **32**, pp. 88-96.

Von Gerhardt, K., van Niekerk, A., Kidd, M., Samways, M., Hanks, J. (2014). The role of elephant *Loxodonta africana* pathways as a spatial variable in crop-raiding location. *Oryx*. **48**, pp. 436-44.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A. (2010). Tropical forests were the primary sources of new agricultural land 1980s and 1990s. *PNAS*. **107**, pp. 16732-7.

Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., Meron, E. (2004). Ecosystem engineers: from pattern formation to habitat creation. *Physical Review Letters*. **93**, p.098105.

Gobush, K.S., Edwards, C.T.T., Balfour, D., Wittemyer, G., Maisels, F., Taylor, R.D. (2021a). *Loxodonta africana* (amended version of 2021 assessment). *The IUCN Red List of Threatened Species 2021*. E.T181008073A204401095.

Gobush, K.S., Edwards, C.T.T., Maisels, F., Wittemyer, G., Balfour, D., Taylor, R.D. (2021b). *Loxodonta cyclotis* (errata version published in 2021). *The IUCN Red List of Threatened Species 2021*. E.T181007989A204404464.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*.

Grandos, A., Weladji, R.B., Loomis, M.R. (2012). Movement and occurrence of two elephant herds in a human-dominated landscape, the Bénoué Wildlife Conservation Area, Cameroon. *Tropical Conservation Science*. **5**, pp. 150-62.

Grubb, P., Groves, C.P., Dudley, J.P., Shoshani, J. (2000). Living African elephants belong to two species: *Loxodonta africana* (Blumenbach, 1797) and *Loxodonta cyclotis* (Matschie, 1900). *Elephant*. **2**, pp. 1-4.

Gubbi, S., Poornesha, H.C., Madhusuda, M.D. (2012). Impact of vehicular traffic on the use of highway edges by large mammals in a South Indian wildlife reserve. *Current Science*. **102**, pp. 1047-51.

Guisan, A., Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*. **8**, pp. 993-1009.

Guldemon, R.A.R., Purdon, A., van Aarde, R.J. (2017). A systematic review of elephant impact across Africa. *PloS ONE*. **12**, e0178935.

Han, X., Huang, J., Yao, J., Xu, Y., Ding, Y., Zang, R. (2021). Effects of logging on the ecological strategy spectrum of a tropical montane rain forest. *Ecological Indicators*. **128**, 107812.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*. **342**, pp. 850-3.

Harich, F.K., Treydte, A.C., Ogutu, J.O., Roberts, J.E., Savini, C., Bauer, J.M., Savini, T. (2016). Seed dispersal potential of Asian elephants. *Acta Oecologia*. **77**, pp. 144-51.

Hartig, F. (2021). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.4. <https://CRAN.R-project.org/package=DHARMA>

Hatton, J.C., Smart, N.O.E. (1984). The effect of long-term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park, Uganda. *African Journal of Ecology*. **22**, pp. 23-30.

Hyvarinen, O., Te Beest, M., le Roux, E., Kerley, G., de Groot, E., Vinita, R., Croomsigt, J.P.G.M. (2021). Megaherbivore impacts on ecosystem and earth system functioning: the current state of the science. *Ecography*. **44**, pp. 1579-94.

Iravani, M., Schütz, M., Edwards, P.J., Risch, A.C., Scheidegger, C., Wagner, H.H. (2011). Seed dispersal in red deer (*Cervus elaphus* L.) dung and its potential importance for vegetation dynamics in subalpine grasslands. *Basic and Applied Ecology*. **12**, pp. 505-15.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*. **104**, pp. 501-28.

Jorritsma, I.T.M., van Hees, A.F.M., Mohren, G.M.J. (1999). Forest development in relation to ungulate grazing: a modelling approach. *Forest Ecology and Management*. **120**, pp. 23-34.

