Elephants and aboveground carbon stocks in a South African protected savanna

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Master thesis • 60 credits
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Department of wildlife, Fish and Environmental studies
Master in Ecology and Conservation
Examensarbete/Master's thesis, 2022:14
Umeå 2022

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Credits:	60 credits
Level:	Second cycle, A2E
Course title:	Master Thesis in Biology, A2E
Course code:	EX0971
Programme/education:	Master in Biology in Ecology and Conservation
Course coordinating dept:	Department of Wildlife, Fish and Environmental studies
Place of publication:	Umea
Year of publication:	2022
Cover picture:	Camille Schröcker
Copyright:	All featured images are used with permission from the copyright owner.
Title of series:	Examensarbete/Master thesis
Part number:	2022:14

Keywords:	above-ground carbon stocks, climate change mitigation, elephant impacts, megaherbivores, conservation, wood density

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Abstract

Savanna elephants (*Loxodonta africana*) are known to exert transforming impacts on the vegetation. Due to these impacts, one would expect elephants to have significant effects on aboveground carbon stocks. However, we still know relatively little about the magnitude and direction of the effects of elephants on aboveground carbon stocks. Here, I combined historical data from vegetation surveys and wood density field measurements to estimate the change in aboveground carbon stocks between 1999 and 2017 in relation to different elephant impact levels in Hluhluwe-iMfolozi Park, South Africa. Despite an increasing and relatively high-density elephant population compared to other South African reserves, aboveground carbon stocks did not generally decrease over time, although we found weak evidence for a reduction in aboveground carbon stocks at extreme elephant impact levels. In addition, variation in stem diameter and elephant impact among individuals influenced the wood density of these individual for certain tree species but not for others. This demonstrates the importance of considering drivers of wood density and how their effects vary among tree species when estimating aboveground carbon stocks. Our findings support previous findings and show that elephants might not necessarily conflict with goals focused on conserving aboveground carbon stocks.

Keywords: above-ground carbon stocks, climate change mitigation, elephant impacts, megaherbivores, conservation, wood density

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Abbreviations

HiP	Hluhluwe-iMfolozi Park
AGC	Aboveground carbon stocks
AGB	Aboveground biomass
CCF	Carbon conversion factor

1. Introduction

Understanding the drivers of the carbon cycle is essential to mitigate climate change, and one important previously underestimated driver is the effect of mammals on carbon dynamics (Schmitz *et al.,* 2014). Megaherbivores (<1000kg adult biomass) have been hypothesized to play an important role in carbon dynamics since they have disproportionate impacts on vegetation due to their size (Asner *et al.,* 2012, Davies *et al*., 2019, Vanak *et al.,* 2012). Savanna elephants (*Loxodonta africana*) can be major drivers of vegetation and landscape change in African savanna systems by exerting transforming impacts on vegetation through their feeding behavior (i.e. bark stripping, branch breaking and uprooting trees) (Birkett *et al*., 2005, Mukwashi *et al.,* 2012). African savannas are carbon-productive regions (Grace *et al*., 2006) and changes in tree density disrupt the atmospheric CO_2 fluxes (Sandhage-Hofmann *et al*., 2021). Therefore, a deep understanding of the impacts of savanna elephants on the local carbon cycle of African savannas can help us understand how these megaherbivores influence climate systems. Through vegetation consumption, elephants change the structure and height of plants and increase moisture stress and exposure to fire for trees (Smit *et al.,* 2011, Shannon *et al*., 2008, Vanak *et al*., 2012). Those combined impacts may increase tree and shrub mortality and thus influence aboveground carbon stocks (AGC) (Smit *et al.,* 2011, Sandhage-Hofmann *et al.,* 2021). However, the extent and direction of these elephant impacts on vegetation and resulting aboveground carbon stocks remain uncertain (Davies *et al.,* 2019).

Elephants affect different carbon pools and fluxes in savanna ecosystems (Figure 1). Through browsing and consumption of vegetation, elephants directly influence the CO_2 uptake and release by reducing the number of plants available for photosynthesis in savannas (Schmitz *et al*., 2014). They also transfer carbon to the soil carbon pool by excretion and may affect soil carbon pools spatially by redistributing carbon across different locations. I.e., they consume plant matter in one site and deposit urine and dung after digestion in another area (Sandhage-Hofmann *et al.,* 2021, Beirne *et al.,* 2019, Sitters *et al.,* 2020). Once the carbon enters the soil from organic matter in a decomposable form such as excrements or litterfall, it is decomposed by microbial activity. A part of it is stored in the ground, while another portion is released as carbon dioxide into the atmosphere via microbial respiration (Tanentzap *et al*., 2012). Plants will then fix a part of the atmospheric CO_2 through photosynthesis which can be consumed by herbivores (Schmitz *et al*., 2014).

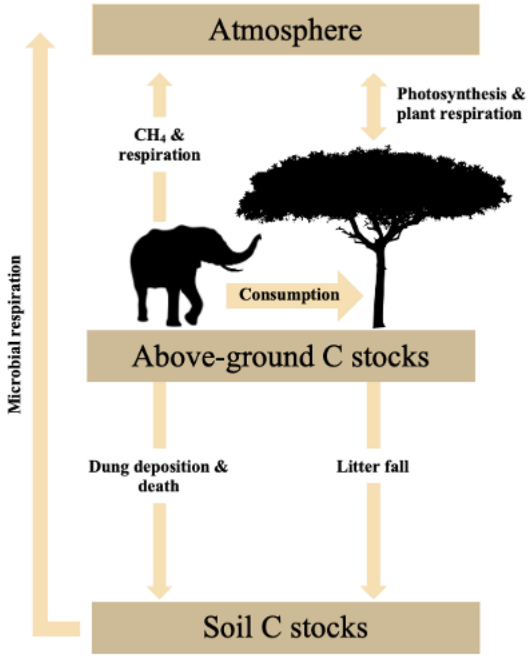

Figure 1: Conceptual framework showing how elephants interact with the carbon cycle within an ecosystem (for example vegetation consumption or dung deposition).

Previous studies found contradictory results on the potential impacts of savanna elephants on aboveground carbon stocks. A study using herbivores exclusion plots showed that the exclusion of a combination of herbivore species resulted in an average increase in aboveground carbon stocks and led to an increase in soil carbon pools (Wigley *et al*., 2020). In the latter study, elephants' effects were not separated from other herbivores, but Sandhage-Hofmann et al (2021) showed that, indeed high elephants densities reduced woody biomass and related carbon stocks. However, results showed an increase in carbon in soil pools with increasing elephant densities due to input sources like decaying woody biomass from elephant impact and dung deposition from megaherbivores. On the other hand, another study demonstrated that the aboveground carbon density increased in most of the surveyed areas in the Kruger National Park between 2008 and 2014 despite the increasing elephant population and high tree fall rates (Davies *et al*., 2019). The ways elephants influence woody vegetation and carbon stocks are complex. They induce a decline in taller trees, but they also convert taller trees to shrub vegetation species which might not necessarily lead to a loss in aboveground biomass, hence aboveground carbon stocks but simply shows a change in vegetation structure (Skarpe *et al*., 2004).

Carbon stocks are assessed (Figure 2) through (1) the estimation of aboveground biomass (AGB) via measurements of tree traits such as tree diameter, wood density and tree height and (2) the conversion of AGB to carbon content by the multiplication of AGB with a carbon conversion factor (CCF) (Martin *et al*., 2018). Wood density is a key parameter for converting wood volume into biomass estimates and is defined by the amount of mass per volume of wood (Nam *et al*., 2018, Chave *et al.,* 2006, Fearnside, 1997). It varies with tree species, age, height, and tissue type (Chave *et al*., 2009, Martin *et al*., 2018). Wood density is a highly variable factor that can influence carbon estimates (Flores *et al*., 2011). The interspecific and intraspecific variation in wood density might thus be important to consider when estimating the change in carbon content in relation to elephant impacts. Carbon stocks are usually estimated using a 47-50% CCF, assuming that 47-50% of wood biomass is carbon. However, studies showed that such a generic CCF may bias the estimation of carbon stocks as there is a significant variation of carbon content among tree species and tissue types (Martin *et al*., 2018, Thomas *et al*., 2012). Previous studies (Davies *et al*., 2019, Wigley *et al*., 2020, Sandhage-Hofmann *et al.,* 2021) assessing carbon stocks change in relation to elephant impacts assumed no interspecific or intraspecific variation in wood density and CCF. I.e., these studies treat the woody vegetation as one species, ignoring species may differ in wood density and carbon content (Martin *et al*., 2018, Thomas *et al*., 2012). As elephants interact with a wide range of woody species through browsing (Campos-Arceiz *et al*., 2011, Dudley *et al.,* 2000, Bunney *et al*., 2017), they affect the composition of woody species, and this effect might be strong in fenced reserves (Wiseman *et al*., 2004). In response to browsing pressure, woody communities change, where tree species that elephants prefer might become less common whereas species that elephants avoid may increase in numbers (Wiseman *et al*., 2004). These effects of elephants on the species composition of woody communities in savannas suggest it might be important to consider interspecific variation in wood density and carbon content when assessing aboveground carbon stocks as it might influence the overall above-ground carbon stocks of an area.

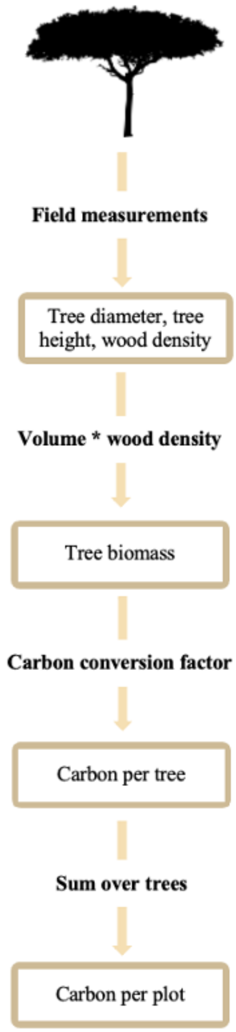

Figure 2: Conceptual framework showing the process of carbon stocks estimations.

The aim of my thesis was to test the effects of elephant impacts on changes in aboveground carbon stocks in Hluhluwe-iMfolozi Park (HiP), South Africa. To accurately understand the effects of elephants on the carbon cycle, all the carbon pools should be examined in detail, however, the focus of this thesis is on the aboveground carbon stocks only. I integrated field measurements of species-specific woody density and existing data from long-term vegetation monitoring surveys to quantify the change in carbon stocks in relation to elephant impact.

I addressed the following research questions:

(1) How do elephants shape aboveground carbon stocks through browsing in Hluhluwe-iMfolozi Park (HiP) between 1999 and 2017?

