Contrasting elephants and humans as agents of disturbance in Miombo woodlands

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Declaration

I declare that this dissertation is my own work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted by me before for any other degree, diploma or examination at any other university or tertiary institution.

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14/10/2019

Abstract

The Miombo woodlands are “disturbance driven savannas”, where people, elephants and fire prevent canopy closure and maintain tree-grass coexistence. Since the end of the 18th century, the woodlands have undergone dramatic changes to their disturbance regimes, through increases in human and decreases in elephant populations. This has resulted in a high concentration of human-driven disturbances in some areas of the woodlands and low disturbances in other areas. Consequently, in the areas affected by humans, there are high levels of biomass loss, while other areas experience woody plant encroachment. The ecological impacts of humans and elephants are comparable, but there are important differences. Although both remove woody biomass, they might impact vegetation composition and structure differently. The aim of this study was to investigate whether people can perform a similar functional role to elephants, with regards to biomass removal and potential changes to savanna structure and composition.

Aboveground woody biomass estimates were obtained from Synthetic Aperture Radar backscatter and used to (1) compare biomass change at different levels of human (2010 human population density) and elephant influence (2009 Niassa elephant density); and (2) identify how the intensity of biomass loss differs for humans and historical elephant densities (1.4 elephants/km^2) under different rainfall and initial biomass conditions. Biomass change was calculated between 2007 and 2010 and compared across equal areas inside and outside of Niassa National Reserve. For human influence, a regional analysis was also done. Published estimates of past elephant densities without poaching for Niassa National Reserve were used as the historical elephant density. Biomass loss increases with population density, for both people and elephants. However, rainfall responses show opposite patterns: biomass loss decreases with rainfall within Niassa National Reserve (under elephant influence) but increases outside of protected areas (under human influence). Under more mesic conditions, humans tend to remove more biomass than elephants. This suggests that woodlands with low rainfall and low human influence have more trees and higher biomass than if elephants were still present at their historical densities, and that some harvesting by people may be beneficial.

People and elephants both remove woody biomass; however, they do not necessarily select the same stems. Therefore, species and size class preference of humans and elephants were compared, to identify potential differences in their impacts on vegetation structure and composition. I found that humans prefer a wider range of species than elephants, so might filter the canopy layer more strongly. Elephants’ preference for slightly larger stems suggests that areas utilised by elephants might result in a more left-skewed size-class distribution than humans in areas without a charcoal industry. The high regeneration ability of many species, the large overlap in stems used by people and elephants and the relative flexibility in what stems can be used for a specific purpose, suggests that many of these differences in impacts on composition and structure could be mitigated.

While elephants and people clearly have different impacts on woody vegetation, people are a totally novel ecological and evolutionary force due to some similarities in how both use woody biomass. The type of human utilisation will determine the stems used and I suggest that since almost all aboveground woody biomass can be utilised for charcoal, the human impact on the woodlands could be reduced by decentralising the charcoal industry. Encouraging small scale production in low rainfall, low human impact areas, could alleviate the pressure on the hotspots of biomass loss. This could provide rural populations with an additional source of income, and the woodlands with a disturbance necessary in maintaining, to some extent, the ecosystem structure and functioning. However, care needs to be taken as increasing accessibility in remote areas could result in rampant deforestation. Results from this thesis suggest that forest management principals developed in other ecosystems, which haven't had mega-fauna for thousands of years, need to be tailored to African ecosystems. African forest managers therefore need to develop policies that consider the past and present disturbance regimes of these ecosystems.

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Chapter 1

Introduction

Disturbances - including fire, mammalian herbivory and wind (Spinage & Guinness 1971) - play an important role in the dynamics of savannas, particularly in maintaining their characteristic tree-grass coexistence (Sankaran *et al.* 2005). In the Miombo woodlands, the most common savanna of the southern hemisphere (Campbell *et al.* 1996), woody plant dynamics are affected by three interacting disturbance factors; people, elephants and fire (Frost 1996; Ribeiro *et al.* 2015). The woody components of these systems play an important role in the ecosystem functioning of the Miombo, particularly in nutrient cycling (Frost 1996; Ribeiro *et al.* 2013) and the storing of carbon (Ribeiro *et al.* 2015; Ribeiro *et al.* 2013).

The Miombo ecoregion covers 3.6 million km^2 from the west coast of Angola to the east coast of Mozambique and Tanzania (Figure 1; Timberlake & Chidumayo 2011). It is characterised by trees from the Detariodeae (previously Caesalpinioideae) subfamily and a grass layer (Timberlake & Chidumayo 2011). The Miombo has been classified as savanna (Frost *et al.* 1986), woodland (White 1983; Hansen *et al.* 2016) and forest (Malaisse 1978; Hansen *et al.* 2013), partly due to the high structural variability as within this region tree cover can vary from about 20% to an almost closed canopy (Timberlake & Chidumayo 2011). The ecoregion includes nine different vegetation types (Figure 1). Rainfall is a key driver in the structural and compositional variability of this region (Timberlake & Chidumayo 2011) as the Miombo is often divided into the Wet and Dry Miombo. The Wet Miombo is found in the higher rainfall areas, which support higher woody biomass (Frost 1996) and faster regrowth rates (Trouet *et al.* 2010) than the Dry Miombo found in areas of lower rainfall. Fire is also common in most Miombo vegetation types. Annual fires open up the woodlands through the loss of tree biomass, while in the absence of fire the woodlands gain woody biomass and become more closed canopy (Ryan & Williams 2011). The high variability in canopy cover, or woody biomass, and their resprouting ability makes it difficult to assess the ecological impact of changes in woody biomass due to disturbances. This is because unlike other vegetation (such as tropical forest) it is not possible to simply use changes in structure to define whether Miombo vegetation is in a degraded state, because these changes in structure appear to be part of the natural variability of Miombo vegetation.

Since the end of the 18th century the Miombo woodlands have undergone dramatic changes; widespread land use transformation (Bond *et al.* 2010; Campbell *et al.* 1996), an increasing human population (Misana *et al.* 1996) and the reduction in the abundance and distribution of elephants (Ntumi *et al.* 2009; Misana *et al.* 1996, Hempson *et al.* 2015). Therefore, over much of the Miombo region elephants have been replaced by humans. Humans and elephants can have similar ecological impacts as they both remove woody biomass, but they are not identical (Frost 1996). When trying to understand the natural dynamics of the Miombo woodlands, and considering that Miombo woodlands have evolved under elephant disturbance, it is important to account for the ecological impacts elephants would have had in areas where they are no longer found. We should be able to use our understanding of elephant impacts to assess ecologically relevant or acceptable rates (i.e. those under which the ecosystem evolved) of human-caused tree loss.

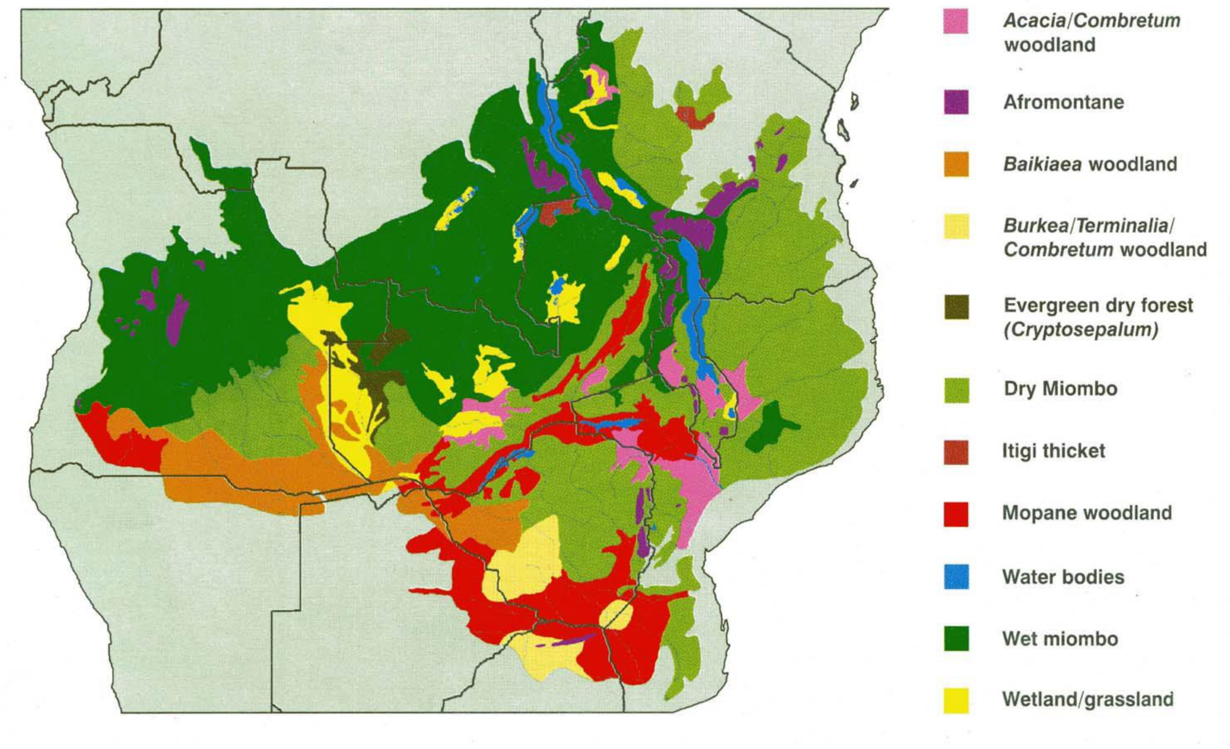


Figure 1: Vegetation types of the Miombo ecoregion (WWF SARPO 2003)

Deforestation and Degradation

The FAO (2010) defines deforestation as “The conversion of forest to other land use or the long-term reduction of the tree canopy cover below the minimum 10 percent threshold” and degradation as “The reduction of the capacity of a forest to provide goods and services”. Ryan *et al.* (2012), in the context of Miombo, describes deforestation as a decrease in aboveground biomass, so that there is a shift from the forest (greater than 15 Mg C/ha) to non-forest (less than 15 Mg C/ha) class. He defines degradation as a decrease in biomass, while remaining in a forest or non-forest class (Ryan *et al.* 2012) therefore degradation is simply a less severe form of biomass loss but it can accumulate and result in deforestation. However, there is no rate associated with these definitions. It is estimated that degradation accounts for about 67% of the net biomass loss, but there is high uncertainty around measuring degradation (Ryan *et al.* 2012). As most measurements of biomass change/tree cover change are over short time periods, 3-10 years, it is not easy to determine whether this structural change is temporary or permanent, which, in a system with rapid regrowth potential like the Miombo, again complicates the definitions. The multiple definitions for deforestation and degradation and high levels of uncertainty mean that it is difficult to measure and come to a consensus as to what is classified as deforestation and degradation.

Under both definitions above it is clear that the Miombo woodlands are threatened by widespread deforestation and degradation, primarily due to an increasing human population (Misana *et al.* 1996; Bond *et al.* 2010; Campbell *et al.* 1996; Timberlake & Chidumayo 2011). A 40% loss of the woodlands is predicted by the middle of the century (Green *et al.* 2013), which has raised concerns over how the loss of big trees will affect the biodiversity, woody biomass and the ecosystem goods and services (Ribeiro *et al.* 2015) that characterise Miombo ecosystems. The Miombo provides a great potential for pro-poor carbon-based payment to prevent deforestation and degradation, such as REDD+ (Ribeiro *et al.* 2015), because a loss in woodlands is linked with a decline in livelihood in the region (Bond *et al.* 2010). Many people rely on the woodlands goods, such as firewood and charcoal, and it is suggested that low rates of extraction can be sustainable (Bond *et al.* 2010). The aim is to give communities incentives for afforestation, to enhance the livelihoods of subsistence economies by placing a financial value on the carbon stored in the woodlands (Ribeiro *et al.* 2013).

For carbon-based payment for ecosystem services to work researchers need to understand how biodiversity and carbon uptake changes under different land use as well as how the woodlands recover from disturbances (Ribeiro *et al.* 2013). Many Miombo species are well adapted to recovering after a disturbance because of their ability to resprout (Luoga *et al.* 2004; Chidumayo & Frost 1996). Current levels of wood harvesting could potentially be sustainable, as biomass losses from degradation and deforestation are currently offset by extensive growth across the Miombo region (McNicol *et al.* 2018). Thus conservation of Miombo does not require eliminating all human resource extraction, but it does require adaquate information of what level of resource extraction is appropriate. This could be achieved through detailed knowledge of regrowth rates and demographic processes under different levels of utilisation (bottom up approach). However, as this is lacking in many parts of the region, a broad-scale “top-down” approach, which aims to quantify the extent and types of disturbances characteristic of Miombo can also contribute to this debate. Researchers therefore need to account for the change in woody biomass induced by elephants to understand the natural dynamics of the Miombo woodlands (Frost 1996).

Human Impacts

The Miombo woodlands can be viewed as a 'socio-ecological' system as people have played an important role in shaping their structure and composition since the early Stone Age (Timberlake & Chidumayo 2011). The woodland resources are important to the livelihoods of the approximately 150 million people living within the region (Ryan *et al.* 2016); but they are disappearing at a considerable rate (Bond *et al.* 2010; Ryan *et al.* 2012; Ryan *et al.* 2014). These high levels of biomass loss are primarily due to increases in the human population (Ryan *et al.* 2014; Timberlake & Chidumayo 2011). Historically the woodlands have been cleared for a variety of reasons including; tsetse eradication programmes, cultivation (for cash crops such as tobacco, cotton and peanuts) and political resettlement (Misana *et al.* 1996). Today small- scale agriculture is the primary cause for woodland biomass loss; but construction activities, charcoal production, logging and commercial agriculture also contribute to this change in biomass and woodland cover (Ryan *et al.* 2014; Sitoe *et al.* 2012).

The Miombo woodlands are also the primary source of energy for both rural and urban areas, providing 76% of total energy use in the region (Ryan *et al.* 2016), in the form of firewood and charcoal respectively (Clarke *et al.* 1996; Jones *et al.* 2016; Brigham *et al.* 1996). Fuelwood (firewood and charcoal) is a key contributor to the livelihoods of millions of people across the region (Jones *et al.* 2016).

Specific tree species and size classes tend to be favoured for firewood, charcoal production (Brigham *et al.* 1996; Jones *et al.* 2016; Luoga *et al.* 2002) and for logging (Fath 2001); although 90% of the aboveground biomass is suitable for charcoal (Chidumayo *et al.* 1996). This species and size preference can lead to changes in species composition and the community structure (Luoga *et al.* 2002). *Brachystegia spiciformis*, *Brachystegia boehmii* (Jones *et al.* 2016), *Combretum molle* and *Julbernardia globiflora* (Luoga *et al.* 2002) were all identified as preferred species for charcoal production, but preference also depends on the abundance and ease of extraction (Luoga *et al.* 2002). Trees selected for charcoal production tend to be slightly larger and use a wider range of size classes than those used for firewood (Luoga *et al.* 2002, Table 2).

The utilisation of the woodlands are affected by: 1) the proximity to the main road, 2) proximity to the settlement and 3) biomass availability, as a result of previous utilisation (Luoga *et al.* 2002), creating predictable spatial patterns of woody biomass loss (Ribeiro *et al.* 2015; Ahrends *et al.* 2010). Many have shown that areas close to main roads have higher biomass loss than those further away (Ryan *et al.* 2014; Ryan *et al.* 2012; Luoga *et al.* 2002; Misana *et al.* 1996; Monela *et al.* 1993). This is because informal trading of woodland products occurs along the main roads (Luoga *et al.* 2002). Charcoal production sites are generally within 5-15 km from main roads (Brigham *et al.* 1996) and they provide transport for charcoal from the rural areas; where it is produced, to the urban areas, where it is consumed (Brigham *et al.* 1996; Misana *et al.* 1996). Cities and towns have been described as the "epicentre of biomass loss" as woody biomass tend to be low around urban areas, with biomass increasing with distance from the settlement (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010). Settlement size also influences how quickly the biomass of the surrounding areas decrease. Settlements with smaller populations have a lower pressure for woodland resources, particularly charcoal; that is why a small town in central Mozambique has a much lower decrease in biomass per year, 0.43 Mg C/ha/year (Ryan *et al.* 2012), than a large city like Dar es Salaam which loses 0.8 Mg C/ha/year (Ahrends *et al.* 2010).

Direct human impacts on Miombo vegetation structure can therefore be classified as 1) total transformation, 2) harvesting for charcoal, 3) harvesting for firewood and 4) logging. Each of these would have different ecological consequences and can have indirect impacts on, for example, fire regimes. Humans alter fire regimes (through ignition, suppression or changing fuel loads; Archibald 2016) which can indirectly affect vegetation structure (Ryan & Williams 2011). Humans do not only influence vegetation and woody plants of the Miombo, but also have indirect impacts on the ecosystem. Hunting and simply the presence of people or livestock will influence the behaviour and spatial utilisation of many wild animals (Valls-Fox *et al.* 2018).

Elephant Impacts

Elephants are one of the main disturbance factors affecting the dynamics of Miombo woodlands (Frost 1996); but understanding their impacts on the woodlands can be challenging, mainly because elephant numbers have been dramatically reduced and they have been lost to vast areas of Miombo (Hempson *et al.* 2015; Bakker *et al.* 2016; Ntumi *et al.* 2009; Owen-Smith 1988), such that they are now only found in or near protected areas (Ntumi *et al.* 2009). Trophic downgrading is the loss of an apex consumer, in this case elephants, from a system. This loss of top-down forces can have far reaching and unanticipated consequences (Estes *et al.* 2011). It is therefore important to understand how this removal of elephants, has and could affect the structure and function of ecosystems; to understand the consequences of trophic downgrading (Bakker *et al.* 2016; Estes *et al.* 2011; Gill 2015; Hempson *et al.* 2015).

Elephants dominate African (Hempson *et al.* 2015) and Miombo (Frost 1996) herbivore biomass and it is widely known that they have a strong effect on woody plants (Bakker *et al.* 2016; Guldemond & Van Aarde 2008). Elephants are known to push down trees for food and as a social display (Barnes 1979). They can damage a tree in multiple ways: 1) through bark stripping which can kill the tree through ring barking it or make the tree more susceptible to fire, insects and infection; 2) breaking branches, which can result in a resprouting response of many trees and also increases the susceptibility to other factors (Barnes 1979; Owen-Smith 1988); 3) pushing over trees (Owen-Smith 1988); many trees are still able to coppice after being pushed over as long as they are not completely uprooted . Elephants can therefore completely transform savanna landscapes (Guldemond & Van Aarde 2008; Owen-Smith 1988); converting relatively dense woodland into a more open shrubland or grassland with scattered tall trees, resprouting tree stumps and a dense layer of shrubs (Frost 1996).

Elephants, like people, show preference for specific species and size classes which impacts the size class distribution of species (Barnes 1979; Owen-Smith 1988) and community structure (Mapaure & Moe 2009; Owen-Smith 1988). *Brachystegia* species, a Miombo dominant, tend to have high rates of elephant damage (Barnes 1979; Owen-Smith 1988; Holdo 2007), particularly *Brachystegia boehmii* (Thomson 1975; Anderson & Walker 1976; Jachmann & Bell 1985; Mapaure & Moe 2009). Barnes (1979) estimated that 0.16 *Brachystegia* trees are killed, through ring barking, per elephant per day in the Miombo woodlands of Ruaha National park. In Chizarira National Park elephants killed 18% of the *Brachystegia boehmii*, the dominant tree species, in just one year (Thomson 1975). In Niassa Reserve elephant damage has led to decreases in *Julbernardia globiflora* and *Brachystegia manga* (Ribeiro *et al.* 2008b). Jachmann & Bell (1985) found that selected and non-selected tree species were pushed over by elephants at the same frequency and that they showed size class preference towards preferred species, pushing over preferred trees greater than 2 m in height more often, but no preference for size class for non-selected species.

Elephants tend to forage in specific patches, and trees, within a landscape, but there are many questions as to why elephants select particular patches or trees. Elephants may be attracted to a patch by certain tree species or it could be influenced by location, such as near permanent water (Gadd 2002; Owen-Smith 1996) or nutrient-rich patches (Pretorius *et al.* 2011). Elephant damage on woody plants is higher close to permanent water (Gaylard 2003; de Beer *et al.*2006; Chafota & Owen-Smith 2009; Scholes & Mennell 2009), as they tend to concentrate their foraging activities close to water during the dry season (Gaylard 2003). Elephants are water dependent are also generally found less than 12-16 km from surface water (Gaylard 2003; Scholes & Mennell 2009; Robson *et al.* 2017).

Higher elephant density is known to result in an increase in their impacts on woody vegetation (Barnes 1979; Guldemond & Van Aarde 2008; Mapaure 2013). In a modelling study Mapaure (2013) calculated that an elephant population growing from a relatively low level of 0.27 per km^2 would convert woodland into coppice within 120 years, but that at a higher initial density of 2 per km^2 this is expected to occur within just 10 years (population growth rate estimated at 5% per year). In contrast, when elephant densities were maintained between 0.6 - 1 per km^2 the woodlands are not converted to coppice in the model.

As with people, various factors will affect the intensity of use by elephants. Along with elephant density, tree density can also influence the number of trees impacted by elephants. The number of trees impacted by elephants increases with tree density (Jachmann & Bell 1985; Barnes 1983; Gadd 2002) until a certain point, where utilisation levels off and the proportion of trees impacted decreases (Jachmann & Bell 1985). The effect of tree density seems to be species specific as Barnes (1983) found that the proportion of trees impacted by elephants is constant in *Commiphora ugogensi* and *Sclerocarya birrea* (Gadd 2002), but the proportion of trees impacted increases with density of trees in *Faidherbia (Acacia) albida* (Barnes 1983).

Localised severe elephant damage tends to occur in conjunction with other episodic events such as low rainfall (Baxter & Getz 2008), fire and frost; as a result of a decrease in the availablility of alternative forage thus they have to rely heavily on woody vegetation (Chafota & Owen-Smith 2009). A similar pattern is also seen seasonly as elephants cause the most damage to woody vegetation during the dry season, as they tend to feed mainly on the woody parts of trees and shrubs, which represent several seasons of growth and are therefore not easy to replace (Barnes 1979; Loarie *et al.* 2009; Owen-Smith 1988). During the dry season Miombo woodland was also preferred elephant habitat (Mpanduji *et al.* 2008), likely because there are large amounts of forage available.

