



**Effects of African elephant (*Loxodonta africana*) on
forage opportunities for local ungulates through
pushing over trees**



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Examensarbete
i ämnet biologi

2013:12

**Effects of African elephant (*Loxodonta africana*) on
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**Påverkan av afrikansk elefant (*Loxodonta africana*) på lokala
hovdjurs betesmöjligheter genom trädvältning**

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Keywords: African elephants, cascade effects, forage, treefalls, fallen trees, common duiker; kudu, black rhinoceros, Karoo

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30 hp, A2E

Kurskod EX0633

Program: Skötsel av vilt- och fiskpopulationer - masterprogram

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Umeå 2013

Abstract

African elephants (*Loxodonta africana*) are ecosystem engineers that have the ability to alter the physical structure of the landscape it inhabits and subsequently affect the livelihood of other local species. This study evaluated the landscape and plant level impacts by elephants by means of fallen trees in the Karoo ecosystem. Fourteen transects were walked and found the proportion of fallen trees inside the Kuzuko section of the Addo Elephant National Park was higher than outside the game reserve. Potential shoot bites were higher for standing trees than fallen trees but percentage cover of coppiced re-growth remained similar for all fallen treatments except the Dead treatment. Standing trees were especially important as nurse plants, having a higher density of woody saplings and forbs coverage. Average foliage surface area from the canopy was better than foliage collected from coppiced re-growth outside the reserve. There was a noticeable effect from elephant presence. My data showed that both forage availability and quality decreased from a standing to a fallen tree. However, additional studies should be conducted for a better understanding of foliage quality differences.

Introduction

The study of organisms interacting with other species and their environment is a central topic for ecology (Hastings et al. 2007). Treefalls in any ecosystem is an important structural change that can influence many organism interactions (Whyte 2004). Primary effects may involve the immediate change in forest structure and composition, where habitats and forage opportunities are affected due to alteration of the physical environment and height of forage materials (Makhabu, Skarpe & Hytteborn 2006). Secondary effects include the opening of spaces in the ecosystem for secondary plant growth (Cowling & Kerley 2002). While animals and plants are often impacted by this structural change, there are only a few animals capable of causing treefalls. One example in the North American and European landscape is the North American beaver (*Castor canadensis*), a species well documented for its ability to break trees down and build structures that can modify existing habitats (Johnston & Naiman 1990; Hastings et al. 2007). In the African ecosystem, one animal that share the same treefall capability is the African elephant (*Loxodonta africana*). The largest species among the animals roaming the African savannas, the African elephant can be described as an environment engineer (Jones, Lawton & Shachak 1994; Asner & Levick 2012); these are organisms with the capability to shape and change the physical structure of the landscape they live in. Some studies have suggested that elephant engineering have reduced habitat complexity on the landscape level (Caughley 1976; van Aarde & Jackson 2007) but at the patch scale, this can mean increased exposed woody material and opening of habitats (Pringle 2008; Nasseri, McBrayer & Schulte 2010). While all organisms interact with the physical environment in some manner, the changes that environmental engineers can cause in the environment are at a landscape level and have a greater impact than the typical organism. Many studies have previously been conducted on the impact of elephants in the African savannas (Kohi et al. 2011; Kerley et al. 2008) but the same research has yet to be applied in the Karoo biome. The Karoo is an ecosystem that is vulnerable to degradation and becoming increasingly important to be protected as less than 1% of the ecoregion is conserved (Cowling 1986; Barnard et al. 1998). Furthermore, the study of the cascading effects of elephants is still relatively uncharted. The key to biodiversity and species survival is the ability to fill niches in the environment that allow

certain species to thrive (McNaughton & Wolf 1970). How elephants change the environmental landscape and how animals react to these changes is the central themes to the study of cascading effects. In this study, I explored the topic of the changes that elephants could bring to the environment, both at the landscape level and at the plant level.

My purpose for this study was to investigate a component of the cascading effects and apply it at a landscape level. My interest was to study how elephants can change the Karoo landscape and to what extent does forage opportunities change for other herbivores inhabiting the same areas. Different sized herbivores have different access to resources, depending on their body size and environmental factors like abundance in tree species and distribution of plant material (Gordon 1989). The co-existence of species requires resource partitioning where individual species make use of resources that cannot be utilized by others (Basset 1995). In this study I looked at how different sized herbivores were affected by changes in the landscape and how forage opportunities changed for individual trees when felled and over time.

I was also interested in which tree species was most likely to be found fallen over in the landscape and if the presence of elephants contributed or modified the likelihood of certain tree species falling over. For the landscape level analysis, I hypothesized that as a result of having elephants: there was a significantly higher amount of fallen trees inside a reserve with elephants compared with the sites sampled without elephant presence. I also identified *Pappea capensis* as the tree species with the most dominant effect across the landscape from falling over. I suspected that *Pappea capensis* was one of the most utilized trees by elephants and I would find a significant amount of this species fallen over. This tree is also well represented in the landscape and is an important food resource for local ungulates.

I was particularly influenced by the elephant's role as an environmental engineer and focused my plant level analysis around the concept of fallen trees and how forage opportunities change as a result. As part of the forage opportunities assessment, I also studied the effect of time on fallen trees by sampling forage opportunities across four stages of fallen tree degradation: Recent; Intermediate; Old; and Dead. For my plant level analysis, I chose to conduct the analysis in four components: (1) potential bites in the canopy; (2) amount of coppiced re-growth available; (3) effectiveness as nurse plants; and (4) forage quality difference between canopy and coppiced re-growth. For the plant level analysis, I tested for potential bites and coppiced re-growth using herbivore bite limitation models developed by Wilson and Kerley (2003). These models measured and recorded the bite diameters different ungulates bit for various tree species. The maximum shoot diameters that each ungulate bit were recorded as the measured bite diameters. I included three animal bite models in my study: the common duiker (*Sylvicapra grimmia*), kudu (*Tragelaphus strepsiceros*) and black rhinoceros (*Diceros bicornis*). All three of these species are inhabitants in my study area and were differentiated from each other by the range of their measured bite diameters and forage heights. I only used bite models measured from *Pappea capensis* shoots. I hypothesized that fallen trees would create: (1) additional forage opportunities, particularly for the smaller sized common duiker, in the Recent stage before decreasing over time as fallen trees degrade; (2) more foliage availability from coppiced re-growth compared with standing trees and that forage opportunities would decrease the longer a tree has fallen over because of tree degradation; and (3) opportunities and protection for new growth. I also hypothesized that foliage quality

was more optimal in the canopy layers and that quality would decrease with time in the Old and Dead treatments.

Materials and Methods

Study Area

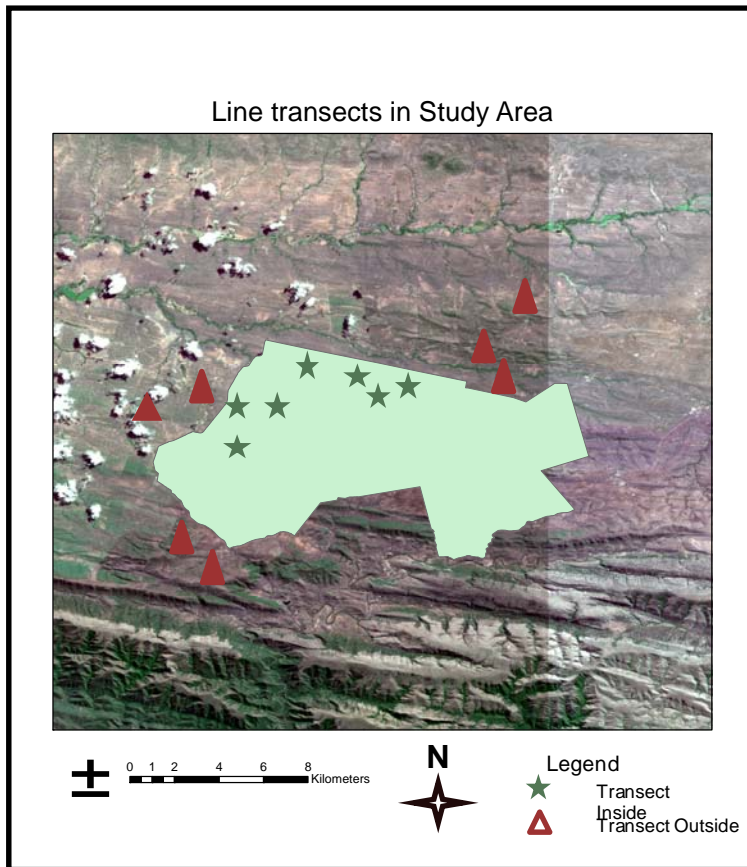
Addo Elephant National Park

In 1931, the Addo Elephant National Park (AENP) was established to protect the African elephants in the Addo area (Hoffman 1993). Since then, the park had expanded and the elephant population had increased to over 550 individuals (Stuart-Hill 1992; Kerley et al. 2008). The expansion of the AENP in 1995 and 2006 had expanded the conservation and management plans of the AENP (SANParks 2008). Conservation efforts in the AENP are no longer focused on the African elephant but include the biome and vegetation types as well as all other components of biodiversity (Kerley & Landman 2006). The AENP is comprised of many different sections, combining to make it the third largest national park in South Africa at nearly 1640 km² (SANParks 2008).