I expect that the change in aboveground carbon stocks will depend on the intensity of elephant impacts. Elephants will have a negative effect on aboveground carbon stocks at extreme levels of impact. (Davies *et al.,* 2019, Sandhage-Hofmann *et al.,* 2021).

(2) How is the estimation of aboveground carbon stocks influenced by using species-specific wood density values or one average wood density value for all species?

I expect that the use of species-specific wood density values will give different results for carbon stocks estimations and therefore carbon stock changes over time than when using an average wood density value for all tree species (Yeboah *et al.,* 2014).

Moreover, since disturbances such as fire impact and elephant impact are important in savannas (Druce *et al.,* 2017, Archibald *et al*., 2017) and affect individual trees, I assessed how these factors influenced the intraspecific wood density variation. Therefore, I addressed the following research question:

(3) How is wood density driven by factors such as stem diameter, elephant, or fire impact?

I expect that, in general, stem diameter will influence wood density depending on the species. I expect that disturbances, such as elephant impact and fire, will reduce wood density by affecting the viability of stems of individual trees.

2. Material and methods

2.1 Study area

This study was conducted in Hluhluwe-Imfolozi Park (HiP), located in the north of the province of KwaZulu-Natal (28°00’-28°26’S and 31°43’-32°09’E) (Figure 3) in South Africa (Boundja *et al*., 2010). The reserve was proclaimed as a protected area in 1895. The total area of 950 km^2 is fenced and supports different vegetation types, and biomes vary from semi-arid to mesic savanna (Cromsigt *et al*., 2017). The vegetation communities in HiP are diverse and hold about 300 tree species and 150 grass species (Ezemvelo KZN Wildlife 2011a). The variability in local weather in HiP is related to topography. The altitude ranges between 60m to 580m above sea level (Boundja *et al.,* 2010), and mean annual rainfalls vary between 990mm in the northern high-altitude regions to 650mm in the lower southern regions (Balfour *et al*., 2002, Ezemvelo KZN Wildlife 2011a). The mean temperatures range between 13 to 35 C° during winter and summer (Balfour *et al.,* 2002).

Figure 3: A map showing the location of Hluhluwe-iMfolozi Park on the African continent.

2.2 Elephant impact vegetation survey

2.2.1 Plot selection

Since 1999, HiP has a program of elephant impact vegetation monitoring that has been repeated in 2001, 2003, 2007, 2017 spanning different vegetation types across the park (Druce *et al*., 2017). The program consists of the resampling of fixed plots distributed across HiP using a stratified random design covering all main habitat types in HiP (Druce *et al*., 2017). In 1999, 369 plots were surveyed and about half of them were re-surveyed in 2003 (186 plots) and in 2007 (175) (Druce *et al*., 2017). The survey of 2017 (107 plots) only included plots that were surveyed in all the previous three surveys (1999, 2003, and 2007) (Mbongwa, 2020). For the analysis, I used the common plots between all the years and only included savanna plots which makes a total of 105 plots. Plots with forest vegetation type were excluded from the selection as elephants tend not to spend time in the forest plots of HiP. Therefore, they do not affect the forests part of the park.

2.2.2 Survey design and data collection

The sampling design described here was based on Boundja et al (2010). Each plot of 50x50m (0.25 ha) consisted of subplots to effectively sample vegetation in three different size classes (Figure 4). A center line (zero-line), consisting of a 50m measuring tape through the middle of the plot from north to south, separated each plot in two equal parts. Two other measuring tapes were laid out, 10m from and parallel to the zero-line, on both sides of the zero-line. (a) From the zero-line to 2m to the right, all trees below 2m were measured for the full 50m length whereas trees below 0.5m were only measured for the first 25m. (b) From the zero-line to 2m to the left, all trees between 0.5m to 2m tall were measured. (c) From the zero-line to 10m on both sides of the tape, all trees between 2 to 4m tall were measured. (d) From the zero-line to 25m on either side of the tape, all trees taller than 4m were measured (Boundja *et al*., 2010, Mbongwa, 2020). In terms of the tree measurements, the following was recorded for each individual tree: tree species, diameter, height, and number of stems. Stem diameter was recorded in different classes: 0-1cm, 1-3cm, 3-10cm, 10-20cm, 20-50cm and >50cm. Moreover, the damage by elephants was recorded for each tree for three impact types: branch breaking, bark stripping and tree toppling (Druce *et al.,* 2017,

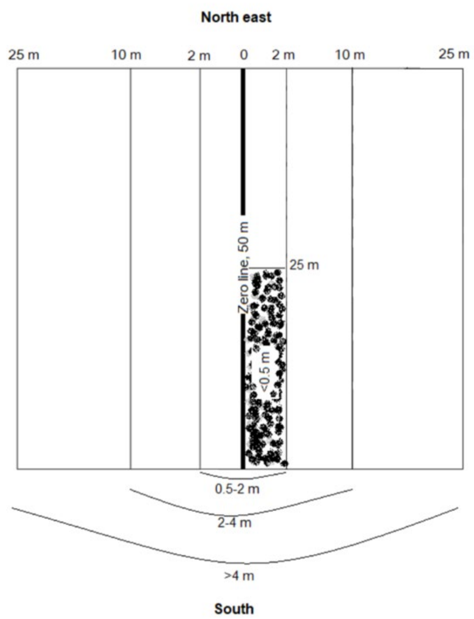

Figure 4: Diagram of the plot design used for the vegetation sampling. Different height classes were measured in the subplots within the plot

Mbongwa, 2020). For first two of these impact types, the impact was classified as percentage of the whole tree broken or stripped. The third impact type was classified as toppled or not (see Appendix 1 for pictures of the types of damages). Finally, for each plot, vegetation type, topography and slope were recorded.

2.3 Data collection

2.3.1 Species selection for wood density measurements

Due to the limited timeframe of my thesis and a considerable sampling effort, I could not sample all tree species present in the elephant impact vegetation survey. Therefore, I selected tree species based on their contribution to the aboveground volume as an indicator of their potential contribution to the carbon stocks (Yeboah *et al.*, 2014). The selection was based on common plots of years 1999 and 2017 to include dominant species of both years for several reasons. If the selection is based only on plots from 1999, there are chances to sample species only present at a time where the elephant impact was low. On the contrary, if the selection is based on 2017 only, there is a probability of missing species that were common in the previous years but are currently less common due to historic elephant impact.
Using the common plots surveyed in 1999 and 2017 (105 plots), I calculated the volume of each stem present in the common plots using a standardized volume formula in 1999 and 2017 separately:

$$V = \pi * r^2 * H$$

where r is the radius of the tree trunk in cm, and H is the tree height in cm. The diameter measured during the vegetation monitoring survey was categorized into six different classes; therefore, I used the average diameter of each class for the volume calculations. Once the volume of each stem was calculated, I selected the species that make up 80% of the plots in volume in 1999 and 2017 so that uncommon species were not included in the sampling since they probably do not add much to the total aboveground volume and biomass and thus carbon content.
For the final list, the duplicated species in both lists (1999 and 2017) were kept which makes a total of 28 species (Table 1).

Table 1: List of the species that make up 80% of the plots in volume in 1999 and 2017. Only species that were dominant in both years were included. Numbers represent the number of plots in which each species makes up 80% of the plots. Species with an asterisk were excluded from the sampling for reasons explained in the main text.

Tree species	1999	2017
Spirostachys africana	23	35
Acacia burkeii	22	18
*Acacia nigrescens**	17	16
Euclea racemosa	12	16
Schotia brachypetala	15	9
Combretum molle	10	10
Acacia nilotica	13	5
Acacia robusta	13	5
Sclerocarya birrea	14	3
Ziziphus mucronata	10	7
Sideroxylon inerme	7	7
Dichrostachys cinerea	1	12
Acacia gerrarrdii	11	1
Acacia tortilis	10	2
Euclea divinorum	8	4
Combretum apiculatum	9	2
Berchemia zeyheri	8	2
Rhus pentheri	4	6
Acacia grandicornuta	7	1
Cassine transvaalensis	2	3
Peltophorum aftricanum	1	4
Pappea capensis	2	2
*Ekebergia capensis**	1	2
Maytenus senegalensis	1	2
*Acacia davyi**	1	1
Dombeya rotundifolia	1	1
Manilkara concolor	1	1
Thespesia acutiloba	1	1

Some species had to be excluded from the sampling. *Acacia nigrescens* was excluded since the wood was too hard to core with the manual corers available. *Ekebergia capensis* and *Acacia davyi* were also excluded since they were only present in one of the selected plots. Ultimately, a total of 25 species were sampled.

2.3.2 Selection of plots where woody density was sampled

To obtain the wood density samples for the 25 selected species and minimize the sampling effort, plots surveyed in the previous years were used as an indicator of species presence. Among the 105 common plots, I first selected the plots that had the highest number of the 25 selected species in previous years. Next, from the selected plots I kept plots that were within 500m from the road to limit the walking time while sampling. This resulted in 21 selected plots spread across the park, in which I collected most of the wood density samples of the 25 species (Figure 5). Depending on a species distribution range, I spread the wood density samples as much as much as possible throughout the park from south to north. This was not possible for species with a limited distribution (see Appendix 2 for location of wood density sampling plots for each species). If species could not be found around the selected plots, they were spotted from the car.

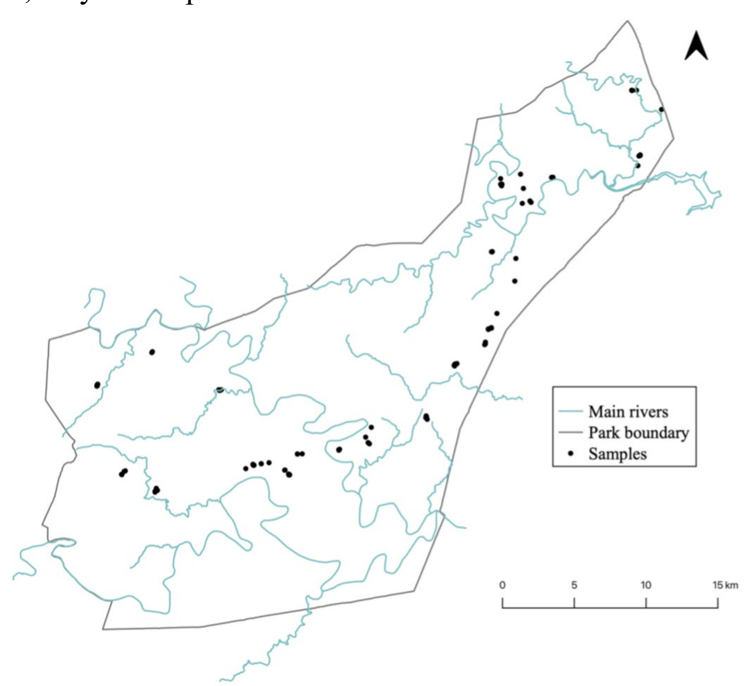

Figure 5: Map showing the sampling locations in HiP.

