Long-term high densities of African elephants clear the understorey and promote a new stable savanna woodland community

African elephant long-term effects on savanna

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Abstract:

Questions: Species defined as ecosystem engineers (e.g. elephant) are able to strongly shape their habitat. In African savannas, elephants have often been shown to reduce woody plant abundance and diversity. However, recent studies highlight more complex elephant-induced effects on vegetation. Here, we assessed if long-term high elephant densities ($>2.\text{km}^{-2}$) in a large open landscape resulted in the depletion of savanna woodland woody communities or if it led to a new alternative equilibrium.

Location: Woodland savanna of Hwange National Park, Zimbabwe. Elephant densities at the study site have remained high for the past two decades ($>2.\text{km}^{-2}$).

Methods: We measured long-term (>15 years) elephant utilization of woody plant communities and their effects on vegetation structure, species composition and functional traits (e.g. N leaf concentration, specific leaf area) in twelve vegetation plots.

Results: We observed opportunistic foraging behaviour by elephants with only a slight temporal shift in species composition, mainly explained by changes in rare species. Further, we did not observe any modification in mean functional trait values, overall height and stem diameters of the woody plant communities. However, we found differential changes in woody plant abundance according to the height layer (decrease in the number of tall plants (>200 cm) and increase in the number of short plants (<50 cm)) and a strong reduction in crown diameter for plants in the 50-200 cm height class.

Conclusion: Our study strongly suggests that long-term high elephant densities have led to a stable state in savanna woodland vegetation in terms of plant community composition and their functional traits. However, high elephant densities did affect vegetation structure, which would have several important indirect effects on this ecosystem (e.g., predator-prey

interactions). We hope that this study stimulates more work on the long-term effects of ecosystem engineers in large and open ecosystems.

Keywords:

Ecosystem engineer, herbivore-plant interactions, vegetation dynamics, woody plant functional traits, plant diversity and structure, megaherbivore, *Loxodonta africana*, semi-arid woodland savanna, alternative stable state.

Introduction

Savanna ecosystems are complex and heterogeneous landscapes with a high diversity of habitats and plant species shaped by different interacting factors such as soil, rainfall, frost, fire and herbivory (Sankaran et al., 2005, Hoffman et al. 2019). Large herbivores play a major role in the shaping and functioning of African savanna ecosystems (Danell et al., 2006; Sankaran et al., 2008; Wigley et al., 2014). Among them, African elephants *Loxodonta africana* consume large quantities of vegetation and a wide range of food items including grass, leaves, twigs, roots and bark (Barnes, 1982; O'Connor et al., 2007). Further, by breaking or uprooting trees and shrubs, elephants can change the physical environment and ultimately the quality of the habitat of other species (e.g. availability of resources or risk of predation), and are thus considered as ecosystem engineers (*sensu* Jones et al., 1994; e.g. Valeix et al. 2011). They are known to exert strong top-down controls on the savanna vegetation (Kerley and Landman, 2006; Guldemond and van Aarde, 2008).

Because of their body size, wide ranging requirements, and the growing demand for ivory, elephants are particularly vulnerable to human threats such as habitat fragmentation, human-wildlife conflict, hunting and poaching (Macdonald et al., 2013), and many elephant populations have collapsed due to negative anthropogenic effects (Chase et al., 2016). However, in many African areas that are well protected, elephant populations have grown to very high densities (Blanc et al., 2005; Hempson et al., 2015). These changes have raised concerns about elephant-induced vegetation changes as they can influence a wide range of processes, such as grass-tree coexistence (Sankaran et al., 2005), fire dynamics (van Langevelde et al., 2003), habitat selection by other species (Valeix et al., 2011), animal biodiversity (Pringle 2008), and predator-prey relationships (Tambling et al., 2013; Ferry et al. 2020).

Elephants can exert a strong filtering on woody plant species (O’Connor et al., 2007) by selecting species with specific traits (e.g., low leaf dry matter content, high specific leaf area) or leaf chemistry (e.g., high leaf nitrogen content, low carbon-base secondary metabolites concentration) (Jachman & Bell, 1985; Viljoen, 1989; Holdo, 2003). This filtering pressure can lead to plant diversity losses (Owen-Smith et al., 2006, O’Connor & Page, 2014; Coetsee & Wigley, 2016) and to a shift in woody plant species over time under high elephant density; a shift also explained by plant species differential vulnerabilities to elephant herbivory (O’Connor et al., 2007). It is still not clear how modifications of woody plant community compositions by elephants affects functional diversity (Rutina & Moe, 2014) and ecosystem functioning in these communities (e.g., resource dynamics or stability, Dìaz & Cabido, 2001). Additionally, because of their large body size, elephants have the physical potential to affect woody plants by pollarding, breaking trunks and uprooting trees (O'Connor et al., 2007). Early studies revealed that woodlands declined in many parks of Eastern Africa in the 1960s-70s and suggested that the conversion from woodland to grassland savannas was driven by high elephant densities - the so-called “elephant problem” (Laws, 1970; Caughley, 1976). While the classic view is that high elephant densities tend to have negative effects on woody vegetation, several studies have demonstrated no or positive effects (review in Guldemond & van Aarde, 2008). For example, elephants have been shown to increase woody plant species richness and beta diversity (Coverdale et al., 2016; Pringle et al., 2016). The complexity of elephant-induced vegetation changes is due to (i) the influence of local environmental conditions (Guldemond & van Aarde, 2008), and (ii) the different time scales at which studies are conducted. Indeed, African savannas are characterized by a tree cover that does not respond smoothly to climatic conditions, disturbances (fire, herbivory) and their interaction, but exhibit abrupt transitions between alternative stable states, from a savanna dominated by trees to a treeless savanna and *vice versa* (Dublin et al., 1990; van Langevelde et al., 2003; Staver et al., 2011). The shift from a stable state to another stable state does not depend solely on the actual conditions (climate, fire and herbivory) but on the historical factors that shaped these ecosystems (e.g. drought frequency, frost frequency, fire frequency, herbivore disease outbreaks). Consequently, a system, when disturbed from one state to another, may not return to its original state once the cause of the disturbance disappears (i.e., hysteresis, Beisner et al. 2003). Herbivory can greatly contribute to such shifts but often in interaction with fire (Holdo, 2007). For example, browsers may enhance the effect of fire on trees because they reduce woody biomass, thus indirectly stimulating grass growth (i.e. fuel load), which results in more intense fire and may ultimately lead the system to switch from a savanna dominated by trees to a treeless savanna (van Langevelde et al., 2003). In the Serengeti-Mara ecosystem in Eastern Africa, fire was necessary to change the vegetation from woodland to grassland, and once the grassland was formed, elephants held it in that state (Dublin et al. 1990). Hence, the length and timing (during a stable state, during a shift) of studies on elephant impacts on the vegetation clearly determine their conclusions.

Many existing studies were conducted in small fenced reserves that poorly relate to what is observed in open systems where elephants naturally use wide areas to roam (Loarie et al., 2009; Tshipa et al., 2017). Furthermore, many studies were once-off or short-term (review in Guldemond & van Aarde, 2008), and do not allow for the assessment of long-term vegetation dynamics. Finally, the few long-term studies that did assess long-term effects of elephants on vegetation in large open landscapes (Conybeare, 1991; Mosugelo et al., 2002; Skarpe et al., 2004) typically focused on periods of drastic changes in elephant densities. These studies are useful to depict vegetation changes during a transition period but are not able to predict future changes of vegetation dynamics when elephant densities remain high in the long-term.