The study was conducted in and around the Kuzuko section of the AENP (Figure 1). The Kuzuko section was a fully enclosed game reserve that, at the time of the study, had a population of twenty-six elephants. The reserve encompass approximately 162km² and is part of the Karoo ecoregion, an important biological hotspot in South Africa that is threatened by land use change from agriculture activities (Lovegrove 1993; Hoffman et al. 1999). Since being established as a game reserve in 2005, Kuzuko had re-introduced some of Africa's big name animals into the reserve to form the Big 5 within the park: the lion, African elephant, buffalo, leopard and black rhinoceros. This makes Kuzuko one of the newest additions to the AENP and also having the distinction of containing the Big 5 animals. The site location previously comprised of twenty-two farmlands that were purchased and were restored to its natural state. Over 2.5km² of invasive plants were removed from the site and in cooperation with the South African National Park (SANParks), the site was re-stocked with various animal species that historically inhabited the region. Although Kuzuko is independently managed, its incorporation into the AENP means that it is under the protection and legislations of SANParks.

The farmlands and other sections of AENP that surround Kuzuko were included in the study to act as control sites where no elephants have utilised for over 150 years. These farmlands are all near-natural sheep farmlands where sheep grazing is the only land use change to the landscape. The inclusion of these outside sites (hereby termed as "No Elephant Sites") provided an opportunity to determine the effects of elephants at the landscape level. By comparing the amount of fallen trees found inside and outside Kuzuko, a macro-level analysis could be conducted to determine how much disturbance is caused by elephants in their environment. While most felled trees found inside Kuzuko could be caused by elephants, this was not the case for the No Elephant Sites. Since there are no elephants in the study sites outside Kuzuko, the cause of these felled trees can be from natural factors like drought, wind throw and soil degradation. Anthropogenic change is not considered a factor since the No Elephant Sites were conducted either on AENP reserves or on domestic farmlands that have not subjected to high levels of land use change.

Figure 1. Kuzuko study area with locations of line transects



Study species

The African ecosystem is one of many animals and plants, many of which are threatened species and require protection. A giant among its landscape, the African elephant is one such species and is my main study species for this project. To measure potential forage opportunities, I chose three species that could represent the size range and feeding abilities of the animals that inhabit the Karoo ecoregion and occurs in my study area. The three species I chose were the common duiker (*Sylvicapra grimmia*), the kudu (*Tragelaphus strepsiceros*) and the black rhinoceros (*Diceros bicornis*). Within my study area, these three herbivores were the smallest, had the highest foraging ability and the largest measured bite diameters respectively. For my landscape level analysis, I was interested in all tree species but for my plant level analysis, I chose to focus the study on the dominant felled tree species. I chose *Pappia capensis* due to its widespread range in the Karoo, as well as its important role as a valuable food source for many herbivores. By sampling only one tree species, I wanted to maintain a consistent measuring method to help reduce variability in my data collection due to different tree forms and sizes.

African elephant

The African elephant (*Loxodonta africana*) is the only animal in the African ecosystem that has the ability to change the structure of its environment. It is a native species to the

African ecosystems but due to poaching, hunting and land use changes, elephant numbers have dropped and the species is currently classified as a Vulnerable species in the International Union for Conservation of Nature (IUCN)'s Red List (Blanc 2008). The well-publicized illegal ivory trade, combined with its status as a vulnerable species, has made the protection of the African elephant a main concern for many conservation programs in Africa. Increasing elephant numbers is a frequent objective for many conservation programs but recent studies have suggested that many nature reserves in South Africa are already housing densities over its natural carrying capacity (Whyte et al. 1999). Opinions are divided whether this over-stocking of elephants in nature reserves is detrimental to the protection of other animals and plants. Some studies have found that high elephant densities are decreasing forage opportunities for other browsers (Whyte et al. 1999) while other studies have evidence showing high elephant numbers are positive for the ecosystem function (Nasser, McBrayer & Schulte 2010). What is undeniable however is the fact that elephants are at the top of the ecosystem ladder and have the innate ability to change its environment due its sheer size, feeding and migration behaviours (Cowling 1986; Landman, Kerley & Schoeman 2008; Duffy et al. 2002; Jacobs & Biggs 2002). Its role as an environmental engineer means it can change both forage availability and quality for other species (Jones, Lawton & Shachak 1994).

Common duiker

The common duiker (*Sylvicapra grimmia*) is one of the smallest ungulates in South Africa, dwarfed in size by its close cousin, the blue duiker (*Philantomba monticola*). Females are generally larger than males, weighing 16 to 21kg compared to males at 15 to 18kg (Skinner & Chimimba 2006). This species is the smallest herbivore in Kuzuko and has a maximum forage height of 2.2 metres (Furstenburg et al. 1996) with a measured bite diameter of 1.36mm (Wilson & Kerley 2003). The common duiker consumes most parts of a plant, although the species seems to prefer foliage and fruits (Wilson 1966). The common duiker has shown signs of high adaptability, persisting in numbers wherever there is low secondary growth (IUCN SSC Antelope Specialist Group 2008).

Kudu

Not including the African elephant, the kudu (*Tragelaphus strepsiceros*) is the highest browsing herbivore in Kuzuko at a height of 2.2 metres (Furstenburg et al. 1996). Although smaller than the black rhinoceros, this species is able to reach higher foliage due to a longer neck. The kudu has a measured bite diameter of 2.63mm (Wilson & Kerley 2003) and are frequently found in scrub woodland and bush that have reclaimed abandoned fields and pastures (IUCN SSC Antelope Specialist Group 2008). It is a common species in Kuzuko and can weigh up 250kg (Skinner & Chimimba 2006).

Black rhinoceros

The black rhinoceros (*Diceros bicornis*) is the third herbivore I chose. It has the largest bite diameter among local herbivores (not including elephants) and weighs between 800 to 1400kg (Skinner & Chimimba 2006). This species is classified as Critically Endangered on the IUCN Red List and is among the most endangered mammals on the planet due to a history of poaching and hunting (Emslie 2012). The black rhinoceros can forage up to a height of 2.0 metres and has a measured bite diameter of 6.83mm (Wilson & Kerley 2003; Mukinya 1977). The black rhinoceros favours palatable woody species and can be found in savannas and succulent valley bushveld areas (Emslie 2012).

Pappea capensis

The tree species I tested foliage opportunities on was the *Pappea capensis*. This tree is an evergreen in the Karoo, providing a source of food for many ungulates all year round. In addition, its broad crown provides essential shade for species inhabiting the semi-arid environment. A multi-stemmed tree, grazing pressure from farm animals has influenced the growth of *Pappea capensis* to reflect growth of traditional single stemmed trees (personal communication, April 24, 2013). There is a strong coppicing effect among the trees I surveyed where many trees have developed re-growth around the stems. This re-growth is an effect of browsing by farm animals and is a sign that the tree is recovering from a long period of browsing pressures. This “coppiced re-growth” as I have termed it, is an important forage material for ungulates, particularly the smaller sized species that cannot reach the tree crown. The re-growth generates low to the stem and is densely grown together. While farm animals are responsible for creating this coppiced effect, the coppiced re-growth is mainly due to decreased grazing pressure and opportunity for the plant to regenerate.

Landscape-level analysis

For the landscape-level analysis, I used the line transect method to sample the amount of standing and fallen trees inside and outside Kuzuko. I walked fourteen transects of each 500 metres in length and 10 metres wide and the locations were randomly distributed throughout the study area. Seven transects inside Kuzuko and seven transects in the No Elephant Sites were walked and sampled for the proportion of fallen trees (Table 1). On each transect, I measured every standing and fallen tree over 1.5 metres tall and recorded the GPS location, tree species and whether it was standing or fallen. My aim was to estimate the average elephant impact for fallen trees across the study area. To provide a more accurate estimation, I avoided sampling near roads, waterholes and waterways. This was because elephants have been observed to favour using roads and desiccated rivers as migration corridors. Each transect walked was spaced a minimum of 100 metres away from waterholes, rivers and roads to avoid over-estimating elephant impact. Increased elephant activities around water holes and migration corridors could potentially bias the amount of fallen trees recorded. Using the collected data, I estimated the fallen trees for all tree species, as well as the proportion of *Pappea capensis* among fallen trees inside and outside Kuzuko.

Table 1. The fourteen transects used for the landscape-level analysis.

