# Elephants and Woody Plant Diversity: spatio-temporal dynamics of the Linyanti woodland, northern Botswana

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Philosophy

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# Declaration

I declare that this thesis is my own, unaided work, unless otherwise noted within the text. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any other degree or examination at any other University.

Gabriella Teren

5th day of September 2016 in Johannesburg

# Abstract

There is an urgent need to study the effects of elephants on biodiversity given the ability of megaherbivores to transform vegetation composition, structure and function by killing selected plants. Within a biodiversity framework of different aspects of diversity across different scales, we need to understand elephant effects across time and space, acknowledging disequilibrium dynamics of savannas. However, most savanna studies are conducted either over a short time frame, over a limited spatial extent, or without species compositional data. The Linyanti riparian woodland in northern Botswana represents a valuable opportunity to study the effects of elephants as it is subject to extremely high elephant concentrations in the dry season as elephants congregate on the perennial river. Moreover, because of trampling effects by large herbivores and high soil moisture, fire is largely excluded, allowing the study of intense elephant impacts in relative isolation.

This PhD thesis aims to assess long-term (16-18 years) compositional and structural change at a large spatial scale (50 km of riverfront) of the Linyanti riparian woodland, built upon two earlier studies in 1992/2 and 2001. Specifically, it aims to establish the effects of elephants on 1) the spatial heterogeneity of disturbance across the woodland; 2) compositional changes of the canopy tree layer caused by elephant impacts; 3) the potential of the woodland to regenerate from seedlings; 4) structural changes due to woodland decline and shrub increase. It finally aims to synthesise these findings for biodiversity and the implications for conservation and management.

Spatial heterogeneity was assessed by delineating patches of intense disturbance using the clustering algorithm DBSCAN. I manually marked dead trees within a 2000 ha overlapping riparian area from the 1992, 2001, and 2010 aerial photographs and determined these trees were significantly clustered in the landscape to form patches of disturbance. Disturbance patches were highly dynamic over the period where small patches appeared, grew and coalesced over time, whilst a few patches fragmented or disappeared. The overall dynamic was of smaller patches coalescing resulting in the total patch area increasing from 6% in 1992 to 23% in 2010. Mortality increased mostly in the inter-patch areas but the overall dead tree appearance rate of 0.28 trees.ha.yr$^{-1}$ was not much higher than a background tree death rate calculated for exclosures in other areas. The slow mortality rate coupled with progressive decline suggests there was little recruitment into the canopy to replace the trees that were lost. Even though large areas remained that were not classified as disturbance patches, there was

evidence of increased fragmentation where inter-patch areas became increasingly small and isolated. This increase in greater areas of disturbance represents a state shift to decreased heterogeneity although landscape patchiness still remained in 2010. Projections were that mortality rate and patch formation would decrease.

To assess compositional changes, I reconstructed the pre-1992 canopy tree woodland by combining both living and dead trees in 1992, and compared this to the 1992 and 2008 woodland composition. The woodland showed progressive declines from an *Acacia* spp.-*Colophospermum mopane* dominated tall tree woodland pre-1992 to a woodland in 2008 composed primarily of two resilient species (*C. mopane*, *Combretum hereroense*), and one avoided species (*Philenoptera violacea*). I compiled Size Class Distributions of individual canopy tree species and compared proportional high impact on living and dead trees between 1992 and 2008. High elephant impact was defined as more than 50% stem circumference ringbarked or with the main stem or majority of side stems broken. I found that elephant impact was the likely cause of the woodland decline, although wind and natural senescence were variably important for some species. The acacias had nearly disappeared from the woodland, declining in proportional abundance from 30% in the reconstructed pre-1992 woodland to just 4% in 2008. Over time there was a progressive shift in elephant impact from abundant preferred and vulnerable species like *Acacia* spp. and *Terminalia* spp. to species more resistant to debarking like *Combretum imberbe* and *Berchemia discolor*. The abundant species *C. mopane* proved highly resilient to intensive elephant impact. The seedling layer (plants below 0.5m) had high proportions of canopy tree species including the acacias, and all but the rarest species were recorded. This suggests regeneration of the woodland is possible but there was a demographic bottleneck of seedling mortality with few saplings recorded over the time period.

To determine the structural changes which have taken place, I separated shrub species and canopy-forming tree species and assessed density changes in the sapling (<2.5m) and tree (>2.5m) layers. Tall (>2.5m) canopy tree density decreased by half between 1992 and 2008, representing an annual loss rate of 2.7% without replacement. Except for *Colophospermum mopane*, there was no compensatory regeneration in the form of saplings. *Colophospermum mopane* was highly resilient to elephant impacts, coppicing vigorously following impact to form local ‘browsing lawns’ which may benefit other browsers. The overall shrub density increased 2.5 times while one shrub species (*Combretum mossambicense*) increased five-fold in density and came to constitute 50% of the total woody plant density. This shrub species

increased rapidly, at an exponential growth rate of 10.5% per year, representing pervasive shrub encroachment. Its invasion wave was incipient in 1992 and by 2008 many of these plants had grown beyond 2.5 m in height, forming a dense screen. Small plants of this species <1 m in height had become sparse by 2008, suggesting that the invasion had become curtailed by then. I proposed that the spread of this shrub was due to its unpalatability by elephants, although it is an important browse species for ruminants. A potential global driver of enriched atmospheric $CO_2$ or regional aridification could not be ruled out. The state shift from woodland towards dense shrubland caused by differential elephant impacts has potential negative consequences for structural and functional diversity.

I attempted to synthesize the findings for biodiversity and concluded that there was a state shift towards pervasive disturbance with a corresponding decline in spatial heterogeneity, although composition of the disturbance patches was not studied. There has however, not been a state transformation from woodland and stands of tall trees were still present in the woodland. Coupled with the potential regeneration of the woodland from seedlings, these findings highlight the importance of long-term studies of non-equilibrium savannas. The main threat to biodiversity of the woodland was not elephant-induced mortality of large trees, but rather the lack of recruitment and the pervasive shrub encroachment of a single species. It may be, however, that alternate states of canopy trees and unpalatable shrubs exists, enhancing long-term functional diversity, provided the system remains relatively open and elephants are free to move to other areas. Ultimately the only management strategy of relatively open areas with high elephant concentrations is to accept changes and support transfrontier conservation efforts. I further assess the limitations of this study, and make recommendations for future study, specifically highlighting the need for a longer-term palaeo-ecological study to evaluate compositional changes due to episodic recruitment events.