In this paper, we investigate long-term changes in woody vegetation structure, species composition and plant functional traits in relation to elephant impacts and preferences in Hwange National Park (HNP), Zimbabwe. HNP is one of the largest African protected areas where elephant browsing pressure has been high for decades. Hence, HNP provides a unique opportunity to assess the long-term effects of high elephant densities on savanna woodland vegetation. We first assessed the dynamics of elephant impacts and if elephant preferences are still observable after a long period of high elephant impacts. We then analysed which plant traits could drive potential preferences. Six functional traits were assessed: three physiological traits (leaf nitrogen, carbon and phosphorus concentrations) and three morphological traits (leaf dry matter content, stem density and type of spinescence (no spine, spines or thorns)). We tested if continuous heavy browsing pressure by elephants led to changes in species composition and declines in woody plant species and functional diversity or if the vegetation has attained a new equilibrium state. Finally, we assessed if changes in vegetation structure (woody plant abundance, height, crown diameter and stem diameter) occurred during the study period. We predicted a decrease in woody plant abundance, height, crown diameter and stem diameter due to high elephant impact.

Material and methods

Study site

Hwange National Park covers an area of 14 600km², extending from 18°30’ to 19°50’N and from 25°45’ to 27°30’E. HNP is part of a large and open protected area embedded in the world’s largest trans-frontier conservation area (Kavango-Zambezi [KAZA] landscape) where elephants roam freely (Tshipa et al., 2017). The elephant population density has been high for a very long time in this ecosystem where in the early 1980s the Zimbabwe Parks and Wildlife Management Authority implemented culling operations to control the elephant population, which was at *ca*. 1 elephant.km^{-2} (Chamaillé-Jammes et al., 2008). Since elephant culling stopped in 1986, the elephant population density steadily increased, and has stabilised since the early 1990s at an estimated average density > 2 individuals per km^2, which corresponds to a mean population of 30 000 individuals, with large fluctuations around this mean and peaks around 40 000 individuals in some years (Chamaillé-Jammes et al., 2008, Zimbabwe National Elephant Management Plan, 2015-2020). During some dry years, local densities can increase to *ca*. nine individuals per km^2 during the dry season (Chamaillé-Jammes et al., 2009). Rainfall is markedly seasonal, from November to March, with an annual mean of ~ 600 mm and a range of 324 to 1160 mm. The mean annual temperature is 20.3°C. October is the hottest month with a mean daily maximum of 33.2°C, and July is the coldest with a mean daily minimum of 4.1°C. Historical records from the 1999-2004 management plan show a low rate of fires in the study area. The study took place in the Main Camp area, in the north-eastern part of the park in 2001, 2008 and 2015. The Main Camp area is dominated by open woodland savannas on Kalahari sandy soils. We monitored vegetation in the four dominant vegetation types: *Baikiaea plurijuga* woodland, *Combretum* bushed-woodland, *Colophospermum mopane* bushland and *Acacia/Terminalia* bushed-woodland (Rogers, 1993).

Data

In each of the four vegetation types, three plots of 25x50 m were monitored between May and August in 2001 and 2015. In 2008, only plots in the *Baikiaea plurijuga* woodland and *Combretum* bushed-woodland were monitored (political instability in the country due to the presidential elections in 2008 resulted in the team leaving the country prematurely). Each plot was delimited and marked by two concrete blocks: one block was placed in the middle of the plot (GPS coordinates are provided in S1), the other block marked the north-western corner. The location of plots was chosen in areas close to permanent waterholes (mean distance to the closest waterhole = 1271 m, S1) and hence intensively used by elephants in the dry season.

Vegetation structure, composition and elephant impacts

We performed an exhaustive inventory of all the woody plants (≥ 5cm height) in each plot to determine the vegetation species composition and structure. For each woody plant, we recorded the height and the crown diameter (mean of two perpendicular measurements). We recorded the diameter at breast height (DBH hereafter) only for woody plants with a DBH higher than 6 cm. For individuals shorter than 1.5m, heavily damaged and/or with several stems, stem diameter was measured on the largest stem, at the height of the first twig. In addition, for each plant, the degree of utilization by elephants was recorded through several binary variables: trunk broken, twigs browsed, uprooted, root used, bark removed, dead tree. These variables (where applicable) were recorded in the reach of elephant: between 0.5m and 5m in height (Höft & Höft, 1995). Observed damages are very specific to elephants: beyond plant uprooting, breaking (not cutting with teeth) of large stems and branches with their trunk leaves scars that can be typically associated to elephants. These include shredded broken trunks and branches of large diameter, with characteristic scars on the sides and ends of damaged stems. These typical scars have also been identified by other studies (e.g. Nelleman et al. 2002; Holdo, 2003; Staub et al., 2013; Kimuyu et al, 2021). We are therefore confident that most elephant impacts were not confounded with other herbivores' impacts. We also performed a visual estimation of the percentage of twigs and bark removed. We finally summarized this information of whether an elephant impact of any type was present on a plant at the time of observation with a binary variable "used" *vs.* "not used". The different impacts were qualified as old or young (less than one-year-old) following Coetzee et al. (1979) and Ben-Shahar (1998) for the age classification method. Structural information was not recorded for plants that were shorter than 50 cm, but these were included in abundance analyses.

Functional traits

Data on six functional traits were gathered: three physiological traits (leaf nitrogen [N], carbon [C] and phosphorus [P] concentrations) and three morphological traits (leaf dry matter content (LDMC), stem density (SD) and type of spinescence (no spine, spines or thorns)). Functional traits data were gathered from a combination of sources which included the TRY database (Kattge et al. 2011), the Global ^{15}N Database (Craine et al. 2009), the Seed Information Database, TROBIT West Africa (Domingues et al. 2010), The Americans N&P Database (Kerkhoff et al. 2006), Global Wood Density Database (Chave et al. 2009), William Bond's database. Species for which trait data were missing from the different databases were sampled during a fieldwork session in May 2016. Overall, functional trait data were gathered for 26 species which accounted for 90% of the standing abundance in the plots (see list in S2).

Analyses

All analyses were performed using R Software (R Development Core Team, 2017). For all binomial and Poisson error models, we performed a test for overdispersion and computed quasi-likelihood analysis proposed by Bolker (2021) if overdispersion was detected. Significant covariates were selected according to their p-value against $\alpha = 0.05$. All the analytical steps detailed below are summarized in Figure 1.