Kalbitzer, U., McInnis, V., Omeja, P.A., Bortolamiol, S., Chapman, C.A. (2019). Does the presence of elephant dung create hotspots for growth for existing seedlings? *Journal of Tropical Ecology*. **35**, pp. 132-9.

Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U., Christensen, N.L. (2009). Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology*. **46**, pp. 1189-1200.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *PNAS*. **101**, pp. 4854-8.

Keigwin, M., Wabukawo, V., Wasser, S.K., Chapman, C.A. (2016). Impacts on transboundary elephant movements between Queen Elizabeth Conservation Area, Uganda and Parc National des Virunga, Democratic Republic of Congo. *Pachyderm*. **57**, pp. 118-21.

Keith, S.A., Bull, J.W. (2017). Animal culture impacts species' capacity to realise climate-driven range shifts. *Ecography*. **40**, pp. 296-304.

Kleinman, J.S., Goode, J.D., Fries, A.C., Hart, J.L. (2019). Ecological consequences of compound disturbances in forest ecosystems: a systematic review. *Ecosphere*. **10**, e02962.

Kolinski, L., Milich, K.M. (2021). Human-wildlife conflict mitigation impacts community perceptions around Kibale National Park, Uganda. *Diversity*. **13**, p. 145.

Laguardia, A., Bourgeois, S., Strindberg, S., Gobush, K.S., Abitsi, G., Ateme, H.G.B.B., Ebouta, F., Fay, J.M., Gopalaswamy, A.M., Maisels, F., Daouda, E.L.F.S.B., White, L.J.T., Stokes, E.J. (2021). Nationwide abundance and distribution of African forest elephants across Gabon using non-invasive SNP genotyping. *Global Ecology and Conservation*. **32**, e01894.

Landman, M., Mgqatsa, N., Cromsigt, J.P.G.M., Kerley, G.I.H. (2019). Elephant effects on treefall and logfall highlight the absence of megaherbivores in coarse woody debris conceptual frameworks. *Forest Ecology and Management*. **438**, pp. 57-62.

Law, A., Gaywood, M.J., Jones, K.C., Ramsay, P., Willby, N.J. (2017). Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Science of the Total Environment*. **605**, pp. 1021-30.

Lawes, M.J., Chapman, C.A. (2006). Does the herb *Acanthus pubescens* and/or elephants suppress tree regeneration in disturbed Afrotropical forest? *Forest Ecology and Management*. **221**, pp. 278-84.

Laws, R.M. (1970). Elephants as agents of habitat and landscape change in East Africa. *Oikos* **21**, pp. 1-15.

Levey, D.J., Londoño, G.A., Ungvari-Martin, J., Hiersoux, M.R., Jankowski, J.E., Poulsen, J.R., Stracey, C.M., Robinson, S.K. (2009). Urban mockingbirds quickly learn to identify individual humans. *PNAS*. **106**, pp. 8959-62.

Linnell, J.D.C., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczensky, P., Moorter, B.V., Panzacchi, M., Rauset, G.R., Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*. **244**, 108500.

Liu, J., Feng, C., Wang, D., Wang, L., Wilsey, B.J., Zhong, Z. (2015). Impacts of grazing by different large herbivores in grassland depend on plant species diversity. *Journal of Applied Ecology*. **52**, pp. 1053-62.

Liu, Y., Wu, C., Peng, D., Xu, S., Gonsamo, A., Jassal, R.S., Arain, M.A., Lu, L., Fang, B., Chen, J.M. (2016). Improved modelling of land surface phenology using MODIS land surface reflectance and temperature at evergreen needleleaf forests of central North America. *Remote Sensing of Environment*. **176**, pp. 152-62.

Loarie, S.R., van Aarde, R.J., Pimm, S.L. (2009). Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*. **142**, pp. 3086-98.

