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Större träds överlevnad i relation till ”bottom-up” och ”top-down” drivkrafter i Hluhluwe-iMfolozi Park, Sydafrika

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Examensarbete i ämnet biologi
Department of Wildlife, Fish, and Environmental studies
Umeå
2017

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Credits: 60 HEC
Level: A2E
Course title: Master degree thesis in Biology at the Department of Wildlife, Fish, and Environmental Studies
Course code: EX0595
Programme/education:

Place of publication: Umeå
Year of publication: 2017
Cover picture: Petter Madsen
Title of series: Examensarbete i ämnet biologi
Number of part of series: 2017:8
Online publication: http://stud.epsilon.slu.se

Keywords: Elephant, drivers, savanna, South Africa, tree survival

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Abstract

Tall trees are in decline throughout many national parks in South Africa. Many studies have found that trees within a certain size are preferred by elephants which damage trees by either bark stripping, breaking tree branches and/or stems or by knocking over trees (toppling). The decline of trees in relation to growing elephant populations is of growing concern, as tall trees are a key stone feature in the savanna ecosystem. One of the parks where elephant populations are increasing is in Hluwhluwe-iMfolozi Park, KwaZulu-Natal. To investigate whether trees within the park are in decline, we set out to revisit previously tagged trees from 2007 to reassess their condition. When revisiting trees a total of 260 trees were found, resulting in a 92.5% success rate in relocation of individual trees. The analyses showed that elephant impact was not descriptive of tree mortality within the park. Two tree species however, Combretum molle and Spirostachys africana, had a lower mortality risk. The risk of elephant impact was mediated by several abiotic variables, such as slope, aspect and elevation. The results of this study further accentuates the need to research the interaction between various factors to understand the causative agents of tall tree mortality.

Introduction

As in any ecosystem, large trees play a key role in African savannas as they are suitable habitats for other species, constitute a large part of browsers diet, while also regulating biogeochemical processes (Derham et al. 2016, Clegg & O'Connor 2016, Belsky et al. 1989). From numerous independent studies there is a growing concern for the condition of the tree populations in the African savannas. Transformation of savannas by elephants have been widely reported in African savannas (Spinage 2012). Elephants have an impact on community composition (Scholtz et al. 2017), woody vegetation recruitment (O'Connor 2017) and directly impact particular tree species (Hema et al. 2017). Additionally, studies have that elephants target taller trees, making them more vulnerable (Shannon et al. 2008), subsequently decreasing the number of tall trees. This decline of tall trees has often been directly attributed to elephants (Guldemond & van Aarde 2008). Since the end of the ivory trade, elephants have been re-introduced into many reserves and populations of African elephants, Loxodonta a. africana, have steadily increased (Blanc et al. 2005). Often these reserves are fenced, such as Kruger National Park, Addo Elephant National Park and Hluhluwe-iMfolozi Park. An increasing elephant population within a fenced environment will cause an increasing pressure on the vegetation. In some cases, the elephant populations are estimated to be living above the carrying capacity for the environment (Druce et al. 2008). This increase in elephant impact due to their increased density has negative consequences for the parks. Kerley & Landman (2006) showed that an increasing population of elephants increases the percentage of open landscapes, O'Connor & Goodall (2017) show that population size and structure is affected by elephant impact, Rutina & Moe (2014) showed that elephant browsing substantially affected tree-species composition, decreased diversity and decreased species richness. Elephants might also affect vulture populations by making it possible for insects and diseases to harm trees (Vogel et al. 2014). The damage to trees due to elephants has been a rising concern in many parks where elephant populations are increasing.

The consequences from loss of large trees can have major impact on the ecosystem. However, the loss of trees are often wrongfully ascribed to elephants solely, as impact from elephant is often mediated by other drivers, such as fire. In African savannas, fire is one of the main landscape altering drivers capable of changing the environment (Grady & Hoffmann 2012, Holdo et al. 2014). Fire has been shown to interact with elephant impact in driving the loss of tall trees. Elephants remove more tree volume from previously burnt areas, they facilitate more severe fire damage by debarking trees and they are also capable of toppling trees which would otherwise escape fire damage (Shannon et al. 2011). In savannas, the abundance of tall trees is decreasing and certain species are facing a higher pressure from these two drivers resulting in increased mortality, thus it is of interest to monitor and investigate the relationship between elephants and fire on tall trees.

Elephants impact trees in different ways: pushing over the whole tree (toppling), breaking off stems and/or branches, or stripping the bark off the trees. The trees which are more likely to be targeted by elephants are often in the commonly termed “elephant trap”: trees between ~5-9m high and not fully matured (Shannon et al. 2011). Most savanna trees can reach a maximum height higher than this, causing the ‘elephant trap’ to be a bottleneck for trees and reducing the number of trees reaching adulthood. The damage caused during elephant foraging is mostly due to the feeding behaviour of the elephants, but recent studies have also suggested that other reasons, such as sexual display or long term foraging strategies, may also play a role (Midgley et al. 2005). It has been shown that elephant damage is dependent on the distance between the elephant foraging patch and the nearest water source, since elephants do not roam too far from a permanent water source (Western 1975, Nichols et al. 2017). Furthermore, it has been shown that elephants prefer to forage in certain areas determined by elevation and vegetation type due their differences in accessibility, lush vegetation and dietary preference (Nellemann et al. 2002, Clegg 2008). Elephant foraging is also mediated by the foraging intensity, as elephants avoid to utilize previously browsed trees (Clegg 2008). When foraging, elephants may kill all above ground parts of a tree (topkill) while they also facilitate the advent of other harmful agents. When breaking tree branches, the damage caused by elephants can facilitate diseases, insect attacks, increased herbivore pressure, and fire damage. As such, although elephant damage might not directly cause increased mortality to trees, they do facilitate for other deleterious factors.

While there are several deleterious factors in regards to tree survival, fires count as one of the two main drivers in the savannas causing a decrease in trees. Trees which face an elephant trap likewise face a fire trap, in which the younger saplings with a height of maximum three meters are more likely to die from fire damage (Grady & Hoffmann 2012, Wakeling et al. 2011). It has been shown that only a few tree species are able to outgrow this fire trap during fire-free periods. However, these time spans in which trees are able to escape the fire trap is short, limited to only a few years (Wakeling et al. 2012). It is further known that the fires are more likely to harm and kill trees if it is following elephant impact (such as bark stripping) (Pringle et al. 2015). After fires occur in an area, carbon and nitrogen levels available in the soil are reduced, resulting in grass species dominance as they are more proficient in nitrogen fixation, thus reducing tree prominence (Cech et al. 2008). This competition is further accentuated to water prevalence, as wetter areas are dominated by grasses due to their higher growth rate and thus outcompeting trees, driving trees to be excluded to drier areas (Wakeling et al. 2011, Wakeling et al. 2012). However, drier areas, such as ridges or elevated areas where trees are at an advantage in respect to grasses, are limited by decreased growth rate due to colder climate rendering them unable to outgrow the fire trap (Wakeling et al. 2011, Wakeling et al. 2012). In light of this, although fires are necessary to maintain the savanna landscape it proves a challenge for trees.

However, with all this said, it has also been shown that elephants are not always to blame. Guldemond & van Aarde (2008) show this when they conclude that the actual anthropogenic impact, in the form of distance between fences and trees, had a significant correlation to mortality. Furthermore, since elephants prefer to travel along paths and open landscapes to cover larger areas, roads and man-made paths might prove to work as canals for the elephants when they are foraging which might have similar effects on tree mortality as fences. These anthropogenic effects on tree mortality will not be part of the analysis but still offer valuable perspectives to a discussion regarding park management.

To assess the fate of tall trees, long-term monitoring of permanently marked individuals is essential. In this study I resampled 290 trees, which were individually marked in 2007, to investigate survival rate of trees in the savanna over the past ten years in regards to elephant and fire impact together with other biotic and abiotic factors.