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It's a glorious place.

## Disclaimer

This thesis consists of a series of chapters that have been prepared for submission to a range of scientific journals. As a result styles may vary between chapters in the thesis and overlap may occur in order to secure publishable entities.

# Table of contents

# List of figures

## List of Tables

## List of Abbreviations

| | |
|---|---|
| AIC | Akaike's Information Criterion |
| BDF | Botswana Defence Force (camp) |
| CNP | Chobe National Park |
| CSR | Complete Spatial Randomness |
| DBSCAN | Density-based spatial clustering of applications with noise |
| DCM | Digital Canopy Model |
| DEM | Digital Elevation Model |
| DT | Duma Tau Camp |
| DWNP | Department of Wildlife and National Parks, Botswana |
| GCP | Ground Control Point |
| GIS | Geographic Information System |
| GLM | Generalized Linear Model |
| GPS | Global Positioning System |
| HPDP | Hierarchical Patch Dynamics Paradigm |
| IDH | Intermediate Disturbance Hypothesis |
| IUCN | International Union for Conservation of Nature |
| KAZA TFCA | Kavango Zambezi Transfrontier Conservation Area |
| KNP | Kruger National Park |
| KPL | King's Pool Camp |
| LiDAR | LIght Detection And Ranging or also Light raDAR |
| MAP | Mean Annual Precipitation |
| MLE | Maximum Likelihood Estimation |
| MODIS | Moderate-resolution imaging spectroradiometer |
| PPP | Precise Point Positioning |
| REM | Relative Elevation Model |
| SCD | Size Class Distribution |
| SPP | Spatial Point Pattern |
| TFC | Tsetse Fly Control |

# CHAPTER ONE

## Elephants as agents of biodiversity change in riparian woodlands

## 1.1 Study Rationale

At the conclusion of the extensive Elephant Scientific Assessment (Scholes and Mennell, 2008), several questions around the effects of elephants on biodiversity remained and research needs were clearly identified:

"There is an urgent need to study the effects of elephants on biodiversity, specifically those aspects which are considered critical for ecosystem integrity (e.g. species level effects)…The observation that such impacts are often scale- and site-specific or episodic requires that this be undertaken at a range of spatial and temporal scales… The rate of change brought about by elephants as a function of elephant density is key to managing biodiversity in elephant areas, and this needs to be specifically quantified" ( Chapter 3: Kerley *et al.* 2008). This study attempts to contribute this need by evaluating the effects of extreme elephant densities, across time and space, on a riparian woodland in northern Botswana.

## 1.2 Background literature

### 1.2.1 Spatio-temporal dynamics of savanna woodlands

Scholes & Walker (1993) suggested that 'savannas do not represent a stable mixture of trees and grasses, as has been suggested in the past, but an inherently unstable mixture which persists owing to disturbances such as fire, herbivory and fluctuating rainfall'. This statement has been supported by evidence from palaeopalynology which show that savannas are not static in time, but oscillate between more and less woody periods (Gillson 2004a; b), supporting non-equilibrium hypotheses. At large spatial and temporal scales woody vegetation is determined by climate (Sankaran, Hanan & Scholes 2005), but at smaller scales by the disturbance agents of fire and large herbivores (Midgley, Lawes & Chamaillé-jammes 2010) (Fig. 1.1) Although fire has been recognised as the prime disturbance agent in modifying the structure of the woody component of savannas (Bond 2005; Scholtz *et al.* 2014; Schertzer, Staver & Levin 2014), there is increasing evidence of the role that megaherbivores have in changing woody species composition and structure (Asner *et al.* 2015; Bakker *et al.* 2016; Malhi *et al.* 2016). Africa has a comparatively intact Pleistocene megafaunal assemblage (Owen-Smith 1987), where megaherbivore impacts are able to alter ecosystem structure and function (Bakker *et al.* 2016; Malhi *et al.* 2016). African bush elephants (*Loxodonta africana*, Blumenbach 1797) in particular, are major disturbance agents in savannas where they kill trees by uprooting, toppling, and debarking (Barnes 2001; Midgley, Balfour & Kerley 2005; Staver *et al.* 2009; Chafota & Owen-Smith 2009; Teren & Owen-Smith 2010; Owen-Smith & Chafota 2012). The range of spatial and temporal scales of megaherbivore impacts in savannas (Fig. 1.1) means that typical studies are conducted at scales too small to answer questions about elephant effects on biodiversity. Studies conducted at sufficiently large extents (Asner *et al.* 2009; Asner & Levick 2012) or long periods (Mosugelo *et al.* 2002) using remote sensing lack tree species identification and cannot answer questions of compositional changes over time. Conversely, species-scale studies are generally limited in spatial extent and without long-term information (Rutina & Moe 2014) or are based on exclosure experiments (Wigley *et al.* 2014).