Elephants are important seeds dispersers; dispersing large quantities of seeds from many different plant species, including several species that rely only on elephants for dispersal (Bunney *et al.* 2017). The absence of elephants can therefore have implications for woody community dynamics and other ecological consequences (Hempson *et al.* 2017). Elephants play an important role in the redistribution of nutrients, being megaherbivores they disproportionately drive the movement of nutrients (Doughty *et al.* 2016). They also play an important role in making the nutrients available, as digestion increases decomposition thereby freeing up nutrients (Owen-Smith 1988).

People vs Elephants

Both humans and elephants influence the woody biomass in multiple ways, therefore it is important to consider the consequences of these disturbances and how they differ or are similar. The human disturbance of land transformation does not have an elephant disturbance equivalent, whereas people harvesting firewood could be equivalent to elephants breaking branches and harvesting for charcoal and logging to pushing over trees. Elephants and humans are both known to strip bark and break or cut branches, but people are more likely to cut/break trees, and elephants are more likely to uproot trees and strip bark (Table 2). Both humans (Bird & Cali 1998) and elephants can influence fire regimes of an area. The removal of woody biomass means the landscape is more open, so grass increases and therefore there is an increase in fuel for fire (Ribeiro *et al.* 2008b). Humans are also the main source of ignition for fires, thereby potentially influencing the fire regime.

Table 2: A comparison of the types of impacts people and elephants have on the trees they use: estimated occasions of different types of damage. People almost never uproot trees (unless they are engaged in agricultural transformation) but elephants are known to (depending on the tree species). Bark stripping is also more common with elephants. Both people and elephants cut or break many branches.

	People	Elephants	Included in comparison
Uprooted	0	low	Yes
Ploughing/agriculture	High	0	No
bark stripped	low	High	No
Broken or cut	High	High	Yes

Frost (1996) developed a conceptual model of Miombo woodland dynamics – and the factors driving transitions between states (Figure 2). In this model elephants and the harvesting of fuelwood by people essentially perform a similar role in removing woody biomass and encouraging coppice regrowth. Both of which can convert mature Miombo into an open coppice and play a role in preventing the woodlands becoming forest (Figure 2; Frost 1996). It is also important to understand how they differ as disturbances (Table 3) and that human impacts also tend to change the vegetation more rapidly than natural transformation (Neke 2004).

Overall elephant impacts tend to be more extensive across the landscape than the more intensive human impacts as elephant utilised a larger area then people because of their movement patterns and that people are concentrated round settlements and major roads. Both people and elephants utilise a wide variety of species. *Brachystegia* species, a Miombo dominant, are utilised by both people (Jones *et al.* 2016) and elephants (Barnes 1979; Owen-Smith 1988). Elephant utilisation studies focus on tree height selected while human studies focus on stem diameter, making it difficult to compare size class selection in a literature review. Although, elephant seem to prefer the larger trees (>2m in height) while people can utilise a wide range of stem sizes (Luoga *et al.* 2002). Humans impacts seem to occur more uniformly throughout the year, as charcoal and firewood are generally used for cooking not heating. Whereas, elephants predominantly impact woody biomass during the dry season (Chafota & Owen-Smith 2009). Another fundamental difference between the two disturbances is that people remove the woody biomass, along with the nutrients, and transport it the cities whereas elephants distribute the nutrients within the woodlands (Doughty *et al.* 2016; Hempson *et al.* 2017).

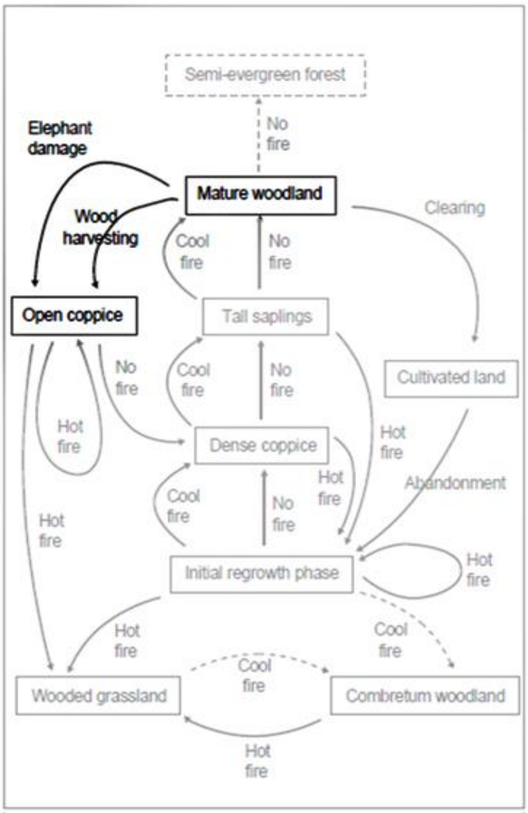


Figure 2: Multiple states and transitions between them within miombo woodland. (Frost, 1996)

Table 3: Table comparing how the impacts of humans and elephants on the woodlands differ

	People	Elephants
Spatial patterns	Near settlements and along main roads (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Ahrends *et al.* 2010)	Within 16km of permanent water (Gaylard 2003; de Beer *et al.*2006; Robson *et al.* 2017)
Species selectivity	Brachystegia spiciformis, B. boehmii (Jones *et al.* 2016), Julbernardia globiflora (Luoga *et al.* 2002) Logging: Afzelia quansensis, Pterocarpus angolensis and Millettia stuhlmannii (Fath 2001)	Uapaca nitida, Brachystegia manga (Jachmann & Bell 1985), Brachystegia boehmii (Jachmann & Bell 1985; Anderson & Walker 1976; Mapaure & Moe 2009; Thomson 1975)
Size class selectivity	Charcoal: 2.4 - 68.6 cm DBH Firewood: 4.2 – 16.9 cm DBH (Luoga *et al.* 2002)	Selected species: greater than 2m, non-selected species: according to relative occurrence (Jachmann & Bell 1985)
Seasonality of impact	All year	Dry Season (Barnes 1979; Loarie *et al.* 2009; Owen-Smith 1988)
Uprooting	Ploughing = yes Harvesting = no	Sometimes
Relationship with tree density	Unknown, but there is a threshold tree density below which human harvesting is no longer productive	Species specific, but generally the number of trees impacted by elephants increases with tree density until about 300 trees per hectare (Jachmann & Bell 1985)
Nutrient extraction	Yes	No

Understanding the potential legacies of megaherbivore extinctions and the consequences of trophic downgrading is an important question facing ecologists today (Sutherland *et al.* 2013; Cromsigt & te Beest 2014). Some have suggested introducing extant megaherbivores to regions of Europe, North America, and Australia to restore the functional roles of their extinct relatives (Donlan *et al.* 2006). However, in many ecosystems it is important to realise that the functional impacts of exterminated wildlife have to some extent been replaced by the impacts of livestock and people (Hempson *et al.* 2017). Which raises the question of whether people, through their harvesting of fuelwood and logging, can perform a similar functional role to elephants in the Miombo woodlands? If so, human use could be seen as maintaining ecosystem functions, without the need for the reintroduction of elephants to the entire Miombo region and increasing human-elephant conflict. Theoretically in the Miombo region, allowing access to vital woodlands resources could be part of an integrated conservation strategy. This scenario depends crucially on determining the level of past elephant impacts in Miombo vegetation.

Study Aim and Objectives

This study aims to compare elephants and people as disturbances of woody biomass in the Miombo woodlands. To investigate whether people can perform a similar functional role to elephants, with regards to biomass removal and potential changes to savanna structure and composition.

Dissertation Outline

This dissertation consists of two data chapters (Chapters 2 and 3), an introduction chapter (Chapter 1) and a conclusion chapter (Chapter 4). Both data chapters have been written in the format of scientific papers and the repetition of information on certain aspects is unfortunately unavoidable in this format. The first chapter in this dissertation contains a general introduction on the challenges of degradation and deforestation facing the Miombo woodlands and a comparison of humans and elephants as disturbances within the region. Chapter 2 compares biomass change at different levels of human and elephant influence, to identify how the intensity of biomass loss differs between humans and elephants. Chapter 3 investigates how elephants and people could potentially change savanna structure and composition, by comparing species and size class selection.

Chapter 2: Biomass change

Biomass change at different levels of human (Human population density) and elephant (elephant density) influence are compared, to identify how the intensity of biomass loss differs between humans and elephants. This is achieved through statistically modelling the effect of 1) human influence and 2) elephant density on biomass change. 3) Human utilisation at different levels of influence were compared to the predicted past elephant density for Niassa National Reserve (1.4 elephants/km^2; Robson *et al.* 2017) across a rainfall and initial biomass gradient to investigate under what conditions human utilisation is similar to that of past elephant impacts.

Chapter 3: Species and size class preference

Species and size class preference of human and elephants were compared, to provide an indication of whether people and elephants may have similar impacts on vegetation structure and composition. Human i) species preference and ii) size class preference of preferred tree species were compared to elephant preference across the Sikumi Forest Reserve (where human utilisation is regulated) and communal land.

Chapter 2

Contrasting biomass change facilitated by humans and elephants

Abstract

The Miombo woodlands are “disturbance driven savannas”. People, elephants and fire are important disturbances which prevent canopy closure and maintain tree-grass co-existence. Since the end of the 18th century the disturbance regimes of the woodlands have been dramatically altered. The abundance and distribution of elephants have decreased while human populations have seen rapid growth and urbanisation. This has resulted in the concentration of disturbances in areas of high human influence causing biomass loss. These woodlands also experience the highest levels of woody plant encroachment across Africa suggesting that there are areas potentially underutilised, due to a lack of disturbance. This raises the question of whether people, through their harvesting of fuelwood and logging, can perform a similar functional role to elephants in the Miombo woodlands by removing woody biomass. Generalised additive models were used to compare biomass change (between 2007 and 2010) at different levels of human and elephant influence (population density). Above ground woody biomass estimates were obtained from SAR RADAR imagery. The intensity of biomass loss between humans and past elephants (1.4 elephants/km2) under different rainfall and initial biomass conditions were compared using the models. Biomass loss increases with population density, above 30 people/km^2 and 0.5 elephants/km^2. Biomass change responds differently to mean annual precipitation in areas under human influence and elephant influence. Humans tend to remove higher levels of biomass under more mesic conditions than elephants, as rainfall decreases the system can handle increased human impacts before exceeding the loss predicted by past elephant estimates. This suggests that woodlands with low rainfall and low human influence have more trees and higher biomass than if elephants were still present, at historical densities, and that some harvesting by people may be beneficial. Promoting human utilisation in these areas would alleviate the pressure on the hotspots of biomass change while providing the people in the rural areas with an additional source of income and the woodlands with a disturbance necessary in maintaining, to some extent, the ecosystem structure and functioning of the Miombo.

Introduction

The Miombo ecoregion covers 3.6 million km^2 across central and southern Africa (Timberlake & Chidumayo 2011) and is an area that should be prioritised for conservation (Mittermeier *et al.* 2003). The Miombo woodlands are under threat by both deforestation due to woodland clearance for agriculture and urbanisation (important to the economy and food security) and degradation through the utilisation of woodland products vital to the livelihood of many living within the region (Ryan *et al.* 2016). On the other hand, these woodlands also experience the highest levels of woody plant encroachment across Africa (Venter *et al.* 2018). Sustainable land management is therefore required: as the region shows potential for pro-poor carbon-based payment to prevent deforestation and degradation, such as REDD+ (Bond *et al.* 2010; Ribeiro *et al.* 2015), but this benefit needs to be considered relative to the current benefit of renewable biofuel energy from woodlands that is currently the main energy source for most people in the region (Ryan *et al.* 2016)

For carbon-based payment for ecosystem services to work, researchers need to understand how biodiversity and carbon uptake change under different land uses as well as the importance of disturbances to the system (Ribeiro *et al.* 2013). Much of the ecoregion is covered by Detariodeae (previously Caesalpinioideae)-dominated Miombo woodlands (primarily *Brachystegia, Julbernardia* and *Isoberlinia* species). Rainfall is a key driver of woody plant dynamics, and more mesic areas can support a higher above ground woody biomass and faster regrowth rates (Trouet *et al.* 2010) than the areas that receive less rainfall. In these ecosystems rainfall is sufficient to create closed canopies, and disturbances are necessary to maintain tree-grass coexistence (Sankaran *et al.* 2005). The woody plant dynamics of Miombo woodlands are affected by three interacting disturbance factors: people, elephants and fire (Frost 1996; Ribeiro *et al.* 2015).

Since the end of the 18th century these disturbance factors have been dramatically altered; with rapid increases in human populations and urbanisation (Misana *et al.* 1996; Jew *et al.* 2016), while the abundance and distribution of elephants have decreased (Ntumi *et al.* 2009; Misana *et al.* 1996, Hempson *et al.* 2015; Robson *et al.* 2017). Hempson *et al.* (2015) estimated that the Miombo woodlands should contain ~2.5 elephants/km^2 without the influence of human hunting with guns, based on relationships with mean annual precipitation (MAP) in protected areas across the continent. However, there is very little information on past elephant densities and fire, creating much debate regarding the ideal disturbance regime of these woodlands, and whether managers should be aiming to maximise tree biomass or promote disturbances. The conservation of Miombo does not require eliminating all human resource extraction, as the systems are adapted to recovering after disturbances (Luoga *et al.* 2004) and some level of tree felling by elephants. The effects of humans on woody biomass can be contrasted to those of elephants, as both remove woody biomass (Frost 1996; Mograbi *et al.* 2017). However, it does require adaquate information of what level and type of resource extraction is appropriate. It is important to understand how the removal of elephants has and could affect the structure and function of the ecosystems; to understand the consequences of the loss of this apex consumer (Bakker *et al.* 2016; Estes *et al.* 2011; Gill 2015; Hempson *et al.* 2015), and whether humans could replace some of their ecosystem functions.

Elephant impacts on woody plants:

Elephants influence woody cover through breaking branches (Barnes 1979; Owen-Smith 1988), pushing over trees (Owen-Smith 1988) and stripping bark (Barnes 1979; Owen-Smith 1988) to access forage or as a social display (Frost 1996; Barnes 1979). Elephants can therefore completely transform savanna landscapes (Owen-Smith 1988; Barnes 1979; Guldemond & Van Aarde 2008; Mapaure 2013); converting relatively dense woodland into a more open shrubland or grassland with scattered trees (Frost 1996). Higher elephant density is also known to result in an increase in their impacts on woody vegetation (Barnes 1979; Guldemond & Van Aarde 2008; Mapaure 2013). The areas in which an elephant lives (it's home range) can vary from 3 km^2 up to 12 800 km^2 (Scholes & Mennell 2009). The home range size and resident time of elephants varies with biotic and abiotic, particularly rainfall, influencing elephants impacts on woody species (Scholes & Mennell 2009). Therfore elephants' impacts on the structure and composition of woody vegetation (Barnes 1979; Owen-Smith 1988; Mapaure & Moe 2009) vary both spatially and temporally; with increased damage in specific patches within the landscape; particularly near (within aproximately 16km of) permanent water (Gaylard 2003; de Beer *et al.*2006; Robson *et al.* 2017), in nutrient rich areas (Pretorius *et al.* 2011) and in more arid areas (Guldemond & Van Aarde 2008).

Human impacts on woody plants:

People have also played an important role in shaping the structure and composition of the Miombo woodlands since the early Stone Age (Timberlake & Chidumayo 2011; Ellis 2011), highlighting the need to treat humans as ecosystem components (Worm and Paine 2016). Woodland resources are important to the livelihoods of many people within the region; providing wild foods, construction materials, medicinal plants, fuel and spiritual value while contributing to the economy (Bond *et al.* 2010; Campbell *et al.* 1996; Clarke *et al.* 1996; Ekman *et al.* 2013; Ryan *et al.* 2016). Human utilisation creates predictable spatial patterns of above-ground woody biomass (biomass) loss (Ribeiro *et al.* 2015; Ahrends *et al.* 2010), which tend to be concentrated near urban areas and along main roads (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010). Cities and towns have been described as the "epicentre of biomass loss" (Ryan *et al.* 2012), due to high demand within urban areas and the proximity to the consumers.

Understanding the potential legacies of megaherbivore extinctions and the consequences of trophic downgrading is an important question facing ecologists today (Sutherland *et al.* 2013; Cromsigt & te Beest 2014; Bakker *et al. 2016*). In many ecosystems the functional impacts of exterminated wildlife have to some extent been replaced by the impacts of livestock and people (Hempson *et al.* 2017). People harvesting firewood, charcoal, construction poles and logging could be an equivalent to elephants breaking branches and pushing over trees and that there has been a dramatic loss in elephants across the region. Both humans and elephants can also influence woody biomass through manipulating fire (humans: Archibald 2016; elephants: Beuchner & Dawkins 1961). Annual fires cause a loss in trees opening up the woodlands, while woody biomass increases, and the canopy closes with a lack of fire (Ryan & Williams 2011). Their impacts will likely differ spatially, as elephant impacts are greatest near permanent water and human impacts are concentrated near urban areas and along main roads. The human disturbance of land transformation does not have an elephant disturbance equivalent. People (harvesting firewood, charcoal and poles) and elephants are performing a similar functional role in removing woody biomass and encouraging coppice regrowth (Frost 1996), although there may be differences in the intensity of biomass loss (Neke 2004), degree of nutrient cycling (as large animals disproportionately drive nutrient movement; Doughty *et al.* 2016), and emergent properties, such as in changes to the vegetation composition and structure (humans: Luoga *et al.* 2002, elephants: Owen-Smith 1988).This raises the question as to whether people and elephant can perform a similar functional role, as both remove woody biomass. If so, human use could be maintaining ecosystem functions, while allowing access to vital woodland resources. Clearly this scenario depends crucially on determining the impacts of past elephants in Miombo vegetation and understanding how the effects of people and elephants may differ.

Using newly available repeat mapping of biomass from RADAR imagery (Ryan *et al.* 2012; Mitchard *et al.* 2009) biomass change at different levels of human and elephant influence (population density) were compared, to identify how the intensity of biomass loss differs for humans and elephants. This was achieved through modelling the effect of 1) human and 2) elephant influence on biomass change. Using these models human utilisation at different levels of influence were compared to the predicted past elephant density for Niassa National Reserve (1.4 elephants/km^2; Robson *et al.* 2017) across a rainfall and initial biomass gradient. The aim was to assess what level of human impact was equivalent to past elephant impact in this region.

Methods and Materials:

Study Site:

Biomass change data were available from three areas within the Miombo region (Figure 1); western Zimbabwe, central and northern Mozambique. Much of the region is characterised by Detariodeae woodlands on gently undulating plains (Timberlake & Chidumayo 2011). *Brachistegia* dominated Miombo woodlands are common across the study area, with patches of T*erminalia sericea* and Baikiaea predominately in western Zimbabwe (Rutherford *et al.* 2005). Western Zimbabwe represents drier conditions than Mozambique, with the areas receiving a maximum MAP of below 860 mm and above 1700 mm respectively. Within eastern Zimbabwe and northern Mozambique (including eastern Malawi) people are clustered around urban areas, as areas with less than 30 people/km^2 cover over 80% of the area. Across central Mozambique under 60% of the areas has a low population density (< 30 people/km^2), with the human population more evenly distributed across the landscape. The road networks are more extensive across eastern Zimbabwe (as 40% of the areas is within 2 hours of a major city) than in Mozambique where over half of the area is more than 5 hours from a major city.

Biomass change data for elephants was collected within the 42 300 km^2 of Niassa National Reserve (NNR; Figure 1) in northern Mozambique (Craig 2009). NNR is predominantly Miombo, dominated by *Julbernardia globiflora* and *Brachystegia* species (Rutherford *et al.* 2005) and receives a MAP increasing from 800 mm in the east to 1200 mm in the west (Ribeiro *et al.* 2017). Approximately 32 000 people live within NNR; much of the human influence is concentrated around the major town of Mecula and Mavago (Craig 2009) and along the main roads (Ribeiro *et al.* 2008a) although at low population densities (Ribeiro *et al.* 2017). The average elephant density of NNR is 0.48 elephants/km^2, with elephant densities across the management units ranging from 1.52 to 0.02 elephants/km^2 (Craig 2009).

Biomass change:

The 2007 and 2010 above-ground woody biomass (MgC/ha; data: McNicol *et al.* 2018) across the study area was estimated from Phased Array L-band Synthetic Aperture Radar (SAR) images obtained aboard the advanced land observing satellite, ALOS PALSAR (McNicol *et al.* 2018). L-band SAR backscatter provides accurate above-ground woody biomass estimates for lower-biomass tropical woody vegetation, such as the Miombo woodlands (Mitchard *et al.* 2009). As the study is at a landscape and regional scale, a lower resolution (1 km^2) was more appropriate. The other explanatory variables used were also at a scale of approximately 1 km^2 and were extracted from the centre of each 1km^2 biomass change pixel. Biomass from 2010 was subtracted from the 2007 biomass for each pixel to calculate biomass change. Therefore, negative change values indicate a loss in biomass between 2007 and 2010.

Areas with a biomass of less than 10 MgC/ha (in 2007 and 2010) were excluded due to the additional error subject to low biomass estimates (Ryan *et al.* 2012). Agricultural areas, with greater than 0.1% of the pixel crops (Ramakutty *et al.* 2008), and urban areas (CIESIN 2017) were also excluded as this large-scale transformation does not allow for woodland regeneration. Due to the influence of moisture on radar backscatter (Ryan *et al.* 2012), areas within 0.5-1 km of rivers were masked out. Data were limited to areas of *Brachistegia* or *Julbernardia* dominated Miombo, Terminalia or Baikiaea woodlands (according to Rutherford *et al.* 2005), as these different vegetation types have similar structure and ecology (Timberlake & Chidumayo 2011).