Transect	Treatment	Starting GPS
3	Inside	S 33.15039 E25.44847
28	Inside	S 33.15685 E25.43354
1	Inside	S 33.14855 E25.43354
27	Inside	S 33.14266 E 25.40149
16	Inside	S 33.16133 E 25.38097
50	Inside	S 33.16401 E 25.35813
9	Inside	S 33.17673 E 25.34926
49	Outside	S 33.16462 E 25.35448
10	Outside	S 33.17394 E 25.34740
6	Outside	S 33.15647 E 25.47692
41	Outside	S 33.15963 E 25.48952
31	Outside	S 33.15487 E 25.47141
36	Outside	S 33.22322 E 25.35426
19	Outside	S 33.21977 E 25.34914

Plant-level analysis

For the plant-level analysis, I measured standing and pushed over *Pappea capensis* to evaluate the impact of fallen trees on ungulate forage availability. I classified *Pappea capensis* as standing or one of four fallen categories: recent; intermediate; old; and dead (Table 2). For each category, I randomly sampled twenty *Pappea capensis* throughout Kuzuko. I also sampled an additional twenty standing *Pappea capensis* in the outside sites to evaluate how forage availability differed between the standing *Pappea capensis* inside and outside Kuzuko. Forage availability was measured in three separate parts consisting of the potential bites, coppiced re-growth and nursery plants.

Table 2. Tree treatment classifications.

Treatment	Description
Standing (Inside)	Standing <i>Pappea capensis</i> that is over 1.5m tall, located inside Kuzuko.
Standing (Outside)	Standing <i>Pappea capensis</i> that is over 1.5m tall, located in the outside sites.
Recent	A pushed over tree with over 50% of leaves still present. Branches are still oriented the same way as if the tree is still standing. No signs of wood deteriorating. Typically no signs of re-sprouting from the root system.
Intermediate	A pushed over tree with over 50% of leaves missing and mostly wilting. Signs of branches starting positive photoaxic vertical readjustment process. Wood condition still solid but signs of deterioration. May have re-sprouting from the roots.
Old	A pushed over tree with no leaves remaining. Strong signs of branches starting positive photoaxic vertical readjustment process. Wood is deteriorating and easy to snap. May have re-sprouting from the root system.
Dead	A pushed over tree with no leaves remaining and deteriorating of wood. No signs of re-sprouting from the root system.

Potential bites

In this study, I defined the number of potential bites by the number of available shoots that the three different ungulates (common duiker, kudu, and black rhinoceros) could feed on. Using bite diameter models developed by Wilson and Kerley (2003) and maximum forage height information on the three study species (Furstenburg et al. 1996; Mukinya 1977), I was able to replicate the measured bite diameter and maximum forage heights for each of the three ungulates I chose to measure (Table 3). Both measured bite size and height stratification are important limiting factors when calculating forage availability on a tree. For this analysis, I used the bite models corresponding to *Pappea capensis* and only measured the crowns of trees and used the line of the longest canopy width as a measuring transect. Each transect line along the tree crown was two centimetres wide. To maintain a consistent sampling method, I measured the number of shoots that intercepted with the line of the longest canopy width. Using a calliper set at the measured bite diameter, I counted the number of shoots that was under the maximum forage height and intersected with my transect line. I repeated the same process for each of the three ungulates, changing the measured bite diameter and maximum forage height corresponding to the ungulate. To maintain a straight transect, I used a four metre pole to show the transect line. To help with counting and avoid over-estimating potential bites, I used clothespin to mark counted shoots.

Table 3. Measured bite diameter and forage heights of the study species

Ungulate	Measured bite diameter	Maximum forage height
Common duiker	1.36 mm	0.6 m
Kudu	2.63mm	2.2 m
Black rhinoceros	6.83mm	2.0 m

Coppiced re-growth

To account for this food source, I measured the amount of coppiced re-growth by the percentage cover over each the stem(s) of individual trees. I measured this availability for two of the three ungulates, the common duiker and the kudu. The percentage of coppiced re-growth available for the common duiker and kudu was recorded for each tree. The percentage available was recorded separately for both species due to difference in maximum forage heights. For the common duiker and kudu, I recorded coppiced re-growth up to 0.6 and 2.2 metres respectively (Table 3). The percentage was a reflection of coppiced re-growth available on the entire tree and not just up to their maximum foraging height.

Standing and fallen trees as nurse plants

The third set of measurements I took for calculating forage availability was the abundance of forbs and woody seedlings under the tree. For the woody plants, I was able to count each individual plant and for forbs, I estimated the percentage ground cover. For each tree, I measured forbs and woody seedlings both under the tree cover and in a control site that was five metres away. The direction of the control site from the tree was randomly chosen by which direction the “sweep” hand (the second hand) on a watch was pointing. The ground area under a tree was calculated by multiplying the length and width of the tree crown. The same ground area measurement was used for the control site of that tree. I calculated the density of woody species (per metre squared) instead of using woody plant counts to have a standardized measurement.

Forage quality analysis

The fourth analysis I conducted was a forage quality analysis to compare the foliage availability and nutrient quality from bite samples collected in the tree crown and coppiced re-growth among treatments. I studied the quality of forage in two parts: the amount of forage available by bites (calculated by leaf surface area) and leaf greenness as a proxy for the level of nitrogen in the leaves (using photographs of the samples). Leaf greenness as a proxy for nitrogen levels had been used by other studies like the International Rice Research Institute as a grassroots method to quickly determine levels of nitrogen in the field (Witt et al. 2005). Ten trees from each treatment were sampled, including standing trees inside and outside Kuzuko. For each tree, I took three samples from the tree crown and coppiced re-growth respectively (totalling six samples from each tree). Each sample was a 2cm x 2cm square and only the first layer of foliage was collected. For each sample collected, I laid out the foliage collected on an A4 sized white sheet of paper and took a photo of it using a digital camera (flash on). To maintain consistency, each picture was taken under direct sunlight with no shade cover. I used a clear sheet of paper with 4 cm² grids to indicate the scale of the foliage. Those samples with no foliage collected were still recorded. For each of the trees I sampled, I averaged out the leaf surface area and colour saturation separately. Using the software Adobe Photoshop Creative Suites 4, I calculated the total surface area for each sample. Using the same software and photographs, I also did a colour measurement by using the “Colour Sampler” tool. For each photograph, I averaged five randomly selected colour points (only on leaves) using the standard RGB colour

scheme. I did not collect colour samples from the photographs without any foliage collected. The colour saturation measurements from the three samples collected from each tree's tree crown and coppiced re-growth were averaged to provide a general leaf greenness for their respective sections. In total, I had ten averaged leaf surface area measurements and ten leaf greenness measurements for each treatment.

Data analysis

For the landscape level analysis, I tested for significant differences for the proportion of fallen trees inside and outside Kuzuko using the Pearson's Chi-square test. For the plant level analyses, I tested for normality of errors in order to use the standard ANOVA statistical tests but my dataset did not follow these conditions. Since my data did not follow a normal distribution, I employed the Kruskal-Wallis rank sum test (a non parametric statistical method) instead to test for significant differences between treatments. I used the Kruskal-Wallis rank sum test for all response variables, followed by a Kruskal-Wallis Multiple Comparison to test differences among individual treatment levels. All statistical analyses were performed in R (Version 3.01) with the additional package `pgirness` to access the Kruskal-Wallis Multiple Comparison (`kruskalmc`) function. For my forage quality analysis, I followed the same procedures for the surface area component of the study. I was not able to perform a statistical analysis for the nitrogen level/leaf greenness analysis due to the format of the RGB colour system.

For the density in woody plants and forbs cover, I also conducted Correspondence Analyses to determine any associations between treatments and the number of woody plants or percentage forbs cover found. I conducted the Correspondence Analyses in R after installing the 'FactoMineR' package. Because my data had a lot of zeros, I decided to categorize both the woody plant densities and percentage forbs cover. I categorized the woody plant densities into five classes (Table 4) and separated the percentage forbs cover into four classes (Table 5) for this analysis.

Table 4. Classification for the density of woody plants.

Classes	Woody plant densities (per m ²)
Class 1	0
Class 2	0.01 – 0.25
Class 3	0.251 – 0.50
Class 4	0.501 – 0.75
Class 5	0.751 – 1.00

Table 5. Classification for the percentage cover of forbs.