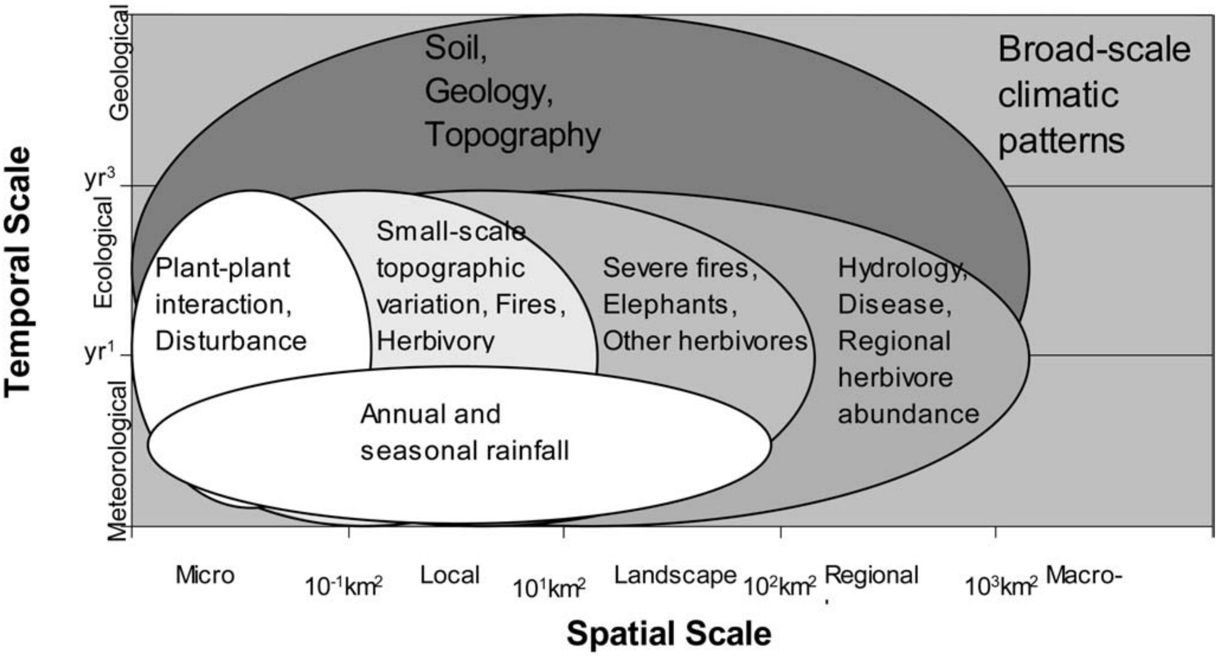

**Figure 1.1** The spatio-temporal framework for processes influencing tree density in savannas (Source: Gillson (2004))

### 1.2.2 Elephants as selective agents of composition, structure, and heterogeneity

Unlike most other disturbance agents, elephants are highly selective for plant species and sizes (Vesey-Fitzgerald 1973; Anderson & Walker 1974; Jachmann & Bell 1985; Kerley *et al.* 2008; Owen-Smith & Chafota 2012). Fire by comparison, destroys most vegetation irrespective of species (Bond 2005) but is structurally selective as fire cannot directly kill adult trees (Higgins, Bond &

Trollope 2000; Staver *et al.* 2009; Sankaran, Augustine & Ratnam 2013) and has its greatest effect on the mortality of savanna trees below the ‘escape height’ of 3m (Higgins, Bond & Trollope 2000).

However the synergistic effects of elephants and fire can cause the decline of large trees in savannas and a central topic in savanna ecology for decades has been the loss of large trees, without apparent replacement (Laws *et al.* 1975; Thomson 1975; Ben-Shahar 1998a; Holdo 2007; Valeix *et al.* 2011; Shannon *et al.* 2011; Vanak *et al.* 2012; Helm & Witkowski 2013; Levick, Baldeck & Asner 2014). Widespread declines in woody species density, following elephant population increases, have been documented right across Africa: Murchinson Falls National Park (NP), Uganda (Buechner & Dawkins 1961); Tsavo NP, Kenya (Leuthold 1977), (followed by a recovery when elephants declined from poaching (Leuthold 1996)); Chobe National Park (CNP), Botswana (Skarpe *et al.* 2004; Rutina & Moe 2014); Tarangire NP, Tanzania (van de Vijver, Foley & Olff 1999); and Kruger NP, South Africa (Eckhardt, Wilgen & Biggs 2000; Levick *et al.* 2009).

Elephants preferentially feed on species of *Acacia*[1] (*A. erioloba, A. nigrescens, A. tortilis, A. xanthophloea*), species from the *Combretum* and *Terminalia* genera ((Ben-Shahar 1993; Skarpe *et al.* 2004; Neke, Owen-Smith & Witkowski 2006; Owen-Smith & Chafota 2012); and *Colophospermum mopane* (Ben-Shahar 1993, 1996a; Styles & Skinner 2000; Hartnett *et al.* 2012).

Feeding may not necessarily lead to tree death, but if more than 50% of the stem circumference is stripped of bark or the main stem has been broken (uprooted) or snapped (pollarded), susceptible trees are likely to die (O’Connor, Goodman & Clegg 2007) . Some species, notably *C. mopane*, are resilient to impact and coppice readily following pollarding, into a hedged growth form with increased browse availability at a lower height, and of greater nutritional value, thereby benefitting subsequent browsing by elephants and other browsers (Smallie & O’Connor 2000; Styles & Skinner 2000; Kohi, Boer & Peel 2011).

Linked to the decline in large trees is the apparent lack of replacement by recruiting sizes. Savanna woodlands are likely a result of variable if not true episodic recruitment, where seedlings are only able to recruit into large size classes in exceptionally good rainfall periods and by escaping the browser trap (Midgley & Bond 2001; Moustakas *et al.* 2006; Helm 2011). Studies have commonly not addressed the potential replacement of tree mortality from seedlings and saplings and there is a gap in knowledge on regeneration of elephant impacted woodlands (Helm 2011; Shannon *et al.* 2011; Vanak *et al.* 2012; Levick & Asner 2013; Levick, Baldeck & Asner 2014).

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[1] I have persisted in using the *Acacia* genera name as it presents a cohesive group ecologically, and enables easier comparison with historical records of composition. All plant nomenclature follows Coates-Palgrave( 2002).

Elephants concentrate their feeding on intermediate size classes and largely plants taller than 1m (Croze 1974; Pellew 1983; Jachmann & Bell 1985; Gadd 2002; Boundja & Midgley 2009) except for some preferred species like *A. erioloba* (Croze 1974; Barnes 2001). Chafota (2007) and Stokke and du Toit (2000, 2014) found that elephants predominantly concentrated their feeding within a narrow height range of 1-3m in the Chobe riverfront, northern Botswana.

Because of elephant selectivity for species and size classes, in woodlands where elephant impact is intense we would expect to see selected species and size classes decline while neglected species become proportionally more abundant (Bakker *et al.* 2016). This could lead to increased compositional and structural diversity if impact does not spread to less preferred species and sizes.

Most of the elephant-vegetation studies in northern Botswana have focussed on the Chobe Riverine vegetation, with the conclusion of a recent large-scale study by a Norwegian group (Skarpe *et al.* 2004; Skarpe, du Toit & Moe 2014). The most interesting findings to come out of this long-term study was the documentation of an almost complete transformation from woodland to shrubland along the Chobe River where mixed woodland aerial cover decreased from 60% to 30% over 36 years (Mosugelo *et al.* 2002). Whilst elephant impact was the main cause of large tree decline (Rutina, Moe & Swenson 2005; Rutina & Moe 2014), impala (*Aepyceros melampus*) were implicated in preventing regeneration through seedling predation (Moe *et al.* 2009, 2014). Shrub encroachment is a global phenomenon and has been well documented across sub-Sahara and within non elephant impacted areas (O'Connor, Puttick & Hoffman 2014). Shrub encroachment is driven by both local drivers (such as overgrazing limiting fire disturbance) (Roques, O'Connor & Watkinson 2001) and global drivers of enriched atmospheric $CO_2$ (Wigley, Bond & Hoffman 2010; Buitenwerf, Swemmer & Peel 2011).