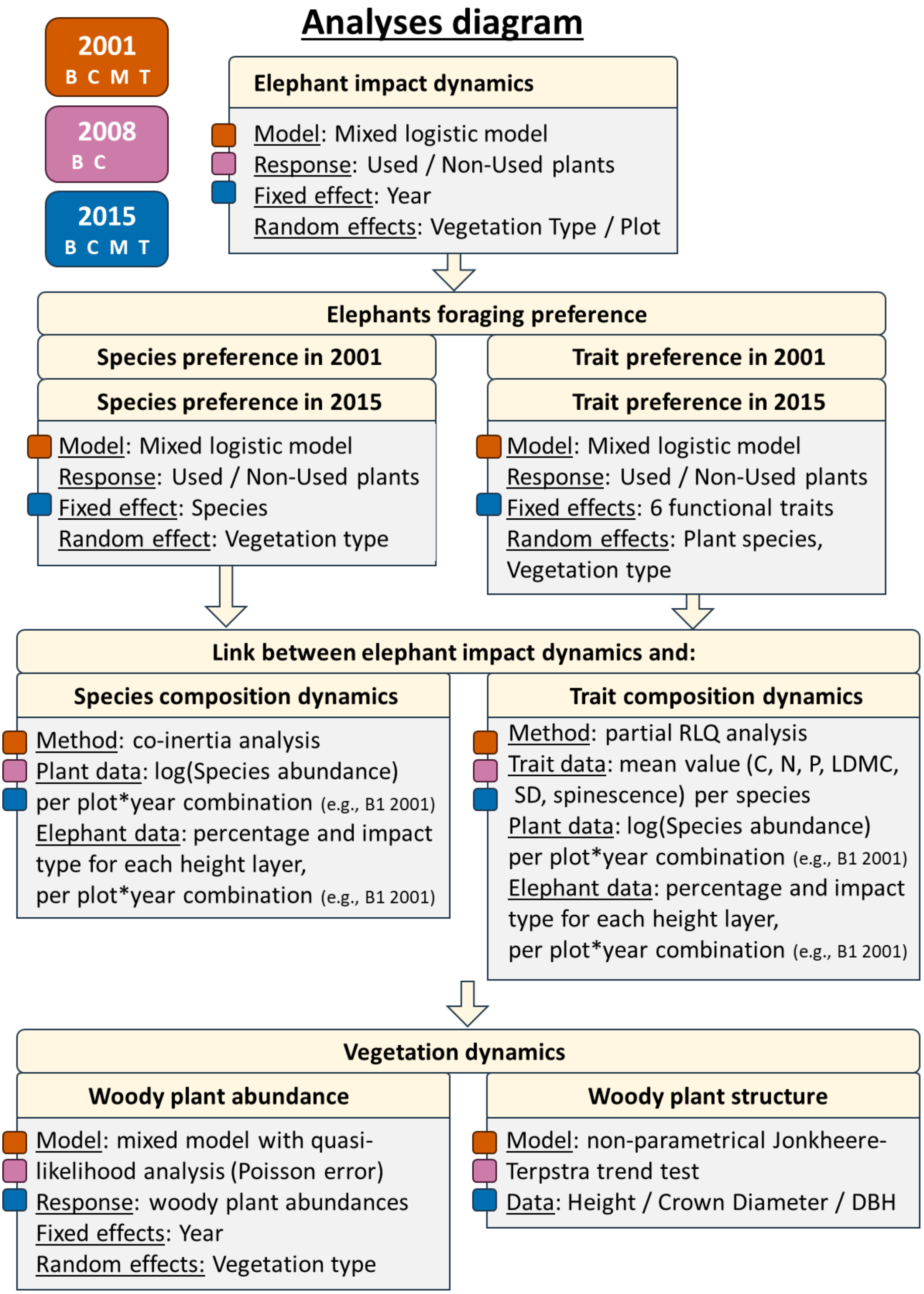

Figure 1: Diagram depicting the framework of the different analyses. Coloured boxes represent the part of the data was used for each analysis (i.e., data from 2001, 2008 or 2015).

White letter B, C, M and T represents the vegetation type recorded for each year (respectively *Baikiaea plurijuga* woodland, *Combretum* bushed-woodland, *Colophospermum mopane* bushland and *Acacia/Terminalia* bushed-woodland).

Elephant impact dynamics and elephant foraging preference

Impact dynamics – We evaluated the accumulation of elephant impacts on the woody vegetation over the study period by performing a mixed logistic model (using the "lme4" package, Bates et al., 2015). The response variable was the presence (i.e., "used", noted as "1") and absence (i.e., "not used", noted as "0") of elephant impact on woody plants; the vegetation type and the plot identity were used as random effects, with the plot nested within vegetation type, and the year of observation as a fixed effect.

Species preference – We used a mixed logistic model (using the "lme4" package, Bates et al., 2015) to evaluate the species preference by elephants. The response variable was the presence (i.e., "used" noted as "1") and absence (i.e., "not used" noted as "0") of elephant impact on woody plants; the vegetation type was used as a random effect and the plant species as a fixed effect. For each plant species, we thus obtained the log-odd ratio estimation of "success" (i.e., utilisation by elephants) with its statistical test associated. The availability here is the total number of individuals for each species. To assess temporal difference in species preference and reduce model complexity, we did not include interaction terms but computed one model per period (*i.e.*, one for 2001 and one for 2015) and compared the outputs of the two models. Only species occurring both in 2001 and 2015 with at least 10 individuals in each year were considered in the models. We adjusted all the p-values obtained (i.e., number of species multiplied by two as we ran two models) with the "fdr" method (Benjamini & Hochberg, 1995), which controls the false discovery rate, the expected proportion of false discoveries amongst the rejected null hypotheses.

Functional trait preference – We evaluated whether elephant preference was driven by plant functional traits using a mixed logistic model (using the “lme4” package, Bates et al., 2015). The response variable was the presence (i.e., “used” noted as “1”) and absence (i.e., “not used” noted as “0”) of elephant impact on woody plants; the vegetation type and the plant species were used as random effects and the six functional traits as fixed effects. To assess temporal difference in the functional trait preference, we fitted two models for 2001 and 2015 separately.

Species and functional trait composition dynamics

Species composition dynamics - We performed a co-inertia analysis (Dolédec & Chessel, 1994) to study if and how the variations of species composition in plant communities are related to the number and type of elephant impacts for each combination ‘plot-year’. This two-table ordination technique aims to find a linear combination of plant species and a linear combination of elephant impacts with maximal covariance. It thus provides a graphical summary of the main effects of the different impacts on plant communities. Prior to the co-inertia analysis, species abundances were log-transformed and we used a within-class analysis to partial out the differences between vegetation types and ensure that the analysis focused only on the temporal effect. Analyses were performed with the ade4 package for R (Dray and Dufour, 2007).

Functional trait composition dynamics - We applied a partial-RLQ analysis (Wesuls et al., 2012), using the “ade4” package (Dray & Dufour, 2007) to determine if and how the functional trait composition of plant communities varied with elephant impacts after controlling for differences in vegetation types. RLQ analysis is an ordination technique that extends co-inertia analysis to study the relationships between three tables (instead of a pair of tables). The method finds a linear combination of plant traits and a linear combination of elephant impacts with a maximal covariance taking into account abundances of plant species in plots. This allowed us to identify if and which types of elephant impacts mainly drive differences in functional traits among communities.