Classes	Percentage cover of forbs
Class 1	0
Class 2	0.01 – 0.05
Class 3	0.06 – 0.10
Class 4	>0.10

For the nitrogen level/colour saturation test, I was unable to perform a standard statistical analysis so I decided to graph the RGB values onto a 3D scatterplot to visually determine differences between treatments instead. I postulated the average RGB values for each sample onto a 3D scatterplot to determine the different levels of greenness for the samples and compared the plotted 3D scatterplot with a standard RGB colour cube, both of which I

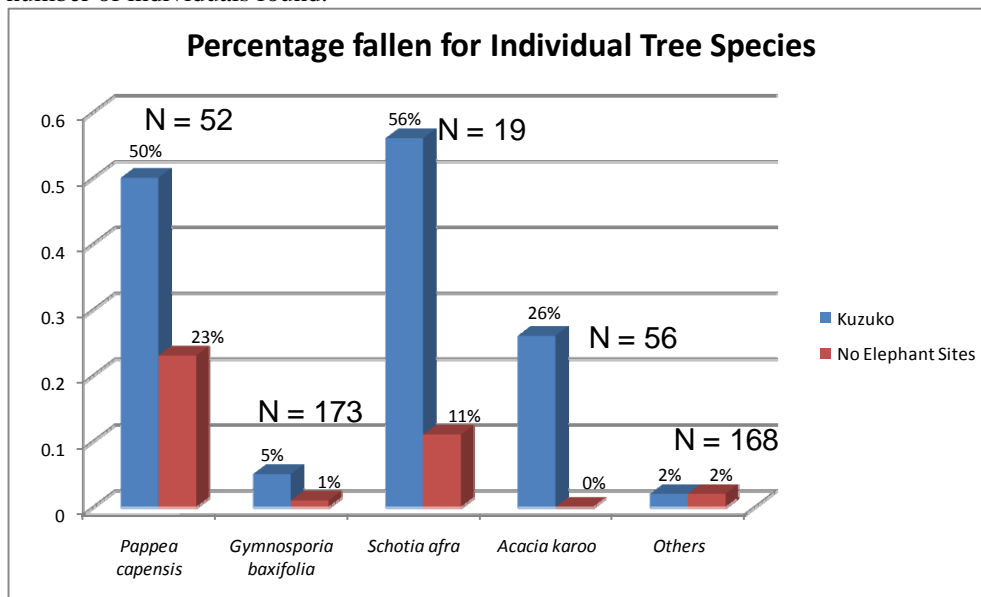
re-created in R. The 'plot3d' function, found in the 'rgl' package was used to create an interactive 3D scatterplot. I used the 'scatterplot3d' package to produce the graphs presented in the result section.

Results

Landscape-level Analysis

Of the fourteen transects I conducted, I recorded 27 out of 243 and 11 out of 244 trees that were fallen inside Kuzuko and in the No Elephant Sites respectively. The proportion of fallen trees I recorded was significantly higher inside Kuzuko than outside ($\chi^2 = 7.38$, $df = 1$, $p = 0.0066$). Among fallen trees, the dominant species recorded was the *Pappea capensis*. Both in Kuzuko and in the No Elephant Sites, I found nearly twice as many fallen *Pappea capensis* as the nearest tree species. I found that the proportion of fallen *Pappea capensis* was higher inside Kuzuko than in the No Elephant Sites ($\chi^2 = 4.11$, $df = 1$, $p = 0.0426$) (Figure 2). Although I found that *Schotia afra* was more prone to have fallen, I recorded only 19 individuals compared to the 51 *Pappea capensis* I counted on my transects. The tree species that I encountered the most was *Gymnosporia baxifolia* with 175 individuals across the study area. However, I rarely encountered fallen *Gymnosporia baxifolia* (Figure 2).

Figure 2. Fallen trees inside and outside Kuzuko, by proportion for individual tree species (n = number of individuals found).



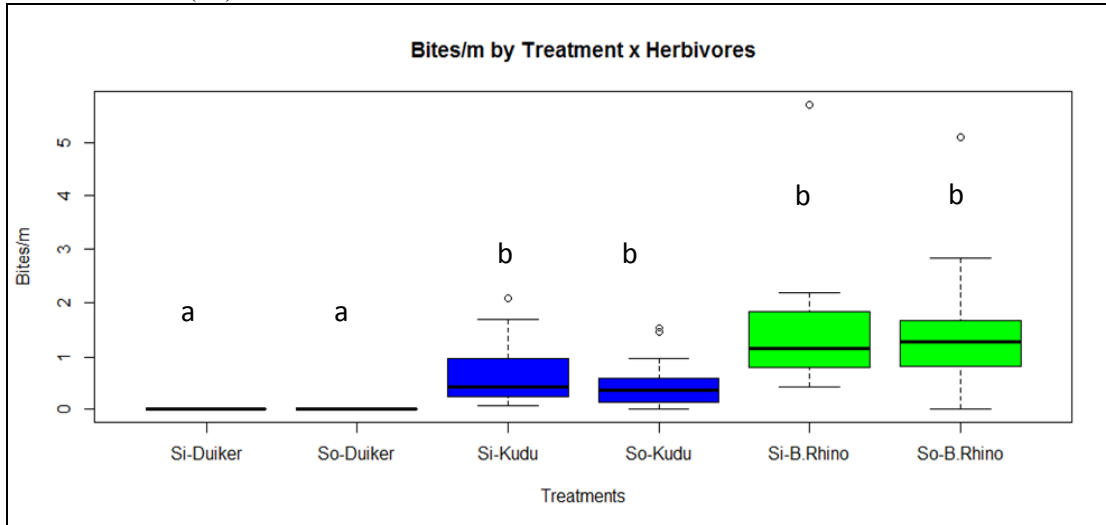
Plant-level Analysis

Potential bites

I found a difference between potential bites sampled from standing trees inside and outside Kuzuko ($H = 88.24$, $df = 5$, $p < 2.2e-16$). However, the difference was between herbivores and not by treatments (Figure 3). Black rhinoceros had on average, the highest number of bites per metre while the common duiker had the least amount of potential bites. Because I did not find a difference for any of the study species potential bites between the standing treatments, I decided to compare only one standing treatment with the fallen tree

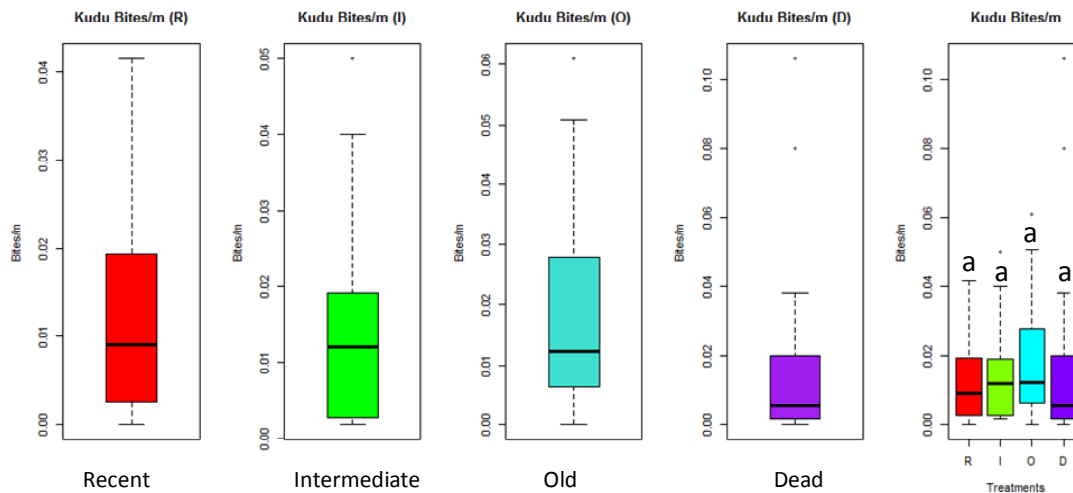
treatments. I chose to test the fallen treatments against the standing inside samples so all treatments could be recorded from inside Kuzuko.

Figure 3. Potential bites for all herbivores, tested between the standing treatments inside (Si) and outside Kuzuko (So).



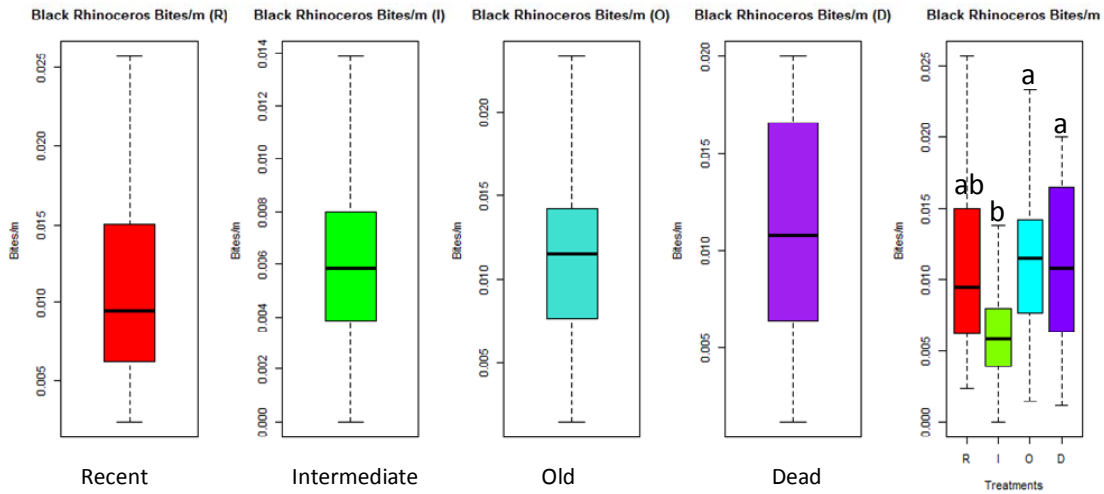
I found a difference between treatments for the common duiker ($H = 10.20$, $df = 4$, $p = 0.04$) but was not able to detect which treatments were different using the Multiple Comparison test. Across all treatments, the number of potential bites that was estimated was near zero with most treatments not recording a single bite during my sampling stage. The maximum number of potential bites that I predicted for the common duiker was in the Dead treatment with 0.005 bites per metre. For the kudu, I recorded higher number of potential bites for the standing treatment compared with the fallen treatments ($H = 49.03$, $df = 4$, $p = 5.75e-10$). Excluding the standing treatment, I did not find a difference between the fallen treatments ($H = 2.96$, $df = 3$, $p = 0.3984$) (Figure 4).