Savannas are inherently patchy systems, and where certain types of patches (for example, groves of an abundant tree species) decline, this can increase heterogeneity, and lead to greater diversity at the landscape scale. Chafota and Owen-Smith (2009) hypothesized that elephant disturbances to canopy trees that are spatially concentrated while sufficiently widely spaced in time could lead to a mosaic of patches in different phases of recovery, enhancing heterogeneity. If impact is pervasively spread, or frequent, a greater area of the landscape would be considered disturbed, and could promote homogeneity. Elephants are highly selective where they select for patches of vegetation based on characteristics such as high cover (Cushman, Chase & Griffin 2005; de Knegt *et al.* 2008; Harris *et al.* 2008). By contrast, the other main disturbance agents of fire and wind can kill vegetation in large swathes (Schertzer, Staver & Levin 2014) or on an individual tree basis (Ulanova 2000) respectively. There is a large gap in knowledge on the effect of elephants on spatial heterogeneity, with only one recent study addressing the spatial implications of tree disturbance in a savanna subject to mixed disturbance (Levick & Asner 2013). The authors found that treefall in selected river catchments was significantly spatially clustered in space (Levick & Asner 2013) but the question remains whether patches of dead trees spread in the landscape or increase and decline in a shifting mosaic (Turner 2010).

### 1.2.3 Elephants in northern Botswana

Northern Botswana has the largest contiguous African Elephant population in the world, with the most recent reliable estimates placing the Botswana population upwards of 134 000 (see Appendix 1.1 Fig. 1) (Blanc *et al.* 2007). For northern Botswana the most recent (2011) reliable population estimate for elephants was 120 000 animals with a regional density of 1.75 km$^2$ (Chase 2011). There is evidence that this population stabilised around 2004 (Chase 2011) with recent dispersal of elephants into neighbouring Angola, Namibia and Zambia (Chase & Griffin 2009; Cushman, Chase & Griffin 2010) although others have argued that the population is still increasing (Kalwij *et al.* 2010).

Elephants are water bound (Owen-Smith 1988) and congregate along the perennial Linyanti and Chobe Rivers in the north of the country in extreme densities in the dry season (April-October) (see Appendix 1.1 Fig. 1). During the wet season elephants disperse to take advantage of ephemeral pans in upland areas. Elephant density recorded during the dry season in 2010 for the Linyanti concession NG/15 (a survey area of 1232 km$^2$) was 2.35 elephants.km$^{-2}$ during the dry season of 2010 (Chase 2011). High elephant densities have also been recorded for a long time, as 12 elephants.km$^{-2}$ in 1000 km$^2$ of the Linyanti area was recorded in the dry season of a 1987 survey (Spinage 1990)). By comparison, around large perennial rivers within Kruger National Park (KNP), local dry-season elephant density reached around 2 elephants.km$^{-2}$ in 2007 (Smit & Ferreira 2010).

#### 1.2.3.1 Historical accounts of elephant and other impact in northern Botswana

There has been concern since the 1960s over elephant impact causing changes in the woody vegetation composition and structure along the Linyanti and Chobe Rivers (Child 1968). There are few records of historical vegetation composition along the Linyanti apart from a survey conducted in 1966-1967 by Child (1967) and another in 1973-74 by Sommerlatte (1976).

In the 1960's the Linyanti riparian woodland was described as acacia riparian forest composed of *Acacia erioloba* and *A. nigrescens* interspersed with open woodland and shrubland (Child, 1967). Sommerlatte (1976) identified two main vegetation types at a broader scale along the Linyanti, dominated by either *C. mopane* or *Acacia* spp (*A. nigrescens, A. erioloba, A. luederitzii*) depending on the soil type. *Acacia erioloba* dominated the acacia areas with a relative frequency of 54.2% in the tree layer (>3m in height) and 8.3% in the shrub layer (<3m in height). There was concern over the lack of acacia regeneration and Sommerlatte suggested episodic recruitment was the cause, and noted that the acacia stands along the Linyanti appeared old. There was concern over elephant impacts, particularly of the acacia which were declining rapidly with high mortality rates. In the Linyanti area 29% of trees were dead and 81.1% of total mortality was attributed to elephant impact. The Linyanti had a higher tree loss rate of 7.3% per annum compared to Chobe which had 4.8% (Sommerlatte 1976). Sommerlatte also noted high densities of shrub species along the Chobe, which had double the shrub density of the Linyanti area.

Before historical European demand for ivory (which started to have large effects from the 1860's), the earliest European explorers noted large numbers of elephant in Botswana (Oswell, 1900, In: Meredith, 2001). The very high historical concentrations of elephants are supported by a recent reconstruction of high megaherbivore biomass on the Linyanti-Chobe 1000 years ago (Hempson, Archibald & Bond 2015). By 1900 there were few remaining elephants in the northern areas of Botswana (Sommerlatte 1976; Campbell 1990; Vandewalle & Alexander 2014). With the creation of the Chobe Game Reserve in 1961 the elephant population recovered and sightings became more numerous along the Chobe River (Sommerlatte 1976).

Apart from the removal of elephants, the rinderpest pandemic struck northern Botswana in 1895/1896, decimating ungulate populations such as buffalo (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*) and bushbuck (*T. sylvaticus*) (Elephants were immune) (Caughley 1976; Walker In: Lewin 1986; Skarpe *et al.* 2014). With almost no browsers present, this probably resulted in an extreme recruitment event for trees. It has been hypothesised that the *Acacia* woodlands along the Chobe River are an artefact of the disturbances of the rinderpest epidemic and ivory hunting (Walker, 1986; Skarpe *et al.*, 2004). Additionally, evidence from archival records, field investigations and remote sensing suggests there has been increased aridity over the past few centuries in northern Botswana (Ringrose *et al.* 2007; Hamandawana, Chanda & Eckardt 2008) and the wetter past may have promoted recruitment of certain woodland species, especially deep rooted species like acacias.