Material and methods

Sampling

The study was conducted in Hluhluwe-iMfolozi Park (HiP) in the province of KwaZulu-Natal, South Africa ((28°0′ to 28°25′S, 31°42′ to 32°0′E). The park is a fenced park consisting of 960km2 with various biomes, ranging from grasslands to dense thickets (Whateley & Porter 1983). The climate is semi-arid in the south-western parts of the park, while the northern parts, where the marked trees are located, is a mesic area (Whateley & Porter 1983, Charles-Dominique et al. 2015) with an average rainfall between 600~1000mm (Balfour & Howison 2009), where the most part of the precipitation occurs during the wet season (October-March). Average temperature ranges from 13°C (winter months) to 33°C (summer months).

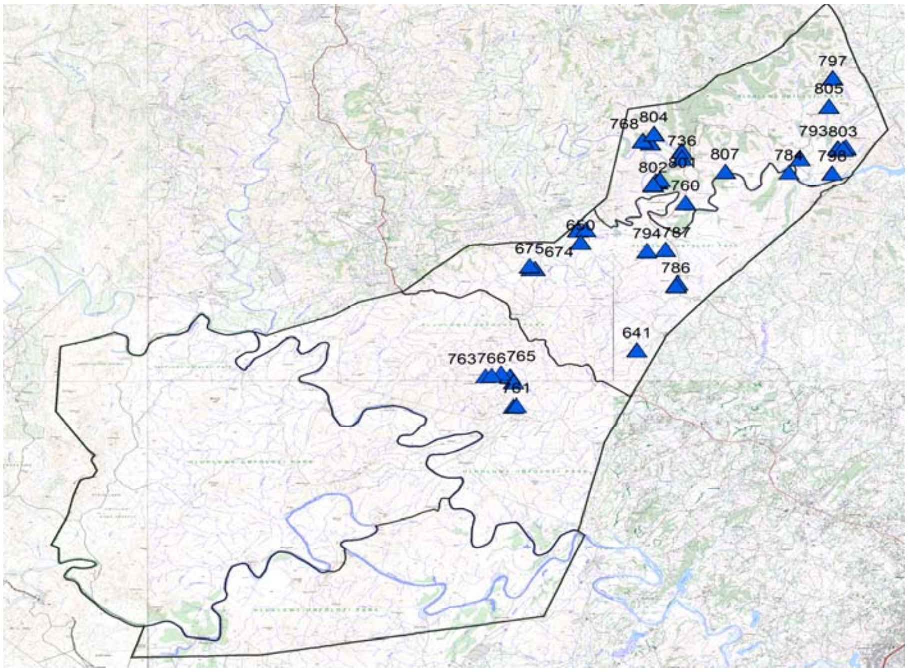


Figure 1. Map showing the distribution of plots within Hluhluwe-iMfolozi Park, Kwa-Zulu Natal, South Africa. In total, 40 plots were assessed and GPS-tagged in 2007.

Throughout the park, a total of 40 different plots were tagged with GPS in 2007, and each plot included individually marked trees, marked with metal tags and its GPS-coordinates. Plots were 50*50m, aligned along a North-South direction. The distribution of the plots covered a majority of the park, with the exception of the southernmost region (Figure 1). Nine trees were not sampled. The reason for this was that the plots contained several trees, where portions of the trees within a plot clustered kilometres apart, making it impossible to know where the actual plot was. The plot size varied from one tree to 34 trees, with an average of 7.25 trees/plot (Figure 2).

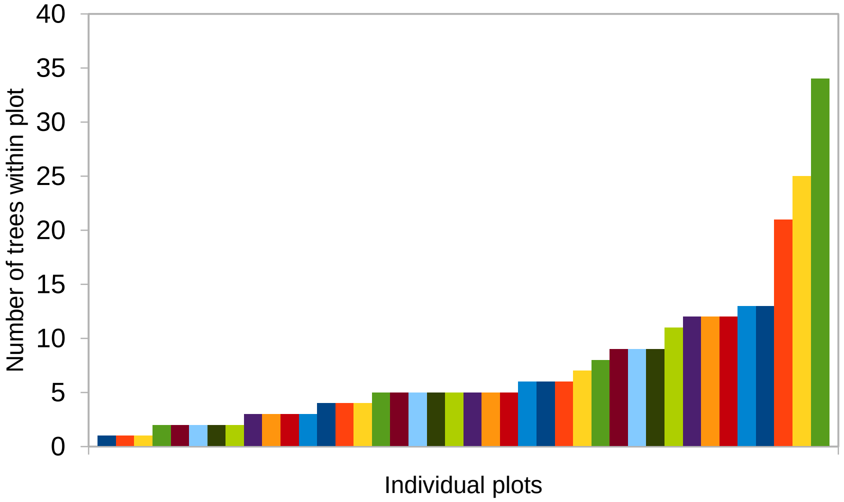


Figure 2. Bar plot showing the number of trees per plot. The smallest plots only had 1 tree, the largest had 34 trees, with an average of 7.25

Between January and March 2017, I revisited the individually marked trees for a second assessment of a range of variables (Table 1). I found back individually marked trees based on their species ID, GPS-coordinates and metal tags. All measurements were not possible to make for all found trees. In the event that no tree was found at the GPS-coordinate we scanned the area for remnants of trees and other possible trees, knowing that the GPS-coordinates might be inaccurate. If we found tree remnants (such as logs, branches, tree trunks, or the occasional metal tag in the dirt) without any other tree nearby, we assumed the tree to be dead. If we did not find any tree remnants and no other trees were found within a radius of +/- ten meters from the GPS-point, the tree was assumed to be dead even if we did not find the metal tag (since the tag might have been buried by hoofs, blown away by the wind, rusted into the dirt or been removed by for instance tusks scraping across the tree trunk). If a tree was found in the area near the GPS-coordinate, we assessed tree species and looked for a tag. If species matched and we found a tag we assumed this to be the tree we were looking for. However, if we did not find a tag the tree was denoted as not found. This was done to ensure individual trees were not mixed up. The measurements were conducted by the same group of people during all revisits with highly experienced personnel to assist in species identification, while also maintaining a strict sample protocol with little variation in measurements (Figure 3). Along with field measurements, estimates of abiotic factors were obtained for the individual plots using ArcGIS and ArcMAP (ArcMAPTM Version 10.4.1.5686, Esri inc®) to extrapolate the values (Table 1).

Table *1* Description of measurements taken in the year 2007 and 2017. Also showing the variables obtained from GIS.

Measurements	**Description**	**2007**	**2017**
Survival	Measure as either dead(=1) or alive(=0)	Yes	Yes
Tree height	Measured in meters (m)	Yes	Yes
Stem diameter	Measured in classes (1=0-1cm, 2=1.1-3cm, 3=3.1-10cm, 4=10.1-20, 5=20.1-50cm, 6=>50cm)	Yes	Yes
Stripping	Amount of damage done to trees by stripping. Measured in classes based on removed bark to circumference (0=0%, 1=>0-5%, 2 =5-35%, 3=35-65%, 4=65-95%, 5=>95%)	Yes	Yes
Breaking	Amount of damage done to trees by breaking of branches and/or stems. Measured in classes based on estimated removed/broken branches/stems (0=0%, 1=>0-5%, 2 =5-35%, 3=35-65%, 4=65-95%, 5=>95%)	Yes	Yes
Species	Tree species	Yes	Yes
Insects	Insect presence, measure as yes or no. This was estimated by visual confirmation of borehols and/or insects	No	Yes
Fire damage	If possible the height of a fire scar was measured in meters. If we found individuals which had been burnt but unable to assess height (e.g. a burnt log) they were marked as Burnt/Not burnt	No	Yes
Cause of damage	An estimate of how certain we were the damage that had been made was from elephants. Measured in classes, 1=certain of elephant impact, 2=relatively certain of elephant impact, 3=probably other source of damage, 4=other source of damage.	No	Yes
Topple	Measured as Yes, defined as roots exposed and trunk/stem in horizontal plane, or No	No	Yes
Slope	The degree of slope for the plots. Obtained both as a continuous variable and broken into a categorical variable (1=0-3°, 2=3-5°, 3=5-8°, 4=8-11°, 5=11-15°)		GIS
Aspect	Categorical variable. Cardinal direction of plot (North, West, South or East).		GIS
Elevation	The elevation for the plots. Obtained both as a continuous variable and broken into a categorical variable (1=105-175m, 2=175-200m, 3=200-260m)		GIS
Distance to water	Measured in kilometers as the distance between plot and nearest main river		GIS
Vegetation type	Functional vegetation type, defined as five different groups: Riverine woodlands, broad leafed woodlands, fine leafed woodlands, thickets and unclassified woodlands.		GIS
Fire frequency	Obtained from yearly reports of fires within HiP		GIS

Figure 3. Example of how measurements of height would be conducted using a 2m long rod to estimate height of individual trees. Picture taken by Petter Madsen.