Losapio, G., Schmid, B., Bascompte, J., Michalet, R., Cerretti, P., Germann, C., Haenni, J.P., Neumeyer, R., Ortiz-Sánchez, F.J., Pont, A.C., Rousse, P., Schmid, J., Sommaggio, D., Schöb, C. (2021). An experimental approach to assessing the impact of ecosystem engineers on biodiversity and ecosystem functions. *Ecology*. **102**, e03243.

Lüdecke et al., (2021). Performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*. **6**(60), 3139.
<https://doi.org/10.21105/joss.03139>

Lum, S., Min, N.K. (2021). Lessons in ecology and conservation from a tropical forest fragment in Singapore. *Biological Conservation*. **254**, 108847.

Ma, L., Lian, J., Lin, G., Cao, H., Huang, Z., Guan, D. (2016). Forest dynamics and its driving forces of sub-tropical forest in South China. *Scientific Reports*. **6**, pp. 1-10.

Makhabu, S.W., Skarpe, C., Hytteborn, H. (2006). Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica*. **30**, pp. 136-46.

- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.C., Terborgh, J.W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *PNAS*. **113**, pp. 838-46.
- Malhi, Y., Lander, T., le Roux, E., Stevens, N., Macias-Fauria, M., Wedding, L., Girardin, C., Kristensen, J.A., Sandom, C.J., Evans, T.D., Svenning, J.C., Canney, S. (2022). The role of large wild animals in climate change mitigation and adaptation. *Current Biology*. **32**, pp. R181-R196.
- Månsson, J., Jarnemo, A. (2013). Bark-stripping on Norway spruce by red deer in Sweden: level of damage and relation to tree characteristics. *Scandinavian Journal of Forest Research*. **28**, pp. 117-25.
- Matos, F.A.R., Magnago, L.F.S., Miranda, C.A.C., de Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., da Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P. (2020). Secondary forest fragments offer important carbon and biodiversity cobenefits. *Global Change Biology*. **26**, pp. 509-22.
- Matsushita, B., Yang, W., Chen, J., Onda, Y., Qiu, G. (2007). Sensitivity of the enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) to topographic effects: a case study in high-density cypress forest. *Sensors*. **7**, pp. 2636-51.
- McNaughton, S.J., Banyikwa, F.F., McNaughton, M.M. (1997). Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science*. **278**, pp. 1798-800.
- Merz, G. (1981). Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt, *Loxodonta africana cyclotis* Matschie, 1900. *Mammalia*. **45**, 299-312.
- Messina, S., Costantini, D., Tomassi, S., Cosset, C.C.P., Benedick, S., Eens, M., Edwards, D.P. (2021). Selective logging reduces body size in omnivorous and frugivorous tropical forest birds. *Biological Conservation*. **256**, p. 109036.

Mills, E.C., Poulsen, J.R., Fay, J.M., Morkel, P., Clark, C.J., Meier, A., Beirne, C., White, L.J.T. (2018). Forest elephant movement and habitat use in a tropical forest-grassland mosaic in Gabon. *PloS ONE*. **13**, e0199387.

Moe, S.R., Rutina, L.P., Hytteborn, H., du Toit, J.T. (2009). What controls woodland regeneration after elephants have killed the big trees? *Journal of Applied Ecology*. **46**, pp. 223-30.

Molina-Vacas, G., Muñoz-Mas, R., Martínez-Capel, F., Rodriguez-Teijeiro, J.D., Le Fohlic, G. (2019). Movement patterns of forest elephants (*Loxodonta cyclotis* Matschie, 1900) in the Odzala-Kokoua National Park, Republic of Congo. *African Journal of Ecology*. **58**, pp. 23-33.

Mondol, S., Moltke, I., Hart, J., Keigwin, M., Brown, L., Stephens, M., Wasser, S.K. (2015). New evidence for hybrid zones of forest and savanna elephants in Central and West Africa. *Molecular Ecology*. **24**, pp. 6134-47.

Morrison, T.A., Bogler, D.T. (2012). Wet season range fidelity in a tropical migratory ungulate. *Journal of Animal Ecology*. **81**, pp. 543-52.