By all accounts historic human settlement along the Linyanti appears to have been sparse, due to the presence of the tsetse fly (*Glossina* spp.) which spreads trypanosomiasis in humans and cattle

(Spinage 2012). According to Sommerlatte (1976) the elephant range (in northern Botswana on the 19th Century "was sparsely populated by the baSubiya, a riverine people who cultivated the flood plains of the Chobe River". At the beginning of the 20th century there was an influx of baTawana from Ngamiland and the Chobe River became the focal point of a flourishing cattle industry (Sommerlatte 1976) but this cattle industry did not spread to the Linyanti. By the late 1940s the cattle population was virtually reduced to nil by outbreaks of trypanosomiasis and streptothricosis (Sommerlatte 1976).

### 1.2.3.2 Previous studies of elephant impact in the Linyanti woodland

Since Sommerlatte's (1976) survey there have been four studies of elephant impact in the Linyanti region.

Coulson (1992) surveyed the densities of the most common trees and shrubs in the Linyanti riparian woodland in 1992, as well as elephant impact. He reiterated what previous surveys had found- that acacias were the most impacted species, owing to their stringy bark which was easily removed in long strips. He also hypothesised that as tree species continued to decline, the total abundance of shrubs would increase, and found that there was dense undergrowth of *Dichrostachys cinerea* along the Linyanti.

Ben-Shahar conducted broad-scale surveys in northern Botswana in 1991-1993 and in 1995, which included sites along the Linyanti, Chobe and Kwando Rivers (Fig. 1.4). He found elephant impact to be selective for tree species and size classes (Ben-Shahar 1993) and that there was high elephant impact in highly resilient *C. mopane* woodlands (Ben-Shahar 1998b). He also recorded low seedling recruitment rates (Ben-Shahar 1998b) and high mortality rates for *A. erioloba* woodlands, but which were attributed to natural attrition and not elephant impact (Ben-Shahar 1996a, 1998b).

Wackernagel (1993) followed up on Sommerlatte's 1973-1974 survey and conducted a survey in 1992-1992 of plant species, physiognomy, and level of elephant impact within regularly spaced transects across 35 km of riverfront. He found differential impact on tree species where elephant impact was concentrated on *A. erioloba* and *A. nigrescens* trees. He found that most elephant impact was old with only 1% of recorded impact from the previous dry season. He also fortuitously captured a windstorm which impacted a high proportion of trees, illustrating another substantial disturbance agent in the Linyanti woodland. There was a distinct lack of recruiting size classes but woodland regeneration potential from seedlings was not assessed. He found a week spatial gradient of impact across the riparian woodland, but could not detect patchy disturbance which appeared at a smaller scale than his transects. Chafota & Owen-Smith (2009) documented recent debarking of trees along the Linyanti related to low rainfall in August 1993.

Bell (2003) analysed loss rates from the canopy across the woodland, as well as spatial variability of losses, from aerial photographs taken in 1992 and again in 2001. Seventy-five percent of the canopy tree population was dead by 2001, with *A. erioloba*, *A. nigrescens* and *P. africanum* making up most of the canopy tree loss. Overall the loss rate was 1.85% of canopy trees per year. This rate was surprisingly not very high considering the rates of natural attrition are around 1% per year for *A. erioloba* (Moustakas *et al.* 2006), as well as Northern Hemisphere hemlock forest trees (Lorimer, Dahir & Nordheim 2001). Mortality was also heterogeneous across the landscape with cells of localised high mortality as large as 4 ha, and loss rates were also spatially variable.

Studies on the consequences of elephant impact on animals in the Linyanti have been limited to a study on birds (Herremans 1995) and dragonflies (Samways & Grant 2007). Both studies found similar results, that greater spatial heterogeneity of elephant impact supported different species assemblages and diversity was not negatively impacted by high elephant impact as long as these were interspersed with areas of lower impact.

These studies highlight the importance of spatial heterogeneity effects of elephant impact, in addition to the selectivity of impact on species and size classes.

### 1.2.4 Biodiversity

Biodiversity encompasses different levels of landscape patterns, habitat heterogeneity, species diversity and genetic diversity; with each level portrayed at three different aspects: that of structural, compositional and functional diversity as described by Figure 1.2 (Noss 1990). Defining biodiversity according to these aspects and levels reflects a shift from a paradigm of ‘the balance of nature’ towards a conceptual shift over the past 3 decades acknowledging the importance of flux and change within ecosystems over time and space (McNaughton, Ruess & Seagle 1988; Wu & Loucks 1995; Gillson, Sheridan & Brockington 2003). This paradigm shift has meant that how we measure biodiversity change has also evolved. Ecologists have moved away from traditional methods of measuring the number and type of organisms in species richness indices which concentrate on competitive or facilitative interactions (see review by Chiarucci, Bacaro & Scheiner (2011)). For example, early diversity-disturbance studies were focussed on what levels of disturbance lead to the greatest species richness by allowing both pioneering and less common species to co-exist, known as the Intermediate Disturbance Hypothesis (IDH) (Fox & Connell

1979). There is actually little empirical evidence to support the IDH in fluctuating environments (Fox 2013). Instead, ecologists are now measuring how ecosystem properties and processes change over time and space (Reiss *et al.* 2009; Loreau 2010). At the landscape scale, this can involve the Hierarchical Patch Dynamics Paradigm (HPDP) which explores ecosystem dynamics as a composite of patch changes in time and space incorporating a pattern-process perspective (Wu & Loucks 1995.