Analysis

All analyses were done using R (R Core Team 2015) in Rstudio (Version 0.99.87, Rstudio Team 2015). I used generalized linear mixed effects model (GLMER) from the package lme4 (Bates et al. 2015) with a binomial response variable, dead or alive/ Elephant impact or No elephant impact, to see assess likelihood of tree mortality and risk of elephant impact respectively. I used the command glmer(ResponseVar~IndependentVar+(1|RandEffect),family=binomial) to make my models. The elephant impact data used as a binomial response variable is data from measurement done in 2007. Plot was used as a random effect to account for clustering of trees within the plots. Using different independent variables I made several univariate models. The independent variables I used have all been shown to affect tree mortality. I had abiotic variables (slope, elevation, aspect, fire frequency (from 1955 to 2016) and distance to water), elephant impact variables (stripping (bark stripping) and breaking (breaking of branches, stems, etc.) and tree variables (tree height, stem diameter, tree species and functional vegetation type). The abiotic variables were obtained for plots and not individual trees, meaning that trees within each plot have identical values. This was done because of the inaccuracy for the individual tree GPS-coordinates. The amount of variation explained by adding the random effect to the model was checked by running a generalized linear model (GLM) and then comparing the two models (the GLMER and the GLM) by using anova(GLMER,GLM). The various independent variables are either continuous (e.g. elevation) or categorical (e.g. stripping). The OddsRatio (OR) was computed as 1/(1+exp(-x)), where x is the estimated coefficient of the respective levels within each model which was obtained using the command summary(GLMER). OR should be interpreted as the likelihood of event occurring (e.g. OR=0.5 suggest a 50% probability of event occurring). The command confint.merMod(GLMER, method="Wald") from the package lme4 (Bates et al. 2015) was used to compute the confidence intervals for each model.

Results

290 trees were marked in 2007, out of which 9 trees were disregarded from sampling. From the remaining 281 trees, a total of 260 trees could be relocated, yielding an approximate 92.5% success rate in relocation (Figure 4). When we look at the percentage of survived trees for the variables within their respective category (Figure 5-6) we can see that within each variable the trees are relatively evenly distributed between the different levels with the exception for the vegetation type, where the unclassified woodlands are more abundant (Figure 5d). When looking at the surviving percentage of trees based on elephant impact (Figure 6) we can see that for stripping, the survival percentage is the higher when there is no strip damage at all (Figure 6a), whereas in regards to breaking the survival rate seems to be more even throughout the different levels (Figure 6b).

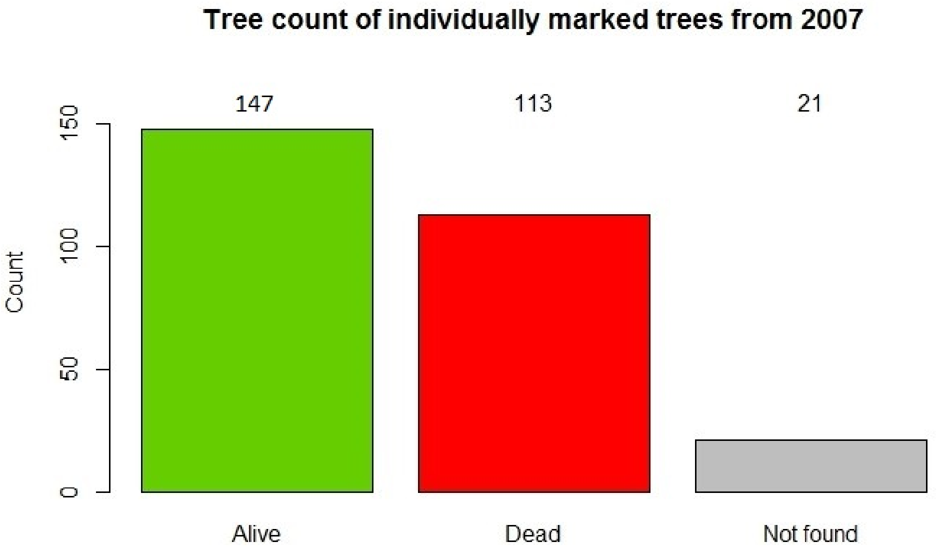


Figure 4. Bar plot showing the number of found individual trees within the categories Alive (147 trees), Dead (113 trees) and Not Found (21 trees). In total, 260 trees out of 290 possible trees were found.

Abiotic factors

Aspect proved significant only as a categorical factor and not as a continuous variable (Table 2). When analysed as a categorical factor, the west facing slope was shown to be the only significant out of the four separate levels, by increasing mortality rate (P=0.0127, OR=0.74) (Table 2). Similar to aspect, slope as a continuous variable was not significant. However, as a factor with 5 levels slope had a significant effect on tall tree survival. Mortality was lower at the steepest slopes (P=0.02, OR=0.12) (between 11-15°) (Table 2). Elevation was also insignificant, both as a categorical and continuous variable (Table 2). Distance to water, only analysed as a continuous variable, was not significant (Table 2). Fire frequency was also insignificant, both on a long term scale with fire data from 1955 up until 2016 and on a short term scale with fire data from 2007 up until 2016. Both long term and short term fire damage was analysed as a continuous and a categorical variable, neither being significant (Table 2).