Woody plant abundance and structure dynamics

Woody plant abundance dynamics – We evaluated the dynamics of woody plant abundance between 2001 and 2015 using a mixed Poisson model. The response variable was the abundance of woody plants, the vegetation type was used as a random effect, and the year, the height and their interaction as fixed effects. Three classes of height were used: (i) below 50 cm height, as elephants were assumed to not substantially affect this layer (feeding height of elephant ranging from 50 cm to 5.5 m, Shannon et al. 2006) and this layer represents the dynamics of recruitment, (ii) between 50 cm and 200 cm and (iii) above 200 cm height (i.e., tall plants supposed to be more impacted by elephants, Cumming et al., 1997; Asner & Levick, 2012). Overdispersion being detected, we computed quasi-likelihood analysis proposed by Bolker (2021) - i.e., we adjusted the coefficient table by multiplying the standard error by the square root of the dispersion factor and recomputing the Z- and p- value accordingly.

Woody plant structure dynamics - For these analyses, woody plants below 50 cm height were removed, as we assumed this layer to have a low importance on global vegetation structure. For each plot, we performed a non-parametric Jonkheere-Terpstra trend test of global trend (Jonckheere, 1954) on the height. We also performed the same test on DBH and crown diameter considering the two height classes: 50-200 cm and >200 cm.

Results

Elephant impact dynamics and elephant foraging preference

Impact dynamics - The probability (mean ± SD) that a woody plant was used by elephants increased over the study period, from 0.34 ± 0.11 in 2001 to 0.45 ± 0.12 in 2008 and 0.52 ±

0.12 in 2015 ($\beta_{2001\text{-}2008} = 0.53$, $z_{2001\text{-}2008} = 9.2$, $p < 0.001$, $\beta_{2008\text{-}2015} = 0.29$, $z_{2008\text{-}2015} = 5.28$, $p < 0.001$; see also Fig. 2). However, only 10% of the impacts were recorded as fresh (i.e. from the year) so the increase detected mainly reveals accumulation of the impacts over the years. Among used plants, broken trunks consistently represented the main impact by elephants (87% of all elephant impacts, see details in S3), followed by browsing (39%). Uprooted trees only represented 19 individuals.

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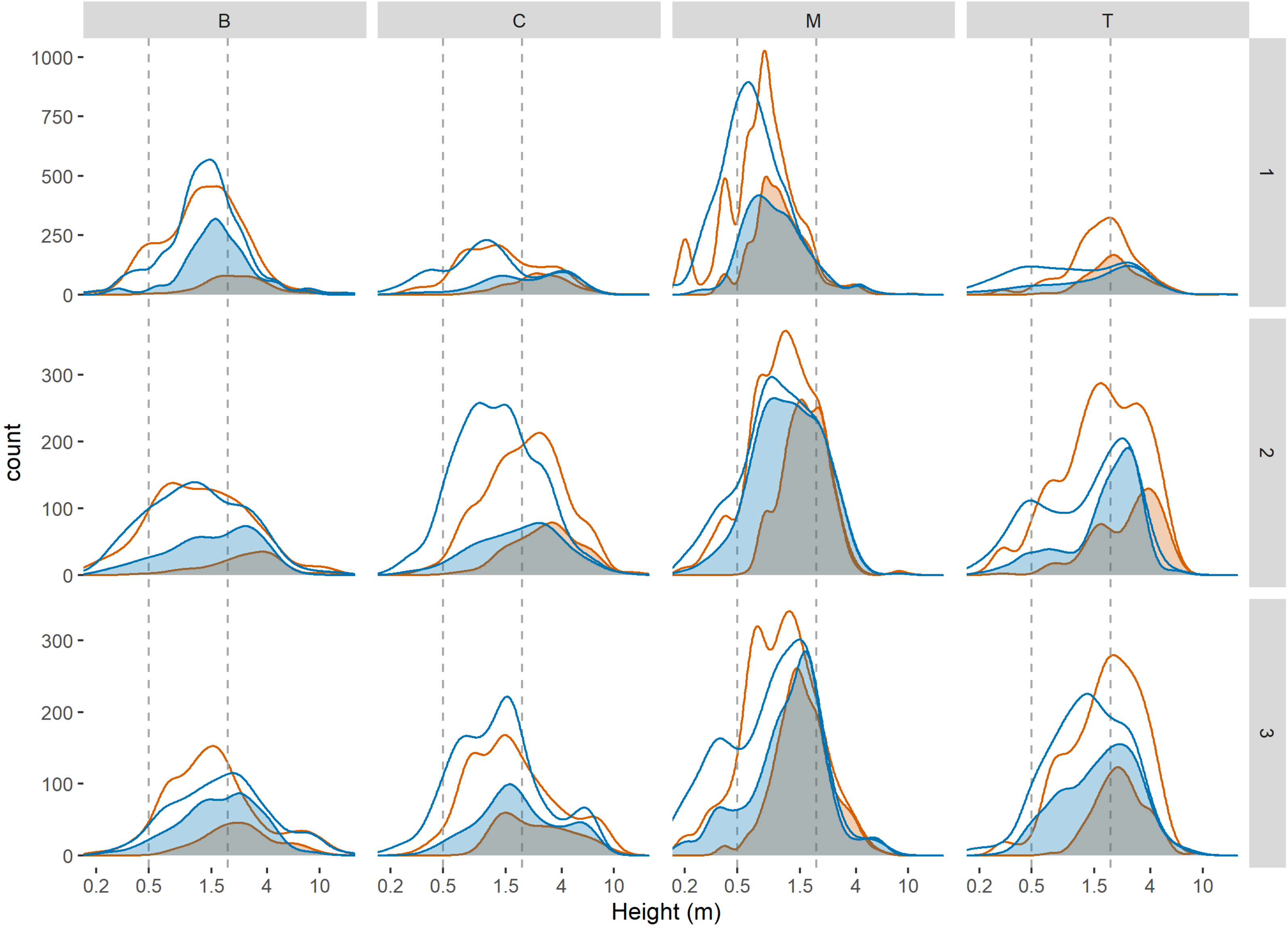


B
C
M
T
1
2
3
count
1000
750
500
250
0
300
200
100
0
300
200
100
0
0.2
0.5
1.5
4
10
Height (m)

316

Figure 2: Density distribution of the log-transformed height of woody plants for the three plots monitored (1, 2 and 3) for each of the four vegetation types (B = *Baikiaea plurijuga* woodland, C = *Combretum* bushed-woodland, M = *Colophospermum mopane* bushland and T = *Acacia/Terminalia* bushed-woodland). Orange density distributions represent 2001 and blue density distributions represent 2015, for visual convenience 2008 was not represented here. Simple lines represent density distributions for all woody plants whereas full-coloured density distributions represent plants used by elephants. Vertical lines indicate the heights of 50 cm and 200 cm respectively. Note that y-axis scales differ but have been scaled to similar height for visual convenience.

Species preference - Of the 39 plant species considered, *Colophospermum mopane* was the only species selected for by elephants for the two study years (2001 and 2015, Fig. 3). Among all the other species, none was selected for in 2001 and only *Combretum celastroides* was selected for in 2015 (Fig. 3). Several species were avoided by elephants in 2001, but were used in accordance to their availability in 2015 (i.e. not avoided and not selected), leading to 14 plant species avoided in 2001 against 7 in 2015 (Fig. 3). For more intuitive overview of the results, we back-transformed the log-odd ratio into probability of utilisation for each species (see Fig. 3).