2.3.3 Sampling of wood density

For all the selected 25 species, I collected 5 wood samples to determine wood density. Concerning the third research question, to test the effects of elephant impact and fire impact on wood density, I used species that were both common in HiP and either highly impacted by elephants or by fire. I chose Marula trees (*Sclerocarya birrea*) to investigate the influence of elephant impact on wood density since Marula trees are a preferred species of elephants. To investigate whether fire affected wood density, I chose *Dichrostachys cinerea* because it is highly damaged by fires. Therefore, 20 samples were collected for *Sclerocarya birrea* and *Dichrostachys cinerea* respectively to look at intraspecific wood density variation. A total of 165 samples were collected.

To avoid biased woody density, and thus ultimately carbon stock estimations, towards healthy trees, I sampled trees of varying viability (e.g., due to impacts of herbivores/insects/fire or other disturbance). However, fully dead trees were excluded. Moreover, to avoid biases in wood density estimates caused by variation in tree size, I sampled representative diameter classes for each species. A percentage of the number of stems for each diameter class was calculated. The number of stems in each diameter class from the historical data were counted and divided by the total number of stems per species. The five samples were then divided across the most common diameter classes for each species to make sure to sample representative diameter sizes of each species (see Appendix 3 for distribution of the samples across diameter classes for each species).

2.3.4 Wood cores collection

I used two methods to collect wood for wood density estimation: sampling with a wood corer and stem cutting. I used the wood corer for trees with a diameter at breast height (1.3 to 1.4m) larger than 10cm. I used the stem cutting method for stems smaller than 10cm of diameter. For these smaller stems, I cut a piece of the stem with the help of a saw.

The wood core samples were collected using an increment borer which consists of three parts: (a) the auger, (b) the handle, (c) the extractor (Grissino-Mayer, 2003). The auger is composed of a threaded bit and a hollow shaft and squared end that can be attached to the handle. The handle consists of two handles attached to a central connector with a hole where the auger can be attached perpendicularly to the handle with a clip (Grissino-Mayer, 2003). The extractor is composed of a serrated end to grasp the core when inserted in the auger and a main incurved part where the core rests (Grissino-Mayer, 2003). Reliable estimates of wood density are possible with core samples that extend from the bark to the pith of the tree (Gao *et al*., 2017). The length of the increment borers used in my study is 300mm and 200mm. To core the trees, the tip of the borer should be placed at breast height with one hand on the auger and turning the handle with the other hand to help the tip of the auger to penetrate the outer bark while applying inward pressure on the borer. Once the tip of the auger entered the bark and is steady, the borer can be turned with both hands until it reaches the estimated inner center of the tree. Next, the extractor can be inserted in the auger and slid under the core sample. The handle can be turned counterclockwise for one full turn to break the core from the inner wood of the tree so that once the extractor is removed, the core can be pulled out. The core should be placed in a bag.

2.3.5 Laboratory measurements

I determined wood density (WD) by dividing the dry mass by its fresh volume:

$$WD = \frac{M}{\frac{\pi}{4} * d^2 * L}$$

where L is the total length of the core sample (cm), d is the diameter of the core sample (cm) and M is the dry mass of the sample (g) after oven-drying at 100 degrees to constant mass (Chave, 2006). This oven-drying procedure can take 24 hours to 72 hours depending on the size of the samples. To test for constant weight, samples were weighed at regular intervals until the mass was constant (Chave, 2006).

The fresh volume of wood cores was measured assuming a regular cylindrical shape with a caliper. Measurements included length (L) and diameter (d) of the core sample and the volume is given by the formula $\frac{\pi}{4} * d^2 * L$ (Chave, 2006).

For irregularly shaped wood samples, especially the smaller stems cut with a saw, I used the water-displacement method. A graduated container capable of holding the wood sample was filled with water to a certain volume (V_1). The sample was carefully sunk in the water until it was completely underwater and displaced the water (V_2). The difference between the V_1 and V_2, which equals the displaced the water, gave the volume of the sample (Barnett *et al.,* 2003).

2.3.6 Change in aboveground carbon stocks

Calculations of aboveground carbon stocks

Carbon stocks were estimated for each sampling year separately. For each plot, I estimated the volume of each individual tree using a standardized allometric equation considering trees as cylinders:

$$V = \pi * r^2 * H$$

where r is the radius of the stem in cm, and H is the tree height in cm. These measures came from the field measured diameter and height historical data. The diameter measured during the vegetation monitoring survey was categorized into six different classes; therefore, I used the average diameter of each class for the volume calculations. I then calculated the radius by dividing the average diameter in 2. I included individuals with multiple stems in the calculations by calculating the volume of each stem of one individual. I then turned the volume of each tree individual into biomass by multiplying volume with wood density values (g/cm^3). Species-specific wood density values were used for the 25 selected species (Table 2), whereas the average wood density value of these species was used for the other, less common, species. I then converted the estimated biomass of each tree individual into total carbon using a carbon conversion factor of 0.47. I.e., the tree biomass was multiplied with 0.47. Finally, I summed the estimated total carbon of all individual trees per plot to obtain the total carbon stock per plot. I then converted the carbon stocks from a gram measurement to a ton measurement to get a more common unit to quantify carbon stocks. In order to get carbon stocks in tons/ha (plot size was 0.25ha), I divided the carbon stocks in tons per 0.25. Dead trees were excluded from the calculations.

Estimation of carbon stocks change over the years

The change in carbon was estimated for each plot individually, by fitting a linear regression through the yearly (1999, 2001, 2007, 2017) total carbon stocks estimates per plot. The slope of the regression for each plot was used as the change in carbon per plot.

2.3.7 Elephant impact

Elephant impact categories

I determined an elephant impact score for each of the monitoring plots based on the measured elephant impact types: branch breaking, bark stripping and tree toppling. These impact types were recorded for each individual tree and categorized in classes as percentage of the whole tree broken or stripped (see Appendix 4 for detailed classes of impacts). For each individual tree, I used the middle of the percentage range. On the other hand, the toppling impact is categorized for individual trees as “Yes” or “No”, therefore, the number of “Yes” was summed divided by the number of “No” to obtain a percentage.

Next, I calculated an average of all impact types (branch breaking, bark stripping and tree toppling) per individual tree and then made an average per plot for each year. I then averaged the impact per plot across all years to get an overall average impact score for each plot.

Using the averaged individual impact scores per plot, I classified these plot impact scores into five impact levels; “Low”, “Semi-low”, “Medium”, “High” and “Extreme” impact. The plots were divided evenly into the five levels based on their overall average impact.

2.4 Statistical analysis

All data processing and statistical analyses were done using R Studio© (version 1.3.1093). All maps were computed with the software QGIS©.

2.4.1 Wood density

A comparison of the collected wood density values and the published values was made to see if they correspond to each other and how it could influence our overall results. The analysis was done using the stats R package (R Core Team 2020). To test how the wood density values collected in HiP compared to published values a Pearson correlation test was performed.

2.4.2 Relationship between elephant impacts and aboveground carbon stocks

To analyze the effects of the different elephant impact levels on carbon stock change, a one-way analysis of variance (ANOVA) was used. This analysis was done for two types of aboveground calculations, one with an average wood density value for all species and one with species-specific wood density values.
To test the effects of the two types of aboveground carbon calculations and elephant impacts on aboveground carbon stocks, a two-way analysis of variance was performed.

2.4.3 Drivers of wood density

Effect of elephant impact on wood density using Sclerocarya birrea as model species

To analyze the effect of elephant impact on wood density for *Sclerocarya birrea*, a simple linear regression was used.

Effect of fire impact on wood density using Dichrostachys cinerea as model species

To analyze the effects of stem diameter and and fire impact on wood density of *Dichrostachys cinerea* a two-way analysis of variance (ANOVA) was performed.

3. Results

3.1 Wood density

Tree species showed a wide variation of wood density values. The wood density of the 25 species ranged from 0.248 g/cm^3 to 1.092 g/cm^3 across all collected samples (Table 2). On average, *Dombeya rotundifolia* had the lowest wood density and *Sideroxylon inerme* the highest (Figure 6). Some species showed a high intraspecific variation such as *Thespesia acutiloba, Pappea capensis, Manilkara concolor* or *Cassine transvaalensis* (Figure 6).

Table 2: Mean wood density values of 25 tree species measured in the field in Hluhluwe-iMfolozi Park as well as the standard deviation, maximum and minimum value for each species. A total mean wood density across all tree species was also calculated. This mean was used for the estimation of carbon stocks that ignored interspecific variation in wood density.

Tree species	n	Mean wood density (g/cm^3)	Standard deviation	Max	Min
Dombeya rotundifolia	5	0.354	0.087	0.490	0.254
Maytenus senegalensis	5	0.459	0.098	0.603	0.348
Rhus pentheri	5	0.565	0.228	0.886	0.249
Combretum molle	5	0.578	0.158	0.691	0.333
Sclerocarya birrea	5	0.604	0.060	0.701	0.539
Acacia robusta	5	0.614	0.131	0.781	0.471
Acacia gerrarrdii	5	0.620	0.100	0.712	0.466
Thespesia acutiloba	5	0.642	0.218	0.890	0.332
Pappea cappensis	5	0.664	0.236	0.943	0.350
Manilkara concolor	5	0.667	0.243	1.003	0.363
Dichrostachys cinerea	5	0.669	0.072	0.772	0.570
Spirostachys africana	4	0.679	0.070	0.741	0.586
Euclea divinorum	5	0.684	0.058	0.749	0.608
Ziziphus mucronata	5	0.699	0.091	0.790	0.565
Euclea racemosa	5	0.699	0.117	0.841	0.577
Cassine transvalensis	5	0.703	0.228	0.943	0.358
Acacia tortillis	5	0.732	0.057	0.829	0.687
Peltophorum africanum	5	0.739	0.072	0.815	0.633
Combretum apiculatum	5	0.774	0.109	0.922	0.629
Acacia burkeii	5	0.785	0.077	0.861	0.669
Acacia grandicornuta	5	0.789	0.111	0.954	0.647
Berchemia zeyheri	5	0.794	0.157	0.986	0.573
Acacia nilotica	4	0.802	0.076	0.892	0.710
Schotia brachypetala	5	0.811	0.048	0.881	0.754
Sideroxylon inerme	4	0.939	0.126	1.093	0.786
Mean wood density		0.683			

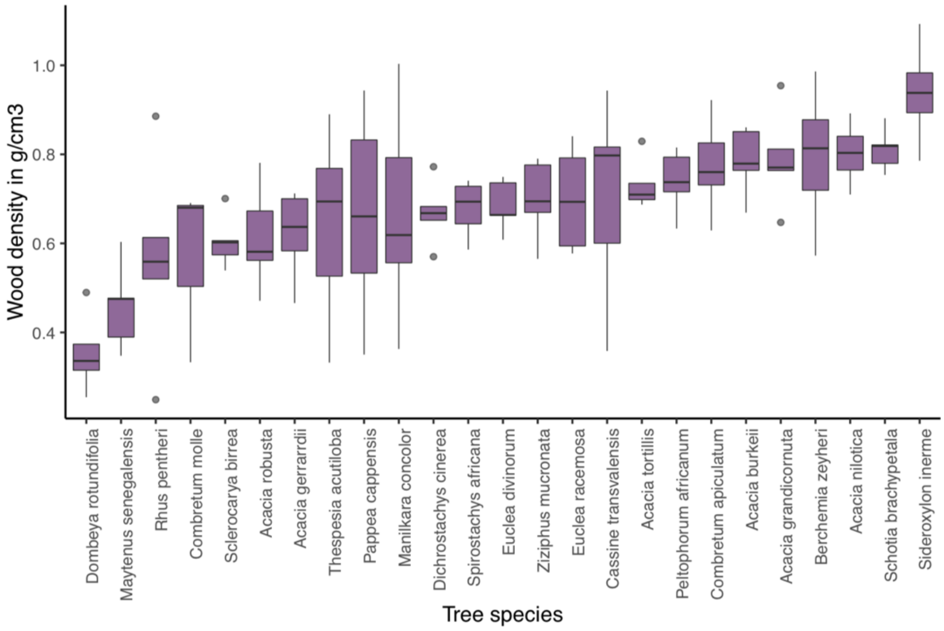

Figure 6:Boxplots showing wood density values in g/cm³ from field measurements. Wood density values are based on 4 to 5 samples per species.