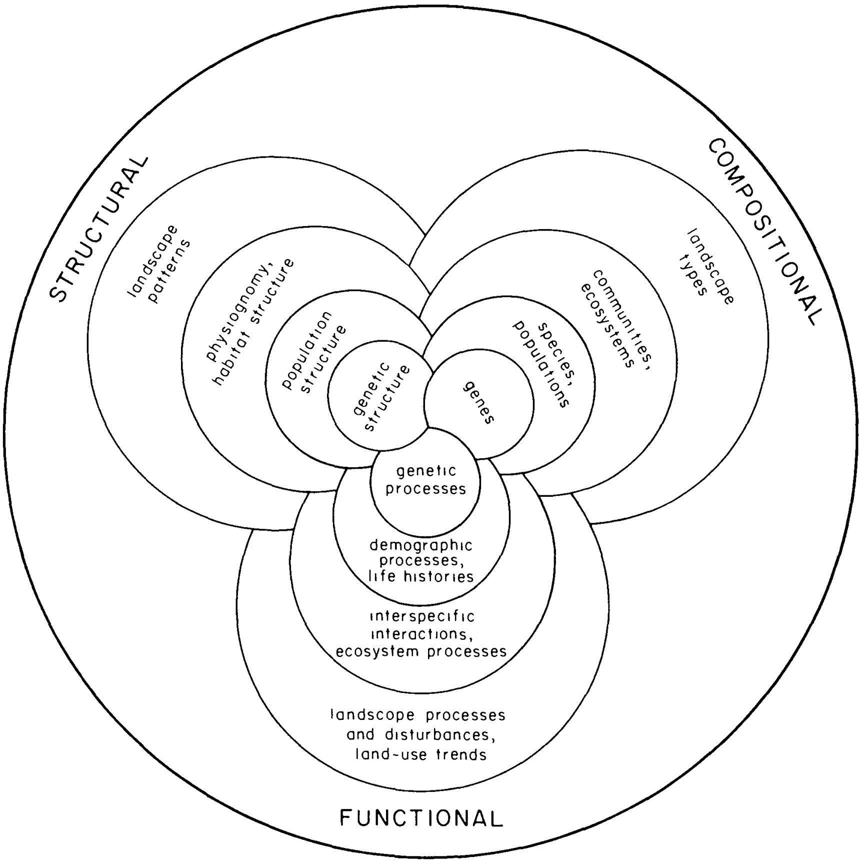


**Figure 1.2** The three main aspects of biodiversity: compositional, structural and functional, across different scales (Source: Noss (1990))

My study will measure the changes in structural, compositional, and by inference, functional diversity at three different scales as described by Noss (1990) (Fig 1.2):

1) At the species-population level I will measure the effects of elephant impact on individual species (compositional aspect) and the changes to population structure (structural aspect) and discuss the demographic processes affected by elephant impact such as regeneration and recruitment into the canopy.

2) At the community-ecosystem scale I will measure the change in composition of the canopy tree layer (compositional aspect) and also the potential shift in structure between woodland and shrubland (structural aspect) caused by elephant effects on ecosystem processes such as recruitment of resilient species (functional aspect)

3) At the landscape scale I will measure the spatial pattern (structural aspect) of disturbance (functional aspect) across the woodland using a landscape ecology approach. I will not be measuring the compositional pattern of landscape types at a larger scale.

## 1.3 Research aim, objectives and outline of the thesis

The aim of my study was to establish how the riparian woodland had been changed by elephant and other impacts over 18 years and the consequences for biodiversity.

There were four objectives:

1) To establish whether canopy tree disturbance is heterogeneous with respect to structure and composition
2) To establish whether shrub expansion is heterogeneous with respect to structure and composition
3) To establish whether tree regeneration is heterogeneous with respect to structure and composition
4) To evaluate the consequences of elephant impacts on canopy tree disturbance, shrub expansion and tree regeneration for structural and compositional diversity of the woodland

The structure of the thesis is such that each chapter is based on an aspect of biodiversity as defined by Noss (1990). Each content chapter has also been written up in a manuscript format for publication in a scientific journal. Thus there will be repetition in Chapters Two, Three, and Four of descriptions of the study site, methods, as well as motivation between chapters.

Figure 1.3 gives an overview of the thesis layout, and the main research questions related to aspects of biodiversity which elephants affect.

- *Chapter one* lays the foundation of the study and gives a brief rationale of the study, background literature, the aim and objectives, as well as a more detailed description of the study site not given in the manuscript-formatted chapters.

- *Chapter two* is related to my first objective and to the spatial patchiness aspect of biodiversity. It sets out to examine the spatial distribution, rates of increase, and patchiness of dead trees in the landscape.
- In *Chapter three,* I examine the causes of the high densities of dead trees by examining the incidence of severe elephant impact. I also address the compositional aspect of biodiversity, and investigate the compositional changes of living canopy trees that have taken place over 17 years. This chapter also addresses tree regeneration and the potential of compositional recovery from seedlings and saplings, fulfilling Objective three.
- *Chapter four* is related to Objective two and examines the structural diversity changes caused by shrub encroachment (as well as tall tree decline) in the woodland. The potential drivers of shrub encroachment in the context of the riparian woodland and elephant impact are evaluated.
- *Chapter five* assimilates the empirical findings of Chapters two, three, and four for biodiversity, and highlights some key functional diversity implications pertinent to riparian woodlands. It also attempts to synthesise the contribution of this study in advancing our current knowledge of how elephants can impact biodiversity.

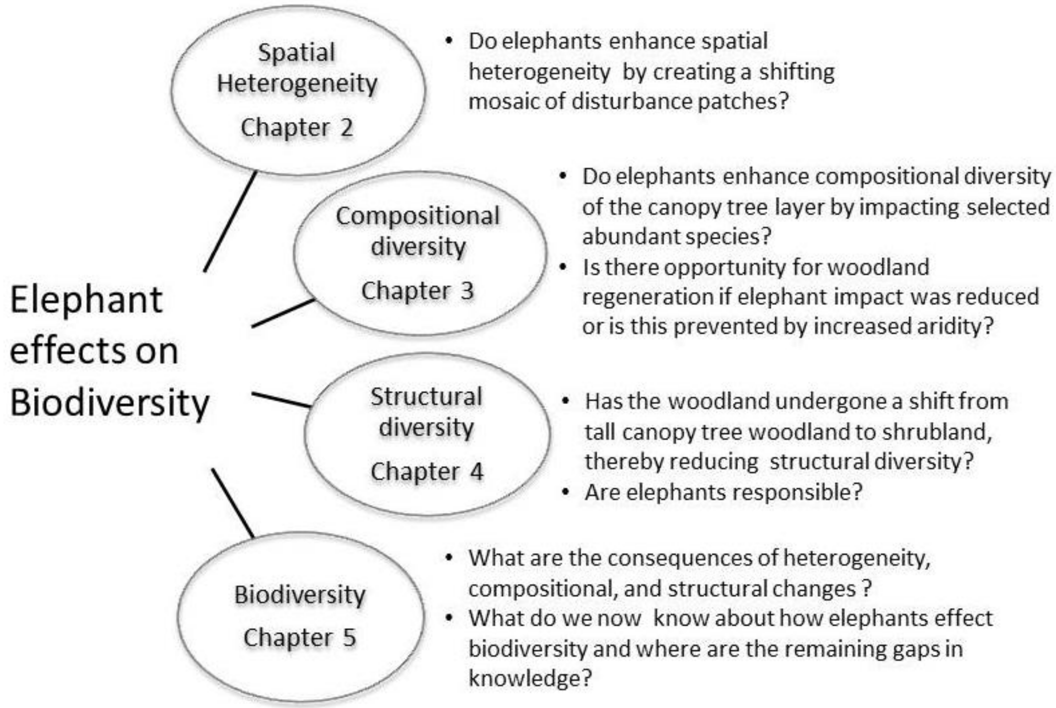


**Figure 1.3** Structure of thesis and main research questions related to three aspects of biodiversity as defined by Noss (1990) forming Chapters 2-4 with a synthesis in Chapter 5

For brevity I have not duplicated study area maps across the chapters, and all maps appear here in Chapter one. Initial observations and hypotheses were published in an article in the peer-reviewed IUCN Species Survival Commission (SSC) Journal *Pachyderm* (47:18- 25) and presented here as Appendix 1.1.