Moss, C.J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology*. **255**, pp. 145-56.

Mukherjee, T., Sharma, L.K., Thakur, M., Saha, G.K., Chandra, K. (2019). Changing landscape configuration demands ecological planning: retrospect and prospect for megaherbivores of North Bengal. *PLoS ONE*. **14**, e0225398.

Müller, A., Dahm, M., Bøcher, P.K., Root-Bernstein, M., Svenning, J.C. (2017). Large herbivores in novel ecosystems – habitat selection by red deer (*Cervus elephus*) in a former brown-coal mining area. *PLoS ONE*. **12**, e0177431.

O'Farrill, G., Galetti, M., Campos-Arceiz, A. (2013). Frugivory and seed dispersal by tapirs: an insight on their ecological role. *Integrative Zoology*. **8**, pp. 4-17.

O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W. (2011). Are the long-term effects of mesobrowsers on woodland dynamics substitutive or additive to those of elephants? *Acta Oecologica*. **37**, pp. 393-8.

O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W. (2012). Heavy impact on seedlings by the impala suggests a central role in woodland dynamics. *Journal of Tropical Ecology*. **28**, pp. 291-7.

O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W. (2013). Model highlights likely long-term influences of mesobrowsers versus those of elephants on woodland dynamics. *African Journal of Ecology*. **52**, pp. 192-208.

Omeja, P.A., Jacob, A.L., Lawes, M.J., Lwanga, J.S., Rothman, J.M., Tumwesigye, C., Chapman, C.A. (2014). Changes in elephant abundance affect forest composition or regeneration? *Biotropica*. **46**, pp. 704-11.

Omeja, P.A., Lawes, M.J., Corriveau, A., Valenta, K., Sarkar, D., Paim, F.P., Chapman, C.A. (2016). Recovery of tree and mammal communities during large-scale forest regeneration in Kibale National Park, Uganda. *Biotropica*. **48**, pp. 770-9.

Owen-Smith, R.N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press.

Paul, J.R., Randle, A.M., Chapman, C.A., Chapman, L.J. (2004). Arrested succession in logging gaps: is tree seedling growth and survival limiting? *African Journal of Ecology*. **42**, pp. 245-51.

Pekor, A., Miller, J.R.B., Flyman, M.V., Kasiki, S., Kesch, M.K., Miller, S.M., Uiseb, K., van der Merve, V., Lindsey, P.A. (2019). Fencing Africa's protected areas: costs, benefits, and management issues. *Biological Conservation*. **229**, pp. 67-75.

Phiri, D., Morgenroth, J. (2017). Developments in landsat land cover classification methods: a review. *Remote Sensing*. **9**, doi: 10.3390/rs9090967.

Pike, D.A., Mitchell, J.C. (2013). Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Animal Conservation*. **16**, pp. 694-703.

Plumptre, A.J. (1996). Changes following 60 years of selective harvesting in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management*. **89**, pp. 101-13.

Poulsen, J.R., Rosin, C., Meier, A., Mills, E., Nuñez, C.L., Koerner, S.E., Blanchard, E., Callejas, J., Moore, S., Sowers, M. (2018). Ecological consequences of forest elephant declines for Afrotropical forests. *Conservation Biology*. **32**, pp. 559-67.

Pradhan, N.M.B., Wegge, P., Moe, S.R., Shrestha, A.K. (2008). Feeding ecology of two endangered sympatric megaherbivores: Asian elephant *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in lowland Nepal. *Wildlife Biology*. **14**, pp. 147-54.

Putz, F. (1985). Woody vines and forest management in Malaysia. *The Commonwealth Forestry Review*. **64**, pp. 359-365.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Ramirez, J.I., Jansen, P.A., Poorter, L. (2018). Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: a semi-quantitative review. *Forest Ecology and Management*. **424**, pp. 406-19.