To compare the wood density values collected in HiP and published values, there was data available for 18 species (Appendix 5). Both sets of wood density data did not strongly correlate (r=0.3935, p=0.1061). Our collected wood density values did not significantly correlate with published values (p=0.1061). For 12 species out of 18 species, the collected wood density values were lower than the published ones and fall under the dotted 1:1 line (Figure 7).

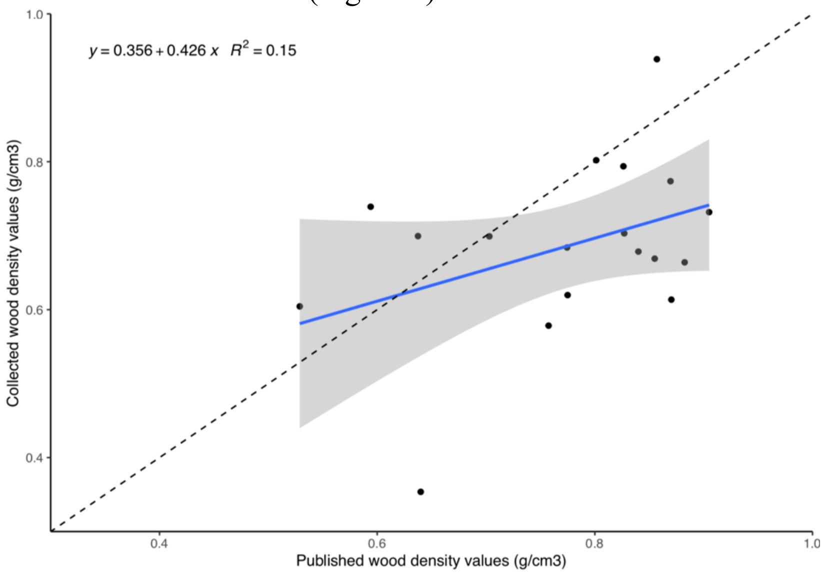

Figure 7: Scatterplot showing the relationship between wood density values found in this study and published values. Correlation test showed low correlation (0.3935846). The blue line indicates the linear regression, and the grey band shows the 95% confidence interval. The black dashed line is the 1:1 line. Published values were not available for seven species of the twenty-five studied species, hence there are only 18 data points on the plot.

3.2 Relationship between elephant impacts and aboveground carbon stocks

For all elephant impact levels, on average, the change in carbon stocks was relatively stable (close to 0), although with strong variation among plots (Figure 8). Elephant impact did not induce a change in aboveground carbon stocks between 1999 and 2017 (Table 3 and Table 4). This result was similar for carbon stocks change calculated based on species-specific wood density values (p=0.3435) and stocks calculated using an average wood density value for all species (p=0.3439). I found weak evidence (p=0.0517 & p=0.0573) for a reduction in aboveground carbon stocks at extreme elephant impacts for both methods (Table 5 and Table 6). No transformation was applied to the data (see Appendix 6 for the distribution of the residuals).

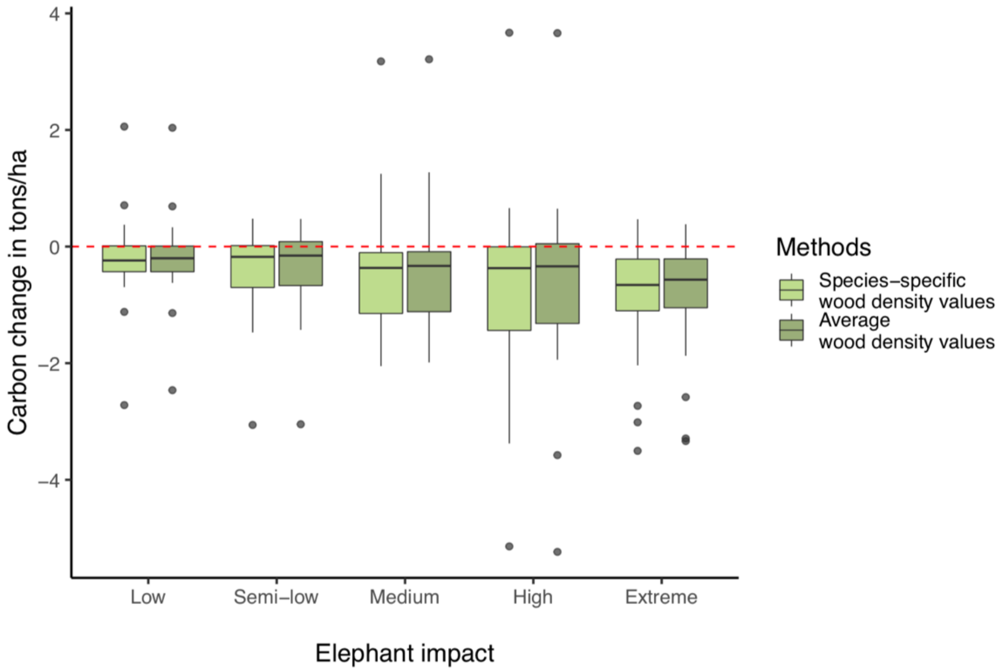

Figure 8: Boxplots depicting the change in carbon stocks in relation to elephant impacts for each plot between 1999 and 2017. The change in carbon was calculated using species-specific wood density values in light green and using an average wood density value in dark green. The red dotted line represents no change in above-ground carbon stocks. Plots were categorized in the elephant impact levels using quartiles of the mean of all impact types as a cut-off.

Table 3: Analysis of Variance table of the effects of impact levels on carbon stocks change using species-specific wood density values for 25 species.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact levels	4	6.117	1.5293	1.137	0.3435
Residuals	100	134.501	1.345		

Table 4: Analysis of Variance table of the effects of impact levels on carbon stocks change using an average wood density value for all species.

	Df	Sum Sq	Mean Sq	Fvalue	Pr(>F)
Impact levels	4	6.025	1.5064	1.1233	0.3499
Residuals	100	134.105	1.3411		

Table 5: Summary table from linear model for the response 'Carbon stock change' among the different elephant impacts levels using species-specific wood density values for all species.

	Estimate	Std.Error	tvalue	Pr(>|t|)
(Intercept)	-0.2076	0.2531	-0.82	0.4139
Impact Semi-low	-0.2478	0.3579	-0.692	0.4903
Impact Medium	-0.189	0.3579	-0.528	0.5986
Impact High	-0.4556	0.3579	-1.273	0.2059
Impact Extreme	-0.7049	0.3579	-1.969	0.0517

Table 6: Summary table from linear model for the response 'Carbon stock change' among the different elephant impacts levels using an average wood density value for all species.

	Estimate	Std.Error	tvalue	Pr(>|t|)
(Intercept)	-0.1912	0.2527	-0.756	0.4512
Impact Semi-low	-0.247	0.3574	-0.691	0.4911
Impact Medium	-0.1733	0.3574	-0.485	0.6287
Impact High	-0.4713	0.3574	-1.319	0.1903
Impact Extreme	-0.6873	0.3574	-1.923	0.0573

A two-way ANOVA was performed to analyze the effect of elephant impact and the use of species-specific or average wood density value on above-carbon stocks change. There was no evidence of interaction between the effects of elephant impacts or the method (p=1.000). Interactions between the method and each impact levels were not significant (Table 7) suggesting that the effect of elephant impact on change in carbon stocks did not depend on the way we calculated carbon stocks (i.e., with or without species-specific wood density).

Table 7: Analysis of Variance table (two-way ANOVA) of the effects of the method and impact levels on carbon stock change.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Method	1	0.021	0.02134	0.0159	0.89981
Impact levels	4	12.135	3.03376	2.2589	0.06414
Method:Impact levels	4	0.008	0.00192	0.0014	1.000
Residuals	200	268.606	1.34303		

Table 8: Summary table of the two-way ANOVA.

	Estimate	Std.Error	tvalue	Pr(>|t|)
(Intercept)	-0.1911569	0.2528909	-0.756	0.4506
Method	-0.0164631	0.3576418	-0.046	0.9633
Impact Semi-low	-0.2470019	0.3576418	-0.691	0.4906
Impact Medium	-0.1733293	0.3576418	-0.485	0.6285
Impact High	-0.4712753	0.3576418	-1.318	0.1891
Impact Extreme	-0.687276	0.3576418	-1.922	0.0561
Method:Impact Semi-low	-0.0008132	0.5057819	-0.002	0.9987
Method:Impact Medium	-0.0157021	0.5057819	-0.031	0.9753
Method:Impact High	0.0156318	0.5057819	0.031	0.9754
Method:Impact Extreme	-0.0176099	0.5057819	-0.035	0.9723

3.3 Drivers of wood density

Stem diameter

Looking at species individually, there were positive, neutral and negative linear relationships between wood density and stem diameter, although the significance of those relationships was not tested.
For most of the species, the relationship between stem diameter and wood density showed positive trends with a strong effect for some species such as *Acacia tortillis, Acacia robusta, Ziziphus mucronata* and *Thespesia acutiloba* (Appendix 7). For some species, woody density did not differ with stem diameter and showed a neutral trend, such as for *Dichrostachys cinerea* and *Dombeya rotundifolia*. While for species such as *Sideroxylon inerme* wood density decreased with stem diameter (Appendix 6).