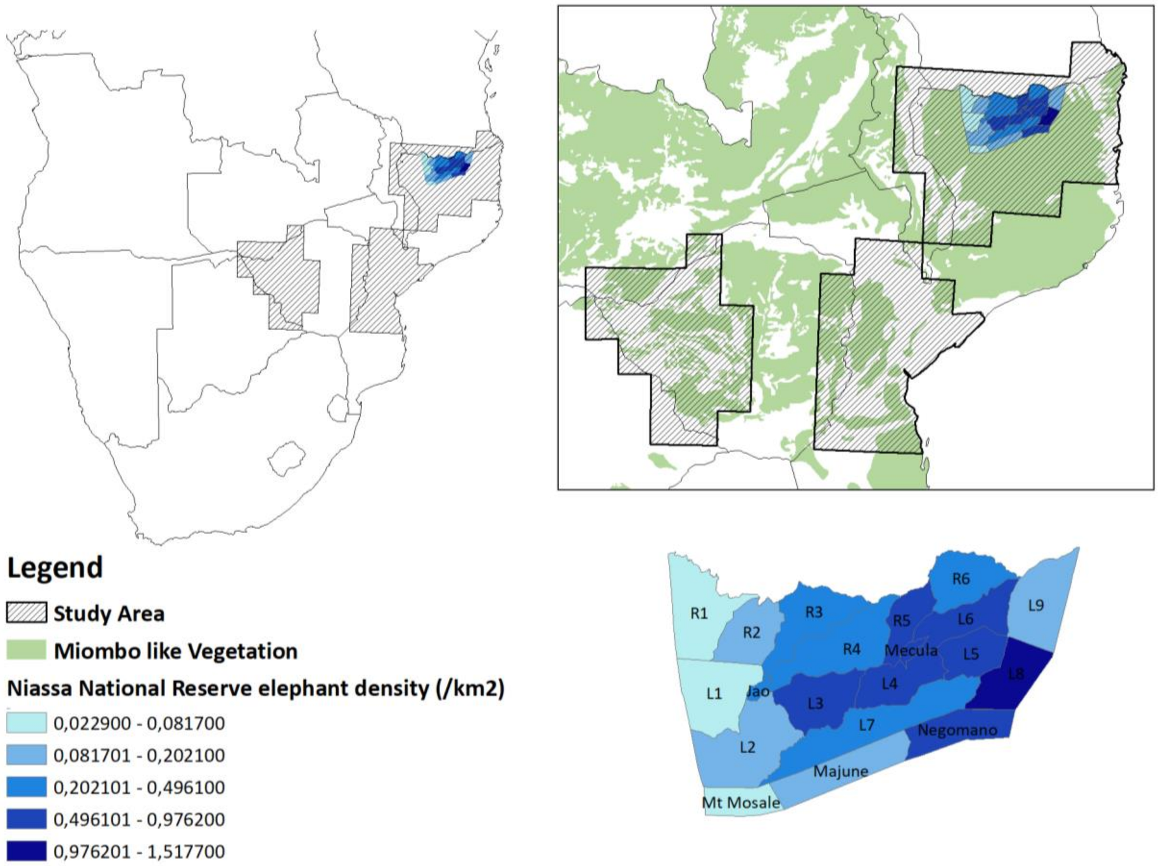


Figure 1: Locations of the three study areas in in the Miombo woodlands of southern Africa, where estimated biomass data was available. Miombo like vegetation include true Miombo (*Brachistegia* or *Julbernardia* Dominated), Terminalia and Baikiaea woodlands (Rutherford *et al.* 2005). Niassa National Reserve, Northern Mozambique, was the study site to assess the effect of elephants on biomass change within the Miombo.

Explanatory variables for biomass change:

The Miombo is dominated by light demanding species, therefore disturbances which remove biomass and increase light also improve the establishment and regeneration of Miombo dominants (Syampungani 2009). The 2010 human population density (data: CIESIN 2016) and estimated travel time to the nearest city of 50,000 or more people (data: Nelson 2008) were used to assess the level of human utilisation across the study areas outside protected areas (PA); providing estimates of the number of people potentially utilising woodland resources within a given area and the ease of access to the primary demand centres of the major cities. Travel time to the nearest city of 50,000 or more people was calculated using a cost distance model. The model includes information on the transport network (road and rail networks and navigable river), environmental factors (land cover, vegetation type and slope) and political factors (national boundaries and border crossings) that all affect travel time (Nelson 2008). The 2009 elephant density per management unit (data: Craig 2009) was used to quantify the level of elephant utilisation across NNR spatially. Areas within 2km from roads within NNR were excluded to minimise the effects of humans on this analysis of elephant impacts: human utilisation is concentrated along roads (Ribeiro *et al.* 2008a). The L9 NNR management unit was excluded due to high levels of illegal logging (Craig 2009).

Rainfall (MAP data: Hijmans *et al.* 2005) is thought to influence regrowth rates of Miombo, with increased growth rates in areas that receive higher MAP (Frost 1996). The available biomass affects human woodlands utilisation (Luoga *et al.* 2002) , elephants' utilisation and regrowth rates of the woodlands. People (Sandel & Svenning 2013) and elephants (Wall *et al.* 2006) both show lower utilisation of steep slopes, due to increased difficulty in accessing these areas. Slope was calculated using a digital elevation model (data: Lehner *et al.* 2006; Slope, ArcMap 10.5). Fire frequency (how many times a decimal degree burnt between 2000 and 2010) was included as fire interacts with disturbances of people and elephants to remove woody biomass (Frost 1996). Percentage area crops (Ramakutty *et al.* 2008) were included as a measure of human influence as agriculture is a key driver of woodland biomass loss (Ryan *et al.* 2014). All factors were continuous except for initial biomass class.

Data Analysis:

Two separate analyses were run. One inside NNR to assess the impact of elephant density on woody biomass change, and one on regional data outside PA to assess the impact of human population density/land use intensity on woody biomass change. The regional human analysis covered a much larger area than the analysis within NNR. To account for this I ran a second human impact analysis just on data from northern Mozambique, within 300km of NNR, and found similar responses to the regional model. Data outside of PA in northern Mozambique were randomly sampled by 15 minute travel time classes, to ensure that both models (human and elephants impacts on biomass change) have a similar sample size and that the data from outside of PA covers the full range of travel times and human population densities.

Gaussian generalised additive models (GAM) were used to calculate an explanatory model for human and elephant impacts on biomass change. GAMs allow for nonlinear response shapes and gaussian distribution allows for the continuous positive and negative biomass change data (Zuur *et al.* 2009). The distribution is symmetrical, although there are outliers on both sides meaning that the model underrepresents the extreme biomass change values. GAMs were fitted using the “mgvc” package in R language (R Core Team 2017). Thin plate regression spline smoothing function was used, the generalized cross-validation method was used to fit smoothers and select the number of knots (Wood 2006; Zuur *et al.* 2009). Following Woods (2006) a spatial term (latitude and longitude) was included in each candidate model to account for spatial autocorrelation. The explanatory variables used for both models were MAP, fire frequency and initial biomass class. An initial biomass (2007) of less than 15 MgC/ha was classified as low biomass, this is considered the forest/non-forest threshold (Ryan *et al.* 2012). Initial biomass between 15 and 30 MgC/ha was classified as medium biomass and greater than 30MgC/ha was classified as high biomass. Human population density and travel time to nearest major city and percent area crops were also used as additional explanatory variables for the human impacts on biomass change. Niassa elephant density and slope were included as additional explanatory variables in the elephant impacts on biomass change. Candidate models were created for each human (regional: Table A2.1, northern Mozambique: Table A2.2) and elephants (Table A2.3), starting as a null model and selectively adding variables using a forward stepwise method. Collinearity was low; therefore all variables could potentially be included in the models (Appendix A). The AIC, GCV, R^2 and deviance explained were calculated for each candidate model.

The model with the best explanatory power was selected based on the lowest AIC value (Wood 2006; Zuur *et al.* 2009). Influence data points with hat values greater than twice the mean were excluded (Wood 2006; Zuur *et al.* 2009).

The model parameters for the best human and elephant model were used to predict the influence of different human and elephant levels of utilisation on biomass change, across the three different initial biomass classes, a rainfall gradient from 1000mm to 1350mm increasing in 50mm, where all other variables were set to the mean. The MAP across the Miombo region is between 650 mm and 1500 mm (Ribiero *et al.* 2012), although the rainfall range for valid data for areas outside of PA within northern Mozambique was between 930 mm – 1350 mm MAP.

The modelled effects of human population density on biomass change were compared to those estimated for elephant densities of 1.4 elephants/km^2, which is the ecological benchmark for NNR (Robson *et al.* 2017) and a conservative estimate of past elephant numbers (Hempson *et al.* 2015). This was done across a rainfall gradient and under different initial biomass classes. Rainfall and available biomass are important determinants of biomass change and will influence how elephants and people affect the woodlands. This comparison aims to identify under what conditions human utilisation results in greater or lower biomass removal than 1.4 elephants/km^2. Conditions where human influence resulted in greater biomass removal than 1.4 elephants/km^2, indicated by the human response below the elephants, would represent areas of potential concern due to the high impact of humans. Whereas conditions where human influence resulted in lower biomass removal than 1.4 elephants/km^2, indicated by the human response above the elephants, might potentially benefit from higher levels of human disturbance.

Results:

Regional human facilitated biomass change:

The best model included human population density, travel time to major city, MAP, fire frequency, percentage area crops, the initial biomass class and a spatial term (latitude and longitude) as predictor variables. This model explained 27,13% of the variation in biomass change at a regional scale across western Zimbabwe and much of Mozambique (Table A2.1). All variables, except the spatial term, had a similar contribution to the model, explaining approximately 13 to 14 percent of the variance (Table A3).

Under low population density levels biomass loss decreases slightly with an increase in human population density (when other values are held constant) until it reaches approximately 20 people/km^2, however biomass loss increases drastically above this threshold as human population density increases (Figure 2 a i; F=203.79, P<0.001). Biomass loss is also greatest close to major cities: loss decreases as travel time to these cities increases (Figure 2 a ii; F=18.36, P<0.001). Biomass loss was greatest in areas of high agricultural pressure: loss increases with the percentage area covered by crops (Figure 2 a iii; F= 22,39, P<0.001). Therefore, as human impacts on the landscape intensify (higher population density, proximity to major cities or increased agricultural pressure) the level of biomass loss increases.

Across the region biomass loss is greatest in areas of high initial biomass, while areas below 30MgC/ha (medium and low) initial biomass show similar levels of biomass change (Figure 2 a iv). Abiotic factors, such as rainfall (F= 157,89, P<0.001) and fire frequency (F= 28,59, P<0.001) are also key factors of biomass change across the region. At a regional scale biomass loss increases with an increase in rainfall (Figure 2 a v). Biomass gains will likely only occur under lower rainfall conditions, below ±600 mm. At this scale, there is slightly less biomass change when fire is excluded (a fire frequency of 0) compared to when fire is frequent (Figure 2 a vi).

Northern Mozambique human facilitated biomass change:

The best model included human population density, travel time to major city, MAP, fire frequency, the initial biomass class and a spatial term (latitude and longitude) as predictor variables. Including percentage area crops did not improve the model ($F_{1,\ 17343.42}$= 0.05, P = 0.82). The best model explained 15,07% of the variation in biomass change at a local scale of northern Mozambique. While the explanatory power was low, it was still significantly better than the null model (Table A2.2). All variables, except the spatial term, had a similar contribution to the model, explaining approximately 14 to 15 percent of the variance (Table A3).

On a smaller scale of northern Mozambique, and on a regional scale, the intensification of human impacts on the landscape (higher population density and proximity to major cities) results in an increase in biomass loss. Biomass loss occurs when population density is greater than ±43 people/km^2; although biomass loss increases with human population density above 30 people/km^2 (Figure 2 b I; F= 38,95, P<0.001). Biomass loss decreases dramatically with an increase in travel time, within approximately two hours from a major city (Figure 2 b ii; F= 7,274, P<0.001). Further than two hours from a major city, travel time has little influence of biomass change.

Biomass loss is greatest in areas of high initial biomass, while areas of low and medium initial biomass show similar levels of loss (Figure 2 b iv). Abiotic factors, such as rainfall (F= 31,73, P<0.001) and fire (F= 24,03, P<0.001) are also key factors of biomass change across northern Mozambique. Biomass gains are more likely under low rainfall conditions, below 1050 mm MAP; as biomass loss increases with an increase in rainfall (Figure 2 b v). Biomass loss also increases with fire frequency (Figure 2 b vi)

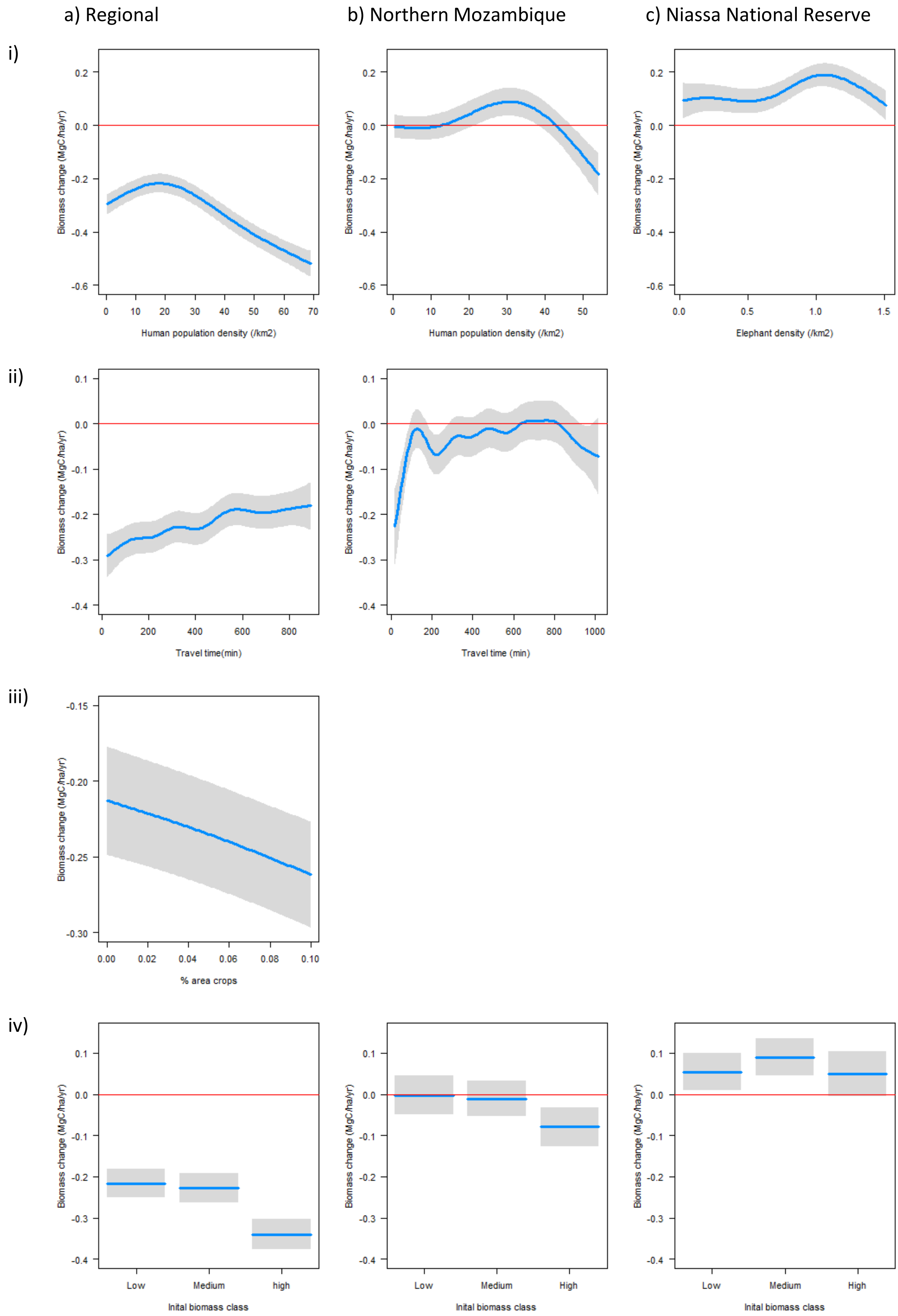
Elephant facilitated biomass change:

The optimal model included elephant density, MAP, fire frequency, initial biomass class and a spatial term (latitude and longitude) as predictor variables explains approximately 49,67 % of the biomass change across NNR (Table A2.3). Slope was not included as a predictor variable as it did not improve the model ($F_{2.55,18336.39}$= 2.56, P = 0.06).

Biomass change was positive for all elephant densities experienced in the park (maximum 1.52 elephants/km^2), although above 1 elephant/km^2 biomass change decreases with an increase in elephants (Figure 2 c ii; F= 12,34, P<0.001). Elephant density is an important factor in biomass change in NNR, explaining 35% of the variation in the model (Table A3). The GAM model predicts that only when elephant density is greater than 1.4 elephant/km^2 does biomass loss start to match regrowth rates (biomass change ~0MgC/ha/year), whereas human facilitated losses were consistently negative. However, at low rainfall levels biomass loss was still observed to occur in NNR (Figure 2 c iii; F= 12,34, P<0.001). Under low rainfall conditions biomass loss is the greatest within NNR (Figure 2 c v; F= 91,49, P<0.001), while outside of PA biomass loss is greatest under high rainfall conditions (Figure 2 c vi; F= 4,83, P<0.001). Unlike outside of PA, areas of high initial biomass within NNR are not more likely to experience a greater loss of woody biomass (Figure 2 c iv). Biomass gains were only slightly higher when fire was excluded compare to yearly fires (Figure 2 c vi). Fire frequency is an important biomass change factor accounting for almost half of the variation seen in the model (Table A3).

Comparing humans and elephants:

Overall, biomass change is negative outside of PA and positive within NNR (Figure 2). Moreover, areas outside PA show different responses to MAP (Figure 2 i) and initial biomass (Figure 2 iv) to those within the NNR. The level of human use equivalent to 1.4 elephants/km^2 therefore varies in different environmental contexts (Figure 3 & 4). Humans appear to substitute for elephants as agents of biomass loss between 1100mm and 1150mm MAP, although it is also dependent on human population density and initial biomass (Figure 3 & 4). The human population density equivalent to past elephants as agents of biomass loss is greater at 1100 mm MAP (~52 to 65 people/km^2 and ~54 to 65 people/km^2 under medium and low initial biomass respectively) than under the lower rainfall of 1150 mm MAP (~20 to 42 people/km^2 and ~25 to 36 people/km^2 under medium and low initial biomass respectively). Humans are only equivalent to past elephants as agents of biomass loss at 1100 mm MAP between 27 and 65 people/km^2 under high initial biomass conditions. At low rainfalls (below 1100 mm MAP), humans do not appear to substitute for elephants: biomass change associated with humans is lower than that associated with past ecologically-relevant elephant densities (Figure 3 & 4). However, at higher rainfalls (above 1150 mm MAP) human impacts exceed "ecological elephant" impacts regardless of human population density or initial biomass. Areas of lower rainfall could potentially handle higher levels of human impact (higher human population density) than areas that receive more rainfall.


a) Regional
b) Northern Mozambique
c) Niassa National Reserve
i)
ii)
iii)
iv)
Biomass change (MgC/ha/yr)
Human population density (/km2)
Elephant density (/km2)
Travel time(min)
Travel time (min)
% area crops
Inital biomass class
Low
Medium
high
High
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.6
-0.15
-0.20
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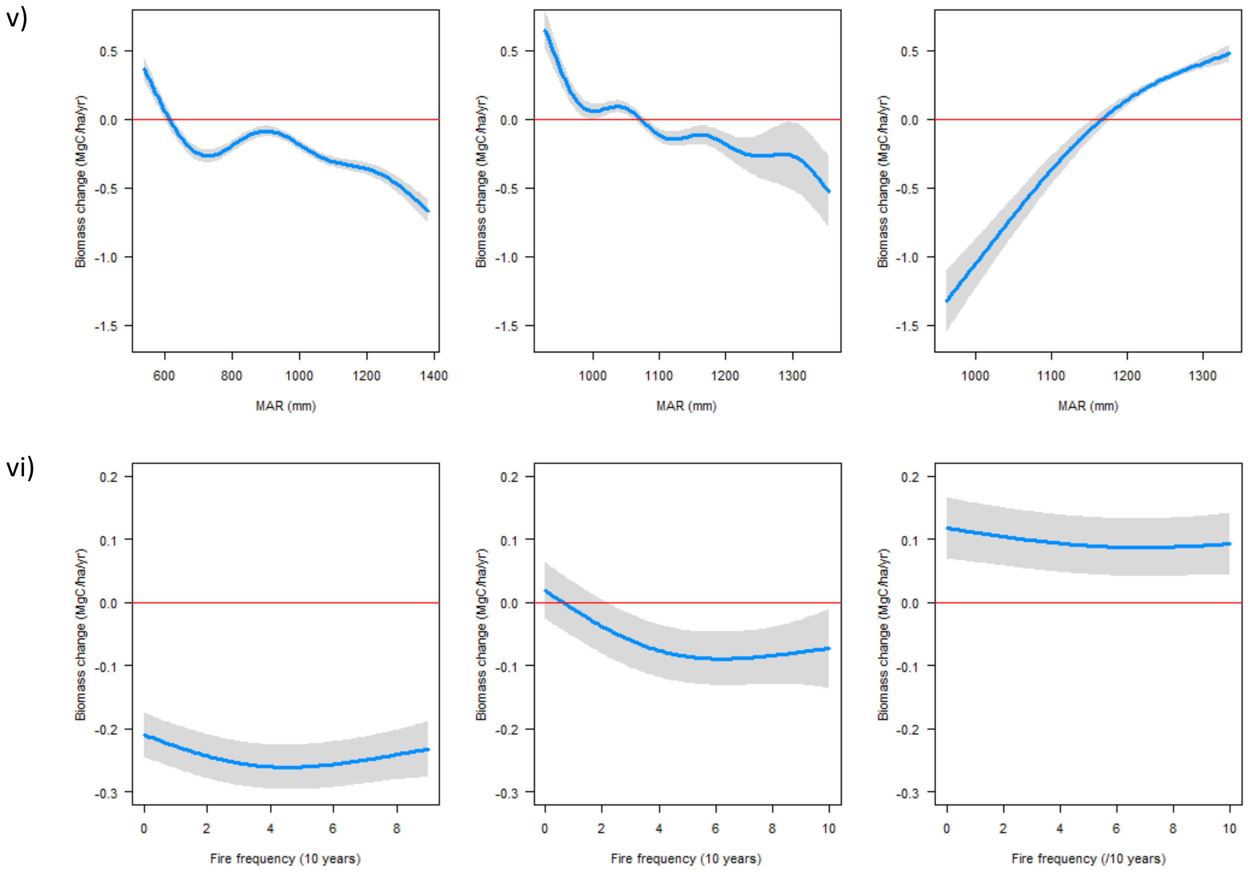

Figure 2: A GAM explains the biomass change outside of PA at a a) regional Miombo scale and b) local northern Mozambique scale where humans are a key disturbance factor and within c) Niassa National Reserve where elephants are a key disturbance factor. The blue line represents the predicted response of biomass change to i) population density ii) travel time to major city, iii) percentage area crops, iv) mean annual precipitation and v) fire frequency when all other variables are held constant. The grey areas represent 95% confidence bands.