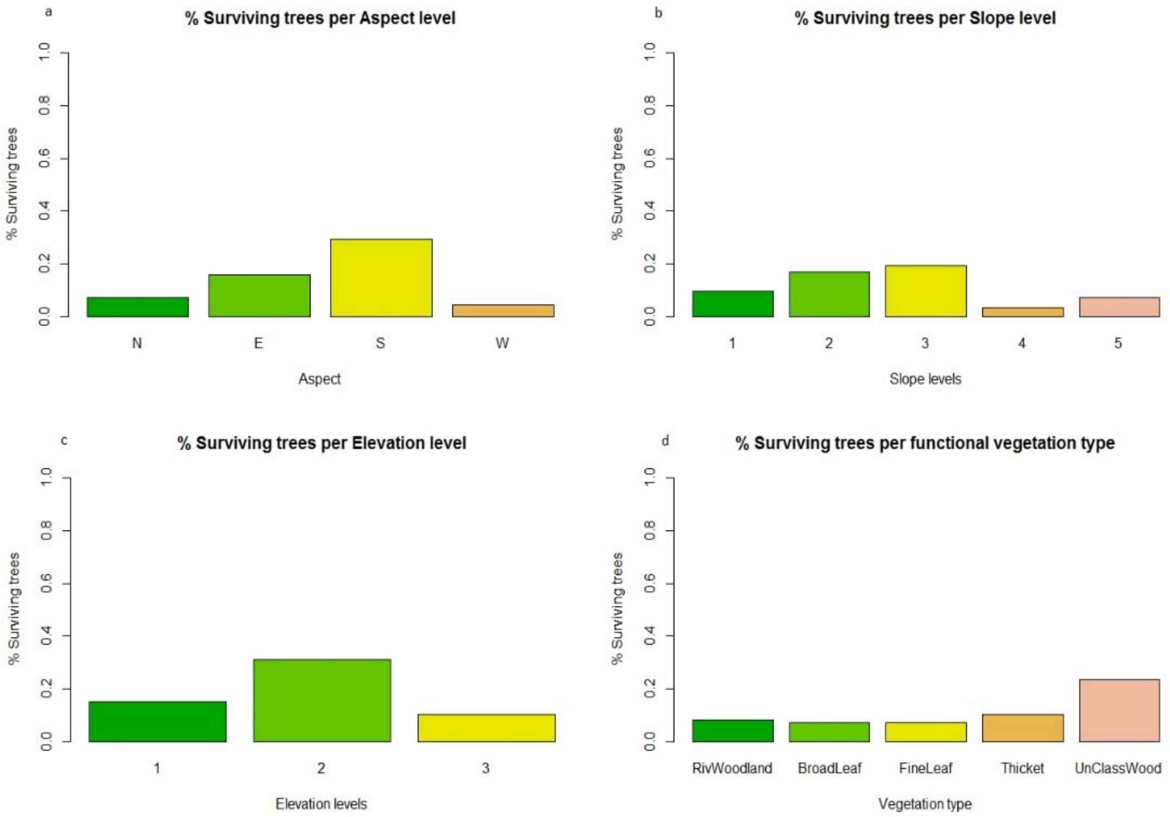


Figure 5. Bar plots showing the percentage of surviving individual trees within their respective categories.

Table 2 Results from single factor models (SFMs) using abiotic factors as independent variables and tree mortality as a binomial response variable. Results in bold are shown to be significant. Only Aspect(W) and Slope(5) were shown to be significantly descriptive of the data, with a reduced mortality risk for both.

	Level	Estimate	Pr(>|z|)	OddsRatio	CI 2.5 %	CI 97.5 %
Aspect	N	-1,1952	0,0671	0,23233021	-2,4744221	0,08403553
	E	0,238	0,0818	0,559220722	-0,1809126	3,04721917
	S	-0,6554	0,4718	0,341773693	-0,9305982	2,01018652
	W	**1,0685**	**0,0127**	0,744311553	**0,4843521**	**4,0431238**
	Continuous	0,001265	0,698	0,50031625	-0,00512008	0,007649386
Slope	Slope1	0,392	0,3577	0,596764066	-0,4433879	1,22736217
	Slope2	-0,2999	0,2697	0,425581929	-1,9205956	0,5367207
	Slope3	-0,766	0,0612	0,317345021	-2,3703284	0,05438263
	Slope4	0,6888	0,7049	0,665699928	-1,2390756	1,83266035
	Slope5	**-2,0039**	**0,0207**	0,118794055	**-4,4257765**	**-0,36609184**
	Continuous	-0,11796	0,107	0,470544148	-0,2612203	0,02530398
Elevation	Elevation1	0,02342	0,959	0,505854732	-0,8658596	0,9126923
	Elevation2	-0,16335	0,756	0,459253065	-1,3625334	0,9889872
	Elevation3	-0,69283	0,318	0,333403822	-2,1224407	0,6899351
	Continuous	-0,004433	0,535	0,498891752	-0,01844763	0,009580784
Water Distance	Waterdistance	-0,0001203	0,787	0,499969925	-0,00099087	0,000750279
Fire07to16	Continuous	0,0001409	0,42	0,500035225	-0,00020136	0,000483258
Fire55to16	Continuous	0,0008917	0,99	0,500222925	-0,1370414	0,1388248
FireLongterm	Fire1	-1,574	0,32	0,171646908	-4,674183	1,525942
	Fire2	-0,535	0,524	0,369351474	-2,152784	4,230215
	Fire3	0,327	0,241	0,581029252	-1,277328	5,078662
	Fire4	-0,453	0,514	0,388647726	-2,247168	4,488829
	Fire5	-21,182	0,999	6,32083E-10	-38997,3491	38958,13343
FireShortTerm	Fire1	-0,3817	0,512	0,405716943	-1,523746	0,7603681
	Fire2	0,0332	0,533	0,508299238	-0,8881178	1,7179959

Biotic factors

Elephant stripping and breaking when analysed with six or two different levels was still shown to be insignificant descriptive factors of tree mortality (Table 3).Tree height was insignificant, both when analysed as continuous and categorical variable (Table 3). Vegetation type was also shown to be insignificant (Table 4). Two of the analysed species however had significantly different mortality levels. Both tall Combretum molle (P=0.0365; OR=0.25) and Spirostachys africana (P=0.0261; OR=0.128) trees showed reduced mortality. None of the analysed interactions were significant (Table 5).

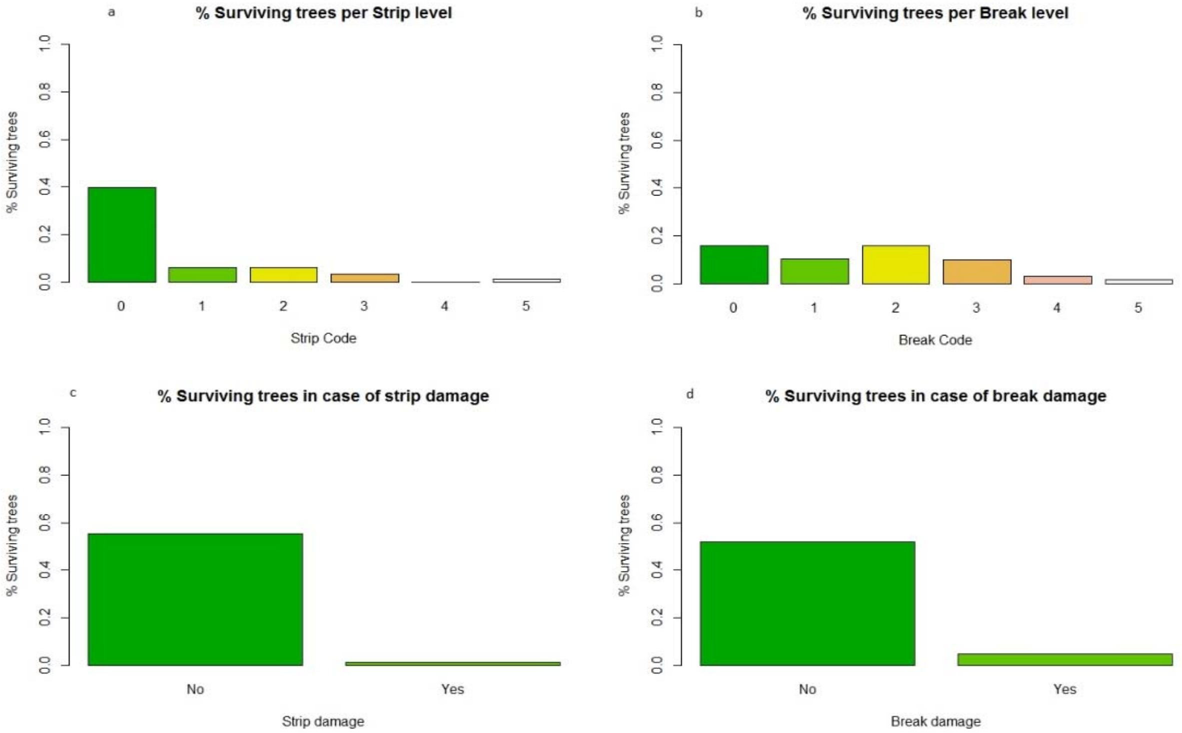
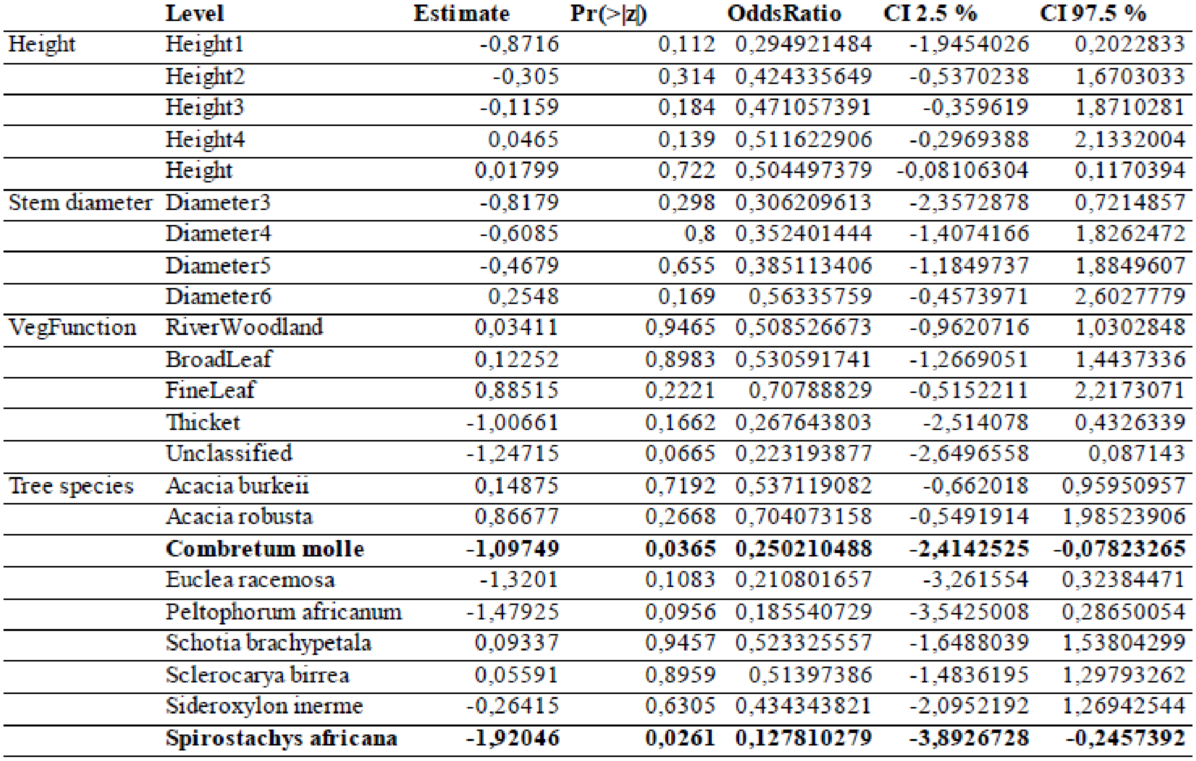