Effect of elephant impact on wood density using *Sclerocarya birrea* as a model species

We found weak evidence for lower wood density at higher elephant impact for *Sclerocarya birrea* (p=0.065, Table 9).

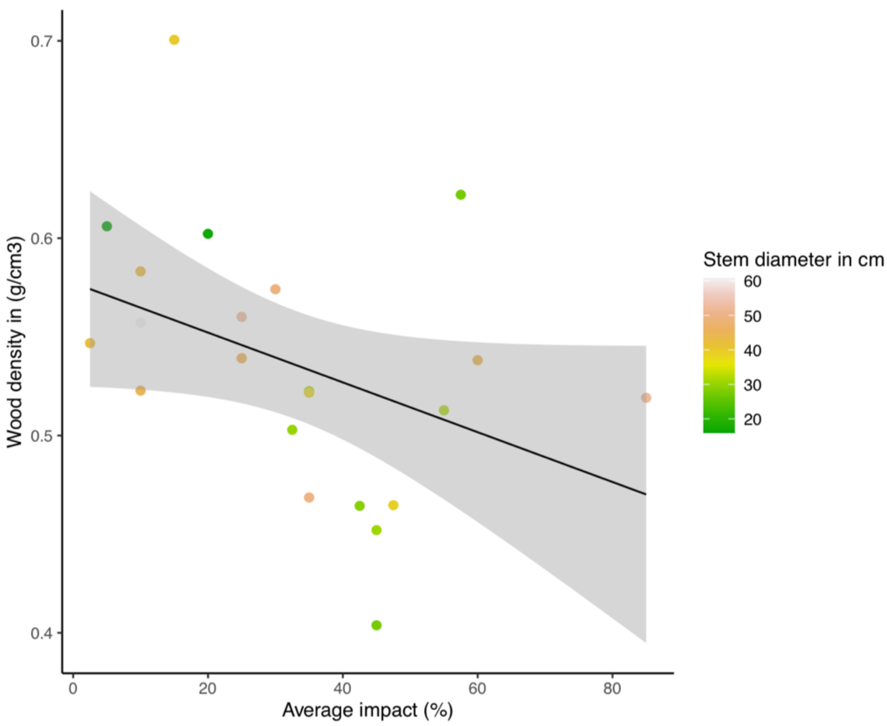

Figure 9: Relationship between wood density and average elephant impact on Sclerocarya birrea. The black trend line corresponds to a linear model based on 20 observations, and the grey band represent the 95% confidence interval. The impact in % is based on an average of two categories of estimated impact: stripping impact and breaking impact.

Table 9: Results of the linear model of the effects of elephant impact on wood density for Sclerocarya birrea. Residuals are normally distributed (Shapiro Wilk test: p-value= 0.6366).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.5773805	0.0251313	22.975	7.54E-16
Average impact	-0.0012617	0.0006478	-1.948	0.0656

Effect of fire impact on wood density using *Dichrostachys cinerea* as a model species

The two-way ANOVA revealed that there was no significant interaction between stem diameter and fire impact (p=0.8629, Table 10). Simple main effects analysis showed that stem diameter did not affect significantly wood density (p=0.2914). Simple main effects analysis showed no evidence of fire impact on wood density (p=0.972) (Figure 10).

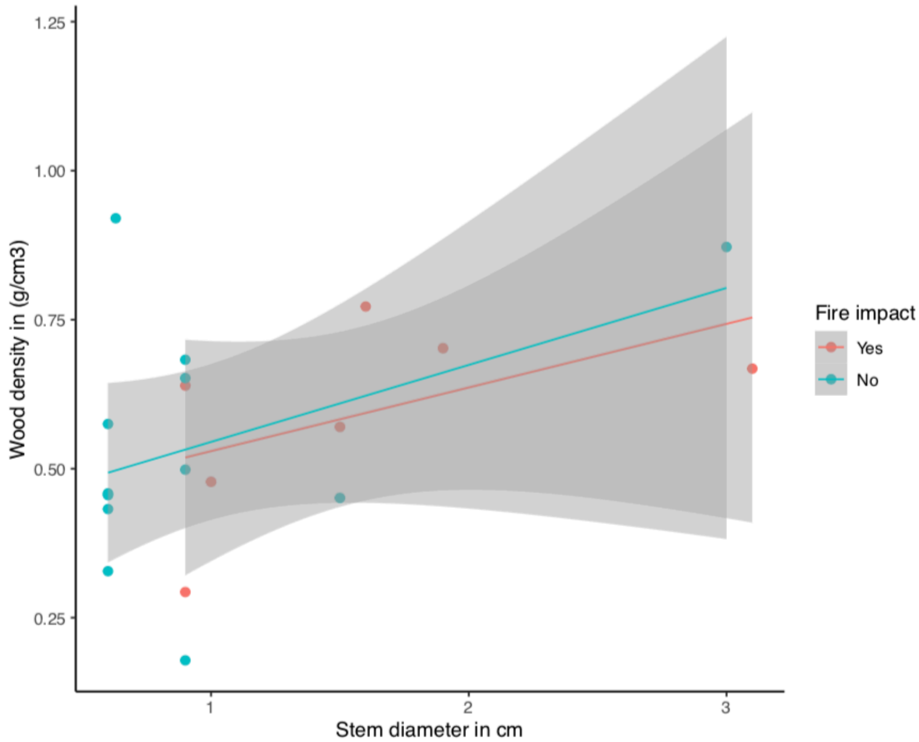

Figure 10: Relationship between wood density, stem diameter, and fire impact based on 18 alive samples of *Dichrostachys cinerea*. The blue trend line corresponds to a linear model of 20 observations, and the grey band represent the 95% confidence interval.

Table 10: Analysis of Variance table (two-way ANOVA) of the effects of stem diameter and fire impact on wood density of Dichrostachys cinerea.

	Estimate	Std.Error	tvalue	Pr(>|t|)	
(Intercept)	0.42267	0.16771	2.52	0.0235	*
Stem diameter	0.10677	0.09764	1.093	0.2914	
Fire impact	-0.00692	0.19356	-0.036	0.972	
Stem diameter:Fire impact	0.0224	0.12747	0.176	0.8629	

4. Discussion

We used field measurements of wood density in combination with historical data from elephant impact vegetation surveys to estimate the change in aboveground carbon stocks in relation to elephant impact levels between 1999 and 2017. Our main results showed that (1) elephant impact did not negatively affect aboveground carbon stocks at levels below extreme impact and that (2) the use of species-specific wood density values compared to the use of an average wood density value did not affect the estimation of the change in carbon stocks. Lastly, we showed that (3) stem diameter depending on the species and elephant impact affected intraspecific variation in wood density, however, fire impact did not.

4.1 Elephant impact on the change of aboveground carbon stocks

I showed that elephant impact did not negatively affect aboveground carbon stocks and that the change in aboveground carbon stocks depends on the intensity of elephant impacts. Despite a growing elephant population in Hluhluwe-iMfolozi Park (Kuiper *et al.,* 2018), the change in aboveground carbon stocks did not show a significant decrease for low, semi-low, medium, and high impact intensity. I found weak evidence for a reduction of aboveground carbon stocks in plots with extreme elephant impact. Several factors could drive this effect. Davies et al (2019) showed that bull elephant densities over 0.5 bulls/km^2 induced the largest declines in aboveground carbon stocks in Kruger National Park (KNP). The impacts of bulls and mixed herds on above-ground carbon stocks seem to differ considering that mixed herds, on the opposite, were generally associated with increases in AGC stocks in KNP. Due to sexual segregation in elephant herds, with bulls roaming more widely and away from herds (Stokke *et al*., 2002), bulls tend to have different foraging behaviors. They topple more trees than mixed herds and increase tree fall which could potentially explain the negative impact of bulls on aboveground carbon stocks (Davies *et al*., 2019). However, the reduction in AGC was not only linked to bulls independently but also to low rainfall. Low rainfall areas are a less favorable environment for tree growth; hence difficult for trees to recover after elephant impacts. Topography and hydrology also seemed to be linked to losses of AGC and bull densities since large declines of AGC stocks have been measured along rivers. Elephants often forage and gather along rivers (Smit *et al*., 2010); therefore, stronger impacts on vegetation might be induced and could explain declines in AGC in those areas (Davies *et al*., 2019). Factors such as bull density, rainfall or topography could also be drivers of extreme impacts in certain plots in HiP.

In Hluhluwe-iMfolozi Park, a total of 174 elephants have been successfully reintroduced to the reserve from 1981 to 1996. The population showed an exponential population growth between 1996 and 2014, which raised concerns about overpopulation and impacts on vegetation and biodiversity (Kuiper *et al.,* 2018). Effects of megaherbivores such as elephants on vegetation might be intensified in small, fenced reserves since the movement of animals is restricted (Wiseman *et al*., 2004). The total area of Hluhluwe-iMfolozi Park is about 950km^2 (Ezemvelo KZN Wildlife 2011a), and it is suggested that areas smaller than the threshold of 1000km^2 fall under the home range size of an elephant. This indicates that the impacts of elephants on the vegetation in HiP might be strong, especially since it holds a growing elephant population (Ezemvelo KZN Wildlife 2011a). However, the ecological carrying capacity of elephants in HiP was projected to be between 960 and 1140 elephants and has not been reached yet; the population was around 700 individuals in 2016. The relationship between elephant numbers and elephant impacts on vegetation is complex (Kuiper *et al.,* 2018). Other South African reserves such as the Kruger National Park (about 20'000 km^2), sheltered over 17'000 individuals in 2015 (MacFadyen *et al*., 2019). Elephant density in HiP (0.73 elephants/km^2) compared to the Kruger National Park (0.85 elephants/km^2) is slightly lower. HiP does not hold the highest density of elephants compared to other reserves in South Africa; however, the density is relatively high. Despite their current density, on average, elephant impact did not affect aboveground carbon stocks in HiP.