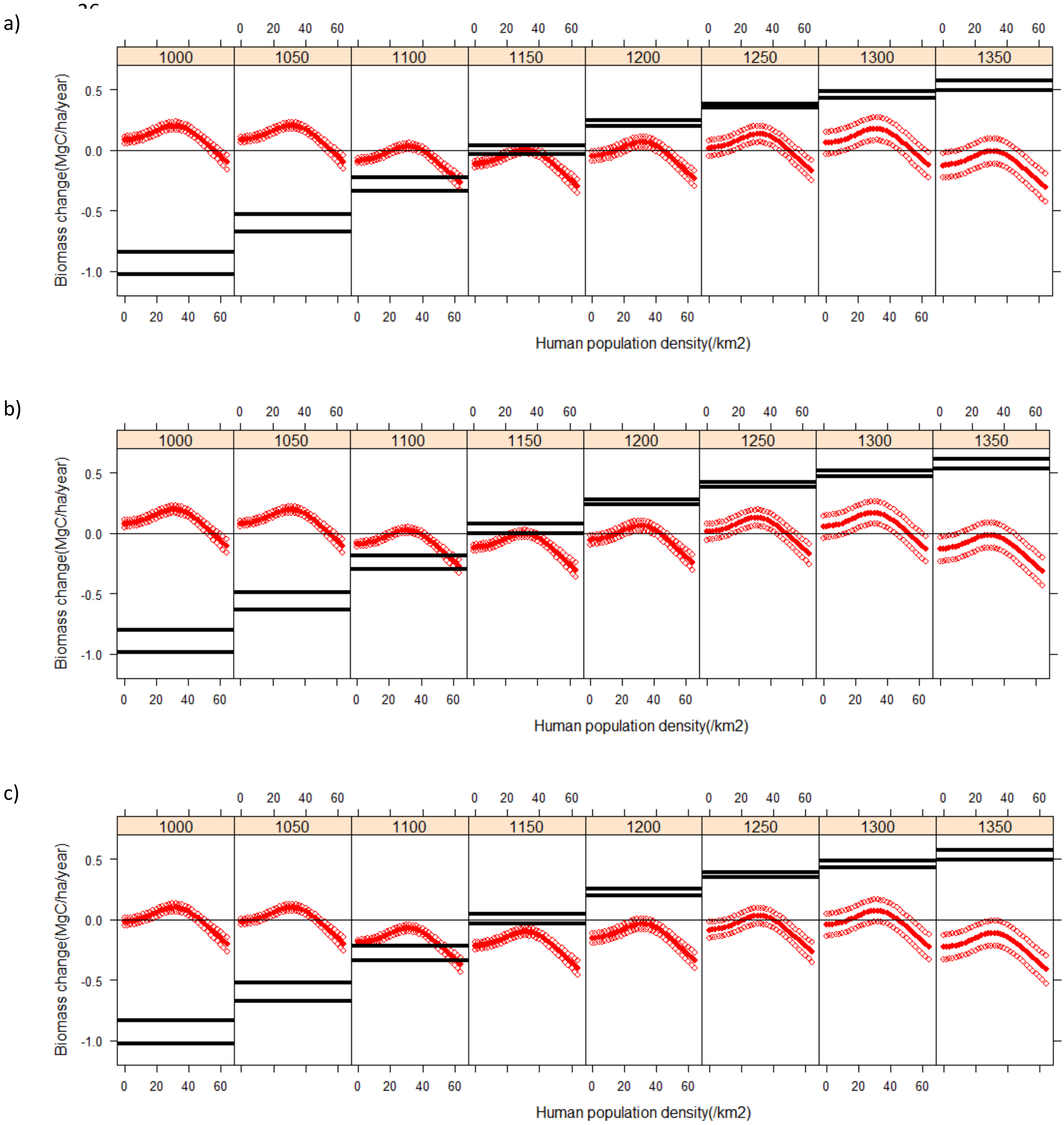

Figure 3: A comparison of the effect of human influence (human population density) and elephants at a density of 1.4 elephant/km^2 (the ecological benchmark for NNR (Robson *et al.* 2017) and a conservative estimate of past elephant numbers) on biomass change. This comparison is across a rainfall gradient (MAP of 975 mm to 1350 mm) and a) low, b) medium and c) high initial biomass. Red indicates human population density response, where the open and solid dots represent standard error and the predicted values respectively. The black dashes represent standard error around the predicted 1.4 elephants/km^2 response. When the red line is above the black line, it indicates that humans are probably removing less biomass than elephants did in the past. When the red line is below the black line, it indicates that humans are probably removing more biomass than elephants did in the past.

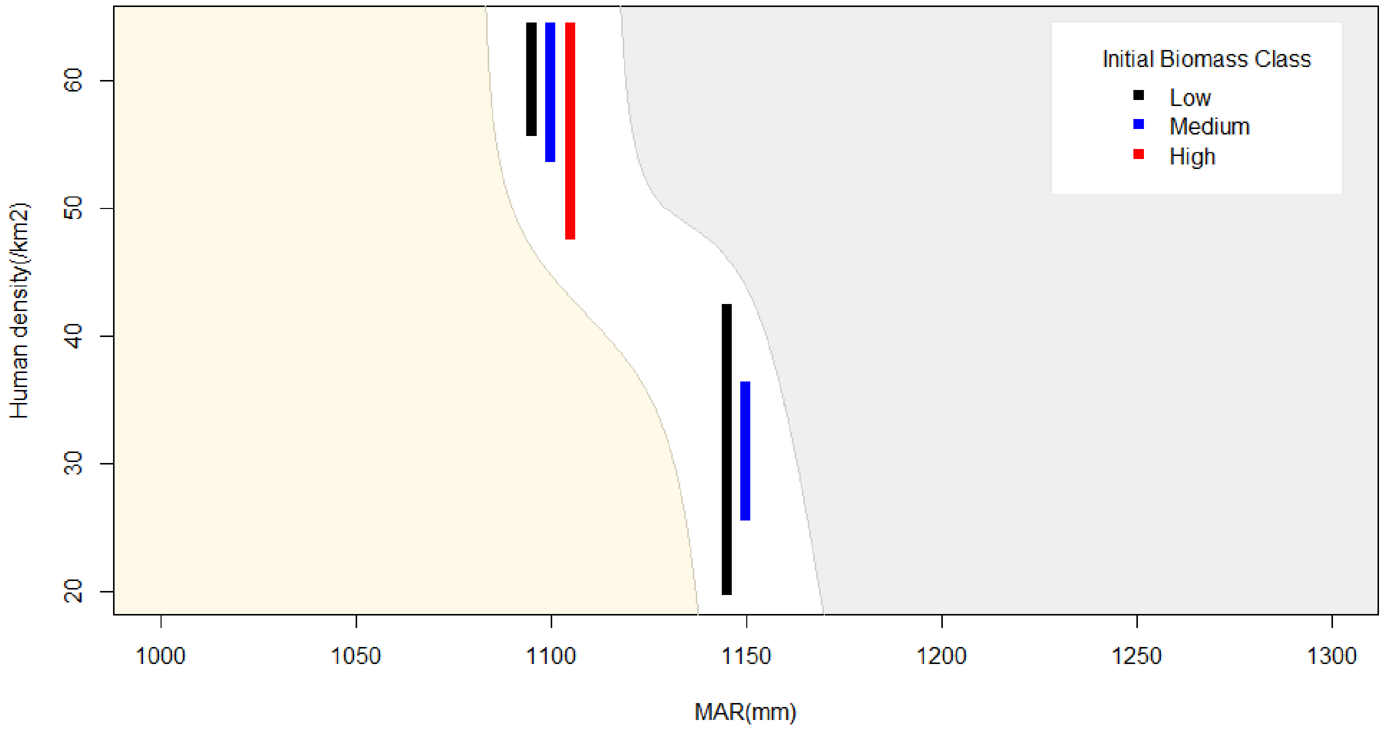

Figure 4: The human population density equivalent to past elephant-mediated above ground woody biomass change across a rainfall gradient and initial biomass categories (Figure 3). 1.4 elephant/km^2 is a conservative estimate of past elephant density for Niassa National Reserve (Robson *et al.* 2017). The grey area (higher rainfall) indicates conditions where human impacts exceed "ecological elephant" impact. The yellow area (lower rainfall) indicates conditions where "ecological elephant" impact exceeds human impacts.

Discussion:

People and elephants are performing a similar functional role in removing woody biomass and encouraging coppice regrowth. To potentially guide what levels of current human facilitated biomass loss are appropriate, the aim of this study was to assess what level of human impact was equivalent to past elephant impact in this region. This was achieved by comparing biomass change at different levels of human and elephant influence (population density), to identify how the intensity of biomass loss differs for humans and elephants across different factors. Human facilitated biomass change is similar to that of 1.4 elephants/km^2 (a conservative estimate of past elephant density; Hempson *et al.* 2015) between 1100mm and 1150mm MAP, although it is also dependent on human population density and initial biomass. Humans tend to remove higher levels of biomass under more mesic conditions than elephants, as rainfall decreases the system can handle increased human impacts before exceeding the loss predicted by past elephant estimates. This suggests that current unharvested woodlands have more trees and higher biomass than if elephants were still present, at historical densities, and that some harvesting by people may be beneficial. Humans tend to remove higher levels of biomass under more mesic conditions than elephants, as rainfall decreases the system can handle increased human impacts before exceeding the loss predicted for past elephant estimates.

Biomass loss increases with population density above 30 people/km^2 and 1 elephants/km^2. Currently it appears that elephant densities recorded within NNR are not high enough to result in net biomass loss – although at low rainfall, negative values were recorded. This lends support to the idea that ~1.4 elephants/km^2 is an ecologically relevant and sustainable level of elephants to have in this reserve (Robson *et al.* 2017), and if past elephant numbers in Miombo were higher than this (as suggested by Hempson 2015) I expect that these ecosystems would have been more open, with lower woody biomass than they are currently.

Human facilitated biomass change:

Areas of medium to high human influence (more than 40 people/km^2 or within approximately 2 hours of a major city) experience the highest levels of biomass loss, with loss increasing with population density and proximity to city. Urban areas are described as the “epicentre of biomass loss” due to their high demand for woodland resources, particularly charcoal, (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010). Charcoal is a highly utilised source of energy in urban areas (Ryan *et al.* 2016) and is thought to be a key driver of biomass loss across the region (Ahrends *et al.* 2010; Luoga *et al.* 2004). Biomass loss hotspots are found near urban areas and along main roads (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010), where transport costs to the urban consumers are minimised (Ahrends *et al.* 2010). Under lower human influence conditions in northern Mozambique, less than 40 people/km^2 or further than two hours from a major city, biomass loss does not increase with human influence. At a regional scale, biomass loss only increases above 20 people/km^2 and continues to increase with distance from major city, even as far as 10 hours from a major city. These areas of lower human influences are generally rural areas or smaller towns, away from the biomass loss hotspots. Rural areas and some towns rely primarily on locally collected dead wood for their energy requirements (Abbot & Homewood 1999; Woollen 2013), which is known to have little or no visible negative impact on woodlands (Abbot & Homewood 1999).

Agriculture, both small-scale and commercial, are key drivers of woodland biomass loss (Ryan *et al.* 2014) at a regional scale and an increase in agriculture results in an increase in biomass loss.

Elephant facilitated biomass change:

Elephant density is a key determinant of vegetation within NNR (Ribeiro *et al.* 2008a ;Ribeiro *et al.* 2008b) and higher elephant density results in increased impacts on woody vegetation (Barnes 1979; Guldemond & Van Aarde 2008; Mapaure 2013). Elephant density across NNR is relatively low, a maximum of 1.52 elephant/km^2, and therefore does not experience the high elephant densities, >2 elephant/km^2, associated with consistent negative vegetation responses (Guldemond & Van Aarde 2008) or high levels of biomass loss. Although biomass loss and significant effects on vegetation have been recorded above ~ 1 elephant/km^2 (Baxter & Getz 2005, Mapaure 2013), within NNR biomass loss only occurred above ~1.4 elephant/km^2. Miombo vegetation, with its root-suckering dominant species, is highly resilient to above-ground disturbance, with higher growth rates recorded in the wet Miombo such as in NNR (Chidumayo 1990; Trouet et al. 2010). This could explain why biomass loss only occurred above ~1.4 elephant/km^2, as woody plants are able to persist under increased elephant influence when growth rates are higher (Baxter & Getz 2005). Elephants typically remove adult trees creating gaps for recruitment, and as many Miombo species require high-light environments to recruit (Syampungani 2009), they could also be facilitating recruitment in these ecosystems (Frost 1996; Baxter & Getz 2005). Thus, even when biomass loss is zero (removal and regrowth rates similar), elephants are still capable of influencing savanna structure and composition even without biomass loss (see chapter 3).

Comparing elephants and people:

Biomass loss was greater when initial biomass is high outside of PA. It has been shown that tree density influences the number of trees impacted by elephants (Jachmann & Bell 1985; Barnes 1979; Gadd 2002) and people (Luoga *et al.* 2002). A further explanation could be that regrowth rates are higher in areas with low initial biomass: as stands dominated by young or small trees will experience higher growth rates per unit biomass than stands of large trees (Frost 1996). The effect of tree density seems to be species specific for elephant impacts (Barnes 1983). Preferred species may not have a high contribution to the overall biomass which may explain why within NNR areas of high initial biomass were not more likely to experience biomass loss, as seen with humans. This suggests that to understand biomass change dynamics some indication of woodland structure may need to be included.

Fire frequency is an important factor in determining woody plant dynamics of Miombo woodlands, with biomass loss greatest when fire frequency is high (Ribeiro *et al.* 2008, Ryan & Williams 2011). This is consistent with my findings as biomass change decreased, even though it was a slight decrease at the regional scale and in NNR, with an increase in the frequency of fire across all three regions. Remotely sensed images of fire are not accurate in closed canopy Miombo (Archibald 2009), which have contributed to the slightly different responses across the different regions.

Rainfall is the primary determinant of biomass at a landscape scale within the Miombo woodlands (Ribeiro *et al.* 2008a) and influences the effects of disturbances on vegetation. Elephants are known to have increased effects on vegetation in more arid areas (Guldemond & Van Aarde 2008). Within NNR biomass loss is typically found in areas which receive less than 1150 mm MAP, with biomass gains found under higher rainfall conditions. Rainfall has the opposite effect on biomass change outside of PA (at both a regional and northern Mozambique scale) to within NNR, as biomass loss is more likely in areas of higher rainfall. One would expect biomass gains across the wetter regions of the Miombo both inside and outside of PAs. The higher regrowth rates of the wet Miombo, suggest that more mesic areas will recover faster after a disturbance and will be able to cope with a higher level of disturbance than drier areas (Trouet *et al.* 2010). Therefore, the mechanism behind the different responses to MAP with NNR and across the rest of the region needs further investigation. This would help to disentangle whether these differences in responses are simply due to the higher levels of elephant impacts under more arid conditions, differences in the seasonality of the impacts or whether the woodlands are better at responding to disturbances from elephants than people, influencing their ability to regrow.

Settlements with smaller populations have a decreased pressure for woodland resources (Ryan *et al.* 2014; Ahrends *et al.* 2010), we can therefore assume that biomass loss will be greater above 65 people/km^2 than under a lower population density. This suggests that above a certain population density (> 65 people/km^2) people will constantly remove more biomass than past elephants regardless of initial biomass classes or rainfall. The maximum human population density of valid data included in the model was only 65 people/km^2, which excludes areas of high human influence and the major cities. These regions with very high human population densities, typically surrounding urban areas and along main roads, are areas of concern due to the high levels of biomass loss (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010) which potentially exceed the biomass loss of past elephants.

In areas of lower rainfall (< 1100 mm) and moderate human influence (< 65 people/km^2) past elephants are predicted to have removed more biomass than people do currently. Due to the high levels of elephant impacts in areas of lower rainfall (Guldemond & Van Aarde 2008) there appears to be the potential for increased human use of these ecosystems which receive low rainfall. Promoting woodland utilisation in lower rainfall and low human influence areas without elephants could provide additional income to rural communities (Misana *et al.* 1996) while maintaining the important disturbance of removing woody biomass (Frost 1996), preventing bush encroachment (Stevens *et al.* 2017) and could help alleviate the pressure on the current hotspots of overharvesting surrounding areas of high human influence.

Current levels of wood harvesting for energy within the Miombo could potentially be sustainable, as biomass losses from degradation and deforestation are currently offset by extensive growth across the Miombo region (McNicol *et al.* 2018). The issue is that biomass loss primarily is occurring in hotspots of overharvesting in areas of higher human influence (Ribeiro *et al.* 2015; Ahrends *et al.* 2010) while other areas are experiencing woody plant encroachment due to changing environmental factors and the lack of herbivores, particularly elephants, or people as disturbance factors (Stevens *et al.* 2017; Venter *et al.* 2018). The charcoal industry has been highlighted as a major cause of woodland biomass loss (Ryan *et al.* 2014; Sitoe *et al.*2012). Therefore, promoting a more extensive charcoal industry across the region, by encouraging small scale production in low rainfall, low human influence areas (outside of PA with elephants), could be a solution to distributing the effects of human woodland utilisation across the region while maintaining necessary disturbances. It has been suggested that changes to the charcoal industry need to be made to allow local communities to generate greater benefits from charcoal production while distributing production away from the high human influence areas associated with biomass loss and aiming at sustainable charcoal production (Baumert *et al.* 2016). Our data shows that areas of lower rainfall and low human influence are underutilised and could be potential areas to promote the charcoal production in to decentralise the industry and potentially reduce utilisation in the biomass loss hotspots.

Under certain conditions people may or could potentially remove a similar amount of woody biomass to past elephants. It is however important to consider how the two may differ. Under human utilisation the nutrients are often lost to the system and transported to urban area whereas with elephants the nutrients are retained by the system whether through the remaining biomass or as dung. Elephants are also important in redistributing nutrients within the landscape (Owen-Smith 1988; Doughty *et al.* 2016) and their absence will likely have consequences of the nutrient cycling. Several species rely only on elephants for dispersal (Bunney *et al.* 2017). The absence of elephants can therefore have implications for woody community dynamics and other ecological consequences (Hempson *et al.* 2017), which people will not be able to replicate. The presence of people, livestock and hunting also impacts the ecosystem, influencing the behaviour and spatial utilisation of many wild animals (Valls-Fox et al. 2018), indirectly also influencing the vegetation. While both people and elephants remove woody biomass, there are many functional roles performed by the one disturbance agent but not the other. It therefore needs to be highlighted that people performing a similar functional role to elephants in the Miombo woodlands is limited to the removal of woody biomass.

The Miombo ecoregion is a highly dynamic and complex system, which makes predicting biomass change challenging. The low explanatory power of many of these models shows that all factors influencing biomass change were not included or that these processes are operating at a different scale, particularly for the areas under human influence. While I included most of the factors that might affect biomass loss, plant species richness (Li *et al.* 2018), dominance biomass (Pelletier *et al.* 2017) and soil nutrients (Frost 1996) are all potentially important determinates of tree growth and the aboveground woody biomass of a stand that I did not include. Incorporating interactions between factors will likely improve the explanatory power of the models, as the Miombo is a complex system with interacting components. Scale is important to consider. Both humans and elephants are making the decision of which trees to utilise at a much finer scale, than at the 1km^2 scale used in this study. Scale can also influence how important a factor is, in NNR fire frequency influenced biomass at a plot level but only when interacting with MAP on a landscape scale (Ribeiro *et al.* 2008a). This dataset could be used to investigate the effect of scale on what driver biomass change, as the biomass estimates are available at a much finer resolution of 25m^2.

Trees in the miombo region are highly adapted to recovering after a disturbance. Currently there are no good models of woody biomass accumulation and regrowth rates for these ecosystems, although the SEOSAW project (https://seosaw.github.io/) is working on developing these. I was able to account for this regrowth ability, to some degree, by accounting for the initial biomass, under the assumption that areas recovering from past disturbance (low initial biomass) will likely grow faster than less disturbed (higher biomass) areas. Although there are properly better ways to account for this. Little is known about how woody plant regrowth differs after human or elephant's disturbance, or the effects of interactions with factors such as: soil nutrients, water availability or the season of the disturbance. The type of human disturbance is also important to consider. Rainfall was a key driver in the biomass change models and to some extent determined under what conditions people could potentially remove more biomass. The responses of biomass change to rainfall differs between NNR, under elephant influence, where biomass gains are more likely under wetter conditions and the rest of northern Mozambique, under human influence, where biomass gains are more likely under drier conditions. The mechanism behind the different responses to MAP within NNR and across the rest of northern Mozambique needs further investigation. To disentangle whether these different responses are simply due to the lower levels of elephant impacts under more mesic conditions, difference is in the seasonality of impacts or if the woodlands are better at responding to disturbances from elephants than people, influencing their ability to regrow. An improved understanding of the determinates of tree growth in these systems is necessary to better model aboveground woody biomass change and to determine how much change the system can handle.

Conclusion:

People could potentially perform a similar functional role to elephants, in removing woody biomass (Frost 1996), preventing bush encroachment (Stevens *et al.* 2017) and mitigating some of the consequences of losing an apex consumer from the system, while allowing people vital access to woodland resources (Bond *et al.* 2010). Biomass loss in the high human influence areas surrounding urban areas and major roads are clearly of great concern (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010) and is much higher than any levels of elephant-mediated loss observed here. There are also vast areas within the region, primarily under low rainfall and low human influence, which appear to be underutilised relative to historical levels.

The results suggest that the current disturbance level of these areas is well below what the system is adapted to as estimated by past elephant utilisation. Distributing the effects of human woodland utilisation across the region, through promoting a more extensive charcoal industry and by encouraging small scale production in low rainfall rural areas, could alleviate the pressure on the hotspots of biomass change while providing the people in the rural areas with an additional source of income and the woodlands with a disturbance necessary in maintaining, to some extent, the ecosystem structure and functioning of the Miombo.