Functional trait preference - In 2001, elephants avoided species with higher leaf N concentrations ($\beta \pm SE = -0.75 \pm 0.23$, $z = -3.05$, $p < 0.01$), and selected species with higher leaf P concentrations ($\beta \pm SE = 0.79 \pm 0.40$, $z = 2.05$, $p = 0.04$). Other traits had no impact. In 2015, no significant selection or avoidance of traits by elephants was detected.

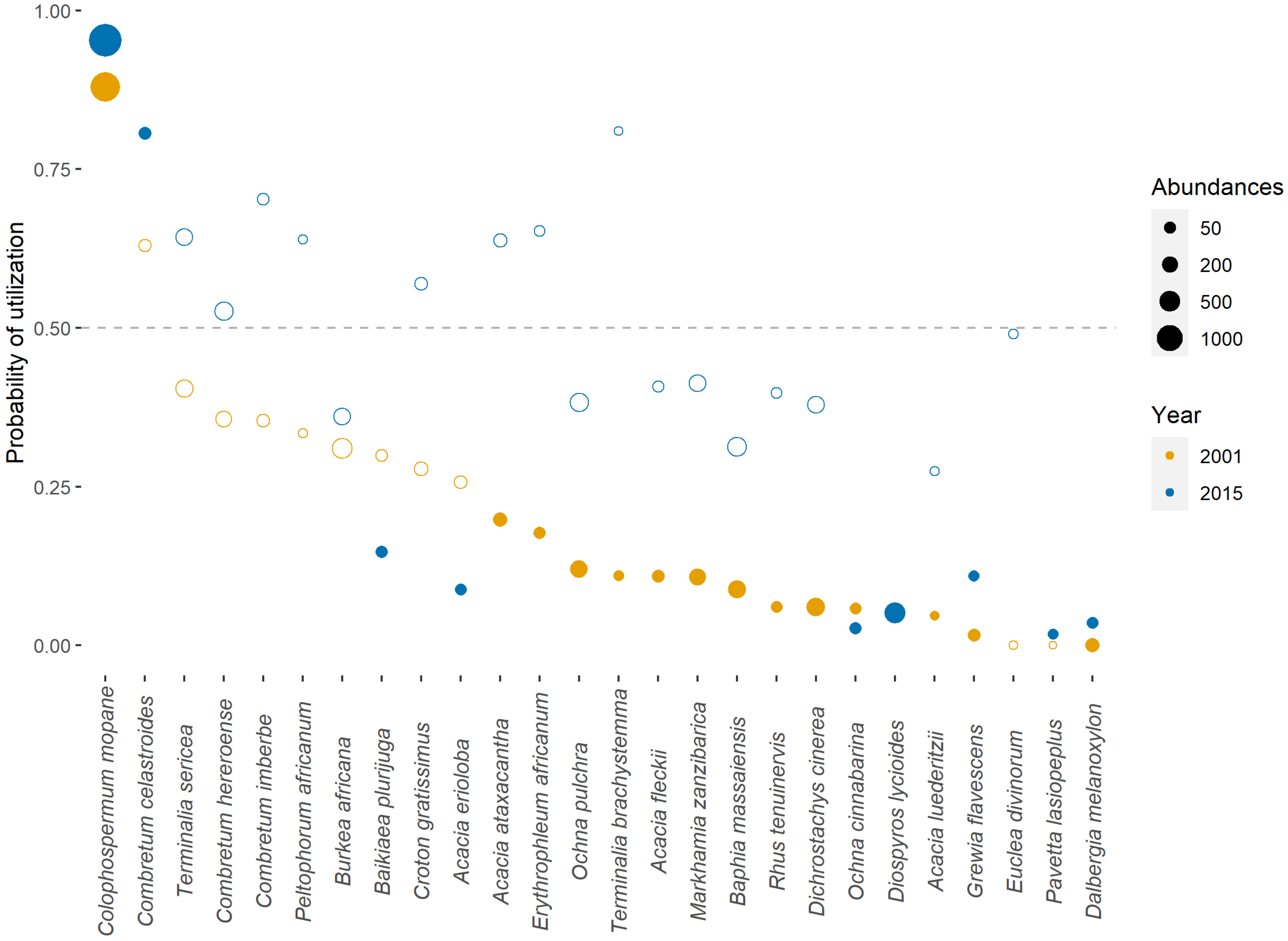

Probability of utilization
1.00
0.75
0.50
0.25
0.00
Colophospermum mopane
Combretum celastroides
Terminalia sericea
Combretum hereroense
Combretum imberbe
Peltophorum africanum
Burkea africana
Baikiaea plurijuga
Croton gratissimus
Acacia erioloba
Acacia ataxacantha
Erythrophleum africanum
Ochna pulchra
Terminalia brachystemma
Acacia fleckii
Markhamia zanzibarica
Baphia massaiensis
Rhus tenuinervis
Dichrostachys cinerea
Ochna cinnabarina
Diospyros lycioides
Acacia luederitzii
Grewia flavescens
Euclea divinorum
Pavetta lasiopeplus
Dalbergia melanoxylon
Abundances
50
200
500
1000
Year
2001
2015

Figure 3: Parameter estimates resulting from the mixed logistic model of woody plant species selection by elephants. Red and blue circles represent estimates for the year 2001 and 2015 respectively. Circle sizes are proportional to the abundance of the species during the year considered. Filled circles are estimates significantly different from 0 whereas empty circles are not significantly different from 0. A high positive Beta estimate value indicates a high selection towards the species regarding its availability (and the opposite for negative value).

Species and functional trait composition dynamics

Species composition dynamics - After removing the variability between vegetation types (which accounted for 70% in the species composition table and 48% in the elephant impacts table), a slight temporal shift in the composition of the vegetation was identified (see S4a). The first axis of the co-inertia analysis captured 70% of the remaining variability, which represented 25.7% of the initial variability (S4b). The slight temporal shift in the composition of the vegetation corresponded mainly to a shift in the rare species of the communities (S4c, d). More than 20 species (e.g. *Tricalysia allenii, Combretum Zeyheri, Commiphora edulis* and *Pterocarpus rotundifolius*) disappeared from the plots while a few new species (e.g. *Mundulea sericea, Gardenia volkensii, Philenoptera violacea* and *Erythroxylum zambesiacum*) appeared in the plots (S4d). Common species such as *Diospyros lycioides, Burkea africana, Baphia massaiensis, Combretum hereoense* were almost unaffected (S4d). The first axis of the co-inertia analysis revealed that this temporal trend was related to an increase in elephant impacts (percentage of broken, of browsed woody plants; S4e, permutation test, $p < 0.001$).

Functional trait composition dynamics – No link was identified between elephant impacts and the mean value of functional trait by the RLQ analysis (permutation test, $p = 0.78$).