Figure 4. Potential bites sampled for kudu in fallen treatments.



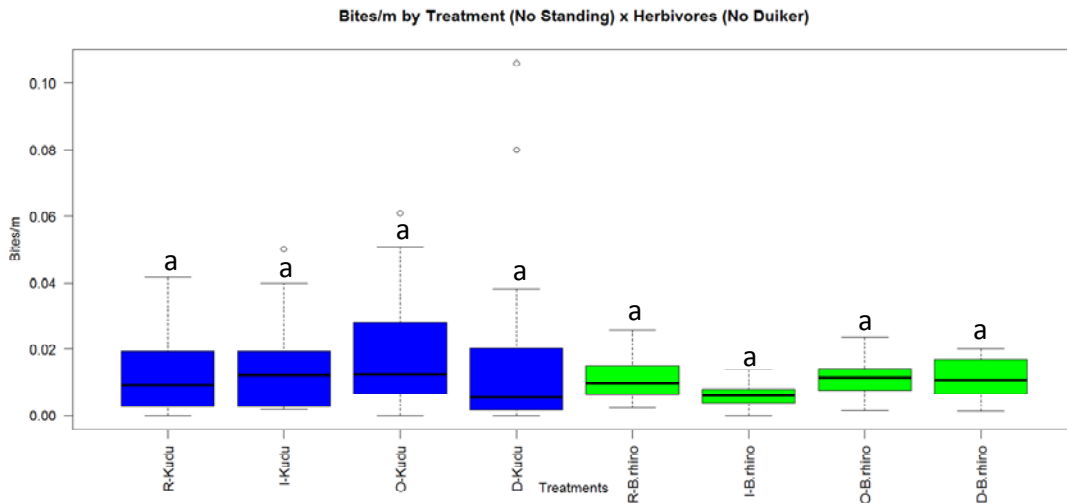
Finally for the black rhinoceros, I also found differences between the standing inside treatment and the fallen treatments ($H = 55.663$, $df = 4$, $p = 2.36e-11$). The number of potential bites I estimated for the standing treatment was higher than the fallen treatments. Similar to the kudu, I also tested for differences between fallen treatments. The potential numbers of bites recorded in the Old and Dead treatments were higher than the potential bites found in the Intermediate treatment ($H = 12.68$, $df = 3$, $p = 0.0054$) (Figure 5).

Figure 5. Potential bites sampled for the black rhinoceros in fallen treatments.



When comparing all herbivores-treatment pairs, I found differences between herbivores but not against all treatments ($H = 242.13$, $df = 14$, $p < 2.2e-16$). There were differences between the common duiker potential bites and the kudu and black rhinoceros potential bites for all treatments. Excluding the common duiker data, I did not find differences between kudu and black rhinoceros potential bites within any treatment groups; the only statistical differences is between standing and fallen treatments ($H = 103.72$, $df = 9$, $p < 2.2e-16$). Among fallen treatments, there were no differences between kudu and black rhinoceros treatment groups ($H = 12.45$, $df = 7$, $p = 0.0868$) (Figure 6).

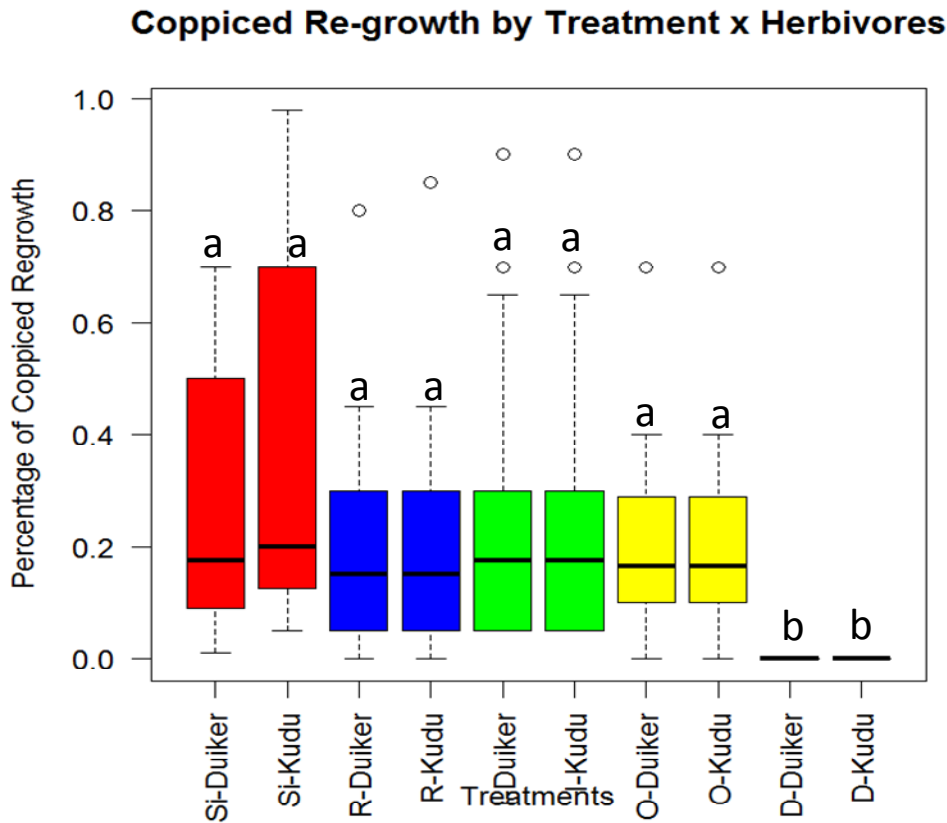
Figure 6. Potential bites between kudu and black rhinoceros, only fallen treatments



Coppiced re-growth

I did not find differences in coppiced re-growth percentage between standing treatments ($H = 3.97$, $df = 3$, $p = 0.265$). The amount of coppiced re-growth available for the common duiker and kudu were similar since I did not find differences between herbivores. Since there were no differences between the standing treatments, I only tested the fallen treatments against the standing inside treatment. I found that the Dead treatment had less percentage cover of coppiced re-growth than the other fallen and standing inside treatments ($H = 46.70$, $df = 4$, $p = 1.77e-09$) (Figure 7). Excluding the Dead treatment, there were no differences among the rest of the treatments ($H = 1.07$, $df = 3$, $p = 0.7835$). For the kudu, I also found similar differences between the Dead treatment and the other treatments ($H = 48.64$, $df = 4$, $p = 6.93e-10$) (Figure 7). When analyzed without the Dead treatment, I did not find differences between the standing and fallen treatments ($H = 3.98$, $df = 3$, $p = 0.2638$).

Figure 7. Coppiced re-growth available to the common duiker and kudu across treatments.

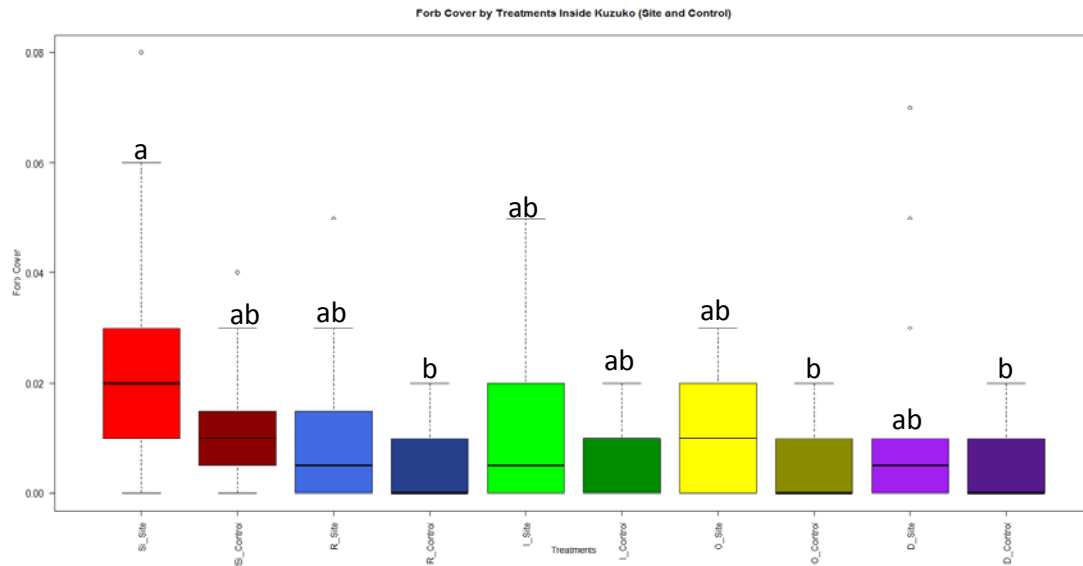


A final significant test for all effects of herbivores and treatments also showed that the Dead treatments were less than the other treatments ($H = 96.07$, $df = 9$, $p < 2.2e-16$) (Figure 7). Removing the Dead treatment yielded the same results, I did not find differences between any other treatments ($H = 5.47$, $df = 7$, $p = 0.6025$). The amount of coppiced re-growth available for both herbivores was only different when comparing against the Dead tree treatment; otherwise there were no differences between standing and the other three fallen treatments.