Figure 6. Bar plots showing the percentage of surviving individual trees within their respective categories. In c and d, the previous strip and break categories have been merged into two groups (1,2,3=No elephant damage, 4,5=Yes elephant damage).

Table 3 Results from single factor models (SFMs) using tree characteristics as independent variables with and tree mortality as a binomial response variable. Results in bold are shown to be significant. C.molle and S.africana are significant, with reduced mortality risk.



	Level	Estimate	Pr(>|z|)	OddsRatio	CI 2.5 %	CI 97.5 %
Height	Height1	-0,8716	0,112	0,294921484	-1,9454026	0,2022833
	Height2	-0,305	0,314	0,424335649	-0,5370238	1,6703033
	Height3	-0,1159	0,184	0,471057391	-0,359619	1,8710281
	Height4	0,0465	0,139	0,511622906	-0,2969388	2,1332004
	Height	0,01799	0,722	0,504497379	-0,08106304	0,1170394
Stem diameter	Diameter3	-0,8179	0,298	0,306209613	-2,3572878	0,7214857
	Diameter4	-0,6085	0,8	0,352401444	-1,4074166	1,8262472
	Diameter5	-0,4679	0,655	0,385113406	-1,1849737	1,8849607
	Diameter6	0,2548	0,169	0,56335759	-0,4573971	2,6027779
VegFunction	RiverWoodland	0,03411	0,9465	0,508526673	-0,9620716	1,0302848
	BroadLeaf	0,12252	0,8983	0,530591741	-1,2669051	1,4437336
	FineLeaf	0,88515	0,2221	0,70788829	-0,5152211	2,2173071
	Thicket	-1,00661	0,1662	0,267643803	-2,514078	0,4326339
	Unclassified	-1,24715	0,0665	0,223193877	-2,6496558	0,087143
Tree species	Acacia burkeii	0,14875	0,7192	0,537119082	-0,662018	0,95950957
	Acacia robusta	0,86677	0,2668	0,704073158	-0,5491914	1,98523906
	Combretum molle	**-1,09749**	**0,0365**	**0,250210488**	**-2,4142525**	**-0,07823265**
	Euclea racemosa	-1,3201	0,1083	0,210801657	-3,261554	0,32384471
	Peltophorum africanum	-1,47925	0,0956	0,185540729	-3,5425008	0,28650054
	Schotia brachypetala	0,09337	0,9457	0,523325557	-1,6488039	1,53804299
	Sclerocarya birrea	0,05591	0,8959	0,51397386	-1,4836195	1,29793262
	Sideroxylon inerme	-0,26415	0,6305	0,434343821	-2,0952192	1,26942544
	Spirostachys africana	**-1,92046**	**0,0261**	**0,127810279**	**-3,8926728**	**-0,2457392**

Elephant impact as response variable

When analysing the likelihood of elephant impact as a response variable, here estimated with a binomial outcome (Yes or No) due to the various biotic and abiotic independent variables I found many significant outcomes. A northern aspect significantly reduced the risk of elephant impact (ORS=0.003,ORB=0.07) (Table 6-7). Slope was also shown to have a significant effect, both when analysing it as a continuous and as a categorical variable. When analysed as a categorical variable the flattest slopes (Slope1), had a significantly reduced impact risk (ORS=0.01, ORB=0.12) (Table 6-7). Distance to water was not significant for either stripping or breaking (Table 6-7). Trees in the lowest altitudes (Elevation1) when analysing the elevation as a categorical variable had a significantly reduced impact risk (ORS=0.003, ORB=0.08) (Table 6-7). When analysing the vegetation function it was only riverine woodlands that were significantly reduced in their impact risk (ORS=0.01, ORB=0.1) when analysing the functional vegetation type (Table 6-7). When I analysed the risk for individual species to be impacted by elephants only Acacia burkeii had a significantly increased risk of impact, but only for break damage (P=2.56e-7, Estimate = -2.216, ORB=0.902, CILL= -3.058, CIUL= -1.373).

Table 4 Results from single factor models (SFMs) using elephant impact as independent variables with 6 and 2 levels respectively and tree mortality as a binomial response variable. Results in bold are shown to be significant. None of the independent variables used in these models were significant.

	Level	**Estimate**	**Pr(>|z|)**	**OddsRatio**	**CI 2.5 %**	**CI 97.5 %**
Strip damage	Strip0	-0,370779	0,209	0,408352801	-0,9492202	0,2076622
	Strip1	-0,573415	0,699	0,360449205	-1,2296305	0,824358
	Strip2	0,008142	0,401	0,502035489	-0,5061086	1,2639502
	Strip3	0,178862	0,344	0,54459667	-0,5896223	1,6889042
	Strip4	17,276843	0,961	0,999999969	-691,9352103	727,2304538
	Strip5	-0,373835	0,998	0,407614676	-2,1405726	2,13446
Strip damage Y/N	No Strip	-0,273	0,309	0,432170748	-0,7995018	0,2534694
	Strip	-0,6487	0,199	0,343282549	-0,5958637	2,8620256
Break damage	Break0	-0,3757	0,339	0,407164422	-1,1466018	0,395207
	Break1	-0,1217	0,581	0,469612496	-0,6486876	1,1567198
	Break2	0,0482	0,31	0,512047668	-0,3949855	1,2428741
	Break3	-0,5516	0,721	0,365493276	-1,1410513	0,7891562
	Break4	0,0881	0,482	0,522010765	-0,8283161	1,7559214
	Break5	-1,4701	0,41	0,186927415	-3,6989269	1,5100947
Break damage Y/N	No Break	-0,22308	0,407	0,444460136	-0,7500301	0,3038799
	Break	-0,20014	0,966	0,450131351	-1,0291012	1,0749813