Chapter 3

Contrasting human and elephant species and size class preferences

Abstract

Disturbances play an important role in maintaining savanna tree-grass coexistence and determining savanna composition and structure. In recent history southern African woodlands have undergone dramatic changes to their disturbance regimes: rapid increases in human population and urbanisation, while the abundance and distribution of elephants have decreased. Elephants have been replaced by humans across much of the region. Although both have similar ecological impacts by removing woody biomass, they are not identical. Using field collected data on observed human and elephant impacts in communal areas (CA) and the adjacent Sikumi Forest Reserve (SF) species and size class preferences of humans and elephants were compared within areas dominated by typical Miombo tree species. Human's preferred 18 species (in the SF and CA) while elephants only preferred six (in the SF only). Therefore, Humans will likely facilitate decreases in a higher number of species than elephants. Elephants generally prefer slightly larger stems (20-40cm) and humans mostly prefer smaller stems suitable (<20cm in diameter) for firewood and construction poles. This suggests that areas utilised by elephants might result in a more left skewed size-class distribution than people (in areas where charcoal production is uncommon). The large overlap in stems used by both people and elephants, the relative flexibility in what stems people are able to use for a specific purpose and high regeneration ability of many of these species, suggests that many of these differences in impacts on composition and structure could potentially be mitigated.

Introduction

Savanna structure and composition is determined by interactions between resource availability and disturbances (Sankaran *et al.* 2005). However, across large areas of African savanna disturbances are essential in reducing woody cover to maintain tree-grass coexistence (Sankaran *et al.* 2005). The Miombo woodlands of central and southern Africa (Timberlake & Chidumayo 2011) are "disturbance driven savannas", where disturbance is necessary to prevent canopy closure and maintain their tree-grass coexistence (Frost 1996; Sankaran *et al.* 2005). The woody plant dynamics of the Miombo woodlands are affected by three interacting disturbance factors; people, elephants and fire (Frost 1996; Ribeiro *et al.* 2015).

The Miombo woodlands are dominated by *Brachystegia, Julbernardia* and *Isoberlinia* species, of the Detariodeae (previously Caesalpinioideae) subfamily (Frost 1996). Trees of the Miombo region are well adapted to disturbances, as many can resprout from roots and stumps after being cut or damaged (Timberlake & Chidumayo 2011; Luoga *et al.* 2004; Frost 1996; Chidumayo & Frost 1996). Since the end of the 18th century the Miombo woodlands have undergone dramatic changes, affecting the disturbance regimes; land use transformation (Bond *et al.* 2010; Campbell *et al.* 1996), an increasing human population (Misana *et al.* 1996) and the reduction in the abundance and distribution of elephants (Ntumi *et al.* 2009; Misana *et al.* 1996, Hempson *et al.* 2015). Although elephants are not extinct, their numbers are greatly diminished (Ntumi *et al.* 2009; Misana *et al.* 1996, Hempson *et al.* 2015; Robson *et al.* 2017) and over much of the Miombo region elephants have been replaced by humans. Humans and elephants can have similar ecological impacts as they both remove woody biomass, but their size class and species selection must to be considered due to the effect on vegetation structure and composition.

People as a disturbance

People have played an important role in shaping structure and composition of the Miombo woodlands since the early Stone Age (Timberlake & Chidumayo 2011; Ellis 2011). The woodland resources are important to the livelihoods of people within the region (Bond *et al.* 2010; Campbell *et al.* 1996; Clarke *et al.* 1996; Ekman *et al.* 2013); but in some areas they are disappearing at a considerable rate due to increased human pressure (Bond *et al.* 2010; Ryan *et al.* 2012; Ryan *et al.* 2014). Small- scale agriculture is currently the primary cause for woodland biomass loss; but construction activities, charcoal production, logging and commercial agriculture also contribute to this change in biomass and woodland cover (Ryan *et al.* 2014; Sitoe *et al.*2012).

Firewood and charcoal are the primary sources of energy (Brigham *et al.* 1996; Ryan *et al.* 2016) and key contributors to the livelihoods of millions of people across the region (Jones *et al.*

2016). 90% of the aboveground woody biomass can be utilised for charcoal (Chidumayo *et al.* 1996); although specific tree species and size classes tend to be favoured for specific purposes (Brigham *et al.* 1996; Jones *et al.* 2016; Luoga *et al.* 2002) causing changes in the size class distribution and the community structure (Luoga *et al.* 2002) under human use. Miombo dominants such as *Brachystegia spiciformis*, *Brachystegia boehmii* (Jones *et al.* 2016) and *Julbernardia globiflora* (Luoga *et al.* 2002) were all identified as preferred species for charcoal production, but preference also depends on the abundance and ease of extraction (Luoga *et al.* 2002). Trees selected for charcoal production tend to be slightly larger and use a wider range of size classes than those used for firewood and construction poles (Luoga *et al.* 2002). Humans therefore alter savanna structure and composition directly through wood removal and therefore, humans' effects on vegetation can be compared to those of the African elephant (Frost 1996; Mograbi *et al.* 2017*)*.

Elephants as a disturbance

Elephants are able to completely transform savanna landscapes (Guldemond & Van Aarde 2008; Owen-Smith 1988) and have been influencing savanna dynamics since the late Miocene (Carruthers *et al.* 2009). Elephants influence woody cover through breaking branches (Barnes 1979; Owen-Smith 1988), pushing over trees (Owen-Smith 1988) and stripping bark (Barnes 1979; Owen-Smith 1988) to access forage or as a social display (Frost 1996; Barnes 1979). Like people, they also show preference for specific species and size classes which impacts the community structure and composition (Barnes 1979; Owen-Smith 1988; Mapaure & Moe 2009). Elephants are known to utilise a wide range of species, although species preference tends to be site specific and shifts according to quality and quantity of forage (Mapaure & Moe 2009). Few studies investigate elephant preference for stem diameter size, making it difficult to compare size class selection between people and elephants. Although Mapaure & Moe (2009) did show that elephants induced decreases in large trees (greater than 11cm basal stem diameter) and Gadd (2002) showed that only *Sclerocarya birrea* stems less than 40cm in diameter were broken.

People vs elephants

Both humans and elephants influence the woody biomass in multiple ways, including indirectly through manipulating fire (Dublin, Sinclair & McGlade 2010; Holdo 2007). The human disturbance of land transformation for agriculture does not have an elephant disturbance equivalent, whereas people harvesting firewood, charcoal, construction poles and logging could be equivalent to elephants breaking branches and pushing over trees. People (harvesting fuelwood and poles) and elephants are performing a similar functional role in removing woody biomass and encouraging coppice regrowth (Frost 1996), although it is possible that their impacts on emergent properties, like community composition and structure, might differ. It is also important to note that when elephants break trees the biomass is recycled in situ, whereas with charcoal extraction and firewood the biomass is taken out of the ecosystem. Megafauna (Smith *et al.* 2016) and people (Bliege Bird & Nimmo 2018) both play important roles in seed dispersal, and many large-fruited trees are adapted for dispersal via the guts of elephants (Smith *et al.* 2016). It is therefore important to also consider the influence of elephants and people on nutrient cycling and seed dispersal to understand and quantify how they differ as disturbances.

Understanding the consequences of trophic downgrading is an important question facing ecologists today (Estes *et al.* 2011; Sutherland *et al.* 2013; Cromsigt & te Beest 2014). The increase in human and decrease in elephant disturbances raises the question of whether people, through their harvesting of fuelwood and construction poles, can perform a similar functional role to elephants in the Miombo woodlands? If so, human use could be maintaining ecosystem functions, while also supporting livelihoods of rural people. Clearly assessing whether people are positively or negatively impacting woodlands depends crucially on determining the impacts of past elephants, and people, in Miombo vegetation.

In this chapter the tree species and size class preference of humans and elephants were compared in Miombo vegetation at a site in north-western Zimbabwe. The aim was to identify utilisation overlaps between these two agents of disturbance, testing whether they have similar impacts on vegetation structure and composition. Human i) species preference and ii) size class preference of preferred species were compared to elephant preference across the Sikumi Forest Reserve (where human utilisation is regulated) and communal land.

Methods and Materials:

Study Site:

The study area includes the north-western section of the Sikumi Forest (SF) and communal land (CA; four villages) along the north-eastern border of Hwange National Park (HNP) within the Hwange District, Matabeleland North, Zimbabwe (Figure 1). The SF and CA will be referred to as a location. This area is characterised by Kalahari sands soils of low fertility and low erratic rainfall (Guerbois *et al.* 2012), MAR: 606 mm, inter-annual CV =25%. The vegetation is a mosaic of *Brachystegia spiciformis* dominated Dry Miombo woodlands and *Colophospermum mopane* woodlands (Rutherford *et al.* 2005).

The Main Camp area of HNP, adjacent to the study site, contains estimates as high as 4.36 ± 2.67 elephants per km^2 in the late dry season (Chamaille´-Jammes *et al.* 2009) and the SF contains approximately 0.51 elephants per km^2 in the dry season (Dunham *et al.* 2007). Both protected areas

(PA) are unfenced, meaning these elephants are free to roam between these PAs and into the surrounding communal land. Elephants are seldom found in the communal land with an effective density of 0.

The villagers within the study area, rely on subsistence farming and natural resource harvesting (Guerbois & Fritz 2017). Villagers living on the edge of SF utilise the forest reserve within the first few kilometres. Access to natural resources such as firewood collection is permitted and regulated. Only women may collect dead wood once a week, on Thursday, and the use of axes and carts are banned. Timber extraction permits for pole collection are given by the forestry area on request. Charcoal production is uncommon in this area. Following the severe droughts in the 80-90s, local communities were authorized to graze cattle up to 3 km within the Sikumi Forest boundaries. One interesting attribute of the study area is that access to natural resources and land-uses in communal areas are still determined internally, by traditional leaders, and are often managed at the village scale. On some occasions, illegal tree felling was witnessed, but overall, active tree felling was done in the CA and not in the SF.

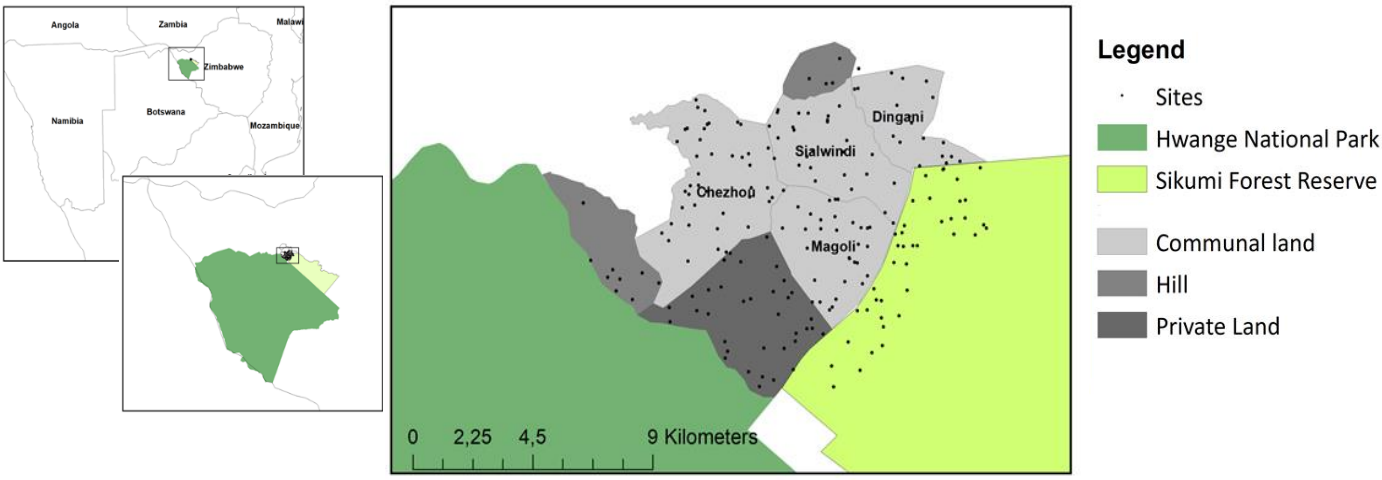

Figure 1: Map of the north-western section of the Sikumi Forest (SF) and land along the north-eastern boarder of Hwange National Park (HNP) within the Hwange District, Matabeleland North, Zimbabwe

Table 1: a)Height and b)stem diameter classes

a)

Height classes
<1 m
1 m-3 m
3 m-8 m
>8 m

b)

Stem diameter class	Stem diameter (cm)
1	<5
2	5-10
3	10-20
4	20-40
5	>40

Experimental design and protocol:

211 sites were randomly selected across the study area and sampled during May and June 2013 by Chloe Guerbois and a team from the Hwange Long-Term Socio-Ecological Research program. A total area of 19 886 m^2 was sampled, approximately 94 m^2 at each site. At each site sampling occurred along two 30 m transects running North and East. Each transect consists of 15 circular plots with a diameter of 2m, with the centres of each circle 2m apart (Figure 2). The species, height class and stem diameter class (at 0.2m and 1.2m above the ground) of all woody plants' stems were recorded in each plot (Table 1). The species, diameter class and height/length of stumps and dead wood and the cause of any disturbance (humans, elephants or other animals) were also recorded. Stems were considered utilised if the agent of disturbance was identified.

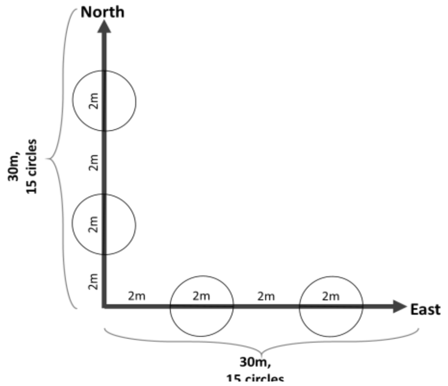

Figure 2: The transect layout, consisting of 15 circular plots in each direction.

Data Analysis:

The vegetation in this area is typically more heterogeneous than classical Miombo areas, as there are significant inclusions of Mopane and Acacia in areas of nutrient rich soils (Timberlake & Chidumayo 2011). These patches of nutrient rich soils show ecological functional differences (Frost 1996) and increased elephant utilisation (Pretorius *et al.* 2011) to the otherwise nutrient-poor landscape.

Mopane (*Colophospermum mopane*) and Acacia (primarily *Vachellia tortilis*) dominated sites were therefore excluded from the analysis, as to only include the broad-leaf Miombo-like vegetation found in dystrophic soils (Timberlake & Chidumayo 2011). Sites with similar vegetation composition dominated by Miombo species (*Brachystegia boehmii, Brachystegia spiciformis, Julbernardia globiflora* and *Burkea Africana*; Timberlake & Chidumayo 2011) were therefore identified through hierarchical clustering using Ward's method and a Bray–Curtis distance matrix of species that make up 80% of the basal area in R (package: Vegan).

Preference ratios (PR) per tree species were calculated for elephants (only within the SF) and people (within the SF and CA), to identify whether these different agents of disturbance select the same species. All the site data was summed within SF or CA to produce a preference ratio at a location level, this ensured a representative sample size per species (Boundja & Midgley 2009). Preference is based on the extent to which a food is utilised in relation to its availability. A species is preferred if it's stems are proportionately more frequently utilised than it is available and avoided if utilised less frequently than it is available (Petrides 1975). PR was calculated using Petrides (1975); where a is the percentage of a specific species available (the sum of removed and unused stems) and R is the number of stems removed of that species.

$$PR = d/a,$$

$$d = 100 * R/\sum R$$

Species with less than 20 stems per location were excluded to deal only with species with a representative sample size (Boundja & Midgley 2009). Species were placed in a preference category based on the preference ratio (Table 2). Bar graphs of species were created comparing relative availability and stems removed by elephants or people within the SF and CA; to contrast the species availability and use between the SF and CA for people and elephants.

Similarly, for species preferred by both people and elephants (*Brachystegia spiciformis*, *Kirkia acuminata, Markhamia zanzibarica* and *Terminalia sericea*) the PR per size class was calculated per location for people (SF and CA) and elephants (SF), to identify whether these different agents of disturbance select the same size classes for preferred species. Size class PR (Petrides 1975) per species were calculated if there were at least five stems per size class and placed in a preference category (Table 2). Bar graphs of these four species were created comparing size class distribution and stems removed per size class by elephants or people for each species; to contrast the species availability and use between the SF and CA for people and elephants.

Statistical tests comparing the distribution of size class utilisation per species (such as Kolmogorov–Smirnov test) were not considered due to the low number and lack of data for some species' size classes. Instead only PR were utilised to compare size class selection across species and between people and elephants.

Table 2: Criteria for preference categories

			Avoided			
Preference Category	**Preferred**	**Neutral**	**Ignored**	**NU**	**U***	**NA**
Preference Ratio	PR > 1.1	PR < 1.1 and > 0.9	PR < 0.9	Not used	< 20 stems available, but still used	Not available

Results:

Site selection and species composition of the sites:

151 of the 211 sites were identified to have Miombo-like vegetation (cluster 3) and were therefore included in the analysis (Figure 3), 37 of these sites are located within SF and 114 in CA. These sites, of Miombo-like vegetation, were dominated by broad-leaf species (excluding *Colophospermum mopane*), with typical Miombo species (Brachystegia boehmii, Brachystegia spiciformis, Julbernardia globiflora and Burkea Africana) covering approximately 13% of the woody plant basal area (Table 3). Sites in cluster 2 are dominated by *Colophospermum mopane*, covering 52% of the woody plant basal area, with the typical Miombo species covering only 3% (Table 3). Sites in cluster 1 are dominated by *Vachellia (Acacia) tortilis*, covering 65% of the woody plant basal area, with the typical Miombo species covering less than 1% (Table 3).

Species preference:

A total of 74 species and 3468 stems were available across both the SF and CA. 44 species were utilised (at least one stem removed); 27 species by elephants and 41 species (SF: 23 species; CA:33 species) by people (Figure 4). 24 species were utilised by both people and elephants, indicating a 54.6% overlap in utilisation. All species utilised by elephants were also utilised by people, except for *Brachystegia boehmii* and *Ochna pulchra*. 17 species are utilised by people but not elephants. Human utilisation also differs between the CA and SF, with only 40.5% of species utilised in both locations.

Within SF 63 species were available, 33 were utilised by either people or elephants and 17 species were utilised by both people and elephants (Figure 4a). Ten species were removed by elephants but not people. SF contained 21 abundant species (more than 20 stems available, meeting the criteria to calculate PR), of these species there is a 47.6% (10 species) overlap in preference categories between people and elephants (Table 4). *Brachystegia spiciformis, Terminalia sericea* and *Kirkia acuminata* were preferred and seven species were avoided by both people and elephants within

SF. Eleven species had different preference categories for people and elephants, indicating potential differences in effects of these agents of disturbance. Three species were preferred by elephants but avoided by people; but only *Pterocarpus angolensis* is not utilised by people in SF. Six species were avoided by elephants but preferred by people, of which only *Canthium frangula* and *Strychnos madagascariensis* were not utilised by elephants. People preferred *Dichrostachys cinerea* and didn't utilise *Diplorynchus condilocarpon* at all, but elephants showed neutral preference towards these two species. Although *Pterocarpus angolensis* and *Diplorynchus condilocarpon* are not utilised by people within the SF, humans use both to some extent within the CA (Table 4). Both people and elephants therefore have the potential to utilise all the abundant species within different preference categories, except elephants do not utilise *Canthium frangula* or *Strychnos madagascariensis*.

Within the CA 64 species were available and 33 species were utilised by people (Figure 4b). 53 species were available in both the SF and CA, of these species 36 are utilised by either people or elephants. Only 14 species had more than 20 stems in both locations. 50% of the abundant species in both SF and CA were in the same preference category for both people in CA and elephants in SF, three species were preferred and four species were avoided by both (Table 4). *Pterocarpus angolensis* is the only species which is preferred by elephants and avoided, yet still utilised, by people. *Baphia massaiensis, Combretum apiculatum* and *Combretum collinum* are all preferred by people in CA and avoided by elephants, yet these fast growing species are known to decline when elephants are present (Holdo 2007). Both people and elephants therefore have the potential to utilise all the abundant species, in both the SF and CA, within different preference categories

People also tend to show preference for a wider range of species, preferring 10 species in the SF and CA (18 species were preferred by people across both locations) compared to the six species preferred by elephants (Table 4). There are 20 preferred species but only four species which are preferred by both people and elephants.

Size class preference:

Brachystegia spiciformis is preferred by elephants and by people in both SF and CA (Table 4), but there are differences in size class preferences between people and elephants for this species (Table 5a). Elephants showed preference for a wide range of intermediate sized *Brachystegia spiciformis* stems, between 5 and 40 cm in diameter. There is some overlap in size preference of this species, as people in both locations and elephants have a preference for stems between 10 and 20 cm in diameter, but people also prefer larger stems, greater than 40 cm in diameter, in SF (Table 5a). Within the CA there are few *Brachystegia spiciformis* stems larger than 10 cm compared to within SF, so it was not possible to contrast preference (Figure 5a).

Terminalia sericea is preferred by people in both SF and CA and elephants (Table 4), but also shows differences in size class preferences between people and elephants for this species (Table 5b). Elephants preferred slightly larger stems, between 5 and 20 cm in diameter, than people; who showed a preference for stems less than 10cm in SF and less than 5 cm in CA (Table 5b). Large stemmed *Terminalia sericea* are rare across both SF and CA; there are no stems greater than 20 cm in CA, with only three stems in the third size class, and no stems greater than 40 cm in SF.

Kirkia acuminata is preferred by people in SF and elephants (Table 4). Both people and elephants prefer stems between 10 and 20 cm (Table 5c), there are very few stems below this size in either the SF or CA (Figure 5c). Elephants also show a preference for slightly larger stems of this species between 20 and 40 cm in diameter, which are avoided by people.

Markhamia zanzibarica is preferred by both people in CA and elephants (Table 4). People show a preference for slightly smaller stems (between 5 and 10 cm) than elephants which prefer stems between 10 and 20 cm (Table 5d). Only small stems of *Markhamia zanzibarica* are found within the CA, almost all are less than 5 cm in diameter (Figure 5d). Large stems, greater than 20 cm were also absent from the SF.

Of the selected species people prefer a wider range of stem sizes than elephants (Table 5). People show a preference for stems in all size classes, except for stems between 20 and 40cm, in at least one of these species; but tend to prefer stems less than 20 cm for most species. Elephants in contrast preferred stems between 10 and 20 cm for all selected species but did also prefer slightly smaller (greater than 5cm) and larger (less than 40 cm) stems for two species.