Richardson, A.D., Braswell, B.H., Hollinger, D.Y., Jenkins, J.P., Ollinger, S.V. (2009). Near-surface remote sensing of spatial and temporal variation in canopy phenology. *Ecological Applications*. **19**, pp. 1417-28.

Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P.A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A., Corlett, R.T., Darimont, C.T., Dickman, A.J., Dirzo, R., Dublin, H.T., Estes, J.A., Everatt, K.T., Galetti, M., Goswami, V.R., Hayward, M.W., Hedges, S., Hoffmann, M., Hunter, L.T.B., Kerley, G.I.H., Letnic, M., Levi, T., Maisels, F., Morrison, J.C., Nelson, M.P., Newsome, T.M., Painter, L., Pringle, R.M., Sandom, C.J., Terborgh, J., Treves, A., Valkenburgh, B.V., Vuchetich, J.A., Wirsing, A.J., Wallach, A.D., Wolf, C., Woodroffe, R., Young, H., Zhang, L. (2016). Saving the world's terrestrial megafauna. *Bioscience*. **66**, pp. 807-12.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., Valkenburgh, B.V. (2015). Collapse of the world's largest herbivores. *Science Advances*. **1**, e1400103.

Ritchie, E.G., Martin, J.K., Krockenberger, A.K., Garnett, S., Johnson, C.N. (2008). Large-herbivore distribution and abundance: intra- and interspecific niche variation in the tropics. *Ecological Monographs*. **78**, pp. 105-22.

Roca, A.L., Georgiadis, N., Pecon-Slattery, J., O'Brien, S.J. (2001). Genetic evidence for two species of elephant in Africa. *Science*. **293**, pp. 1473-7.

Rode, K.D., Chiyo, P.I., Chapman, C.A., McDowell, L.R. (2006). Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of Tropical Ecology*. **22**, pp. 441-9.

Rohland, N., Reich, D., Mallick, S., Meyer, M., Green, R.E., Georgiadis, N.J., Roca, A.L., Hofreiter, M. (2010). Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. *PLoS Biology*. **8**, e1000564.

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J.B., Nicol, S., Pershing, A., Smetacek, V. (2014). Whales as marine ecosystem engineers. *Front Ecol Environ*. **12**, pp. 377-85.

Romero, C., Putz, F.E., Guariguata, M.R., Sills, E.O., Cerutti, P.O., Lescuyer, G. (2013). An overview of current knowledge about the impacts of forest management certification: A proposed framework for its evaluation.

le Roux, E., Kerley, G.I.H., Cromsigt, P.G.M. (2018). Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*. **28**, pp. 2493-9.

Sandhage-Hofmann, A., Linstädter, A., Kindermann, L., Angombe, S., Amelung, W. (2021). Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass. *Global Change Biology*. **27**, pp. 4601-14.

Sarkar, D., Bortolamiol, S., Gogarten, J.F., Hartter, J., Hou, R., Kagoro, W., Omeja, P., Tumwesigye, C., Chapman, C.A. (2021). Exploring multiple dimensions of conservation success: Long-term wildlife trends, anti-poaching efforts, and revenue sharing in Kibale National Park, Uganda. *Animal Conservation*.

Sarkar, D., Chapman, C.A., Kagoro, W., Sengupta, R. (2016). Countering elephant raiding with short message service: challenges of deploying public participation-based systems in a setting with sparse information communication technologies resources. *The Canadian Geographer/Le Géographe canadien*. **60**, pp. 493-504.

Şatir, O., Berberoğlu. (2012). Land use/cover classification techniques using optical remotely sensed data in landscape planning. *Landscape Planning: Rijeka: InTech*. pp. 21-54.

Shaffer, L.J., Khadka, K.K., Van Den Hoek, J., Naithani, K.J. (2019). Human-elephant conflict: a review of current management strategies and future directions. *Frontiers in Ecology and Evolution*. **6**, doi: 10.3389/fevo.2018.00235

Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R., Slotow, R. (2008). The utilization of large savanna trees by elephants in southern Kruger National Park. *Journal of Tropical Ecology* **24**, pp. 281-9.

Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E., Smith, R.J. (2009). The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*. **15**, pp. 776-783.

Shannon, G., Page, B.R., Duffy, K.J., Slotow, R. (2006). The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia*. **150**, pp. 344-54.

Shannon, G., Thaker, M., Vanak, A.T., Page, B.R., Grant, R., Slotow, R. (2011). Relative impact of elephant and fire on large trees in a savanna ecosystem. *Ecosystems*. **14**, pp. 1372-81.

Short, J. (1981). Diet and feeding behaviour of the forest elephant. *Mammalia*. **45**, pp. 177-85.

Short, J.C. (1983). Density and seasonal movements of forest elephant (*Loxodonta africana cyclotis*, Matschie) in Bia National Park, Ghana. *African Journal of Ecology*. **21**, pp. 175-84.

Sintayehu, D.W., Kassaw, M. (2019). Impact of land cover changes on elephant conservation in babile elephant sanctuary, Ethiopia. *Biodiversity International Journal*. **3**, pp. 65-71.

Smart, N.O.E., Hatton, J.C., Spence, D.H.N. (1985). The effect of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biological Conservation*. **33**, pp. 229-45.

Smit, I.P.J., Ferreira, S.M. (2010). Management intervention affects river-bound spatial dynamics of elephants. *Biological Conservation*. **143**, pp. 2172-81.

Snell-Rood, E.C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*. **85**, pp. 1004-11.

Stevens, N., Lehmann, C.R., Murphy, B.P., Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*. **23**, pp. 235-44.

Stokke, S., du Toit, J.T. (2000). Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*. **23**, pp. 70-80.

Struhsaker, T.T., Lwanga, J.S., Kasenene, J.M. (1996). Elephants, selective logging and forest regeneration in the Kibale forest, Uganda. *Journal of Tropical Ecology*. **12**, pp. 45-64.

Struhsaker, T.T. (1997). *Ecology of an African rain forest: logging in Kibale and the conflict between conservation exploitation*. University Press of Florida.

Srinivasaiah, N., Kumar, V., Vaidyanathan, Sukumar, R., Sinha, A. (2019). All-male groups in Asian elephants: a novel, adaptive social strategy in increasingly anthropogenic landscapes of Southern India. *Scientific Reports*. **9**, pp. 1-11.

Sukumar, R., Gadgil, M. (1988). Male-female differences in foraging on crops by Asian elephants. *Animal Behaviour*. **36**, pp. 1233-5.

Talukdar, S., Singha, P., Mahato, S., Shahfahad, Pal, S., Liou, Y.A., Rahman, A. (2020). Land-use land-cover classification by machine learning classifiers for satellite observations – a review. *Remote Sensing*. **12**, doi:10.3390/rs12071135.

- Tang, J., Körner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S.J., Yang, X. (2016). Emerging opportunities and challenges in phenology: a review. *Ecosphere*. **7**, e01436.
- Terborgh, J., Davenport, L.C., Niangadouma, R., Dimoto, E., Mouandza, J.C., Scholtz, O., Jaen, M.R. (2016). Megafaunal influences on tree recruitment in African equatorial forests. *Ecography*. **39**, pp. 180-6.
- de la Torre, J.A., Núñez, J.M., Medellín, R.A. (2017). Spatial requirements of jaguars and pumas in Southern Mexico. *Mammalian Biology*. **84**, pp. 52-60.
- Torres-Romero, E.J., Giordano, A.J., Ceballos, G., López-Bao, J.V. (2020). Reducing the sixth mass extinction: understanding the value of human-altered landscapes to the conservation of the world's largest terrestrial mammals. *Biological Conservation*. **249**, p. 108706.
- Tsalyuk, M., Kilian, W., Reineking, B., Getz, W.M. (2019). Temporal variation in resource selection of African elephants follows long-term variability in resource availability. *Ecological Monographs*. **89**, e01348.
- Tweheyo, M., Tumusiime, D.M., Muhairwe, T., Twinomuhangi, R. (2013). Elephant damage and tree response in restored parts of Kibale National Park, Uganda. *International Journal of Biodiversity and Conservation*. **5**, pp. 371-7.
- UN. (2021). United Nations Decade on Ecosystem Restoration 2021-2030. <https://www.decadeonrestoration.org/>. Accessed: 22/02/2022.
- UNEP-WCMC (2021). Protected Area Profile for Kibale from the World Database of Protected Areas, August 2021. Available at: www.protectedplanet.net
- Vanak, A.T., Thaker, M., Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*. **143**, pp. 2631-7.