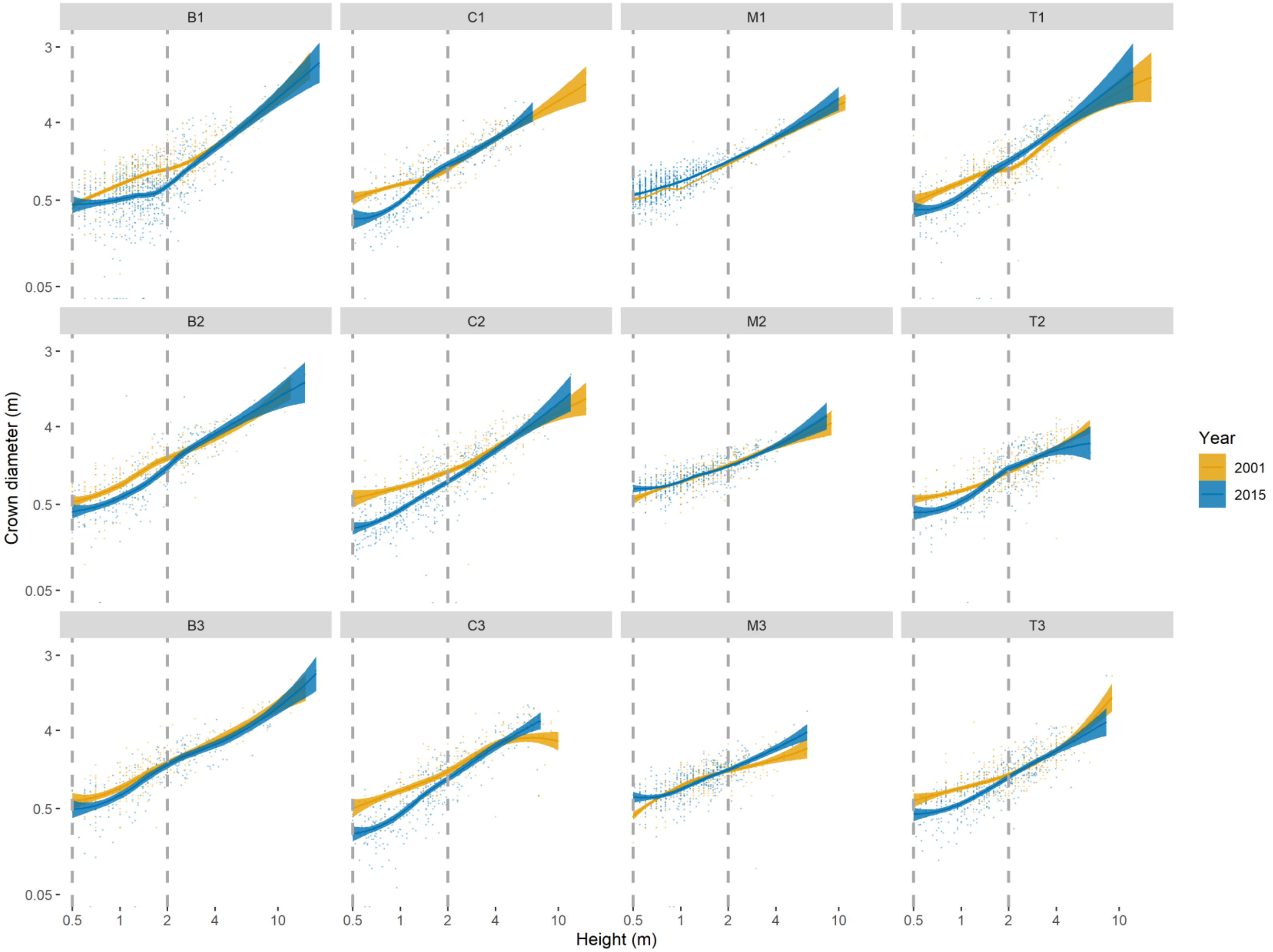
Woody plant abundance and structure dynamics

Woody plant abundance dynamics - The abundance of woody plants under 50 cm had a tendency to increase between 2001 and 2015 ($\beta \pm SE = 0.68 \pm 0.36$, $z= 1.87$, p-value =0.06, see also Fig. 2 and S5 for detailed abundances). The abundance of woody plants between 50 cm and 200 cm had a tendency to decrease ($\beta \pm SE = -0.7 \pm 0.4$, $z= -1.75$, p-value = 0.08; see also Fig. 2 and S5 for detailed abundances), and we observed a decrease in the abundance of woody plants higher than 200 cm ($\beta \pm SE = -0.991 \pm 0.44$, $z = -8.2$, p-value = 0.02; see also Fig. 2 and S5 for detailed abundances).

Woody plant structure dynamics – Overall, plant height did not change except in 4 plots where there was a slight decrease of the median height (Table 1, Fig. 2). Almost no decrease was observed when looking at the DBH (Table 1, S6). Regarding the crown diameter, we observed differential change according to the height layer of woody plants (Fig. 4). No change was observed for woody plants above 200 cm (Table 1, Fig. 4). However, a strong decrease of the median crown diameter for plants between 50-200 cm was observed in almost all plots, except in Mopane plots where an increase was observed (Table 1, Fig. 4).

Table 1: Results from analyses on vegetation structure. For each plot within each vegetation type, the dynamics of each structural variable was assessed with the non-parametrical Jonckheere's test, with the alternative hypothesis as a decrease of the structural characteristics over the study period except for the variable "Crown diameter (m^2) 50-200 cm height", where the alternative hypothesis was a simple difference. Only significant results are represented ($\alpha = 0.05$) with the median value of the structural characteristics in 2001 and in 2015 (H is used for height, CD for crown diameter). * represents the particular case of the *Mopane* plots were an increase of the "Crown Diameter (m^2) 50-200 cm height" was observed.

	Plot	Baikiaea	Combretum	Mopane	Terminalia
Height (cm)	1			H_{2001} =80, H_{2015} =80	
	2		H_{2001} =220, H_{2015} =135		
	3		H_{2001} =150, H_{2015} =145		H_{2001} =200, H_{2015} =145
DBH (cm)	1				
	2		DBH_{2001} =2.86, DBH_{2015} =1.67		
	3				
Crown diameter (m^2) > 200cm height	1				
	2		CD_{2001} =3 .14, CD_{2015} =2.17		
	3				
Crown diameter (m^2) 50-200 cm height	1	CD_{2001} =0.50, CD_{2015} =0.24	CD_{2001} =0.38, CD_{2015} =0.22	*CD_{2001}=0.38, CD_{2015}=0.44	CD_{2001} = 0.75, CD_{2015} = 0.29
	2	CD_{2001} =0.50, CD_{2015} =0.27	CD_{2001} =0.50, CD_{2015} =0.16	*CD_{2001} =0.50, CD_{2015} =0.72	CD_{2001} = 0.50, CD_{2015} = 0.30
	3	CD_{2001} =0.79, CD_{2015} =0.60	CD_{2001} =0.38, CD_{2015} =0.22		CD_{2001} = 0.5, CD_{2015} = 0.32



B1
C1
M1
T1
B2
C2
M2
T2
B3
C3
M3
T3
3
4
0.5
0.05
Crown diameter (m)
0.5
1
2
4
10
Height (m)
Year
2001
2015

Figure 4: Plots showing the relationship between log-transformed mean crown diameters and log-transformed heights of all plants for the three plots monitored for each of the four vegetation types (B = *Baikiaea plurijuga* woodland, C = *Combretum* bushed-woodland, M = *Colophospermum mopane* bushland and T = *Acacia/Terminalia* bushed-woodland). Points represent raw data and predicted values with confidence interval (using local polynomial regression fitting “loess” smoothing method) are represented in orange for 2001 and in blue for 2015. Vertical lines indicate the heights of 50 cm and 200 cm respectively.