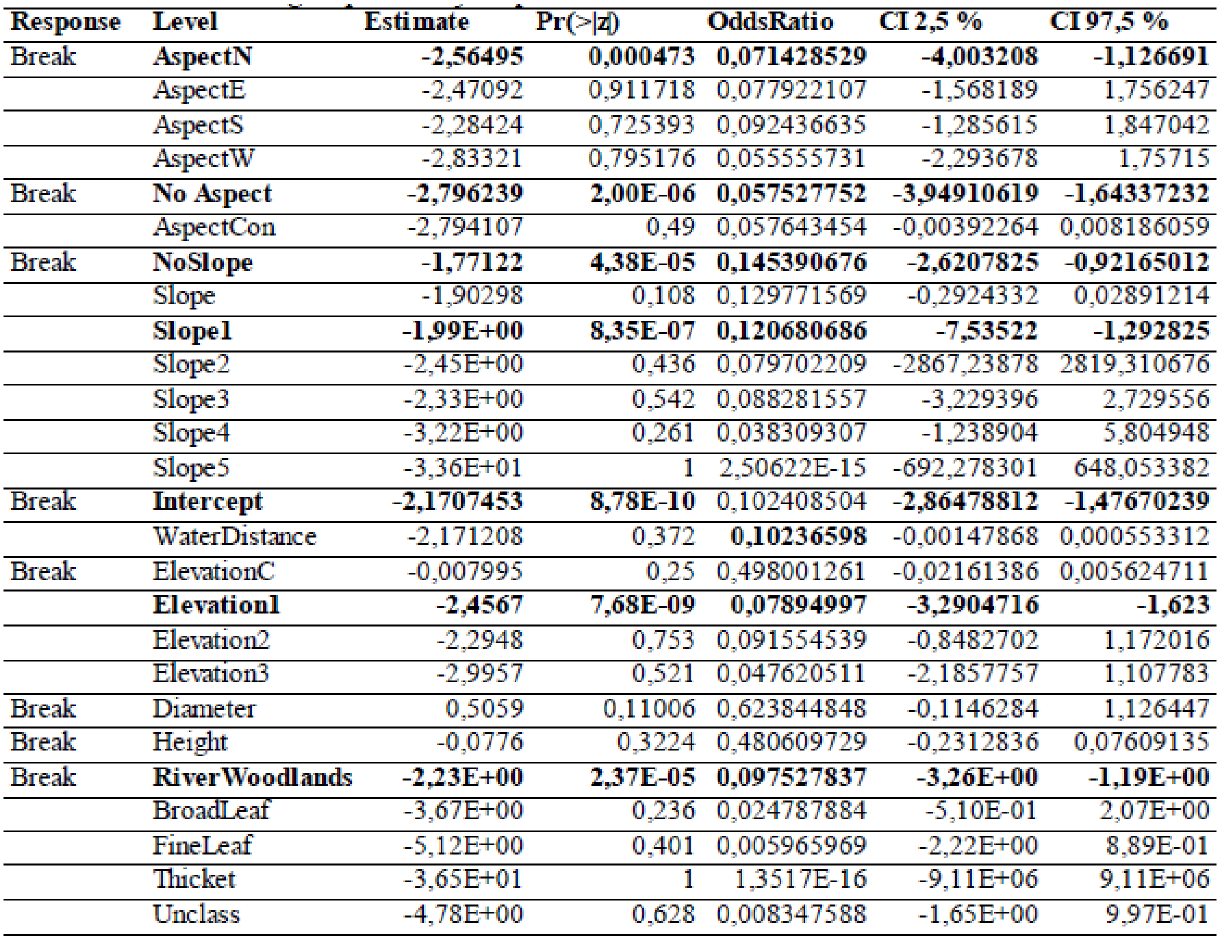
Table 5 A sample of *glmer*s with interactions between independent variables. No interaction was significant. In this table a subset of the outputs from interactions is presented.

	Level	**Estimate**	**Pr(>|z|)**	**OddsRatio**	**CI 2.5 %**	**CI 97.5 %**
Aspect:Slope	TreeData$Aspect,catE:TreeData$SlopeCat2	17,7046	0,9971	0,99999998	-9,47E+03	9,50E+03
	TreeData$Aspect,catS:TreeData$SlopeCat2	32,91204	0,9975	1	-9,47E+03	9,50E+03
	TreeData$Aspect,catW:TreeData$SlopeCat2	51,28156	0,995	1	-1,05E+04	1,06E+04
	TreeData$Aspect,catE:TreeData$SlopeCat3	17,68893	0,9925	0,999999979	-3,26E+00	3,23E+00
	TreeData$Aspect,catS:TreeData$SlopeCat3	17,98079	0,8758	0,999999984	-3,19E+00	3,74E+00
	TreeData$Aspect,catW:TreeData$SlopeCat3	18,65046	0,6002	0,999999992	-2,59E+00	4,48E+00
	TreeData$Aspect,catS:TreeData$SlopeCat4	15,20205	0,1502	0,99999975	-5,91E+00	9,06E-01
	TreeData$Aspect,catW:TreeData$SlopeCat4	16,47409	0,5265	0,99999993	-5,04E+00	2,58E+00
	TreeData$Aspect,catE:TreeData$SlopeCat5	16,38495	0,4727	0,999999923	-4,92E+00	2,28E+00
Aspect:Elevation	TreeData$Aspect.catE:TreeData$ElevationCat2	15,1323	0,9143	0,999999732	-260,552484	290,8170991
	TreeData$Aspect.catS:TreeData$ElevationCat2	34,1154	0,8926	1	-256,7055907	294,6718005
	TreeData$Aspect.catW:TreeData$ElevationCat2	33,0245	0,8988	1	-257,8015141	293,5858773
	TreeData$Aspect.catE:TreeData$ElevationCat3	13,7317	0,5285	0,999998913	-5,7561181	2,9549589
	TreeData$Aspect.catS:TreeData$ElevationCat3	15,9223	0,6013	0,999999878	-2,1733235	3,7532636
	TreeData$Aspect.catW:TreeData$ElevationCat3	14,6386	0,7776	0,999999561	-3,9196857	2,9322654
Slope:Strip	TreeData$SlopeCat3:TreeData$StripCat1	-0,4831	0,8288	0,381520373	-4,8622392	3,8961209
	TreeData$SlopeCat4:TreeData$StripCat1	-1,1845	0,7379	0,234244049	-4,8095279	3,4067025
Strip:Break	TreeData$StripCat1:TreeData$BreakCat1	-0,52553	0,793	0,371560047	-4,4468618	3,3958099
Fire:Strip	TreeData$Fire07to16:TreeData$StripCat1	-0,278274	0,747	0,430876979	-1,968817	1,4122685

Table 6 Results from single factor models using a mix of abiotic and biotic independent variables with and elephant impact as a binomial response variable. Results in bold are shown to be significant. From this we can see that both northern aspects and low altitudes as well as low slopes have a significantly reduced risk of elephant impact. Riverine woodlands are also at a lower risk of being impacted by elephants.