Standing and fallen trees as nurse plants

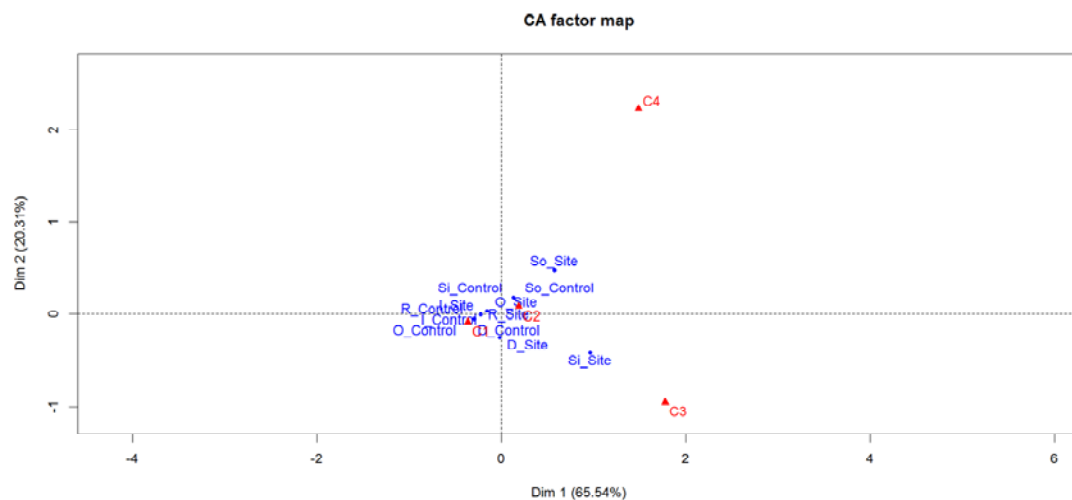
There were no differences between the percentage of forbs cover recorded inside and outside Kuzuko ($H = 7.90$, $df = 3$, $p = 0.05$). When comparing the standing inside treatment with the fallen treatments, I found that the percentage cover of forbs was higher in the Standing Inside-Site treatment pairs than the Recent-Control, Old-Control and Dead-Control treatment pairs ($H = 27.52$, $df = 9$, $p = 0.001$). Comparing Site and Control groups within the standing and fallen treatments did not yield differences however (Figure 8).

Figure 8. Forbs cover by treatments inside Kuzuko (Site and Control).



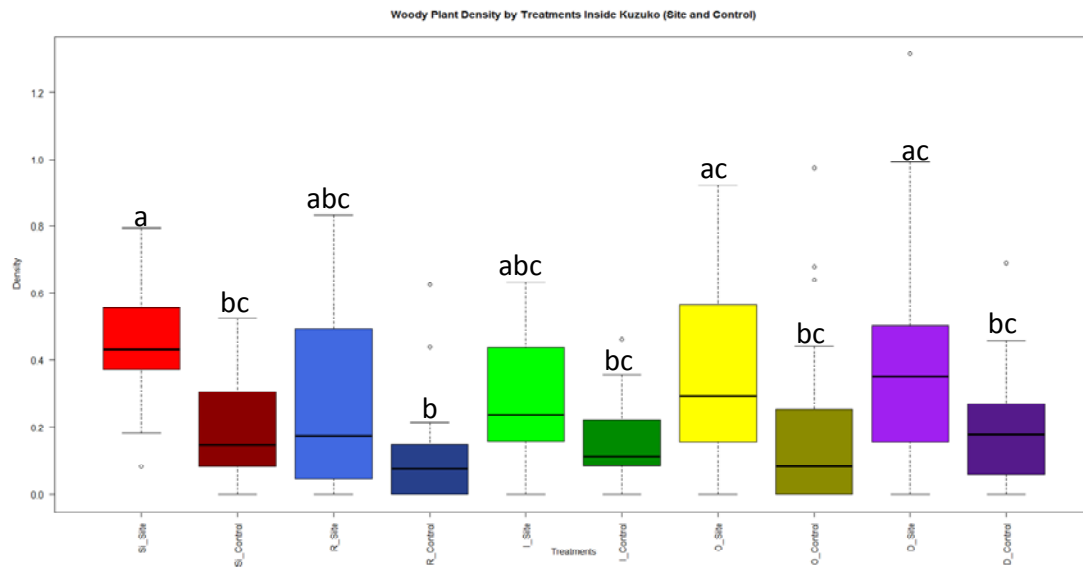
The Correspondence Analysis I ran also showed a slight association between the standing trees outside Kuzuko and the C4 category (see Table 6 for classifications). Standing trees inside Kuzuko also showed a slight association with the C3 category (Figure 9). Overall however, most of the treatments and groups were closely bunched together and association with individual categories were not strong.

Figure 9. Correspondence analysis for forbs coverage.



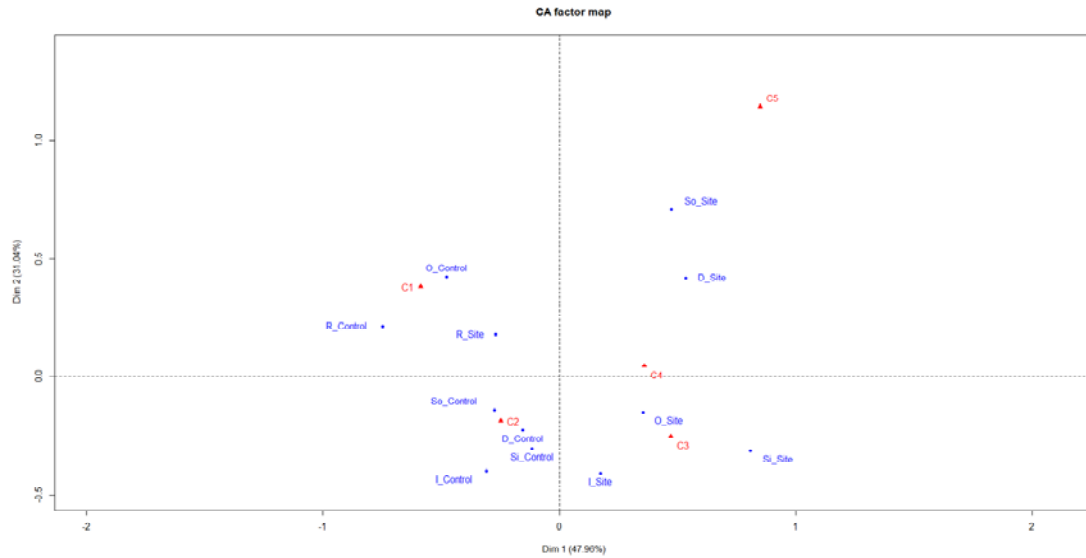
The density of woody plants was higher under the trees (Site) inside Kuzuko than in both Controls for standing trees inside and outside Kuzuko ($H = 21.103$, $df = 3$, $p = 0.0001$). Figure 10 graphed the density of woody plants found between standing and the fallen treatments inside Kuzuko. There were differences between the Si-Site treatment pair and all the Control treatments. I also found that the Recent-Control treatment pair was higher than the Old- and Dead-Site treatment pairs ($H = 45.30$, $df = 9$, $p = 8.105e-07$). There were no differences in the density of woody plants within the fallen treatments when comparing between the Site and Control groups.

Figure 10. Density of woody species inside Kuzuko for all treatments.



The Correspondence Analysis for woody plants also showed signs of association between treatments and the five density categories (See Table 4 for classification). Except for the Recent treatments, all of the other treatments in the Site group were associated with the C3, C4 and C5 (Figure 11). All the Control group treatments were more closely associated with the C1 and C2 categories. There was a trend where the density of woody plants was higher when under tree crowns (Site) compared with to the areas without tree cover (Control).

Figure 11. Correspondence analysis of woody plants.