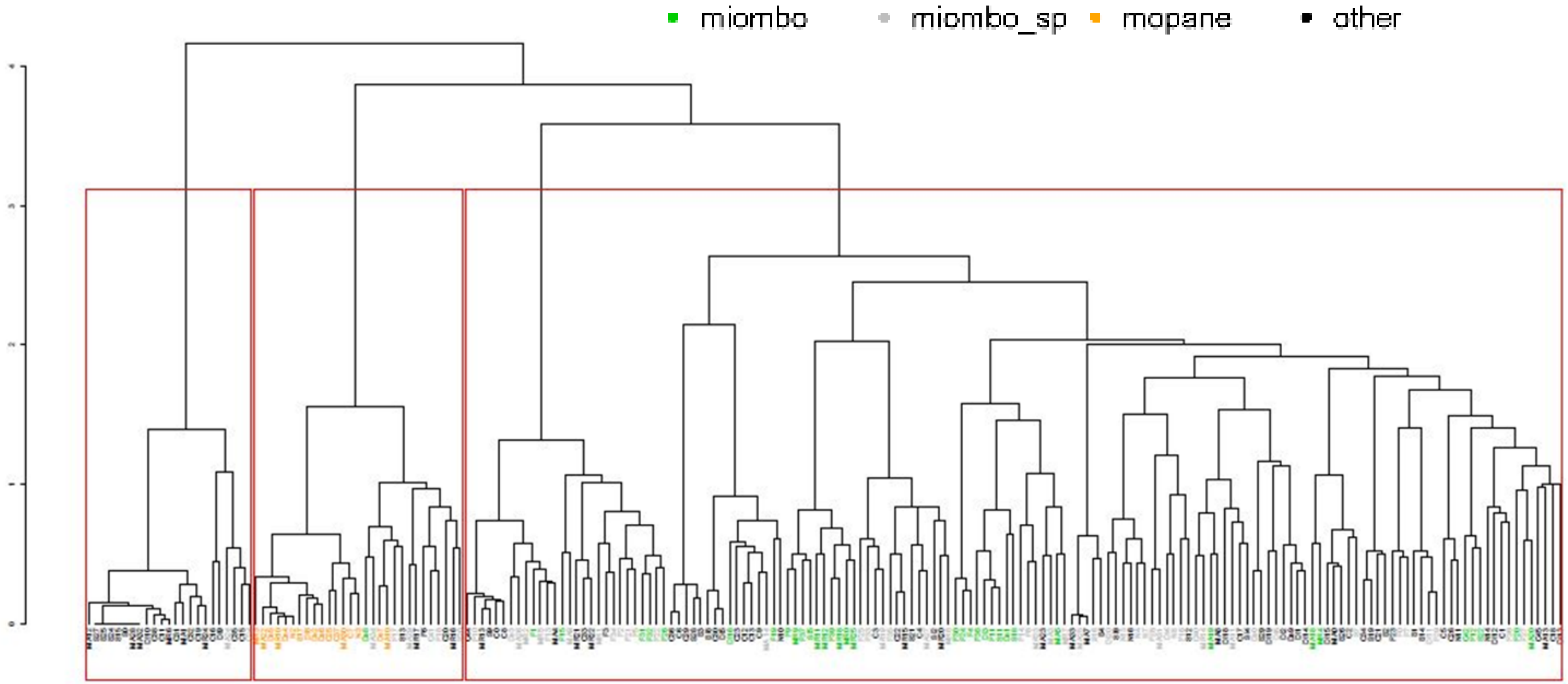

Figure 3: Hierarchical clustering using Ward’s method and a Bray–Curtis distance matrix to identify Mopane and Acacia dominated sites to exclude. Miombo sites (green) contain more than 50% typical Miombo species. Miombo species (grey) sites contain at least one typical Miombo species. Mopane sites contain at least 50% *Colophospermum mopane* (orange). Other sites (black) are not dominated by *Colophospermum mopane* and don’t contain typical Miombo species. *Brachystegia boehmii, Brachystegia spiciformis, Julbernardia globiflora* and *Burkea Africana* are considered typical Miombo species. Cluster 1 is dominated by *Vachellia (Acacia) tortilis*, cluster 2 is dominated by *Colophospermum mopane* and cluster 3 is dominated by broad-leaved trees and contains the typical Miombo species.

Table 3: Details of study species, including growth form (Coates Palgraves 1983; High Branching, 2018), maximum height, resprouting ability (Martin 1939; Strange 1966; Parry 1989; Scholes 1990; Abbot & lowore 1999; Wilson & Witkowski 2003; Neke 2004; Sebata *et al.* 2009; Helm *et al.* 2009; O'Connor 2017; Zulu *et al.* 2018), utilisation and basal area per species across the three vegetation group clusters

							Basal area (cm^2)				
					Uses		**3**		**2**	**1**	
Species	**Family**	**Growth form**	**Height**	**Resprouting ability**	**People**	**Elephants**	**CA**	**SF**	**CA**	**CA**	**SF**
Vachellia (Acacia) nilotica	Fabaceae Mimosideae	Shrub to small tree	< 10 m	high	Direct use	Used	8242	0	103	1909	0
Senegalia (Acacia) nigrescens	Fabaceae Mimosideae	Medium to large tree	< 30 m	Yes	Direct use	Used	29575	3480	785	933	0
Afzelia quazensis	Fabaceae Caesalpiniodeae	Large tree	< 35 m		Direct use	Used	1860	5	0	6067	0
Vachellia (Acacia) tortilis	Fabaceae Mimosideae	Small to medium tree	< 20 m	Yes	Direct use	Used	3736	0	14422	697	5
Burkea africana	Fabaceae Caesalpiniodeae	Medium tree	< 20 m	Yes	Direct use + food/medicinal		1428	761	182	39	177
Brachystegia boehmii	Fabaceae Caesalpiniodeae	Medium tree	< 16 m	high	Direct use	Used	4811	5267	0	1154	0
Berchemia discolor	Rhamnaceae	Medium to large tree	< 20 m		food/medicinal	Used	8399	29	10	5	0
Baphia massaiensis	Fabaceae Papilionoideae	Shrub to small tree	< 8 m	high	food/medicinal	Used	5532	6141	0	0	540
Bauhinia petersiana	Fabaceae Caesalpiniodeae	Small bush to small tree (scrambler)	< 10 m	Yes	food/medicinal	Used	4398	299	0	49	142
Baikiaea plurijuga	Fabaceae Caesalpiniodeae	Medium to large tree	8-16 m	Yes	Direct use	Used	1134	24995	0	226	270
Brachystegia spiciformis	Fabaceae Caesalpiniodeae	Medium to large tree	< 30 m	high	Direct use	Used	7520	18820	10	0	10
Combretum apiculatum	Combretaceae	Small to medium tree (sometimes shrub)	< 10 m	high	Direct use	Used	11364	2680	15	1620	545
Cassia abbreviata	Fabaceae Caesalpiniodeae	Shrub to medium tree	< 10 m	Yes	food/medicinal		3009	44	20	461	0
Commiphora angolensis	Burseaceae	Shrub to small tree	< 6 m				6430	88		54	0

Combretum collinum	Combretaceae	Small to medium tree	< 15 m	Yes	Direct use	Used	7756	4560	29	1973	221
Canthium glaucum subsp. frangula	Rubiaceae	Shrub to small tree	< 5 m				1507	653	0	1183	0
Colophospermum mopane	Fabaceae Caesalpiniodeae	Shrub to tall tree	< 30 m	high	Direct use	Used	10922	2916	2656	46172	2793
Commiphora marlothii	Burseaceae	Small to medium tree	< 13 m	Probably	food/medicinal	Used	24892	7250	5	1016	44
Commiphora pyracanthoides	Burseaceae	Shrub to small tree (scrambling)	< 6 m	Yes	food/medicinal		5326	157	0	5	0
Combretum psidioides	Combretaceae	Shrub to medium tree	< 10 m	Probably	Direct use	Used*	12272	4482	15	1482	98
Combretum zeyheri	Combretaceae	Small to medium tree (sometimes shrub)	< 12 m	high	Direct use	Used	1561	93	0	0	0
Diplorynchus condilocarpon	Apocynaceae	Shrub to small tree	< 20 m	high	Direct use	Used	10809	1708	88	712	54
Dichrostachys cinerea	Fabaceae Mimosideae	Shrub to medium tree	< 12 m	high	Direct use		7756	1797	908	584	0
Diospyros mespiliformis	Ebenaceae	Medium to large tree	< 25 m		Direct use		1409	339	10	785	5
Diospyros quiloensis	Ebenaceae	Small to medium tree	< 10 m	Probably	Direct use		5208	6754	245	520	108
Dombeya rotundifolia	Malvaceae	Small tree	< 10 m	high	food/medicinal		1247	2769	0	0	0
Erythrophleum africanum	Fabaceae Caesalpiniodeae	Medium to large tree	< 12 m	Yes	Direct use		4590	1684	0	0	49
Erythroxylum zambesiacum	Erythroxylaceae	Shrub to small tree	< 7 m	Probably			4182	8050	5	5355	358
Friesodielsia obovata	Annonaceae	Shrub to small tree (scrambling)	< 7 m		Direct use + food/medicinal		1075	3996	0	5	196
Flueggea virosa	Phyllanthaceae	Shrub to small tree (scrambling)	< 8 m		Direct use		2219	2346	0	98	152
Grewia flavencens	Malvaceae	Shrub to small tree (scrambling)	< 5 m				1841	44	0	29	5
Grewia monticola	Malvaceae	Shrub to small tree	< 10 m	Yes	Direct use	Used	1924	825	49	20	49
Julbernardia globiflora	Fabaceae Caesalpiniodeae	Medium to large tree	< 15 m	high	Direct use	Used*	19723	12969	0	785	221
Kirkia acuminata	Kirkiaceae	Medium to large tree	< 20 m	low	Direct use		53147	44026	0	3225	0

Lonchocarpus capassa	Fabaceae Papilionoideae	Small to medium tree	< 10 m		Direct use + food/medicinal		5434	0	0	0	0
Lannea discolor	Anacardiaceae	Small to medium tree	< 15 m		food/medicinal		2670	44	0	358	0
Lonchocarpus nelsii	Fabaceae Papilionoideae	Small to medium tree	< 10 m	Yes			2538	0	15	707	0
Markhamia zanzibarica	Bignoniaceae	Small tree	< 9 m	Yes	Direct use	Used	1301	2759	0	0	29
Pterocarpus angolensis	Fabaceae Papilionoideae	Medium to large tree	< 30 m	high	Direct use	Used	2931	2484	0	383	103
Pteleopsis anisoptera	Combretaceae	Shrub to tree	3-12 m	Probably			6808	9690	0	461	187
Schlerocarya birrea	Anacardiaceae	Medium to large tree	< 18 m		Direct use + food/medicinal	Used	4678	5	0	707	0
Strychnos madagascariensis	Loganiaceae	Shrub to small tree	< 20 m	Yes	Direct use	Used	13960	3740	490	1448	1178
Strychnos potatorum	Loganiaceae	Medium tree	< 15 m	Yes		Used	3574	417	0	152	15
Schrebera trichoclada	Oleaceae	Shrubby bush to medium tree	< 10 m				928	1473	0	177	5
Terminalia sericea	Combretaceae	Small to medium tree (sometimes large)	< 20 m	high	Direct use	Used	2823	8212	20	810	191
Vangueria infausta	Rubiaceae	Shrub to small tree	< 8 m	Probably	food/medicinal		3117	3691	10	79	236

Table 4: Human and elephant species preference across the communal areas and the Sikumi Forest Reserve and the resprouting ability of these species. * indicates species with less than 20 stems available

		Villages		Sikumi forest reserve				
		people		People		Elephants		
	Species	**PR**	**Category**	**PR**	**Category**	**PR**	**Category**	**Resprouting ability**
Preferred or used by all								
BS	*Brachystegia spiciformis*	4,25	Preferred	1,59	Preferred	2,54	Preferred	high
TS	*Terminalia sericea*	5,78	Preferred	3,51	Preferred	2,94	Preferred	high
KAC	*Kirkia acuminata*	U*	Used & Rare	9,21	Preferred	1,77	Preferred	Probably
ANI	*Acacia nigrescens*	1,25	Preferred	U*	Used & Rare	U*	Used & Rare	Yes
Ignored by all								
VI	*Diospyros quiloensis*	0,4	Avoided	0,42	Avoided	NU	Avoided	Probably
FO	*Friesodielsia obovata*	NU	Avoided	0,18	Avoided	0,18	Avoided	Unknown
FV	*Flugia virosa*	NU	Avoided	0,57	Avoided	0,09	Avoided	Unknown
PAN	*Vangueria infausta*	0,3	Avoided	NU	Avoided	0,14	Avoided	Probably
BP	*Bauhinia petersiana*	0,29	Avoided	NU*	Avoided	NU*	Avoided	Yes
Preferred by people in villages but ignored by people in SF and elephants								
BM	*Baphia massaiensis*	1,23	Preferred	0,39	Avoided	0,73	Avoided	Yes
CA	*Combretum apiculatum*	1,67	Preferred	0,66	Avoided	0,66	Avoided	high
CC	*Combretum collinum*	2,06	Preferred	0,73	Avoided	0,73	Avoided	Yes
Used by people in the villages and by elephants in SF								
CPS	*Markhamia zanzibarica*	1,25	Preferred	0,59	Avoided	1,58	Preferred	Probably
BPL	*Julbernardia globiflora*	U*	Used & Rare	0,49	Avoided	1,15	Preferred	Yes
Preferred by people in the villages but rare is SF								
CMA	*Commiphora malothi*	1,82	Preferred	NU*	Avoided	U*	Used & Rare	Probably
CZ	*Combretum zeyheri*	1,21	Preferred	NU*	Avoided	NU*	Avoided	high
CM	*Colophospermum mopane*	3,1	Preferred	U*	Used & Rare	NU*	Avoided	high
Avoided by elephants but preferred by people in SF								
EZ	*Pteleopsis anisoptera*	U*	Used & Rare	1,71	Preferred	0,57	Avoided	Probably
CFL	*Combretum psidioides*	0,92	Neutral	1,37	Preferred	0,69	Avoided	Unknown
SM	*Baikiaea plurijuga*	NU*	Avoided	1,16	Preferred	0,19	Avoided	Yes
DC	*Erythroxylum zambesiacum*	NU*	Avoided	2,57	Preferred	0,57	Avoided	high
DCI	*Canthium frangula*	NU*	Avoided	1,63	Preferred	NU	Avoided	high
DQ	*Strychnos madagascariensis*	NU*	Avoided	1,83	Preferred	NU	Avoided	Probably
MZ	*Dichrostachys cinerea*	0,15	Avoided	1,37	Preferred	0,92	Neutral	Yes
GM	*Grewia monticola*	0,28	Avoided	U*	Used & Rare	NU*	Avoided	Yes
Used by elephants but avoided by people								
JG	*Pterocarpus angolensis*	0,43	Avoided	NU	Avoided	2,73	Preferred	high
CP	*Commiphora pyracanthoides*	0,27	Avoided	NU	Avoided	U*	Used & Rare	Yes
PA	*Diplorynchus condilocarpon*	0,65	Avoided	NU	Avoided	0,96	Neutral	high
Only available in Villages								
AN	*Acacia nilotica*	0,98	Neutral		Not available		Not available	high
AT	*Acacia tortilis*	0,28	Avoided	NA	Not available	NA	Not available	Yes

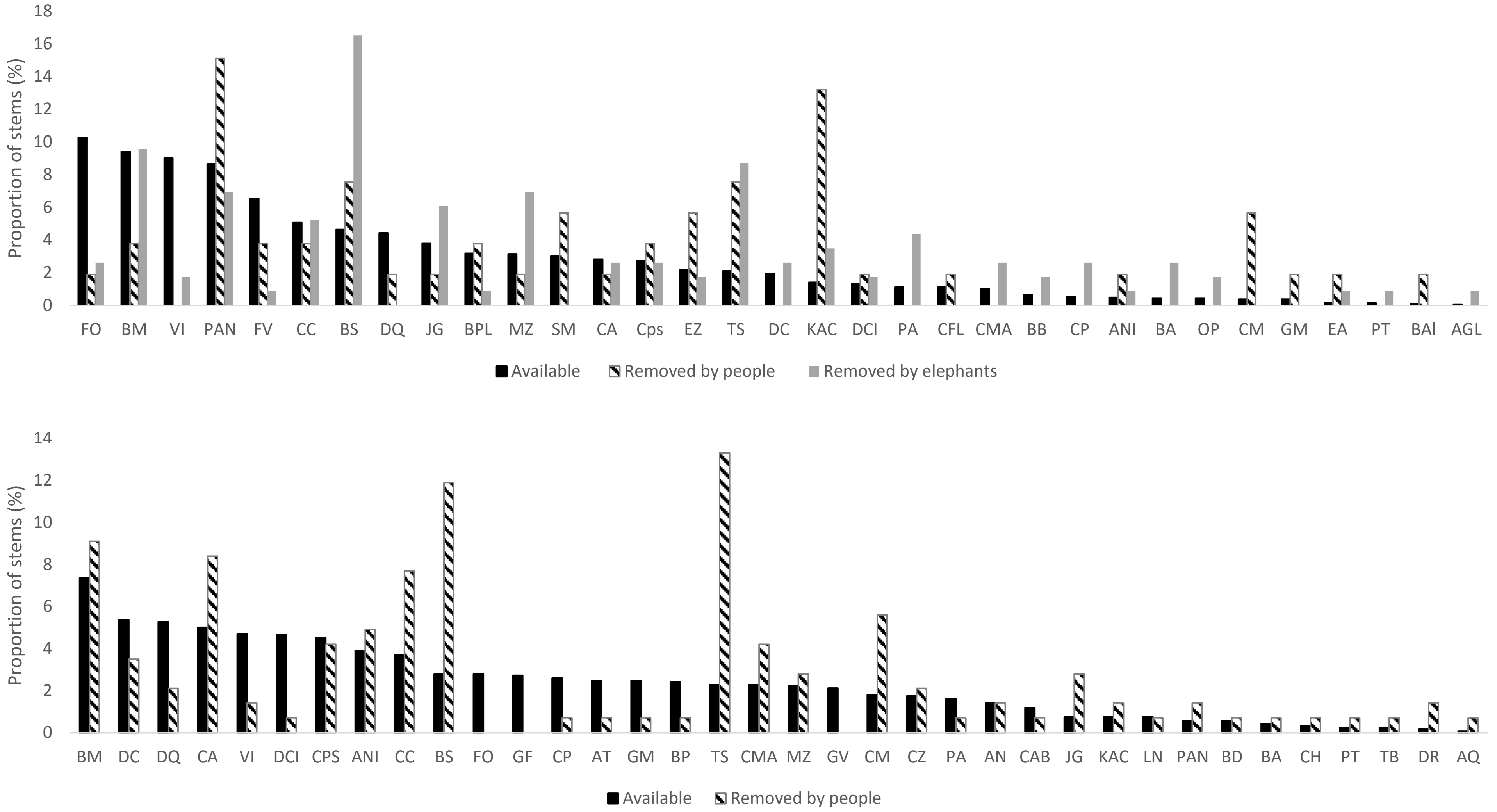

Figure 4: The relative abundance and utilisation of species by people and elephants within a) the Sikumi Forest Reserve (of the 1852 stems available), where human utilisation of woody species is restricted to collection of firewood and poles, and b) communal land (of the 1617 stems available), where human utilisation is not regulated. The black bar represents that proportion of all stems that were of each species. The grey and stippled bar represent the proportion of all utilised stems that were of that species. These bar graphs include any species removed by either people or elephants and the most abundant species in each location.