Discussion

In this study, we provide an overall assessment of the long-term effects of a sustained high elephant population density on vegetation structure and composition in a savanna woodland, which is a large open area.

Elephants: generalist foragers in an ecosystem exposed to long-term high elephant abundance

Among the main plant species of the study plots, *Colophospermum mopane* was the only species that was significantly selected for by elephants, which corroborates previous studies that showed high rates of utilization of this plant species by elephants (Ben-Shahar, 1998; Ben-Shahar & Macdonald, 2002). Interestingly, *Colophospermum mopane,* which was the most heavily utilized species by elephants, also increased the most in abundance, mainly in the lower class size (i.e., < 50cm). This higher abundance of *C. mopane* individuals can result from true recruitment with (a) heavy elephant browsing pressure on adult plants limiting their ability to monopolize resources and hence reducing intraspecific competition with the saplings, or (b) the effect of faeces deposition by elephants with nutrient imports by elephants in areas where they forage, the increased nutrient turn-over rate associated with high elephant abundance, and the increased seed dispersal of the more palatable species, which will ultimately favour the growth of fast growing and more palatable species (Skarpe et al., 2004). The higher abundance of *C. mopane* plants could also be apparent and result from resprouting, i.e., the production of secondary trunks as an induced response to injury or to profound changes in growing conditions (Bond & Midgley, 2003, e.g., on other taxa Heiser et al. 2004 for post-fire resprooting, Lewis 1991 and Lewick & Rogers 2008 in response to herbivory). As *C. mopane* is a root sucker, i.e. new stems grow from existing roots (particularly as a response to disturbance; Makhado et al., 2014), stem density would increase but not population density. Identifying which one of these two persistence strategies, recruitment or resprouting, was responsible of this increase of stem density was not the aim of this study, but would be of interest for further studies at the population scale.

Of twenty-six plant species, fourteen were avoided in 2001, but half of these species were no longer avoided by 2015. Most study species (70%) were therefore neither selected for, nor avoided by elephants in 2015. This tendency of generalist feeding behaviour is also observed when focusing on the plant functional traits: contrary to other studies on elephant preferences (Jachman, 1989; Holdo, 2003), we did not detect any strong association between elephant selection and the functional plant traits measured in this study. We only observed an avoidance of species with high N leaf content in 2001 in complete opposition to expected herbivore preferences (Crawley, 1983; Herms & Mattson, 1992; Wigley et al.; 2014). This surprising result might be explained by the fact that species with high N concentrations may also have high concentrations of compounds that reduce digestibility (e.g., condensed tannins that were not recorded in this study, Herms & Mattson, 1992). The addition of missing important functional traits linked to reduced palatability, such as condensed tannins, would most likely improve our understanding of elephant impacts on species and functional trait composition.

Altogether, our results suggest a foraging behaviour tending to be opportunistic by elephants in HNP between 2001 and 2015 (contrarily to other studies, e.g. Owen-Smith & Chafota, 2012). We cannot rule out a scenario whereby elephants had extirpated their favourite plant species before 2001 and now remain in an ecosystem dominated by non-preferred plant species (e.g. Augustine & McNaughton, 1998), which are therefore utilized in proportion to their availability in the landscape.

A new stable woody vegetation composition

Previous modelling studies suggest that plant communities exposed to elephant herbivory can shift over a 50-year period towards unpalatable species that are highly resistant to elephant disturbances (Holdo, 2007). Our results revealed that elephant impacts did lead to shifts in the abundances of rare plant species (e.g. *Mundulea sericea*, *Trycalia alleni*) but were not associated with shifts in the relative abundance of the common plant species (e.g. *Colophospermum mopane*, *Baphia massaiensis*, *Diospyros lycioides*) between 2001 and 2015 in HNP. In 2001, the elephant population abundance of HNP had been high for at least 20 years (>1.km^{-2}) and among the highest elephant population densities with >2.km^{-2} for a decade (Chamaillé-Jammes et al., 2008). It is therefore highly likely that plant communities had already stabilized by 2001 under high elephant browsing pressure and provides support to the existence of a dynamic equilibrium between elephants and woody plants, with different stable states (Dublin et al., 1990). Further, the overall functional trait composition did not experience significant changes correlated with increased elephant impact, most probably because the dominant species remained more or less stable during the study period. Finally, the rare plant species that disappeared from the plots were not the ones that were most preferred by elephants. Our results suggest that elephant foraging preferences did not cause the changes in species abundance observed between 2001 and 2015 (i.e. these species were not targeted by elephants). These changes may therefore be linked to differences in how well different woody plant species were able to tolerate browsing (O'Connor et al., 2007). However, other explanations cannot be ruled out such as (i) other type of disturbance (e.g., phytophagous herbivory, pathogen), or, because of an initial low abundance, these species could be particularly prone to a local extirpation (ii) "by chance" or (iii) by death due to ageing / senescence of the few individuals occurring initially.

Elephants clear the understorey

Our study, which was conducted over a period of fifteen years of high elephant densities, did not reveal an overall conversion from woodland to grassland as previously reported in the literature from East African savannas (Laws, 1970; Caughley, 1976). We assumed that the response of plants to elephant impacts may be different in Southern Africa, where woodland savannas are often on poorer soils and more diversified (Childes & Walker, 1987; Ben-Shahar, 1998; Asner & Levick 2012). Further, Holdo's (2007) model suggests that elephants are not expected to convert semi-arid savanna woodland to complete grassland as often suggested/observed in East African savannas. Elephants would more likely revert and maintain savanna vegetation in a scrub phase, i.e., a phase dominated by coppiced shrubs and grass, because savanna woody plants are typically able to resprout following disturbance (Holdo, 2007). Our results are in line with previous observations of elephants affecting taller plants (>2m, Cumming et al., 1997; Asner & Lewick, 2012; Morrison et al., 2016). Indeed, during the study period, we observed a decrease of tall plants (>200 cm), which could have been either killed by elephants, or reverted to the lower layer (50-200 cm; i.e. "tree broken into shrub" *sensu* Valeix et al., 2011 or "top-killed" *sensu* Morrison et al., 2016).

Fire and frost are two important agents of tree mortality in African savannas (Holdo, 2007). However, no fire occurred in the study vegetation plots, except in 2015 when 3 plots (T1, T2, T3) burnt in a low intensity fire that only affected the grass layer and woody seedlings. The lack of knowledge on frost in this system limits our ability to disentangle the relative importance of elephants and frost on these abundance modifications, but frost most likely affects young plants (Holdo 2006). Further, elephants are assumed to independently modify savanna vegetation into a scrub phase where frost and fire act, at best, only as a secondary synergistic factor (Holdo, 2007; Morrison, 2016).

Surprisingly, we did not observe an alteration of vegetation structure (plant height, plant crown diameter) of the taller size classes in HNP. The most striking result of our study was the effect of long-term exposure to a high elephant population density on the structure of the vegetation in the understorey (50-200 cm; Fig. 5). The crown diameter distribution in the 50-200 cm layer changed drastically in all plots except in *Colophospermum mopane* bushland. In *Baikiaea plurijuga* woodland, *Combretum* bushed-woodland and *Acacia/Terminalia* bushed-woodland, the crown diameter decreased strongly. Plant crown diameter and height are strongly related to above-ground volume and biomass (Popescu et al., 2003). The observed decrease in crown diameter is therefore linked to a diminution of the spatial volume occupied by woody plants in the 50-200 cm layer (Fig. 5) and is thus expected to lead to a change in available resources for other large herbivores, and a higher visibility in this height layer. As visibility is a key environmental parameter for anti-predator behaviour of prey species (FitzGibbon, 1994; Gorini et al., 2012) and the hunting behaviour of predator species (Loarie et al., 2013), these changes in crown diameter could have consequences on predator-prey relationships (e.g. Tambling et al., 2013; Ferry et al. 2020).