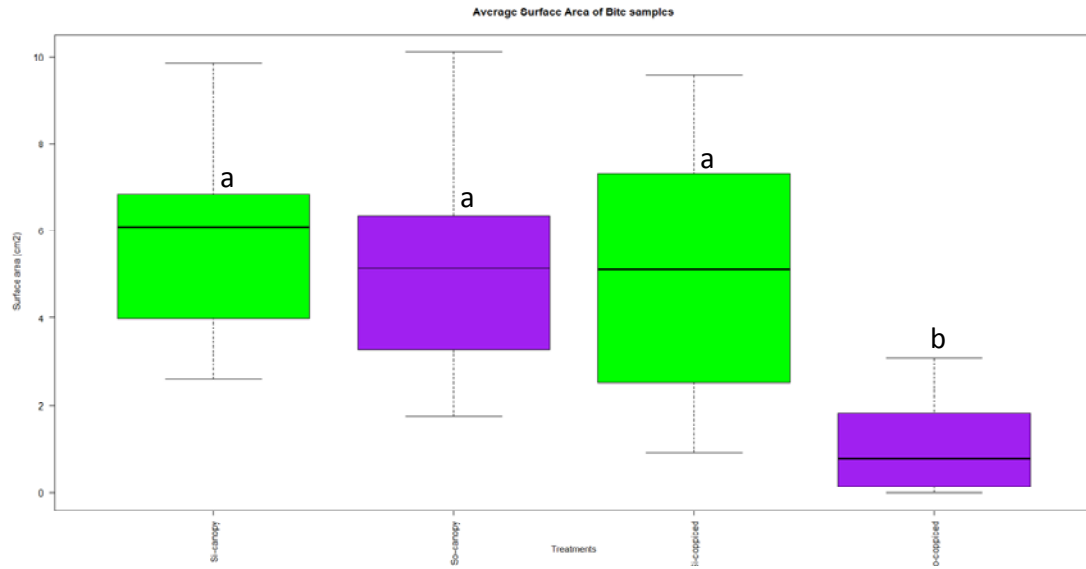
Leaf surface area and nitrogen level analysis

In total I sampled 120 trees from all the treatments but was not able to collect any foliage from forty-three of these samples (Table 7). Samples without foliage collected still counted towards my leaf surface area analysis but was not sampled for the leaf greenness/nitrogen level analysis. The surface area of the coppiced re-growth samples found outside Kuzuko was less than the other treatments I tested for ($H = 17.665$, $df = 3$, $p = 0.0005$) (Figure 12).

Table 6. Treatments where no foliage was sampled for surface area analysis.

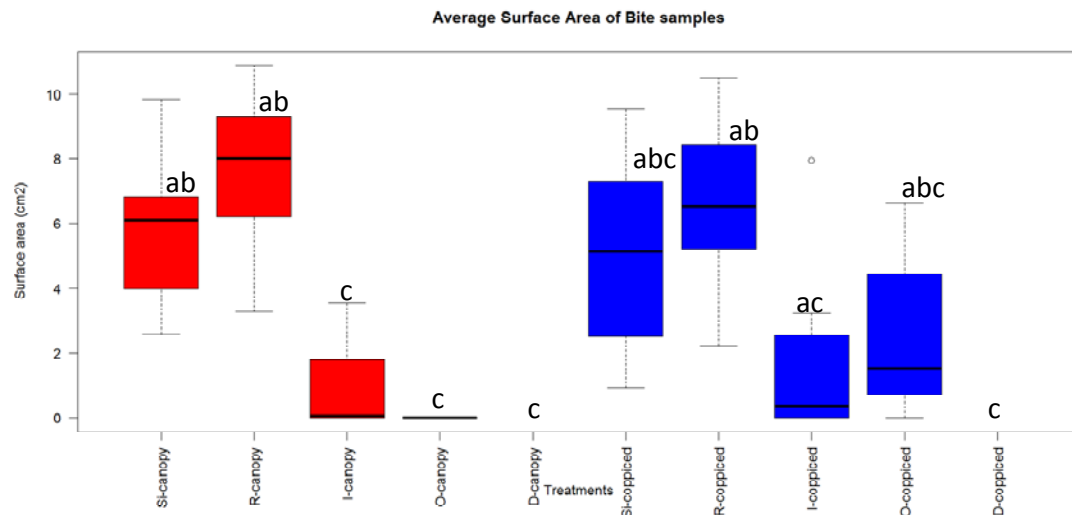
Treatment	Trees with no foliage collected
Canopy (Intermediate)	5
Canopy (Old)	10
Canopy (Dead)	10
Coppiced re-growth (Intermediate)	4
Coppiced re-growth (Old)	2
Coppiced re-growth (Dead)	10
Coppiced re-growth (Standing outside)	2

Figure 12. Leaf surface area sampled from standing trees inside and outside Kuzuko.



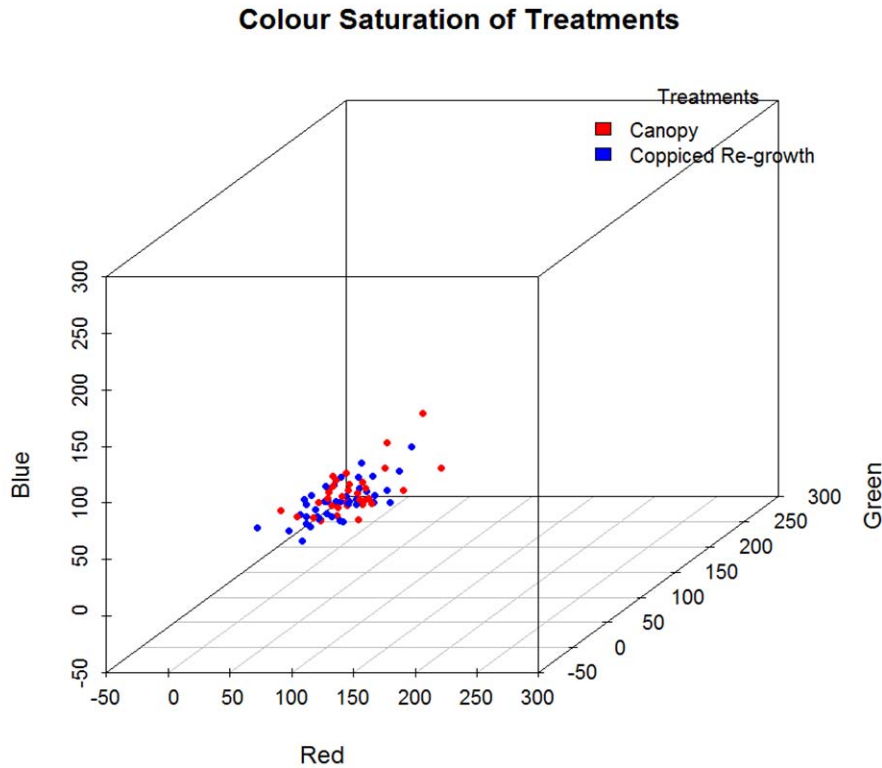
For the leaf surface area analysis, I tested for all standing and fallen (except Dead) treatments due to the difference in coppiced re-growth found for standing trees outside Kuzuko. The reason why I excluded the Dead treatments was because all values recorded for both sections were zeros. I found differences between several treatments ($H = 66.19$, $df = 9$, $p = 8.47e-11$): the Recent treatments were higher than the Intermediate treatments; the Standing Inside-Canopy treatment pair was higher than the Intermediate-Canopy treatment pair; the Old-Canopy treatment pair was less than the Standing Inside and Recent treatments (Figure 13); and the Recent-Coppiced treatment pair was higher than the Standing Outside-Coppiced treatment pair. The surface area of foliage collected from the coppiced re-growth on trees standing outside Kuzuko was also less than foliage collected from the Standing and Recent fallen treatments.

Figure 13. Average surface area of bite samples from all inside treatments.



For the nitrogen level analysis, I plotted 77 points onto the 3D scatterplot. I was unable to collect RGB information from the remaining 43 samples since no foliage was collected in those treatments. I did not find much correlation between canopy groups and a higher intensity of green than foliage collected from the coppiced re-growth (Figure 14). There did not appear to be any difference in nitrogen levels between foliage collected from the standing and fallen over treatments however. However, an expanded sample size and additional studies should be conducted for a better understanding.

Figure 14. Colour saturation test between canopy and coppiced re-growth groups.