4.2 Differences in the estimation of aboveground carbon stocks

The change in aboveground carbon stocks in our study was measured using different wood density values to evaluate the importance of the interspecific wood density variation for estimating aboveground carbon stocks. The magnitude of the change in carbon stocks related to elephant impacts using species-specific wood density values or an average wood density value surprisingly led to similar results. The carbon content of trees is known to be dependent on wood density which is one of the most important predictors of tree biomass (Chave *et al.,* 2009). It has been shown that excluding wood density from allometric equations might lead to poor estimations of aboveground biomass. Therefore, using species level-average wood density values is recommended (Baker *et al*., 2004, Chave *et al*., 2005). Species-specific wood density values might be even more important to consider in areas with a wide variation in species composition. One hectare in Hluhluwe-iMfolozi Park can hold a large variety of tree species and considering them all having similar wood density wouldn't represent the aboveground biomass, hence carbon stocks. However, in our study, using an average wood density value for all species or using species-specific values led to very similar results in estimating the change in carbon stocks over the years. This might be because species-specific wood density values were applied to 25 tree species out of a total of 235 species present in the plots. Because of a lack of species-specific values for the rest of the tree species present in the data, we used an average wood density value meaning that only 10.6% of the total species present in the plots had a species-specific wood density value. So, there might be a difference in carbon stocks estimations when using species-specific wood density values as Baker et al (2004) and Chave et al (2005) showed, but it is not noticeable in my analysis since most of the species were still represented with an average wood density value. Including species-specific wood density values to more species would probably show a difference in carbon stock estimations. In the absence of species level wood density, the use of average wood density values at family or genus level could also potentially show differences as wood density also depends on phylogeny (Baker *et al*., 2004, Chave *et al*., 2006). However, using only 25 species-specific wood density values might not completely explain the similar results between the two types of calculations aboveground carbon stocks. The 25 selected species make up 80% of the plots, which indicates that they are the species that account for most of the aboveground carbon stocks. Therefore, the similar result between the two types of calculations could also be linked to a shift in tree species composition induced by elephant impact. As elephants transform the composition of woody communities over the years (Wiseman *et al*., 2004) and wood density widely varies between tree species, the wood densities of the different tree species might counterbalance each other across time in the species shift. Suppose the wood densities of the different tree species even out over time. In that case, the effect of using species-specific wood density values on the aboveground carbon stocks calculations might be hidden. One approach could be to investigate the species shift between 1999 and 2017 in the plots using the historical data. Then, explore which tree species become more or less dominant over time and compare the corresponding wood density values of the different tree species.

In general, the comparison between collected wood density values and the published values showed that twelve species of my own wood density values out of the 18 species were lower than the published values. For some species, wood density values were similar to published results (Appendix 5). For example, the TRY plant trait database described average wood densities for the tree species *Acacia nilotica* of 0.801 g/cm3 and 0.703 g/cm *Ziziphus mucronata*. These values are close to the mean values 0.802 g/cm3 and 0.699 g/cm3 from my own data collection. However, for some other species, collected wood density values were lower than in previous studies. The regression of the collected wood density values against the published values produced a non-significant linear relationship (Figure 7), indicating a difference between published values and my own values. This suggests that I generally underestimated wood density. An explanation for this result could be due to the methods of wood density measurements by underestimating the dry weight of samples or by overestimating the fresh volume of the samples. Another reason for this result could be that tree species in HiP might show lower wood densities on average than in some other areas simply because wood density varies between local environment conditions (Nam *et al.,* 2018). Moreover, it could potentially be influenced by wood density drivers such as stem diameter. I found that wood density varies with stem diameter for some species (Appendix 7), which might explain the differences between the two datasets. The differences might be due to other studies that focused their sampling on viable individual trees with large diameters only. The discrepancies between published wood density values and my collected values might influence my overall result of carbon stocks estimations. Underestimating wood density values, suggests that I might underestimate aboveground carbon stocks in HiP. However, this shows how much wood density varies between datasets and reflects the importance of including intraspecific and interspecific wood density variation in the estimation of aboveground carbon stocks.

4.3 Wood density drivers

Previous studies quantifying the influence of elephants on aboveground carbon stocks (Davies *et al*., 2019, Sandhage-Hofmann *et al*., 2021) either did not use allometric equations requiring wood density or did not detail their wood density measurements or selection of individual trees. Yet, intraspecific and interspecific wood density variation has been shown to be important to consider when estimating aboveground carbon stocks (Baker *et al.,* 2004, Chave *et al*., 2005, Yeboah *et al.,* 2014). Moreover, because disturbances such as fire and impacts of megaherbivores are important characteristics of savanna biomes (Archibald *et al.,* 2017, Druce *et al.,* 2017), I tested the influence of stem diameter, elephant impact and fire impact on the wood density of individual trees. Therefore, if these factors are drivers of wood density, we should account for them in our sampling method.

There are large variations in diameter size between species and those variations can influence wood density. Tree species can show different shapes depending on natural tendencies. Some tree species are shaped as high standing trees, some others are shrub species, and some species exist in both morphs depending on the environment. In previous studies, the selection of study trees is rarely explained. However, there is a possibility that stem diameter drives wood density depending on the species. As expected, the influence of stem diameter on wood density differed between species. Some species showed an increasing wood density with stem diameter, which means that considering stem diameter is important to avoid biases in wood density measurements. For example, by sampling large trees only, larger stem diameter might be overrepresented and there is a chance for biases in wood density estimates towards higher wood densities for a species. However, based on the number of samples collected per species in my study, it is hard to confirm whether stem diameter affects or not wood density because it is likely to be species dependent. One way to test if stem diameter has an effect on wood density would be to collect more samples per species and apply a linear regression to every species.

I also investigated how wood density was influenced by elephant impacts for Marula trees (*Sclerocarya birrea*) as the species is preferred by elephants. We found weak evidence for lower wood density at higher elephant impact. As a result, using the average wood density value for highly impacted trees might bias the results of carbon stocks estimations. To avoid overestimation, we should consider lower wood density values for impacted trees when estimating aboveground carbon stocks. In nature, woodlands or savannas are composed of trees with different ranges of elephant impacts. Ignoring those impacts on individual trees, if elephant impacts influence wood density, could lead to biased estimates.

Another potential driver of wood density I considered was fire impact. *Dichrostachys cinerea* is a shrub species heavily affected by fire in Hluhluwe-iMfolozi Park. However, we show that fire damage did not significantly affect wood density values and samples from intact or impacted bushes showed similar trends. This could indicate that including samples from post-fire areas would not necessarily influence wood density estimates, hence carbon stocks.

4.4 Study limitations and further research

Despite the results of this study, there are limitations in its conclusions. First, the use of species-specific values for a higher number of species present in the park could lead to more precise results of the estimation of aboveground carbon stocks. I suggest that further studies focus on a wood density data collection that includes more tree species.

Another suggestion concerning the accuracy of the aboveground carbon stocks estimations would be to use a species-specific carbon conversion factor instead of the default value of 0.47. Martin et al (2018) and Thomas et al (2012) recommended incorporating a species-specific CCF into carbon stocks estimations since it varies across biomes and species from the same environment.

In addition, incorporating an analysis of the shift in species composition over the years and test how the species shift influences carbon stocks estimation would be a process to consider. In response to browsing pressure, woody communities change, implying that some dominant large tree species preferred by elephants might become uncommon as they are heavily browsed (Wiseman *et al*., 2004). On the opposite, the establishment of less common species might increase (Wiseman *et al*., 2004). If elephants shift the composition of woody communities in savannas, it might be important to consider the variation in wood density and carbon content between species when assessing aboveground carbon stocks as it might influence the overall aboveground carbon stocks of an area.

Also, savannas are dynamic systems (Skarpe *et al*., 1992). They fluctuate with environmental disturbances such as climate, fires and impacts of animals (Skarpe *et al*., 1992). Due to those changes, savanna ecosystems and processes can show long time-lags that might not be represented in the results of my study. The result of the relationship between elephant impacts and the change in aboveground carbon stocks at plot level might be influenced by processes of the savanna ecosystem on a larger scale.

4.5 Synthesis

In summary, the assessment of aboveground carbon stocks is a complex process influenced by various factors such as tree traits measurements and allometric equations. Nevertheless, this study provides a first comprehensive overview of how elephants influenced aboveground carbon stocks over eighteen years in Hluhluwe-iMfolozi Park. The uniqueness of the available time-series in plot-level tree data and the field measurements of wood density provided insights into the interaction of elephants with aboveground carbon stocks. This study demonstrated a way to incorporate elephant effects in regional carbon stock assessments.

My results support that elephants might not necessarily conflict with goals focused on conserving aboveground carbon stocks. However, given that we found weak evidence that extreme elephant impacts might lead to a decrease in aboveground carbon stocks, a conclusion could be that the conservation of elephants might conflict with the conservation of aboveground carbon stocks if the population continues to grow. However, I only investigated aboveground carbon stocks while other studies (Sandhage-Hofmann *et al.,* 2021) also explored the effect of elephants on carbon in soils. The study showed that the belowground carbon stocks compensate for the loss in aboveground carbon stocks. Moreover, according to my results, extreme impacts of elephants occurred in 20% of the plots in HiP only. Consequently, aboveground carbon stocks in most of the plots (80%), and potentially the majority of the landscape in HiP, were not affected by elephant impacts.

In general, carbon accounting has become an important focus of attention and study in the era of climate change. There is a rising interest in finding strategies to tackle losses of carbon stocks within ecosystems and quantify the positive and negative effects of animals on carbon cycling (Schmitz *et al.*, 2014). Elephant impacts might be strong in certain areas, but the intensity of those impacts is often due to the system of fenced reserves in South Africa. The fences of the reserves are used to protect areas, contain wildlife, and represent state, private or communal ownership (Pretorius et al., 2019). Fences restrict elephants' movements and their historical migration, leading to high localized impacts on vegetation (Wiseman *et al*, 2004, Pretorius et al., 2019). Moreover, we should look at the effects of elephants on a broader scale and not only focus on aboveground carbon stocks. Elephants are ecosystem engineers and affect the savanna ecosystem at different scales (Wright *et al.*, 2006, Asner *et al.*, 2016, Hempson *et al.,* 2017). They create opportunities for biodiversity in those extremely impacted plots as they modify the habitat structure. For example, by opening the vegetation, changing fire patterns, or by creating deadwood, other species benefit from elephants' presence (Asner *et al.,* 2016). Elephants contribute to the savanna ecosystem in many ways and their loss could reduce opportunities for other species since the ecological role of elephants cannot be replaced by smaller species (Owen-Smith, 2013).

If elephants were ever to conflict with carbon stocks in the future, there is a chance that their population management could be discussed. However, this raises a philosophical point of view about how humans value nature and how we hierarchize some nature services above others. What to conserve and what not to conserve? Should we focus conservation actions on one aspect (carbon stocks) to the detriment of another (elephant's presence)? This raises a debate between conservation of nature for nature's sake or conservation of nature for human well-being. However, elephants are part of the savanna ecosystem, and any management decisions should be based on an analytical basis and relevant research.

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Acknowledgements

I would like to start by expressing my deepest gratitude to my supervisors, Joris Cromsigt and Mariska te Beest for their guidance and for giving me the opportunity to work with them on such an interesting project. Your advice, feedback and encouragements helped to shape this thesis and your teaching made me grow as an ecologist and as a person. Thank you for our discussions, your patience and our short time spent in Hluhluwe-iMfolozi Park.