Response	Level	Estimate	Pr(>|z|)	OddsRatio	CI 2,5 %	CI 97,5 %
Strip	**AspectN**	**-5,9308**	**0,0342**	**0,002649319**	**-11,419248**	**-0,4423519**
	AspectE	-6,9615	0,6973	0,000946777	-6,223778	4,1623783
	AspectS	-5,587	0,8758	0,003732268	-3,965953	4,6535437
	AspectW	-5,6502	0,9128	0,003504489	-4,741331	5,3025116
Strip	**No Aspect**	**-7,42186**	**0,0136**	**0,000597678**	**-13,3192365**	**-1,524484**
	AspectCon	-7,415403	0,5282	0,000601548	-0,01360597	0,0265198
Strip	**NoSlope**	**-7,151969**	**<2e-16**	**0,000782707**	**-7,1559624**	**-7,1479752**
	Slope	**0,119407**	**<2e-16**	**0,529816332**	**0,1154128**	**0,1234007**
	Slope1	**-4,414**	**0,00557**	**0,011961837**	**-7,53522**	**-1,292825**
	Slope2	-28,3781	0,98682	4,73748E-13	-2867,23878	2819,310676
	Slope3	-4,6639	0,86941	0,009341528	-3,229396	2,729556
	Slope4	-2,131	0,2039	0,106120096	-1,238904	5,804948
	Slope5	-26,5265	0,94844	3,01778E-12	-692,278301	648,053382
Strip	**Intercept**	**-6,0345748**	**0,0293**	0,002388794	**-11,4622316**	**-0,60691809**
	WaterDistance	-6,0351675	0,7153	**0,002387382**	-0,00377692	0,00259161
Strip	ElevationC	-0,01495	0,523	0,49626257	-0,06082039	0,03091396
	Elevation1	**-5,64675**	**0,0245**	**0,003516557**	**-10,537756**	**-0,7258938**
	Elevation2	-1,07885	0,5539	0,253723705	-4,587199	2,4593284
	Elevation3	-0,95945	0,6702	0,276988328	-5,29163	3,4026474
Strip	Diameter	-0,3885	0,477	0,404078447	-1,460133	0,6831068
Strip	Height	0,1419	0,3264	0,535415594	-0,1414842	0,4252419
Strip	**RiverWoodlands**	**-4,64E+00**	**0,00575**	**0,009527498**	**-7,94E+00**	**-1,35E+00**
	BroadLeaf	-8,52E+00	0,71552	0,000199101	-3,36E+00	4,89E+00
	FineLeaf	-1,02E+01	0,73242	3,86432E-05	-5,88E+00	4,13E+00
	Thicket	-3,54E+02	0,99998	2,2481E-154	-2,16E+07	2,16E+07
	Unclass	-9,69E+00	0,85674	6,17287E-05	-4,80E+00	3,99E+00

Table 7 Results from single factor models using a mix of abiotic and biotic independent variables with and elephant impact as a binomial response variable. Results in bold are shown to be significant. From this we can see that both northern aspects and low altitudes as well as low slopes have a significantly reduced risk of elephant impact. Riverine woodlands are also at a lower risk of being impacted by elephants.



Response	**Level**	**Estimate**	**Pr(>|z|)**	**OddsRatio**	**CI 2,5 %**	**CI 97,5 %**
Break	**AspectN**	**-2,56495**	**0,000473**	**0,071428529**	**-4,003208**	**-1,126691**
	AspectE	-2,47092	0,911718	0,077922107	-1,568189	1,756247
	AspectS	-2,28424	0,725393	0,092436635	-1,285615	1,847042
	AspectW	-2,83321	0,795176	0,055555731	-2,293678	1,75715
Break	**No Aspect**	**-2,796239**	**2,00E-06**	**0,057527752**	**-3,94910619**	**-1,64337232**
	AspectCon	-2,794107	0,49	0,057643454	-0,00392264	0,008186059
Break	**NoSlope**	**-1,77122**	**4,38E-05**	**0,145390676**	**-2,6207825**	**-0,92165012**
	Slope	-1,90298	0,108	0,129771569	-0,2924332	0,02891214
	Slope1	**-1,99E+00**	**8,35E-07**	**0,120680686**	**-7,53522**	**-1,292825**
	Slope2	-2,45E+00	0,436	0,079702209	-2867,23878	2819,310676
	Slope3	-2,33E+00	0,542	0,088281557	-3,229396	2,729556
	Slope4	-3,22E+00	0,261	0,038309307	-1,238904	5,804948
	Slope5	-3,36E+01	1	2,50622E-15	-692,278301	648,053382
Break	**Intercept**	**-2,1707453**	**8,78E-10**	0,102408504	**-2,86478812**	**-1,47670239**
	WaterDistance	-2,171208	0,372	**0,10236598**	-0,00147868	0,000553312
Break	ElevationC	-0,007995	0,25	0,498001261	-0,02161386	0,005624711
	Elevation1	**-2,4567**	**7,68E-09**	**0,07894997**	**-3,2904716**	**-1,623**
	Elevation2	-2,2948	0,753	0,091554539	-0,8482702	1,172016
	Elevation3	-2,9957	0,521	0,047620511	-2,1857757	1,107783
Break	Diameter	0,5059	0,11006	0,623844848	-0,1146284	1,126447
Break	Height	-0,0776	0,3224	0,480609729	-0,2312836	0,07609135
Break	**RiverWoodlands**	**-2,23E+00**	**2,37E-05**	**0,097527837**	**-3,26E+00**	**-1,19E+00**
	BroadLeaf	-3,67E+00	0,236	0,024787884	-5,10E-01	2,07E+00
	FineLeaf	-5,12E+00	0,401	0,005965969	-2,22E+00	8,89E-01
	Thicket	-3,65E+01	1	1,3517E-16	-9,11E+06	9,11E+06
	Unclass	-4,78E+00	0,628	0,008347588	-1,65E+00	9,97E-01

Discussion

The study conducted in HiP proved to be very successful in relocating the individually tagged trees. Given that it has been 10 years since the initial tagging was done, the fact that as many as 260 trees, 92,5% of the total trees sought out, proves that this method of individual marking works as a long term analysis on the tree population. Previous studies have mentioned that long term studies have been lacking when researching elephant impact (Druce et al. 2008, Landman et al. 2012). The success rate at which trees are relocated in this study makes it a helpful start for further improving on the methods. The results I got were somewhat surprising. Based on the previously established theories, I expected a more factors to significantly alter the mortality risk.

Abiotic variables

In the analysis, three variables were used as response variables; the mortality, the stripping and the breaking. The first is used in order to see if, how and where trees are at a higher risk of dying. The second and third response variable, stripping and breaking, is used in order to see if and where elephant impact is more prone.

When analysing the abiotic variables, I found that aspect had a significant effect in influencing mortality risk and risk of elephant impact. Aspect was expected to have an influence on tree mortality in correlation to the elephant impact and to have an optimum in which elephant impact would be greater. This was expected to be a north facing slope, as north facing slopes have a higher degree of sunlight and proportionately higher degree of green biomass. However, when looking at the data, north was shown to be insignificant (P=0.0671). More surprisingly, the OR of north facing slopes showed to have a lower risk of mortality (OR=0.2323), which is the direct opposite of the expected results. Furthermore, west facing slopes was shown to have a significantly increased mortality risk (P=0.0127, OR=0.9058). The most common aspect is southwards facing with 119 plots, whereas west facing has 36 plots. When comparing this to the risk of elephant impact, north was shown to be significantly less likely to be impacted by both strip- and break damage (PS=0.03, ORS=0.003, PB=0.0005, ORB=0.07). One plausible reason for why elephants avoid northern slope could be because of the increased temperature as a consequence of the increased sunlight. Temperature has been shown to affect other herbivores in their foraging patterns (du Toit & Yetman 2005). If this is the case, and the decrease in tree mortality in north aspects is assumed to be due to less elephant impact, this would explain the results.

Slope as a gradient was shown to be insignificant as a predictor for tree mortality (P=0,107) (Table 2). However, when analysed as a categorical variable, very steep slopes (between 11-15°) significantly reduced the mortality risk (P=0.0207, OR=0.0834). Again, this was somewhat counter-intuitive, as it was expected to be a gradual decrease in risk of mortality proportionate to the increase in slope due to the increased difficulty for elephants to access steeper slopes. This however rests upon the assumption that mortality is due to elephant impact. Given the terrain of the area and the rolling landscape it might prove difficult for elephants to discriminate against steep slopes when foraging. Thus they may only disregard the extreme slopes. It may also be that steeper slopes are less crowded for trees while also being difficult for other foragers and browsers to harm the trees in these extreme slopes. As such the steepest slopes may be a refugee from other factors as well, which could explain the results. Interestingly, the opposite was true when looking at elephant impact risk, in which the flattest slopes were significantly less likely to be affected by elephant damage (PS=0.006, ORS= 0.012, PB=8.35e-7, ORB= 0.12). This could be because of elephants avoiding valley beds and hill peaks, as they would have to ascending and descending to enter these areas which is an unnecessary energy expenditure. This suggests that trees in a steeper slopes enjoys lower mortality risk, whereas flatter slopes are less affected by foraging elephants.