## 1.4 Study area

The Linyanti River forms the unfenced international border between northern Botswana and Namibia's Zambezi region (previously Caprivi Strip), and has its sources in the Angolan highlands as the Kwando river, flowing SE before hitting a fault line and abruptly turning NE as the Linyanti River, before becoming the Chobe and Zambezi River downstream to the east (Fig. 1.4). Except for the narrow western corner of CNP, most of the Linyanti riparian region lies in a photographic safari concession (NG/15, Fig 1.4.) currently leased by Okavango Wilderness Safaris (www.wilderness-safaris.com). On the Namibian side lie the Linyanti swamps of the Nkasa Rupara National Park (previously Mamili NP) within Namibia's Zambezi Region (previously Caprivi Strip).

The riparian woodland on the Botswanan side is a narrow (~100-200m wide) strip of mixed woodland occurring on a terrace above the river with no deep alluvium, backing on to vast mopane (*Colophospermum mopane)* woodlands. Mopane is palatable to elephants and resilient to their impacts (Ben-Shahar 1993; Styles & Skinner 2000; Hartnett *et al.* 2012). Although there is a paucity of data on local wildlife density, impala have been reported at lower densities in the Linyanti woodland compared to the Chobe riparian area (Chase 2011), potentially limiting their seedling mortality as shown for the Chobe area (Moe *et al.* 2009).

Fire is a rare event in the riparian zone, with zero extensive fires and only six documented localised (<1km$^2$) single fire events between 2001 and 2016 across the 2000ha study region (NASA FIRMS 2016), none of which were in areas covered by sampling transects.

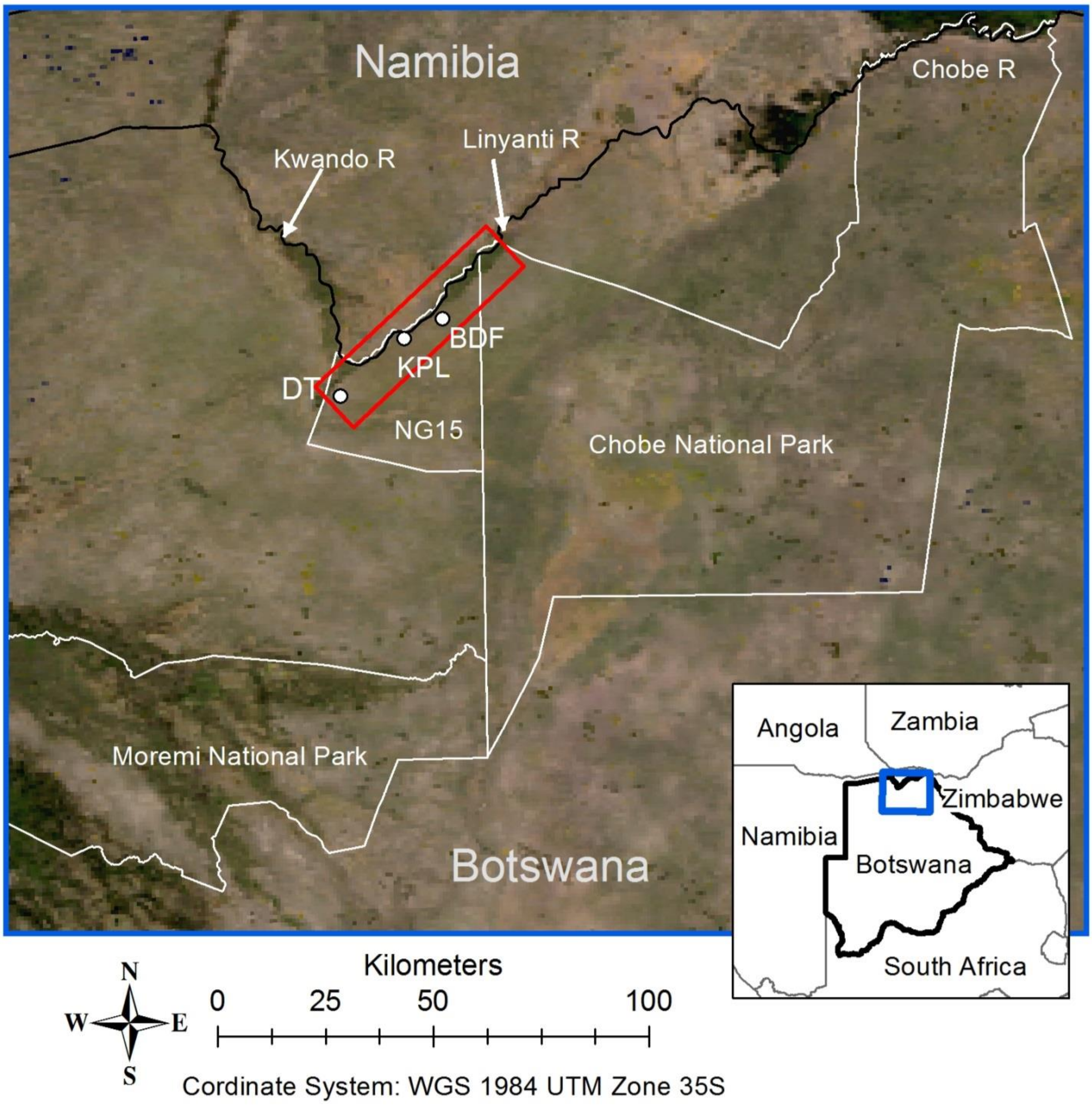


**Figure 1.4** Map of Northern Botswana (extent shown in blue on the country inset) showing the study region outlined in red within the concession area NG/15 and the western corner of Chobe National Park. Country outlines in black and protected areas outlined in white. The locations of various camps are marked: DT Duma Tau; KPL King's Pool, BDF Botswana Defence Force. Spatial data from the United Nations Environment Programme World Database on Protected Areas.