Vanleeuwe, H., Gautier-Hion, A. (1998). Forest elephant paths and movements at the Odzala Naational Park, Congo: the role of clearings and Marantaceae forests. *Afr. J. Ecol.* **36**, pp. 174-82.

van der Waal, C., Kool, A., Meijer, S.S., Kohi, E., Heitkönig, I.M.A., de Boer, W.F., van Langevelde, F., Grant, R.C., Peel, M.J.S., Slotow, R., de Knecht, H.J., Prins, H.H.T., de Kroon, H. (2011). Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia*. **165**, pp. 1095-107.

Wadey, J., Beyer, H.L., Saaban, S., Othman, N., Leimgruber, P., Campos-Arceiz, A. (2018). Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. *Biological Conservation*. **218**, pp. 91-8.

Waldram, M.S., Bond, W.J., Stock, W.D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems*. **11**, pp. 101-12.

Wall, J.L., Loken, B., Brodie, J.F. (2021). Reconciling resource extraction and species conservation in a multi-use landscape: immediate and long-term impacts of logging on rainforest mammal diversity. *Global Ecology and Conservation*. **28**, e01642.

Wanyama, F., Muhabwe, R., Plumptre, A.J., Chapman, C.A., Rothman, J.M. (2010). Censusing large mammals in Kibale National Park: evaluation of the intensity of sampling required to determine change. *African Journal of Ecology*. **48**, pp. 953-61.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*. **2**, pp. 599-610.

- Valtonen, A., Korkiatupa, E., Holm, S., Malinga, G.M., Nakadai, R. (2021). Remotely sensed vegetation greening along a restoration gradient of a tropical forest, Kibale National Park, Uganda. *Land Degradation and Development*. **32**, pp. 1-12.
- Vanak, A.T., Thaker, M., Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*. **143**, pp. 2631-7.
- Weinbaum, K., Nzooh, Z., Usongo, L., Laituri, M. (2007). Preliminary survey of forest elephant crossings in Sangha Trinational Park, central Africa. *Pachyderm*. **43**, pp. 52-62.
- Wing, L.D., Buss, I.O. (1970). Elephants and Forests. *Wildlife Monographs*. **19**, pp. 3-92.
- White, L.J.T., Tutin, C.E.G., Fernandez, M. (1993). Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology*. **31**, pp. 181-99.
- White, L.J.T. (1994). *Sacoglottis gabonensis* fruiting and the seasonal movements of elephants in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*. **10**, pp. 121-5.
- Wu, L., Zhu, X., Lawes, R., Dunkerly, D., Zhang, H. (2019). Comparison of machine learning algorithms for classification of LiDAR points for characterization of canola canopy structure. *International Journal of Remote Sensing*. **40**, pp. 5973-91.
- Young, K.D., Ferreira, S.M., van Aarde, R.J. (2009). Elephant spatial use in wet and dry savannas of southern Africa. *Journal of Zoology*. **278**, pp. 189-205.
- Zaki, N.A.M., Latif, Z.A. (2017). Carbon sinks and tropical forest biomass estimation: a review on role of remote sensing in aboveground-biomass modelling. *Geocarto International*. **32**, pp. 701-16.