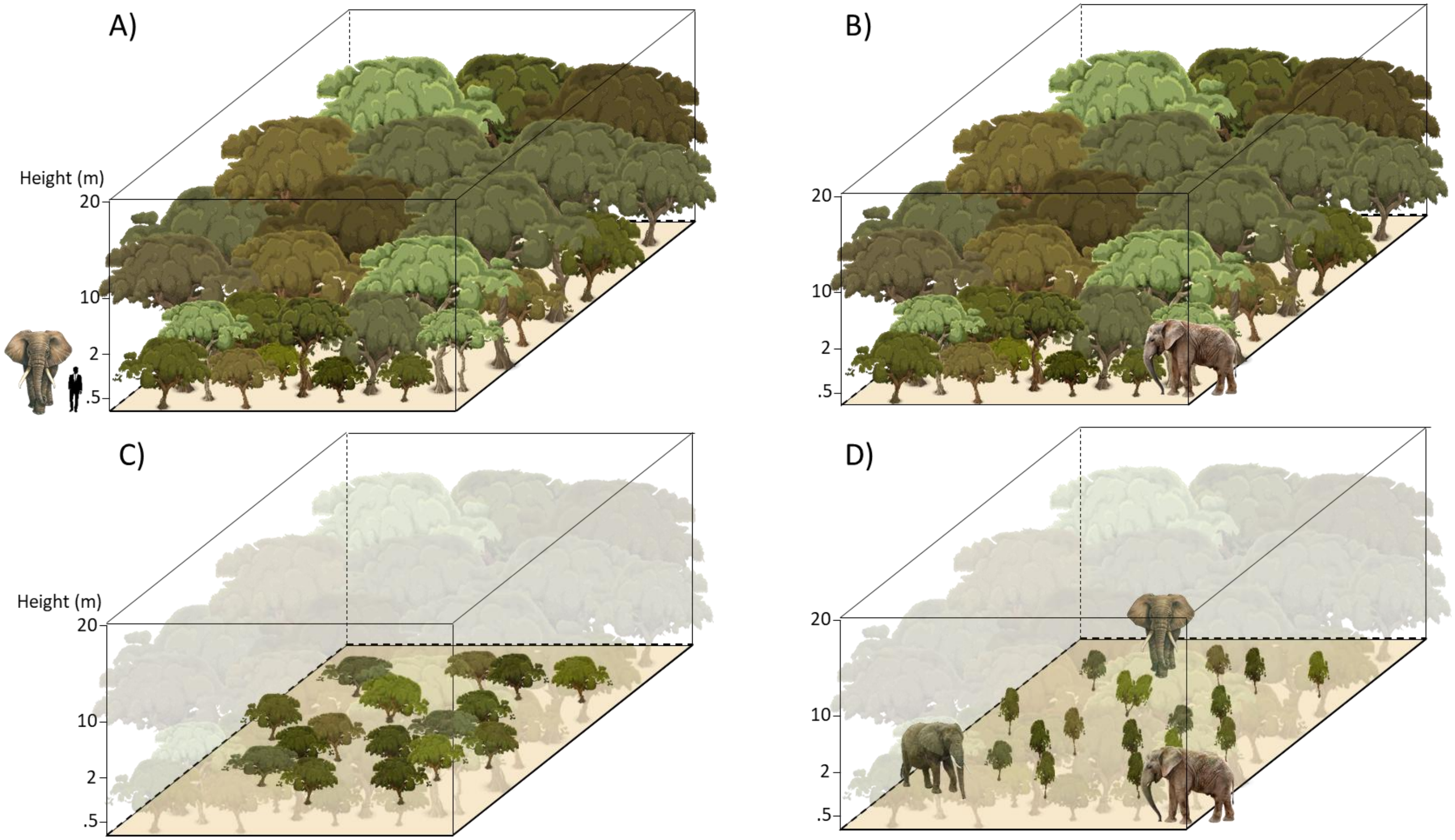


Figure 5: Schematic representation of elephant impact on vegetation structure in Hwange National Park. A) and B) depict the “external morphology” of the woodland (i.e. canopy view), and C) and D) the “internal morphology” of the woodland (i.e. understorey). A) and C) are

habitat without elephant whereas B) and D) are habitats with high elephant density and where a decrease of woody plants’ crown diameter in the 50-200 cm height layer is observed.

Conclusions

The vegetation changes observed were modest despite the long-term exposure to high elephant browsing pressure. The relatively modest vegetation changes revealed here are highly different from previous studies done in the Chobe National Park riverfront, Botswana, where local elephant densities are extreme during the dry season because this is the only source of water in the region during the dry season (Rutina & Moe, 2014; Teren et al., 2018), but are in accordance with another study carried out further into the Chobe National Park (>50 km from the river) where there are small effects of elephants on the woodlands (Kalwij et al., 2010). These and our results, taken together, suggest that elephant might have a drastic impact in large ecosystems that reached an equilibrium but only close to water sources. An alternative explanation suggested by Skarpe et al. (2004), states that elephant abundances and savanna woodlands might be in perpetual changes with multiple stable states suggesting that conservation success should be evaluated by shifts in alternative stable states in addition to elephant induced changes when they reach high density.

Overall, our study suggests that the species composition of the woody community in this savanna woodland has reached a stable state. In terms of vegetation structure, the two main effects revealed here are (i) a decrease in the number of tall plants and an increase in the number of saplings, and (ii) a reduction in crown diameter in the 50-200 cm height stratum. This latter result suggests that elephants may influence other herbivore foraging or predator-prey interactions in ecosystems where they are present in high densities. This finding encourages future studies to assess these potential environmentally-mediated trophic interactions modifications (Wootton, 1993) by elephants.

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Author's Contributions

AI, HF, MB, LS and MV conceived the ideas and designed methodology;

NF, AI, TCD and BW collected the data;

NF, SD, and MV analyzed the data;

NF, SD, and MV led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

A list of data sources used in the study are provided in detailed data collection in the Material and Method section.

The dataset and the R script for analysis has been deposited in Zenodo repository [doi: 10.5281/zenodo.5564836].

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Appendices list

Appendix S1. GPS location of the twelve vegetation plots monitored (Zone UTM 35S) with distance to the closest waterhole.

Appendix S2. List of the 26 species contributing to the 90% standing abundance in the plots for which functional traits were gathered.

Appendix S3. Distribution of the different elephant impact types.

Appendix S4. Outputs of co-inertia analysis for the first two axes.

Appendix S5. Total number of woody plants per plot per year a) lower than 50cm height, b) between 50cm and 200cm height and c) higher than 200cm height.

Appendix S6. Graph of log-transformed DBH in function of log-transformed height of all woody plants.