Elevation was not significant, neither as a continuous or categorical variable. However, looking at the OR, we can see a clear trend in the risk of mortality decreasing with increased elevation, which is in accordance with the current literature (Bellingham & Sparrow 2009, Wakeling et al. 2012). However, the argument could be made that when viewing the results from the perspective that elephants are responsible for the mortality of trees, it would be plausible that given the elevation difference between the lowest and highest points were only around 150m (Lowest 106m~Highest 259m) it might not prove challenging for them to ascend/descend when foraging and as such there is no reason to expect a difference between the different altitudes. But looking at the risk of elephant impact, we can see that lower altitudes are far less likely to be affected by strip or break damage (Table 6-7). This would be coherent with the theory that the elephants avoid valley beds due to the excess energy expenditure required to enter and leave said areas.

Distance to water does not significantly affect tree mortality, which is contrary to the established theories. If the mortality is affected by elephant impact in the park, it would be expected that the trees furthest away would enjoy a “partial refugia”. This absence of refugia can probably be due to the fact that no tree was further away than ~3km away from a water source, whereas the foraging/roaming thresholds for elephants extent up to 50km (Shannon et al. 2009, Boundja & Midgley 2009). By encompassing the area completely, this factor would be neglected by the elephants. This is further supported by the results when analysing elephant impact risk, where neither strip damage or break damage is influenced by distance from water (Table 6-7). This was previously suggested by (Boundja & Midgley 2009). Given these results, HiP is shown to be a very specific system, as water distance is otherwise estimated to be a firm predictor of elephant impact.

Fire frequency was insignificant, both in short terms (fire frequency from 2007 until 2016) and long terms (fire frequency from 1955 until 2016) (Table 2). Both short and long term fire frequency was additionally analysed as categorical variables to see if there is a threshold of fires needed for it to have a deleterious effect, however it still showed to be insignificant (Table 2). This is not completely surprising since the fire trap, in which younger trees are killed off, is discussed to have an escape height of ~3 meters (Grady & Hoffmann 2012, Wakeling et al. 2011, Wakeling et al. 2012). The smallest tree recorded in this dataset was 4,1 m which would suggest that the trees in this study has already escaped the directly deleterious effects from fire impact. However, it was expected that fire frequency were to have a significant interaction with some of the other variables, especially with strip damage. However, there was no significant interaction between fire frequency and strip damage (Table 5) which was surprising.

Other interactions were tested, however none were shown to have a significance. In Table 5 some of the results from these interactions are shown which were thought to have a connection, but since none were significant they will not be discussed to a greater extent.

Tree variables

Both tree height and tree diameter were insignificant in describing the mortality of trees (Table 3). This is very surprising since a lot of the literature suggest that specifically taller trees are in decline. These results argue this, suggesting that neither height nor diameter of the trees are determinants in the mortality rate. This is even further supported when looking at the risk of elephant impact where, again, neither tree height or diameter is significant for either strip- or break damage (Table 6-7). When analysing the species effect, the set threshold for inclusion in the model was a minimum of 8 individuals/species. This resulted in the sample size of 205 individuals. From this, it was shown that only two tree species, Combretum molle and Spirostachys africana, significantly reduced the mortality risk (Table 2). Due to the green biomass to branch-ratio found in C.molle, this is somewhat counter intuitive. S.africana is however poisonous to a certain degree and apparently also have a pungent taste to it (Phumlani Mangethe, personal communication) which would explain them being more protected from elephant induced mortality simply by being less palatable. Vegetation function not significant in any way in regards of describing the mortality risk (Table 4). However, when looking at the risk of elephant impact we can see that riverine woodlands are less likely to be affected by both strip damage and break damage (Table 6-7). As previously discussed, distance to water was insignificant in both mortality risk and elephant impact risk. That being said, along with the knowledge that flatter areas and lower altitudes are being less affected by elephants, it is possible that elephants disregard this vegetation type nearby water sources in favour of other more palatable vegetation. Additionally, it has been shown that elephants favour grasses, which would concur with these results if the elephants favour grazing over browsing while in wetter areas which are grass dominated (Clegg & O'Connor 2016).

Elephant variables

Both strip and break damage was insignificant in explaining the mortality risk (Table 4). The initial hypothesis for this study was that elephant damage was directly correlated to the tree mortality. However, looking at the results, neither strip damage or break damage showed to be a significant factor for explaining the mortality risk. This could be explained by the measuring methods. Previous studies in the Serengeti show that elephant impact is more explanatory in tree mortality than fire or droughts, when trees experience a continuous, relatively light utilization from elephants under a longer time period (Morrison et al. 2016). Since our measurements of elephant damage was made only once, the possible inference from this is fairly low. This would suggest that the individuals which exhibit a lower degree of elephant impact are more likely to die of because of it, due to the repeated utilization of the same individual. Given the previously discussed mortality risk trees face from continuous elephant impact, elephant "forage frequency" in relation to impact level per foraging opportunity might have proven to be more useful data to record. Nevertheless, these results suggest that elephants have no deleterious impact on trees on a large time scale, which contradicts a great deal of literature. To look aside from these results due to the literature could prove harmful, as perhaps elephant impact is not at all to blame in this park for tree decline. Furthermore, it would be beneficial to further study how anthropogenic effects facilitate and/or deter elephant impact.

Studies have suggested that elephants are living in higher than normal densities within HiP. If so, then a possible anthropogenic effect could be more harmful if shown to facilitate elephant movement and foraging.

Study remarks
Given the variation between the plots in terms of number of trees, the estimates might have proven more solid had they been even throughout with the same amount of trees tagged within each plot. Additionally, spreading plots out evenly within the park in order to minimize clusters of plots would also prove beneficial to get a more even estimate throughout the park. Even though this study had a high recovery rate of trees (92.5%), there were several measurements (e.g. toppling, insect, fire damage) were not possible for all individuals. Because of this, there was a large gap in the data for these variables, which made them useless for analysis. An improvement upon the methods would be to make revisits with shorter intervals to marked trees, in order to establish a change over time and to increase the success in measuring all the variables. This would also be beneficial when investigating whether chronic elephant damage is deleterious to trees in a similar manner which has been found in the Serengeti.

Conclusions

From these results, a one time measurement of elephant impact on trees in Hluhluwe-iMfolozi Park does not seem to be descriptive of tree mortality. Furthermore, trees does not seem to be affected by fire frequency. Interactions between fire damage and elephant impact were also shown to be insignificant. This was directly opposite of the initial hypothesis. However, there findings can not be assumed to disprove that trees are affected by fire damage or elephant impact, as these factor have been proven to be landscape altering forces to be reckoned with. Instead the results should be interpreted that they further accentuates the difficult relationship between several factors which are collectively responsible for the population status of trees. Additionally, these results fall in line with Guldemond & van Aard (2008) as it highlights the importance of not giving the sole responsibility for the outcome of tree mortality to single factors and further highlights the need for continual repeated measures as some impacts are only significant over time (Shannon et al. 2011). Elephants impacting their environment is not unusual as they are naturally occurring in this area. However, when kept at a higher than normal density, which is due to park management throughout history, the following impact on the vegetation might be a too great which possibly can alter the ecosystem. As such, studies on the interaction between anthropogenic effects and e.g. elephant impact would enlighten park management on handling elephant populations further.

Acknowledgements

Firstly I would like to thank my supervisors Joris Cromsigt and Mariska te Beest for making this project possible. I would like to thank Siphesihle Mbwonga, Phumlani Mangethe, Erik Khumalo and Joseph Dlamini for the help in my field work, walking in the savanna with you guys is something I will never forget. I would like to thank my girlfriend Sara for helping me in keeping me motivated throughout my thesis. And last but not least I would also like to thank

Fissrix, Slaipee, BersikaWarrior and PaltWarrior for always raising my spirit and helping me blow off some steam.

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