Table 5: Size class preference for the five most preferred species (these species were species preferred by both elephants and people or the top 2 preferred species from each location). NU indicates size classes that were not used. NA indicates size classes that were not available. * indicated that there were less than 5 stems available

	1		2		3		4		5	
	PR	**Cat**	**PR**	**Cat**	**PR**	**Cat**	**PR**	**Cat**	**PR**	**Cat**
a) ***Brachystegia spiciformis***										
People in CA	0,87	Avoided	1,05	Neutral	2,46	Preferred	NA		NU	Avoided
People in SF	NU	Avoided	NU	Avoided	1,99	Preferred	NU	Avoided	3,76	Preferred
Elephants	0,44	Avoided	1,35	Preferred	1,36	Preferred	1,93	Preferred	NU	Avoided
b) *Terminalia sericea*										
People in CA	1,17	Preferred	0,88	Avoided	NU*		NA		NA	
People in SF	1,95	Preferred	1,49	Preferred	NU	Avoided	NU	Avoided	NA	
Elephants	0,92	Neutral	1,18	Preferred	1,14	Preferred	NU	Avoided		
c) *Kirkia acuminata*										
People in CA	NU*		U*		2,93	Preferred	NU	Avoided	NU	Avoided
People in SF	U*		NU*		3,52	Preferred	0,75	Avoided	0,53	Avoided
Elephants	NU*		U*		2,88	Preferred	1,23	Preferred		
d) *Markhamia zanzibarica*										
People in CA	0,4	Avoided	U*		NA		NA		NA	
People in SF	NU	Avoided	1,8	Preferred	NU	Avoided	NA		NA	
Elephants	0,7	Avoided	0,5	Avoided	6,1	Preferred	NA		NA	

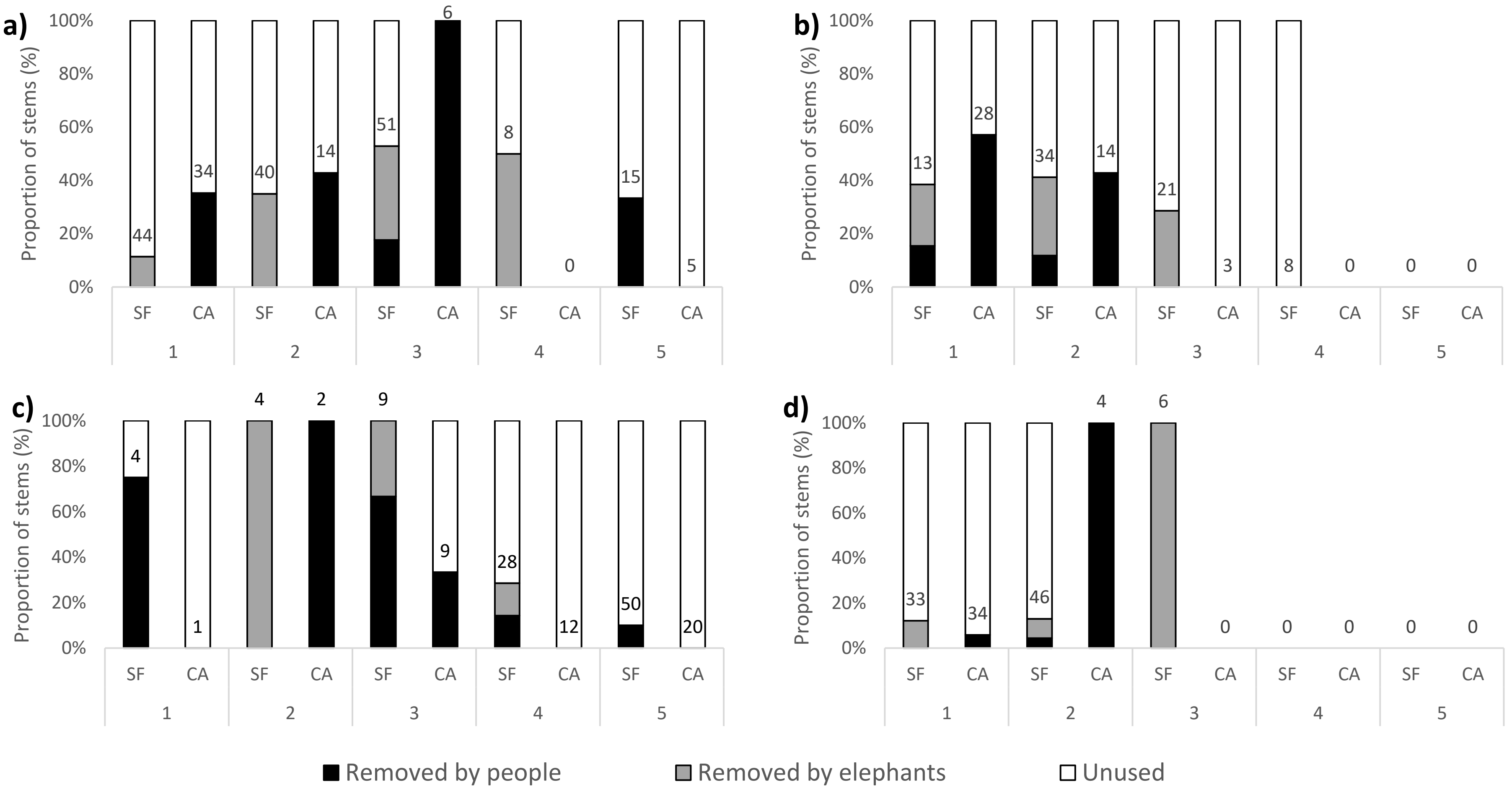

Figure 5: The relative abundance and utilisation of size classes of a) *Brachystegia spiciformis*, b) *Terminalia sericea*, c) *Kirkia acuminate* and d) *Markhamia zanzibarica* by people and elephants within the Sikumi Forest Reserve and communal land. The numbers above each graph are the number of available stems for each category.

Discussion:

Both people and elephants remove woody biomass, but it is important to compare how these two disturbances may differ. Therefore, the aim was to identify utilisation overlaps between these two agents of disturbance. Testing whether they show a preference for similar species and size classes as to better understand the potential impacts vegetation structure and composition. Elephants and people do not prefer the same species or size classes, which will likely lead to differences in species composition between areas with people and elephants. Although some of these differences could potentially be mitigated as there is a large overlap in utilisation as people can potential use all species and size classes utilised by elephants and the high regeneration ability of many of these species.

Species preference:

Eighteen species are preferred by people (10 in each the SF and CA and two in both), whereas elephants only showed a preference for six species. Only four species were preferred by both people and elephants. It is reasonable to assume that tree loss is more likely in preferred species, as these species experience higher levels of impact than expected by chance. A species' high preference or utilisation level does not necessarily indicate the threat of local extirpation and changes to the vegetation composition (O'Connor *et al.* 2007). It is therefore important to consider the species' potential for regrowth when evaluating potential changes to vegetation composition due to elephants (O'Connor *et al.* 2007) or human utilisation. All species preferred by either people or elephants are able to resprout to some degree, although the resprouting ability of *Canthium frangula* is unknown. *Kirkia acuminata* is a candidate for local extirpation from both people (within SF) and elephants; as it is a highly preferred species by both, suggesting a high mortality rate, with an extremely low regeneration ability (O'Connor *et al.* 2007). *K. acuminata* is also rare within the CA which may suggest that humans are facilitating decreases in this species, although repeated sampling studies would be needed to prove their loss in abundance. *Terminalia sericea, Brachystegia spiciformis* (Holdo 2007) and *Colophospermum mopane* will likely be supressed by elephants and people. Local extirpation by people is unlikely for these species, although they are highly preferred species for people their high resprouting ability means they are more likely to experience a state change than die after the disturbance (Holdo 2007; O'Connor *et al.* 2007).

All species preferred by elephants, except *Kirkia acuminata,* experience relatively high resprouting ability, suggesting that in this system elephants will facilitate tree state changes rather than mortality and local extirpation. The relatively low resprouting ability of the species preferred by people but not elephants, suggests that people will likely facilitate decreases in the abundance of *Erythroxylum zambesiacum, Pteleopsis anisoptera, Combretum psidioides, Combretum collinum,* *Strychnos madagascariensis, Baikiaea plurijuga* and *Canthium frangula* while elephants will not. There are only two species preferred by elephants yet avoided by people (*Julbernardia globiflora* and *Pterocarpus angolensis*), both of which show high resprouting ability and can be utilised for fuelwood and carpentry respectively (Luoga *et al.* 2002). Humans will likely facilitate decreases in a higher number of species than elephants, although the effect of elephants on community composition may be mitigated to some extent by the high regeneration ability of the preferred species.

The species utilised by humans and elephants are both affected by what is available (humans: Luoga *et al.* 2002; elephants: Mapaure & Moe 2009). This is partly highlighted by 40.5% overlap of species utilised in both locations the communal lands and the SF. However, it would be misleading to assume that human utilisation within the SF is a true reflection of the choices of the surrounding villages, with regards to the extraction of woody resources, as the removal of woody resources within SF is restricted to the weekly collection of firewood and regulated harvesting of construction poles (per coms. Martin Mzamba). This difference in human utilisation between the SF and CA also indicates that people can be flexible in what species they use, as multiple species (Coates Palgraves 1983; High Branching, 2018) can be used for the same purpose. This suggests that people may be able to, at least to some extent, select species that would be likely used by elephants or those that will be better be able to recover after the disturbance to minimise their impact on the woody plant community.

Elephants can act as the dominant overall agent of mortality and state change for trees (Helm & Witkowski 2012; Cook *et al.* 2017; O'Connor 2017), although the type of impact and mortality rates differ across species (Holdo 2007; O'Connor *et al.* 2007). The mortality rate and type of impact differs across species for human utilisation as well, and specific species may be preferred for different reasons (Jones *et al.* 2016; Luoga *et al.* 2002). It is therefore necessary to consider the type of impact (loss of a branch or main stem, uprooted or ringbarked) experienced by a tree as this will greatly impact the mortality rate (O'Connor 2017). The regeneration ability of a species (Twine & Holdo 2016; O'Connor 2017) and the duration of the disturbance play an important role in determining whether a tree simply changes state or dies after a disturbance. If we are to truly understand how people and elephants potentially change community structure, the regeneration response of trees to human and elephant's utilisation needs to be compared.

Size class preference:

Both elephants and people show a preference for and are likely to facilitate decreases in *Brachystegia spiciformis, Terminalia sericea*, *Kirkia acuminata* and *Markhamia zanzibarica*. It is therefore important to consider size class preferences of these preferred species, as both elephants and people are known to impact the size class distribution and community structure (elephants: Jachmann & Bell 1985; Cook *et al.* 2017, people: Luoga *et al.* 2002). People and elephants show size class preference differences for all of these species, suggesting that human and elephant utilisation is likely to result in differences in the size class distribution of these preferred species

Brachystegia spiciformis is preferred by elephants and people in both the SF and CA but there are differences in size class preferences between the two agents of disturbance. People preferred stems of this between 10 and 20cm in diameter, which are of a suitable size for firewood and construction poles (Abbot & Homewood 1999; Luoga *et al.* 2002). Large *Brachystegia spiciformis* (greater than 40cm in dimeter) were avoided in the CA but preferred in SF, as large trees provide shade to those living within communal areas (Grundy *et al.* 1993). Both people and elephants will likely facilitate decreases in stems with a diameter between 10 and 20 cm, while elephants will likely affect a wider range of stem sizes from 5 to 40 cm.

Terminalia sericea is also a highly utilised species, preferred by both people and elephants. Elephants will likely facilitate decreases in slightly larger *Terminalia sericea* stems than people; who prefer smaller stems, less than 10 cm in diameter, which are ideal for firewood and construction poles (Abbot & Homewood 1999; Luoga *et al.* 2002; Grundy *et al.* 1993). People's size class preference for *Terminalia sericea* differs across the two sites, with people only preferring stems less than 10cm in SF and less than 5 cm in CA. This difference in human preference indicates that people can be flexible in what stems they use as a range of stem sizes (Abbot & Homewood 1999; Luoga *et al.* 2002) can be used for the same purpose.

Kirkia acuminata and *Markhamia zanzibarica* are preferred by people (in SF and CA respectively) and elephants. Elephants prefer and will likely facilitate decreases in slightly larger stems (>11 cm; Mapaure & Moe 2009) than people for both species. *Kirkia acuminata* can be utilised as timber for poles (Maroyi 2017) with stems between 5 and 20 cm in diameter preferred for this purpose (Abbot & Homewood 1999; Luoga *et al.* 2002).

People prefer a wider range of stem sizes than elephants regardless of species, as they showed a preference for stems in all size classes, except for stems between 20 and 40cm in diameter. Although people tend to prefer stems less than 20 cm in diameter, a desired size for firewood and construction poles (Abbot & Homewood 1999; Luoga *et al.* 2002), for all selected preferred species. Elephants prefer stems between 10 and 20 cm in diameter for all selected preferred species. This is consistent with high elephant utilisation resulting in a decrease of intermediate trees, greater than 11 cm (Mapaure & Moe 2009) but less than 40cm (Gadd 2002) in diameter. Although for both *Brachystegia spiciformis* and *Terminalia sericea* elephants also show a preference for smaller stems (5 to 10 cm), both are palatable species (Holdo 2007) with few large stems available. Elephants tend to prefer larger stems than people, for all species except human's prefer *Brachystegia spiciformis* stems larger than 40 cm in diameter within the utilisation regulated SF, suggesting that areas utilised by elephants might result in a more left skewed size-class distribution than people.

In Zambian mopane woodlands, where people typically affect larger trees than elephants (Tripathi *et al.* 2019), contrasting with the results from the Miombo woodlands of north-western Zimbabwe. People in these mopane woodlands were selecting larger stems preferred for charcoal production (Tripathi *et al.* 2019). This highlights that human stem size preference changes according to the needs of the surrounding community and what the felled trees will be used for (Abbot & Homewood 1999; Luoga *et al.* 2002). It is important to consider that the charcoal industry is not prominent in this area of north-western Zimbabwe and much of the resource use is limited to firewood and poles. 90% of the aboveground biomass is suitable for charcoal (Chidumayo *et al.* 1996) and larger stems (as large as 69 cm in diameter; Luoga *et al.* 2002) can be selected for charcoal production than for firewood or construction poles (Abbot & Homewood 1999; Luoga *et al.* 2002). Charcoal is used by 70-90% of the urban population in the Miombo region (Ryan *et al.* 2016), with widespread charcoal production occurring in woodlands surrounding most urban areas (Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010). In areas with a charcoal industry human's stem preference will include larger stems than at the study site, which exceed those preferred by elephants (Tripathi *et al.* 2019). Selective harvesting for charcoal, similar to those species and size classes utilised by elephants, could potentially mitigate some of these differences in impacts on vegetation composition and structure between these two agents of disturbance.

The study site (606 mm MAR) represents extreme low-rainfall Miombo (Miombo is typically found between 500 – 1400 mm MAR) and the vegetation is typically more heterogeneous than classical Miombo areas (Timberlake & Chidumayo 2011). Therefore, the study site will not be representative of the full spectrum of species and size classes available across the region, which change along a rainfall gradient (Campbell *et al.* 1996; Timberlake & Chidumayo 2011). However, I have shown that when faced with the same "available" woody communities, with the SF, there are detectable differences between people and elephants in their utilisation (Tripathi *et al.* 2019). These differences are not to the extent that people are a totally novel ecological and evolutionary force; as there was 68% similarity in both species' preference, 50% similarity in size-class preference and all species and size classes utilised by elephants are or could potentially be utilised by people.

Conclusion:

People could potentially perform a similar functional role to elephants, in removing woody biomass (Frost 1996), potentially preventing some of the consequences of losing an apex consumer from the system and mitigating the effects of woody plant encroachment (Venter *et al.* 2018; Stevens *et al.* 2017), while allowing people vital access to woodland resources (Bond *et al.* 2010).

However, their impacts are not identical, and these disturbances could result in changes to the vegetation composition and structure. Humans prefer more species than elephants, so might filter the canopy layer more strongly. Species preference is highly site specific (humans: Luoga *et al.* 2002; elephants: Mapaure & Moe 2009), which could pose a significant challenge if humans are to mimic elephant impacts. Although, selecting species for utilisation based on the regenerating ability may provide a more practical solution. Elephants' preference for slightly larger stems (Mapaure & Moe 2009) and humans' preference for smaller stems suitable for firewood and construction poles (Abbot & Homewood 1999; Luoga *et al.* 2002), suggests that areas utilised by elephants might result in a more left skewed size-class distribution than people. However, the absence of charcoal activities in this area, and the lack of large trees in the CA means that this is likely to be site specific as the opposite was found in mopane woodlands (Tripathi *et al.* 2019).

Area utilised people and elephants will likely differ in species composition and vegetation structure, due to differences in species and size class prefer between the two agents of disturbance. However, these influences on community composition and structure could be mitigated to some extent due to the large overlap in stems used by people and elephants, that people are relatively flexible in the stems they are able to use for a specific purpose and the high regeneration ability of many of these species.

Chapter 4

Synthesis and discussion

Contrasting biomass change facilitated by humans and elephants

People and elephants are important predictors of treefall (Mograbi *et al.* 2017) and woody biomass loss. The degree of biomass change depends on the intensity of influence (primarily population density) and other environmental factors. Biomass loss increases with human influence (increased population density and a shorter travel time to major cities), as transport costs to the urban consumers are minimised (Ahrends *et al.* 2010). Higher elephant density results in increased biomass removal, with net biomass loss only occurring above ~1.4 elephant/km^2. The responses of biomass change to rainfall differs between NNR, under elephant influence, where biomass gains are more likely under wetter conditions and the rest of northern Mozambique, under human influence, where rainfall has little effect on biomass change.

The Miombo woodlands were estimated to contain between 1.4 elephants/km^2 (Robson *et al.* 2017) and 2.5 elephants/km^2 (Hempson *et al.* 2015) before human influence and hunting with guns; 1.4 elephants/km^2 is therefore a conservative estimate of past elephant density. Estimates of past elephant impacts can help guide what current levels of human facilitated biomass loss are appropriate, to maintain ecosystem function. In areas of high human population density, people consistently remove more biomass than past elephants would have, regardless of initial biomass or rainfall. The high human densities therefore probably represent a disturbance to Miombo that it did not evolve with. These regions near urban areas and along main roads (high human influence) are therefore areas of concern due to the high levels of biomass loss (Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010). Elephant impacts were probably higher than current human impacts in low-rainfall areas (Guldemond & Van Aarde 2008), which means that people could theoretically utilise these areas more intensely. Therefore, lower-rainfall regions could potentially handle increased human influence before exceeding the estimated historical elephant-facilitated losses. Promoting woodland utilisation in lower rainfall (< 1150 mm MAP) and low human influence areas without elephants could provide additional income to rural communities (Misana *et al.* 1996) while maintaining the important disturbance of removing woody biomass (Frost 1996) and preventing bush encroachment (Stevens *et al.* 2017). This could help alleviate the pressure on the current hotspots of overharvesting surrounding areas of high human influence.

People and elephants are performing a similar functional role in removing woody biomass and encouraging coppice regrowth (Frost 1996), although there may be differences in emergent properties, such as in changes to savanna composition and structure. Therefore, the species and size class preference of humans and elephants were compared to identify utilisation overlaps, indicating potential similarities in their impacts on vegetation structure and composition.

Species preference

Both people (Luoga *et al.* 2002; Jones *et al.* 2016) and elephants (Barnes 1979; Owen-Smith 1988; Mapaure & Moe 2009) show a preference for specific species. Area utilised people and elephants will likely differ in species composition, due to differences in species preferred between the two agents of disturbance. Elephants, that appear to be more specialised in their species preferences than people, will likely facilitate decreases in a fewer number of species than people, who are more generalist in their harvesting activities. However, these influences on community composition and structure could be mitigated to some extent due to the large overlap in stems used by people and elephants, that people are relatively flexible in the stems they are able to use for a specific purpose and the high regeneration ability of many of these species. If we are to truly understand how people and elephants potentially change community structure, the regeneration response of trees to human and elephant utilisation needs to be compared.

Size class preference

People (Abbot & Homewood 1999; Luoga *et al.* 2002) and elephants (Barnes 1979; Owen-Smith 1988; Mapaure, & Moe 2009) show a preference for specific size classes. Elephants tend to prefer slightly larger stems overall, while humans use smaller stems suitable for firewood and construction poles (Abbot & Homewood 1999; Luoga *et al.* 2002). This suggests that areas utilised by elephants might result in a loss in more left skewed size-class distribution (a loss in big trees but an increase in smaller stems) than people. However, the Hwange system that I studied is different from much of the Miombo in that there is no charcoal industry, only fuelwood harvesting. Stems as large as 69 cm can be used to make charcoal (Luoga *et al. 2002*), this exceeds the largest (<40 cm) stems utilised by elephants (Gadd 2002). Therefore, in areas where charcoal production is present people could potentially utilise larger stems than elephants do (Tripathi *et al* 2019).

Improvements and future research

The low explanatory power of the models (particularly those in areas of human influence) suggests that there are other important explanatory factors for biomass change, or that these processes are operating at a different scale. The data that I had available represented net change in woody biomass (i.e. growth minus losses). Although I included most of the factors that might affect biomass loss, plant species richness (Li *et al.* 2018), dominance biomass (Pelletier *et al.* 2017) and soil nutrients (Frost 1996) are all potentially important determinates of tree growth that I did not include. There are no good predictive models of woody biomass accumulation for these ecosystems yet, although the SEOSAW project (https://seosaw.github.io/) is working on developing these. My modelling approach was also relatively simple and did not include interactions between explanatory factors. Incorporating interactions between factors will likely improve the explanatory power of the models, as the Miombo is a complex system with interacting components (Frost 1996). Scale can play an important role in determining how important a factor is, in NNR fire frequency influenced biomass at a plot level but only when interacting with MAP on a landscape scale (Ribeiro *et al.* 2008a). This study investigated biomass change at a 1km^2 resolution which is relatively coarse. It would be interesting to investigate the effect of scale on what drives biomass change; these biomass data are available at a much finer resolution of 25m^2.

Trees in this region are highly adapted to recovering after a disturbance event by regenerating from stumps and roots (Luoga *et al.* 2004; Chidumayo & Frost 1996). The only way that I included this in the model was to have a term that accounted for initial biomass – under the assumption that systems regrowing from past disturbance will probably be growing faster than systems that are less disturbed. However, there are probably more sophisticated ways to account for this. Little is known about how regeneration differs between disturbances by people and elephants or the effects of interactions with factors such as: soil nutrients, water availability or the season of the disturbance. Rainfall was a key driver in the biomass change models and to a large extent determined under what conditions people could potentially remove more biomass. The responses of biomass change to rainfall differs between NNR, under elephant influence, where biomass gains are more likely under wetter conditions and the rest of northern Mozambique, under human influence, where biomass gains are more likely under drier conditions. The mechanism behind the different responses to MAP within NNR and across the rest of northern Mozambique need further investigation. To disentangle whether these different responses are simply due to the lower levels of elephant impacts under more mesic conditions, difference is in the seasonality of impacts or if the woodlands are better at responding to disturbances from elephants than people, influencing their ability to regrow.

Conclusion

Current levels of woody biomass harvesting across the Miombo are potentially sustainable, as biomass losses are offset by extensive growth (McNicol *et al.* 2018). This is only the case when harvested areas are allowed to regrow naturally. However, if they are classified as “degraded” or “deforested” and ploughed or turned into settlements this is not the case. Therefore, it is very important to demonstrate that heavily harvested parts of Miombo are actually part of the natural cycle of these woodlands, and need to be incorporated into conservation programs, not excluded from them.

The issue is that biomass losses are concentrated in areas of high human influence, near urban areas and along major transport routes (Figure 1a: Ryan *et al.* 2012; Ryan *et al.* 2014; Luoga *et al.* 2002; Misana *et al.* 1996; Ahrends *et al.* 2010). The information presented here suggests that if the charcoal industry were more dispersed, it might be a better ecological fit to the woodlands. As encouraging small-scale charcoal production throughout the woodlands and in low rainfall and low human influence areas, could alleviate the pressure on the current hotspots of overharvesting. These overharvesting hotspots are being utilised at much higher pressures than in the past, while other areas remain underutilised. Charcoal is a key driver of biomass loss across the region (Ahrends *et al.* 2010; Luoga *et al.* 2004). However, ecological representativeness isn't the only consideration here. Evidence from South America shows that once forests are opened up with roads and made accessible, it is not possible to control the degree to which they are used (Laurance *et al.* 2001; Laurance *et al* 2004; Rudel *et al.* 2009). Therefore, the current situation of excessive extraction close to cities, and not high enough further from cities might actually be the most socio-ecologically sustainable, even if not the most representative of past disturbance regimes.