I am sincerely grateful to Dave Druce and Ezemvelo KZN Wildlife for letting me conduct my study in Hluhluwe-iMfolozi Park. It was a privilege to be able to stay at the research station and spend most of my time in the bush. Thank you to Graham Kerley for the organization of the car and my apologies (again) for the damages caused to the rear bumper. A special thank you to Erick Khumalo who was always making sure I was sampling trees in a safe place and who taught me everything about plant species and the bush. Without your knowledge, none of this would have been possible. My greatest appreciation to Siphesihle Mbongwa for his help with the historical data and the organization of the fieldwork days.

My sincerest thank you to both of my parents who have not only been supporting me financially but also mentally and morally. You always have my back and made it possible for me to achieve my studies and goals. I am forever grateful for your support and love.

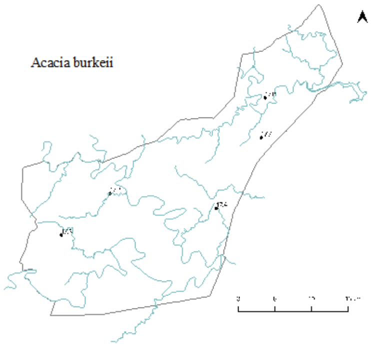
Finally, I would like to thank all my friends for their support during my studies. A special thank you to Philippine, with whom I share a common love for wildlife and nature. I am grateful for our friendship, discussions, your advice, and encouragements. And I also would like to thank all my fellow master students for the support, help and the good laughs.

Appendix

Appendix 1

Figure 11: Different elephant impacts on trees: tree toppling (upper picture), branch breaking (left), bark stripping (right).

Appendix 2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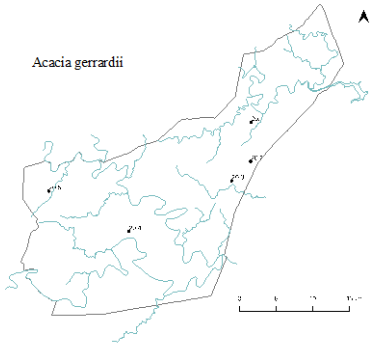
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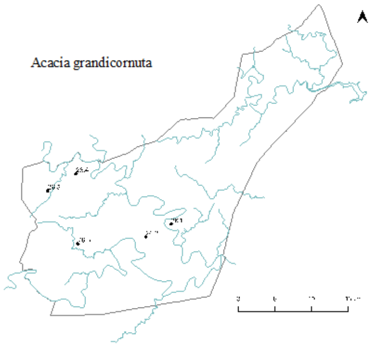
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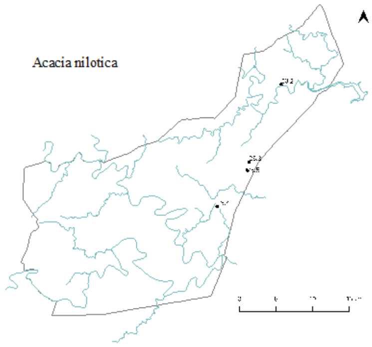
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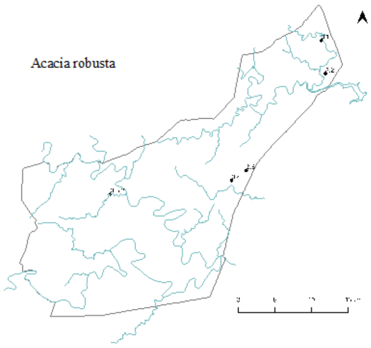
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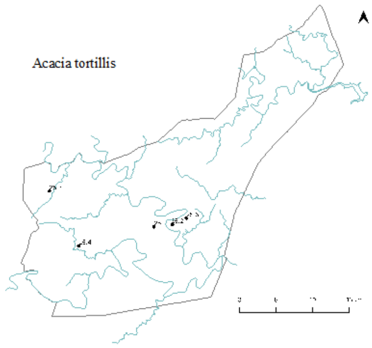
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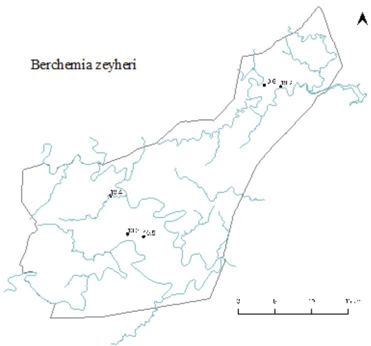
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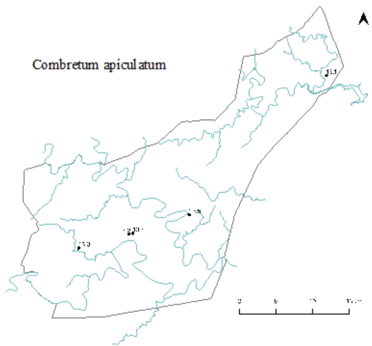
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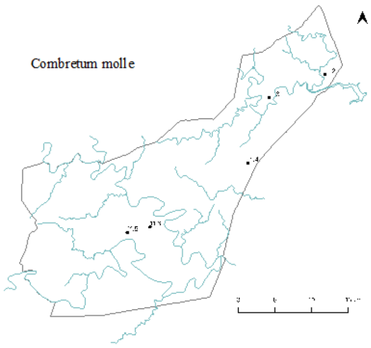
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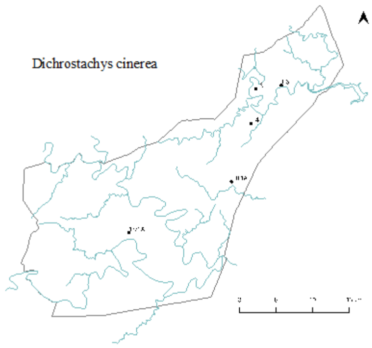
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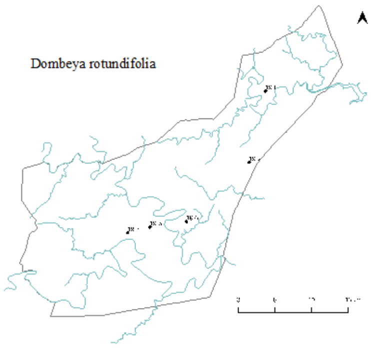
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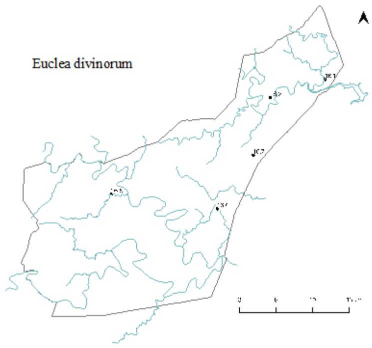
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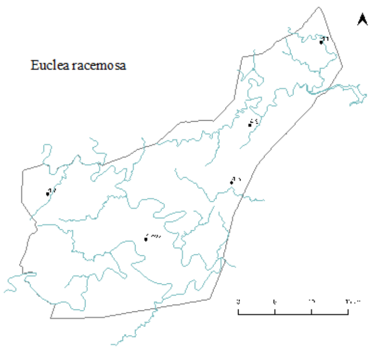
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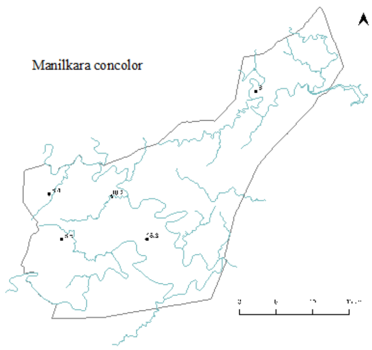
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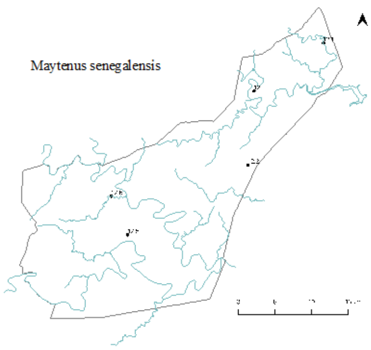
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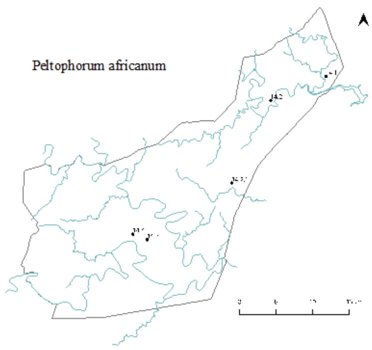
Peltophorum africanum

Figure 12: Sampling locations per species

Appendix 3

Table 11: Tables showing the percentage of stems per diameter class for the 25 species. The 5 samples to collect were divided across the diameter classes according to the highest percentages of each species. n shows how samples have been divided across the diameter class.

	Percentage of stems A.burkeii	n	Percentage of stems A.gerrarrdi	n	Percentage of stems A.grandicornuta	n	Percentage of stems A.nigrescens	n
Diameter class 1 (0-1cm)	9.51		25.17	1	12.32		4.71	
Diameter class 2 (1-3cm)	8.72		24.50	1	14.88		3.14	
Diameter class 3 (3-10cm)	11.41		27.85	2	36.32	3	13.00	
Diameter class 4 (10-20cm)	21.71	2	19.46	1	26.56	2	30.71	2
Diameter class 5 (20-50cm)	31.85	2	3.02		8.64		42.14	3
Diameter class 6 (>50cm)	16.80	1	0.00		1.28		6.29	

	Percentage of stems A.nilotica	n	Percentage of stems A.robusta	n	Percentage of stems A.tortilis	n	Percentage of stems B.zeyheri	n
Diameter class 1 (0-1cm)	16.54	1	14.13		12.86		14.35	
Diameter class 2 (1-3cm)	12.38		17.43	1	9.29		20.83	2
Diameter class 3 (3-10cm)	32.21	2	24.04	2	25.36	2	33.10	2
Diameter class 4 (10-20cm)	32.11	2	20.92	1	33.57	2	16.44	1
Diameter class 5 (20-50cm)	6.48		16.33	1	17.86	1	14.35	
Diameter class 6 (>50cm)	0.29		7.16		1.07		0.93	

	Percentage of stems C.transvaalensis	n	Percentage of stems C.apiculatum	n	Percentage of stems C.molle	n	Percentage of stems D.cinerea	n
Diameter class 1 (0-1cm)	23.17	2	12.89		20.87	1	44.04	2
Diameter class 2 (1-3cm)	23.17	2	23.78	2	28.45	2	36.67	2
Diameter class 3 (3-10cm)	14.63		26.07	2	28.25	2	17.98	1
Diameter class 4 (10-20cm)	17.07	1	19.77	1	11.07		1.29	
Diameter class 5 (20-50cm)	14.63		15.19		9.51		0.00	
Diameter class 6 (>50cm)	7.32		2.29		1.84		0.02	