Discussion

Landscape level impact

Across the study area, I found that there were more fallen trees inside Kuzuko than in the No Elephant Sites. Local farmers, having witnessed the introduction of elephants into Kuzuko from 2007, also had the same observations as I did (personal communication, April 24, 2013). I accepted my first hypothesis that sites with elephants had a higher abundance of fallen trees than sites without elephants. The tree species I encountered most frequently on my transect walks was *Gymnospora baxifolia* although the majority I found were standing. I suspected that the species' shrub-like structure, numerous bunched stems and spinescent properties made it more difficult for elephants to push them down. My study tree species, the *Pappea capensis* was fairly widespread across the landscape and accounted for nearly 50% of fallen trees both inside and outside Kuzuko. Although not the most common tree in the study area, my results showed that *Pappea capensis* was the frequently pushed

down tree inside Kuzuko. This corresponds to past trends that elephants target the larger stemmed tree species to push over (Boundja & Midgley 2009). While *Acacia karoo* had a higher likelihood of being pushed over, there were not enough individuals in Kuzuko to show landscape level impacts. I found that *Pappea capensis* was the most frequently observed fallen tree species both inside and outside Kuzuko and thus, had the greatest influence among the Kuzuko landscape in terms of fallen trees.

Plant level impact

My potential bite analysis showed some interesting trends between species and treatments. While I expected the common duiker to have the least access to potential bites, I did not expect the low numbers I recorded. In most treatments, the common duiker was not able to forage on any of the shoots. I observed that the common duiker's measured bite diameter was often smaller than the shoot diameters. There were no differences in the potential bites for the common duiker across all treatments. For the kudu and black rhinoceros, I found that they were able to access more bites from standing trees than fallen trees. These results were in contradiction to earlier studies that found that elephant impacts positively affected shoot distribution and forage patterns by kudus and black rhinoceros (Makhabu, Skarpe & Hytteborn 2006; Landman & Kerley n.d.). I had to reject my first plant-level hypothesis; my data showed that the potential bites did not increase from standing to fallen treatments. The opposite was shown where potential bites recorded decreased from standing to fallen treatments. This could be due to a potential measurement biased where I underestimated the amount of bites found in the canopy. There were also no difference among fallen treatments, suggesting that time and tree degradation did not affect the number of potential shoot bites recorded.

The coppiced re-growth accessible to the common duiker and kudu was different between the Dead and other treatments. I had to reject my hypothesis that there was additional coppiced re-growth availability in all the fallen treatments. However, I did find that the Dead treatments would offer less foliage compared to the Standing treatments. I was surprised that the amount of coppiced re-growth available for the common duiker and kudu was not significantly different. Both species seemed to be able to access similar amounts of coppiced re-growth, suggesting that both species could make use of this foliage equally. Of course, I suspected that this forage opportunity was more important for the common duiker since it could not access the higher foliage materials that kudus could reach.

There did not seem to be a difference in percentage forbs cover between the Site treatments. There was a noticeable difference between the Site and Control treatments however, especially when comparing the standing Site treatments and the fallen Control treatments. For woody plants, standing trees inside Kuzuko played a more significant role as nurse plants compared to standing trees outside Kuzuko. This was possibly due to overgrazing by farm animals in the No Elephant Sites which consumed the new seedlings. Combining the forbs cover and woody species measurements, there was a trend which showed standing trees as important nurse plants. While a fallen tree could perform the same role, the landscape would rely on these physical structures to provide protection and shelter for new growth. On a landscape level, this would mean that fallen trees should remain as an important resource in the form of a nurse plant while the removal of trees would have a definite long-term impact on new growth. This followed previous understandings of coarse woody debris and its importance as habitats in the ecosystem (Jones, Lawton & Shachak 1994) (Pringle 2008). I rejected my hypothesis that fallen trees acted as a better nurse plant

but found that all tree forms were important for seedlings and as a result, should have long term benefits towards ecological succession. My results showed differences in forage availability between standing and fallen trees and supported Marietjie et al. (2008)'s idea that elephants do impact the environment beyond herbivory.

Having shown that coppiced re-growth was an important source of food for the common duiker and kudu, I did not find significant differences between the quality of foliage found in the tree crown and coppiced re-growth. I quantified forage quality using amount of foliage per bite (efficiency) and leaf greenness as a proxy for nitrogen level (content). Within Kuzuko, I did not find differences in the average surface area of canopy and coppiced re-growth samples. Foliage samples collected from coppiced re-growth on the No Elephant Sites trees however were significantly smaller than the other treatments. These results support past studies that showed the negative effects of goat browsing on tree structures (Moolman & Cowling 1994). As farm animals continued browsing on the coppiced re-growth, new foliage generations would not have had the opportunity to grow to larger leaf sizes. The average leaf surface area of samples I collected from the Standing Inside treatments and Standing Outside-Canopy treatment pairs were similar in size. It was also important to consider that for some treatment pairs, I was unable to collect all foliage samples (Table 7). Among fallen treatments I was unable to collect foliage from, these treatment pairs were all from the Intermediate to Dead treatments. It followed my hypothesis that the quality of forage (in this case, the amount of leaf surface area per bite) decreased with time for fallen trees. I did not see differences in the greenness of foliage collected from the canopy and foliage collected from the coppiced re-growth. Using leaf greenness as a proxy for nitrogen level, the foliage collected from the canopy did not have a higher level of nitrogen compared to foliage from the coppiced re-growth. Based on my results, I could not accept my hypothesis that forage quality was more optimal in the canopy layer and would decrease with time over fallen treatments. However, additional studies should be conducted to enable a better understanding between foliage qualities.

Limits to study

My study provided multiple analyses to evaluate foliage opportunities but there were some improvements that I would like to make to increase the accuracy of the study. The results I obtained from the potential bite analyses were unexpected and I believed I may have underestimated the amount of shoots available for the fallen treatments. I maintained a consistent sampling method but a line transect may have underestimated the actual forage opportunities when a tree had fallen over. My transect measurement method did not include the additional forage opportunities from the top of the tree crown. An improvement would be to use a bite sample analysis similar to the one I used when sampling for foliage quality.

Another improvement may be to increase the study area into multiple locations and elephant densities. As it stands now, I was only able to measure the effect of the 26 elephants inside Kuzuko. How forage availability changed with varying elephant densities would be an interesting topic to study and one that should be pursued in the future. As the density of elephants increase, one could assume that the amount of fallen trees would also increase. How foliage opportunities would be affected by more broken structures would be interesting to study as the landscape level effects would be much stronger than what I observed at Kuzuko.

Conclusions

There were landscape level effects of having elephants in game reserves. Elephants increased the amount of fallen trees in their environment and showed preference for certain tree species over others to push over. In my study area, the most often fallen tree species inside and outside Kuzuko was the *Pappea capensis*. This was the species that would show the most effects at the landscape level when comparing differences between standing and fallen trees.

On the plant-level, I found that forage opportunities decreased from a standing to fallen over position. The common duiker had little access to foliage, depending mostly on the coppiced re-growth material on the *Pappea capensis*. For the kudu and black rhinoceros, they were able to access the canopy layer as well without relying on a tree to be pushed over. The potential bites that kudu and the black rhinoceros had were similar in numbers while the available bites, measured by shoots, did not decrease with the amount of time that a tree had fallen. The amount of coppiced re-growth that the common duiker and kudu could forage on was similar between most standing and fallen treatments. The availability of coppiced re-growth was only less when fallen trees were dead and could no longer regenerate or sustain growth.

Trees, both standing and fallen over, were important as nurse plants. This was important to consider as ecological succession required seedlings to replace old growths. Foliage from the canopy had slightly higher nitrogen levels than foliage from the coppiced re-growth.

Average leaf size remained the same for trees inside and outside Kuzuko except in the coppiced re-growth. Browsing by farm animals resulted in smaller leaf size in the coppiced re-growth of standing trees outside Kuzuko. There was no discernable difference in nitrogen level between foliage collected from the canopy and coppiced re-growth; however additional studies should be conducted to fully assess nitrogen levels.

Within the Kuzuko landscape, my data suggested that elephants did decrease forage availability for local ungulates but additional research should be conducted to reassess potential bites. The coppiced re-growth acted as a food resource buffer when a tree was fallen over due to its ability to persist throughout the fallen treatments until a fallen tree had died. *Pappea capensis* had the dominant impact in the landscape due to its susceptibility to falling over, as well as their abundance in the landscape.

Acknowledgements

I would like to thank my supervisor, Associate Professor Joris Cromsigt, for his guidance and assistance throughout this project. I am grateful for the opportunity to follow him to South Africa and study in this amazing environment. The study was also my first experience in the South Africa and I would like to extend my gratitude to Professor Graham Kerley and Dr. Marietjie Landman for their expertise and assistance during my work, especially in South Africa. I am also grateful to the staff and students at the Center for African Ecology at the Nelson Mandela Metropolitan University for their generosity and hospitality during my stay in Port Elizabeth. Some of the costs related to the field work were covered through the PhD project of Ms. Nokubonga Mgqatsa. My thanks go to her supervisor, Prof. Kerley, for this support. To Nokubonga Mgqatsa, I wish you the best of luck in continuation of your PhD work and thank you for your assistance while in the field. And finally, to my family in Canada: Daniel; Maria; and Hiro, for your continued support throughout the years. And to my SLU-colleagues, I would like to thank you for their friendship and support this year in Sweden. It was a pleasure to have known you all and the experiences we shared together are memories I will cherish.

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