While humans prefer smaller stems and a wider range of species than elephants in the Miombo woodlands of north-western Zimbabwe, these differences are not to the extent that people are a totally novel ecological and evolutionary force. It is important to remember that human species and size class preference depend on what the stems are being used for. This region of Zimbabwe does not have a charcoal industry, but in Zambian mopane woodlands where charcoal is frequently produced people selected larger stems than elephants (Tripathi *et al.* 2019), opposite to that found was in this study. Therefore, when developing wood harvesting management plants, species and size class selection could also be adapted to what would most likely be used by elephants or species with high regeneration ability (O'Connor 2017), to minimise the potential differences in the emergent community composition and structure.

Elephant utilisation was unlikely to have been uniform in the past. Data from other ecosystems indicates that elephants utilise areas near rivers far more than the inter-river areas; as elephants are water dependent species and spend much of their time within aproximately 16km of permanent water (Gaylard 2003; de Beer *et al.*2006; Robson *et al.* 2017). Moreover, areas near permanent water end up accumulating elephant impacts throughout the dry season, when their impacts tend to be greatest (Barnes 1979; Loarie *et al.* 2009; Owen-Smith 1988), while they are more dispersed in the wet season.

Thus, there would also have been patches of heavily and less heavily utilised areas in an elephant – mediated Miombo disturbance regime.

Overall elephant impacts (Figure 1b) are theoretically more randomly distributed across the landscape (Botha *et al.* 2002) than human impacts (Figure 1a) which are concentrated round settlements and major roads. Although elephants do have a greater impact near permanent water, 98% of the Miombo region is within 16km of permanent water (Appendix B) and therefore most of the region could be considered near water.

Human utilisation of Miombo woodlands is a contentious topic, that challenges ecologists, sociologists, and economists to reassess their value judgements and work together to provide guidance on how to create sustainable ecosystems that also provide for their inhabitants. The good news is that unlike many ecosystems globally, the Miombo is adapted to utilisation and disturbance, and this increases the range of management/human use options available. In fact, it could be argued that people are an essential part of a healthy Miombo ecosystem. This thesis does not fully explore the socio-ecology of this issue, but it does provide useful scientific information on our best understanding of past disturbance regimes in these systems, and how they compare with what is observed currently in regions with different types of human utilisation. Ideally the information presented here on size-class preference of people and elephants, and on how harvesting rates compare at different human and elephant densities can help to feed into more informed forest management policies, which currently use very crude estimates of the total allowable cut in different forest types (World Bank, 2018). It is clear that applying forest management principals developed in other ecosystems, which haven’t had mega-fauna for thousands of years, cannot be cut and pasted into African ecosystems, where our mega-fauna were an active and integral part of the ecology until a few hundred years ago. This MSc should help to demonstrate this and encourage African forest managers to develop their own policies that work for their ecosystems.

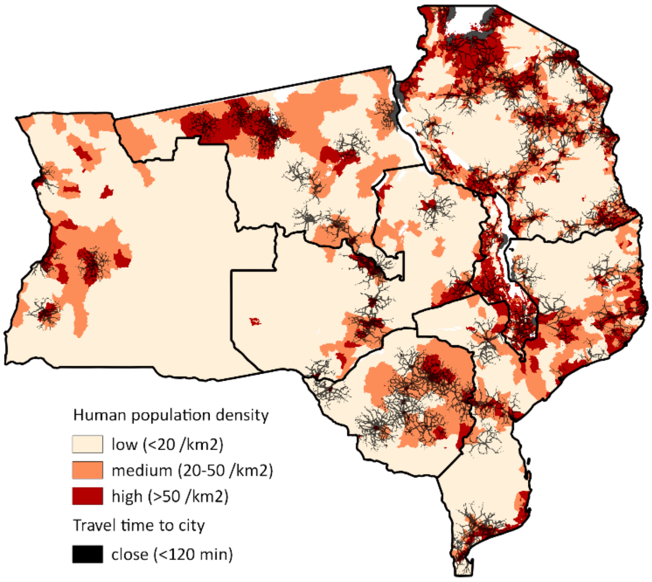

Figure 1a: Human impacts, and the greatest levels of biomass loss, tend to be concentrated around areas of high population density and near major cities. The red, orange and grey areas are therefore likely to be hotspots of biomass change. The region is also covered by large areas of low human utilisation (peach colour).

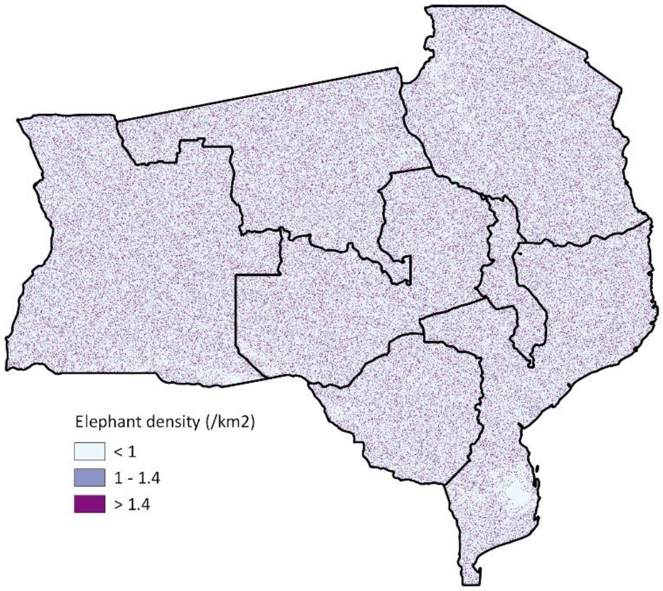

Figure 1b: Estimated past elephant density across the Miombo region (Appendix B). Estimated elephant densities range from 0 to 3.11 elephants/km^2. Areas further than 50km from permenent water have lower predicted elephant densities, see the light area in south-eastern Mozambique, than areas closer to water. There is a mosaic of elephant density across these areas closer to water, with areas of relatively high and low density adjacent to each other.

Appendix

Appendix A: model selection for Chapter 2: Biomass change

There was low correlation between all the explanatory variables, indicating that collinearity was not an issue and that all variables could potentially be included in the models (Table A1, A2, A3).

Table A1.1: Correlation table of explanatory variables in the regional model

	MAP	Travel Time	Population density	% crops	Fire frequency
MAP	1.00				
Travel Time	0.07	1.00			
Pop density	-0.16	-0.06	1.00		
% crops	0.08	0.01	0.12	1.00	
Fire frequency	0.25	-0.01	-0.13	-0.02	1.00

Table A1.2: Correlation table of explanatory variables in the local, northern Mozambique, model

	MAP	Travel Time	Population density	% crops	Fire frequency
MAP	1.00				
Travel Time	0.22	1.00			
Pop density	-0.21	-0.10	1.00		
% crops	0.14	0.19	0.16	1.00	
Fire frequency	-0.10	0.02	-0.11	-0.12	1.00

Table A1.3: Correlation table of explanatory variables in the Niassa National Reserve model

	MAP	Population density	slope	Fire frequency
MAP	1.00			
El_km2	0.03	1.00		
slope	0.21	-0.06	1.00	
Fire frequency	-0.10	0.32	-0.06	1.00

Table A2.1: Selection parameter for candidate GAM explaining variation in biomass change in areas under human influence at a regional scale across Zimbabwe and central and northern Mozambique.

Candidate models	df	AIC	Δ AIC	GCV	R2	Deviance explained (%)
(x,y) + pop + travel + MAP + crop + fire + factor(BM07_class)	**51,81**	**131362**	**0,00**	**0,28**	**0,27**	**27,13**
(x,y) + pop + travel + MAP + crop + factor(BM07_class)	49,33	131440	78,28	0,28	0,27	27,05
(x,y) + pop + travel + MAP + factor(BM07_class)	48,23	131482	119,53	0,28	0,27	27,02
(x,y) + pop + travel + MAP	46,28	131719	357,10	0,28	0,27	26,81
(x,y) + pop + travel	35,22	132655	1292,37	0,28	0,26	25,97
(x,y) + pop	33,93	132735	1373,23	0,28	0,26	25,90
Pop	5,00	156592	25229,3	0,37	0,02	1,68
Null	2,00	158021	26658,6	0,38	0,00	0,00

The candidate models indicate the variable included in each model. The model with the lowest Akaike information criterion (AIC) value was selected (bold), as it has the best explanatory power (Wood 2006; Zuur et al. 2009). Generalised cross validation (GCV) is similar to AIC in that the value can be used to help decide the most appropriate model criteria. GCV are typically used to determine appropriate smoothing parameters, such as the number of knots for each term (Wood 2006; Zuur et al. 2009).

Table A2.2: Selection parameter for candidate GAM explaining variation in biomass change in areas under human influence across northern Mozambique. Including % area covered by crops did not improve the model ($F_{1, 17343.42}$= 0.05, P = 0.82).

Candidate models	df	AIC	Δ AIC	GCV	R2	Deviance explained (%)
(x,y)+ pop + travel + MAP + fire + factor(BM07_class)	**55,44**	**21133,42**	**0,00**	**0,20**	**0,15**	**15,07**
(x,y) + pop + travel + MAP + crop + fire + factor(BM07_class)	56,43	21135,35	1,94	0,20	0,15	15,07
(x,y) + pop + travel + MAP + factor(BM07_class)	53,22	21196,03	62,62	0,20	0,14	15,07
(x,y) + pop + travel+MAP	51,21	21230,18	96,76	0,20	0,14	14,74
(x,y) + pop + travel	44,08	21466,88	333,46	0,20	0,13	14,55
(x,y)+ pop	33,52	21514,33	380,91	0,20	0,13	13,31
pop	4,94	23732,05	2598,64	0,23	0,01	12,97
Null	2,00	20652,99	526,62	0,24	0,00	0,00

Table A2.3: Selection parameter for candidate GAM explaining variation in biomass change in Niassa National Reserve. Including slope did not improve the model ($F_{2.55,18336.39}$= 2.56, P = 0.06).

Candidate models	df	AIC	Δ AIC	GCV	R2	Deviance explained (%)
(x,y) + El_km2 + MAP + fire + slope + factor(BM07_class)	44,067278	9282,92	0,00	0,09	0,501	49,71
(x,y) + El_km2 + MAP + fire + factor(BM07_class)	**41,366448**	**9292,37**	**9,45**	**0,09**	**0,50**	**49,67**
(x,y)+ El_km2 + MAP + factor(BM07_class)	39,297431	9299,97	17,05	0,09	0,50	49,64
(x,y) + El_km2 + MAP	37,317347	9355,45	72,53	0,10	0,49	49,49
(x,y) + El_km2	34,424359	9617,63	334,71	0,10	0,49	48,78
El_km2	5,979768	19335,73	10052,81	0,16	0,15	15,01
Null	2	22466,56	13183,64	0,19	0,00	0,00

It is important to note that while the smoothing parameters from the original full model were used to calculate the deviation explained (Table A3), factors respond differently when other factors are added to the model. Fire frequency, for example, is clearly an important factor in Niassa National Reserve accounting for 48% of the variation in the model. When fire frequency is the only term in the model biomass clearly decreases as the frequency increases, but when all the other variables are included there is little change in biomass across different fire frequencies.

Table A3: Percentage of variance explained by each term.

Variable	Regional scale	Northern Mozambique	Variable	Niassa National Reserve
x,y	1,84	2,64	x,y	1,13
pop	13,61	14,56	Elephant density	34,53
travel	13,49	14,48		
MAP	12,90	13,87	MAP	20,29
crop	14,11			
fire	14,29	15,30	fire	48,01

Appendix B: Maps of historical elephant estimates

Human encroachment and poaching have reduced elephant populations to a fraction of their former numbers and distribution (Ntumi *et al.* 2009; Misana *et al.* 1996, Hempson *et al.* 2015; Robson *et al.* 2017). Elephants are apex consumers; their loss can have far reaching and unanticipated consequences on ecosystems' structure and functions (Bakker *et al.* 2016; Estes *et al.* 2011; Gill 2015; Hempson *et al.* 2015). Estimates of past elephant densities can assist in determining what disturbance levels are appropriate for the Miombo woodlands.

Mean annual rainfall (Hempson *et al.* 2015) and distance to permanent water (Gaylard 2003; de Beer *et al.* 2006; Robson *et al.* 2017) are determinants of elephant density. Miombo is typically found between 500 – 1400mm MAR (Timberlake & Chidumayo 2011), where elephant densities are expected to be at their maximum (~2.5km^2; Hempson *et al.* 2015). However, elephants are water dependent species and spend much of their time within aproximately 16 km of permanent water (Gaylard 2003; de Beer *et al.* 2006; Robson *et al.* 2017). Distance to permanent water was therefore used to estimate past elephant densities across the region.

For our analysis I used 32 year (March 1984 to October 2015) monthly averages of the surface water occurance data from Pekel *et al.* (2016) at a 30m resolution. At 100% occurance many of the smaller rivers, eventhough they are perennial (Weepener *et al.* 2012), were excluded in South africa. As there are no accurate maps of perennial water bodies across Africa (Kummu et al 2011), I assumed that areas with greater than 80% water occurance over 32 years were permanent water bodies. 80% water occurance includes most of these smaller perennial South African rivers and therefore is an estimate of permanent water. It is important to note that this estimate of permanent surface water may still overestimate and underestimate whether water bodies are permanent or not. A distance to water raster (using Euclidean distance, Spatial Analyst, ArcMap 10.5) was created at 500m resolution across Africa. Elephants are also generally found within 16 km of surface water (Gaylard 2003), although during the wet season they can travel up to 50km from permenent water (Owen-Smith 1988). Therefore the distance to permanent water was grouped into three classes: 0-16 km, 16-50 km and greater than 50 km (Figure A1).

Today many elephants survive only in protected areas (PA), where elephant numbers are often monitored (Robson *et al.* 2017; AED 2016). The maximum elephant density per PA was selected from the African Elephant Database (AED 2016), provided there were at least ten elephants. This ensures that only the highest known elephant density estimates are used. AED (2016) is a database of elephant census data from PAs across Africa between 1985 and 2013. To exclude forest elephants, PAs which are predominantly forest according to White (1983) or PAs which contained forest elephants according to Robson *et al.* (2017) were not included in the analysis. Sites with a PIKE greater than 10% were also excluded as these data would be severely effected by poaching. PAs with no permanent water were excluded.

The median distance to water for each of these PAs was calculated to help eludicate the effect of distance to water on elephant density. The elephant densities from the selected PAs were used to fit a nonparametric (kernel) probability density (R Core Team 2017) for each distance to water class. Past elephant densities across the miombo region (Figure A2) were estimated by random sampling from these distributions according to distance to water class. Past elephant densities were created at a 1km resolution.

Elephant densities within the miombo region are expected to reach a maximum density of approximately 3.11 elephants/km^2. Elephant densities were grouped to represent functional elephant densities: 1) less than 1 elephants/km^2, 2) between 1 and 1.4 elephants/km^2 and 3) greater then 1.4 elephants/km^2. Biomass loss and significant effects on vegetation have been recorded above ~ 1 elephant/km^2 (Baxter & Getz 2005, Mapaure 2013) and the past elephant estimates for Niassa National Reserve was 1.4 elephants/km^2 (Robson *et al.* 2017).

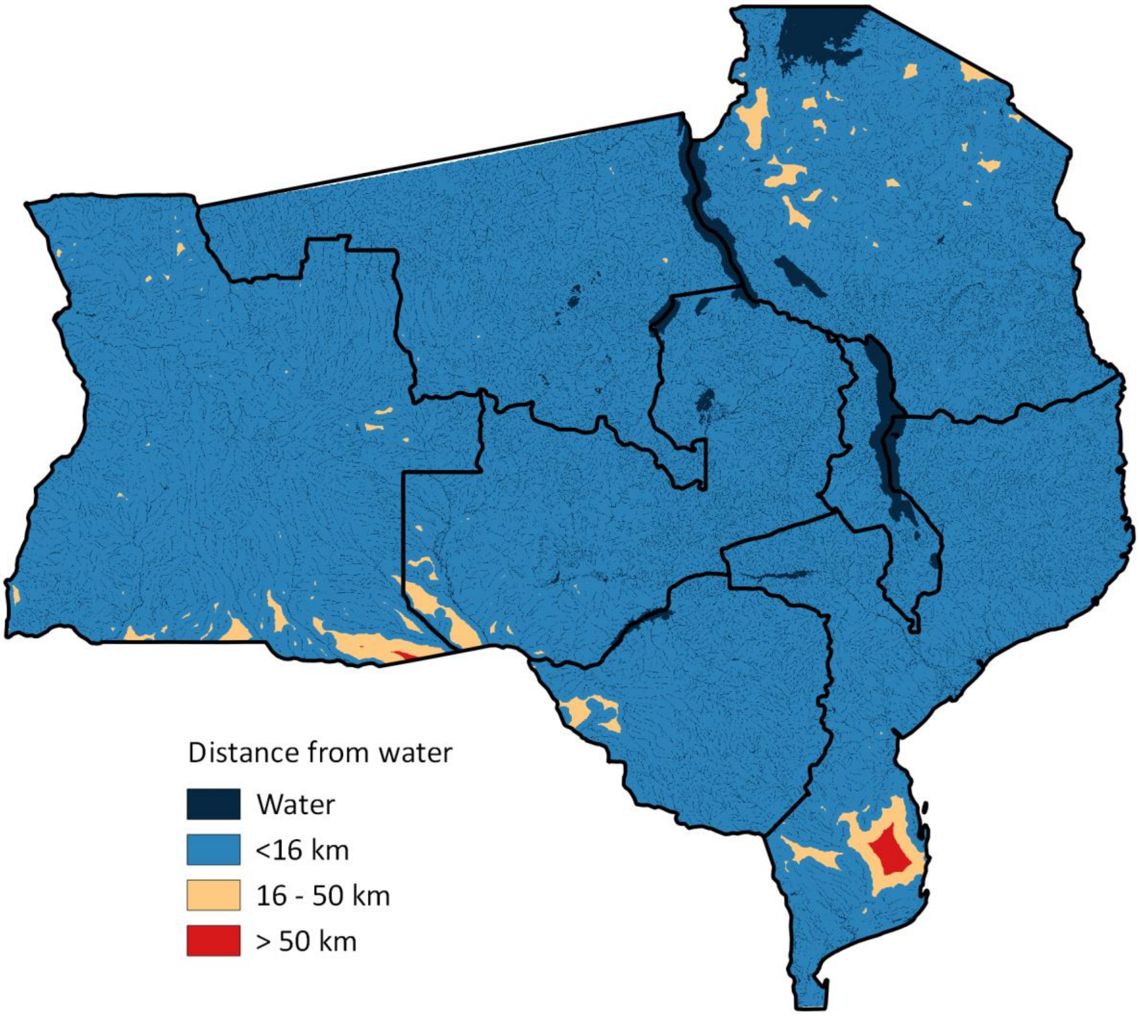

Figure A1: Distance to permenent water classes across the miombo region. Areas where water occurance (Pekel *et al.* 2016) was greater than 80% over 32 years were classified as permenent. 98% of the Miombo region is within 16 km of permenent water. While less than 0.2% of the region is further than 50km from permenent water.

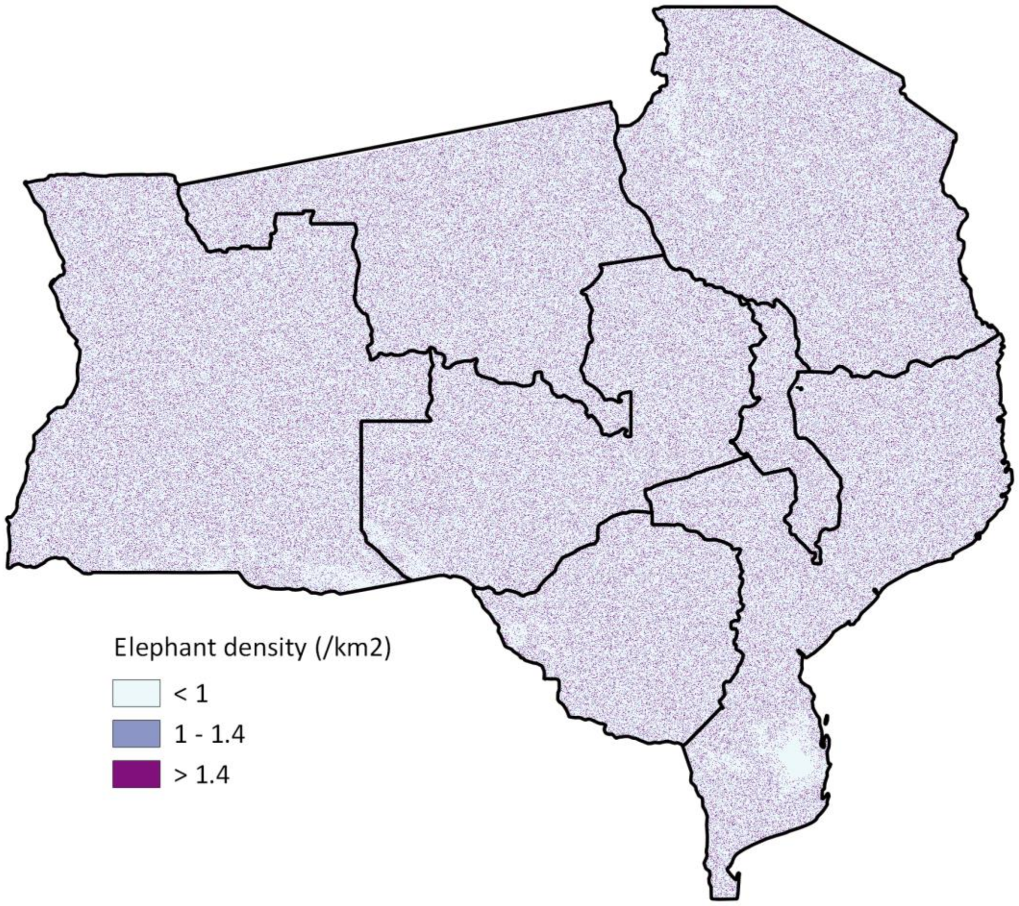

Figure A2: Estimated elephant density across the Miombo region. Estimated elephant densities range from 0 to 3.11 elephants/km^2 . Areas further than 50 km from permenent water have lower predicted elephant densities, see the light area in south-eastern Mozambique, than areas closer to water. There is a mosaic of elephant density across these areas closer to water, with areas of relatively high and low density adjacent to each other.

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