	Percentage of stems D.rotundifolia	n	Percentage of stems E.divinorum	n	Percentage of stems E.racemosa	n	Percentage of stems M.concolor	n
Diameter class 1 (0-1cm)	48.88	3	21.0009814	1	14.56		42.86	3
Diameter class 2 (1-3cm)	26.97	2	27.7723258	2	17.73	1	0.00	
Diameter class 3 (3-10cm)	9.55		34.0529931	2	41.63	2	0.00	1
Diameter class 4 (10-20cm)	11.80		12.2669284		21.29	2	28.57	1
Diameter class 5 (20-50cm)	2.81		4.21982336		4.50		28.57	
Diameter class 6 (>50cm)	0.00		0.68694799		0.30		0.00	

	Percentage of stems M.senegalensis	n	Percentage of stems P.capensis	n	Percentage of stems P.aftricanum	n	Percentage of stems R.pentheri	n
Diameter class 1 (0-1cm)	55.50	4	28.16	2	7.50		21.19	
Diameter class 2 (1-3cm)	28.93	1	12.62		25.83	2	24.28	2
Diameter class 3 (3-10cm)	13.74		18.45	1	22.50	1	31.02	2
Diameter class 4 (10-20cm)	1.70		20.39	1	24.17	1	18.50	1
Diameter class 5 (20-50cm)	0.13		18.45	1	19.17	1	4.05	
Diameter class 6 (>50cm)	0.00		1.94		0.83		0.96	

	Percentage of stems S.brachypetala	n	Percentage of stems S.birrea	n	Percentage of stems S.inerme	n	Percentage of stems S.africana	n
Diameter class 1 (0-1cm)	11.31		5.61		8.92		11.74	
Diameter class 2 (1-3cm)	14.93		2.80		11.27		19.37	1
Diameter class 3 (3-10cm)	15.38	1	3.74		23.94	1	34.06	3
Diameter class 4 (10-20cm)	14.48		14.02		27.70	3	19.15	1
Diameter class 5 (20-50cm)	19.00	2	49.53	2	21.60	1	12.47	
Diameter class 6 (>50cm)	24.89	2	24.30	3	6.57		3.22	

	Percentage of stems T.acutiloba	n	Percentage of stems Z.mucronata	n
Diameter class 1 (0-1cm)	26.32	2	7.65	
Diameter class 2 (1-3cm)	15.79		14.12	
Diameter class 3 (3-10cm)	5.26		37.65	3
Diameter class 4 (10-20cm)	26.32	2	28.24	2
Diameter class 5 (20-50cm)	26.32	1	10.78	
Diameter class 6 (>50cm)	0.00		1.57	

Appendix 4

Table 12: Elephant impact categorized in classes as percentage of the whole tree broken or stripped.

Classes	Percentage
1	0-5%
2	5-35%
3	35-65%
4	66-95%
5	>95%

Appendix 5

Table 13: Table showing my own mean wood density values and published values from different wood density databases. Published values were available for 18 species.

Tree species	Collected mean wood density values (g/cm^3)	Published values wood density values (g/cm^3)
Acacia burkeii	0.784747	-
Acacia gerrarrdii	0.6196742	0.775
Acacia grandicornuta	0.7894111	-
Acacia nilotica	0.8020218	0.801
Acacia robusta	0.6135188	0.870
Acacia tortillis	0.7318038	0.905
Berchemia zeyheri	0.7937987	0.826
Cassine transvalensis	0.7031443	0.827
Combretum apiculatum	0.7735989	0.869
Combretum molle	0.5783933	0.757
Dichrostachys cinerea	0.6689633	0.855
Dombeya rotundifolia	0.3536833	0.64
Euclea divinorum	0.6840089	0.774
Euclea racemosa	0.6994601	0.637
Manilkara concolor	0.6667314	-
Maytenus senegalensis	0.4585333	-
Pappea cappensis	0.66396	0.882
Peltophorum africanum	0.7391009	0.594
Rhus pentheri	0.5652988	-
Schotia brachypetala	0.8108817	-
Sclerocarya birrea	0.6044052	0.528
Sideroxylon inerme	0.938594625	0.857
Spirostachys africana	0.67852175	0.84
Thespesia acutiloba	0.6422059	-
Ziziphus mucronata	0.6990894	0.703

Appendix 6

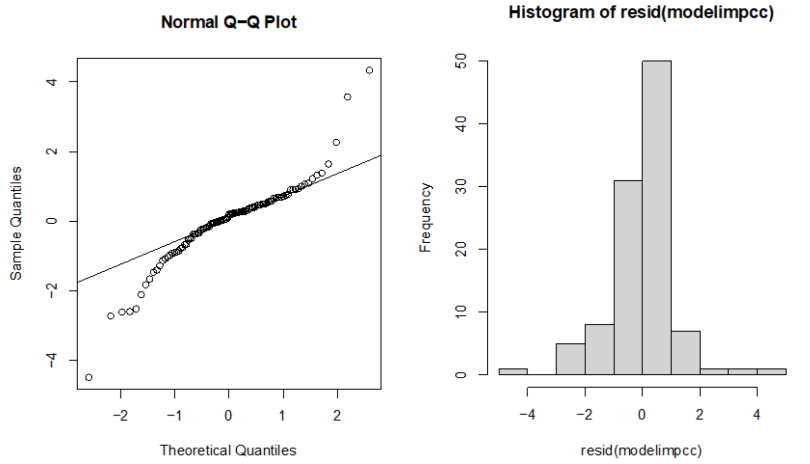

Figure 13: Distribution of the residuals of the model 'Carbon stocks change' against the different elephant impact levels using species-specific wood density values for all species.

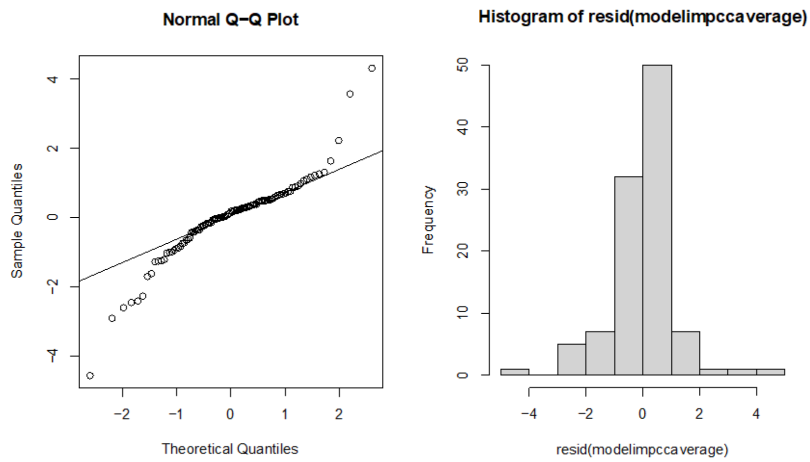

Figure 14: Distribution of the residuals of the model 'Carbon stocks change' against the different elephant impact levels using species-specific wood density values for all species.

Appendix 7

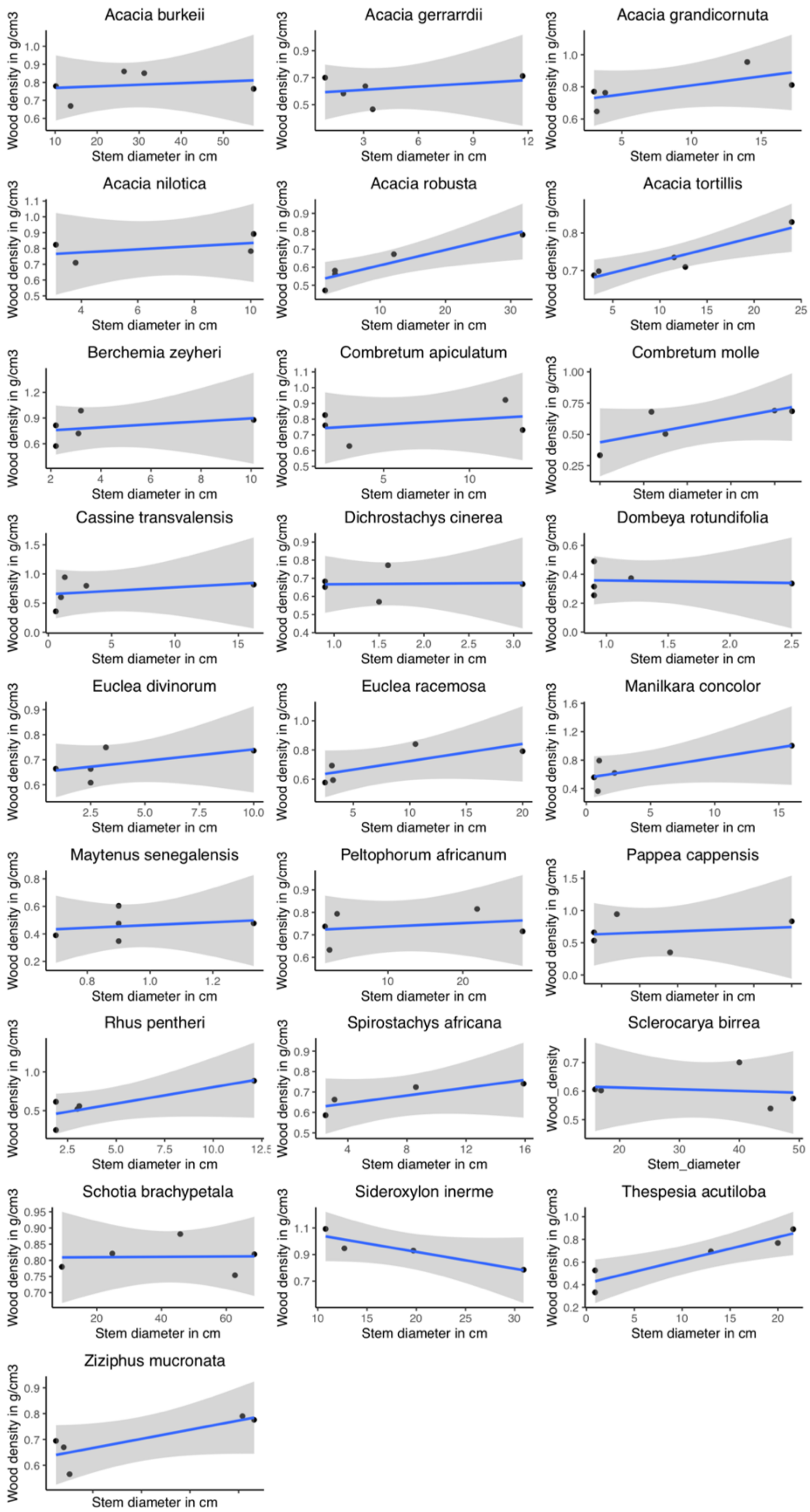

Figure 15: Wood density values in relationship with stem diameter for 25 different species. The blue trend line corresponds to a linear regression of 4 or 5 observations, and the grey band represent the 95% confidence interval.

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