The hottest month October, has a mean daily maximum temperature of 39°C and mean daily minimum of 14°C, with the coldest, July experiencing a mean maximum of 30°C and minimum of 4°C (Aarrestad *et al.* 2011). Rainfall takes place in the summer months between November and April with a mean annual rainfall of 557mm (calculated for 92 years to 2014) at the nearest weather station at Kasane on the Chobe River, 140km away (NOAA 2014) (Fig. 1.5).The studies of Wackernagel (1993) (fieldwork conducted in 1991/1992) and Bell (2003) (fieldwork conducted in 2002) fell in particularly dry periods, whereas the 2007/2008 fieldwork was in the middle of the wettest cycle in 92 years (Fig. 1.5). The implications of this for elephants and trees was that elephants were compressed into the area for a longer dry season and would have exerted high impacts for the earlier surveys. In comparison, elephants would have dispersed towards other areas such as the newly re-flowing Savuti Channel in the last survey and seedling establishment opportunity and survival would have been higher. I chose not to survey age of impact as was previously done in the 1992 survey, and instead measured cumulative impact severity.

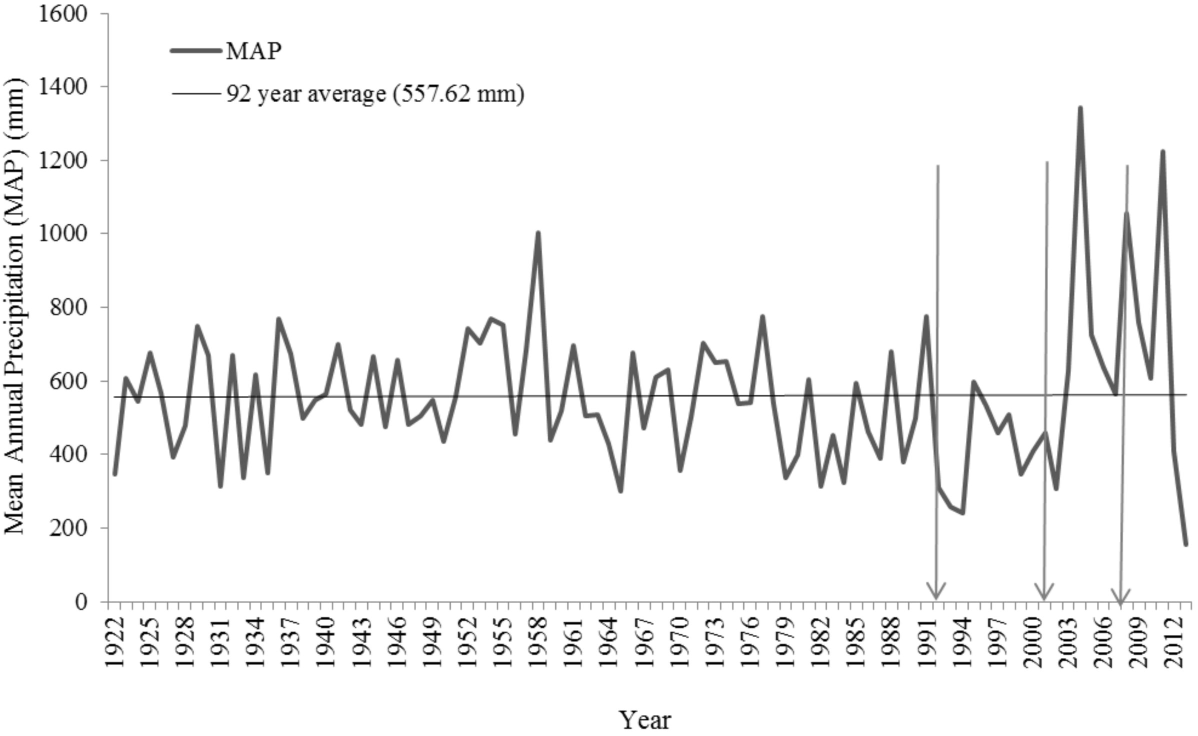


**Figure 1.5** Mean Annual Precipitation recorded for the Kasane weather station over 92 years from 1922 to 2014 (source: NOAA (2014)) Arrows mark survey years of 1992, 2001 and 2008.

## 1.5 Approach to the study

This study is based on the long-term data collected for two unpublished MSc theses: Wackernagel (1993) and Bell (2003). High resolution (1:10 000) aerial photographs were taken in 1992 and 2001 as a baseline for future studies and covered a 40km stretch of woodland along the river. Chafota (2007) concluded a detailed study on the selective utilisation of woody plant species and height classes by elephants adjoining the Chobe River in northern Botswana. His data on acceptance indices of woody species aided in clustering species according to their use by elephants.

Gaining an understanding of spatio-temporal dynamics of disturbance requires spatially explicit data at a landscape scale. I used the earlier aerial photography from 1992 and 2001 and a later set of photography and LiDAR data from 2010.LiDAR provides three-dimensional (3D) images from multiple-return laser pulses where the first return corresponds with the top of canopy and the last return of the ground (for a full description see Lefsky *et al.* 2002).

### 1.5.1 Aerial photography processing and analysis

The 1992 and 2001 colour photography was surveyed by AOC geomatics, and in 2007 they scanned the original negatives at 25 microns to produce digital stereo-images of 25cm pixel size. I used the Leica Photogrammetry Suite (LPS) 9.2 within the ERDAS Imagine® software application to geo-reference and orthorectify the 2001 aerial photos from ground control points (GCPs). The GCPs were collected in the field in January 2007 with a Trimble differential GPS with submetre accuracy. I then georeferenced the 1992 aerial photos to the 2001 orthophotos and mosaicked both time sets. I also extracted Digital Elevation Models (DEMs) from the orthophotos for each year.

I manually marked every dead tree in the 1992 and 2001 aerial photo mosaics to determine areas of high and low density of dead trees. The 2007/2008 transects were stratified to reflect areas of high density of dead trees within a riparian area (Appendix Fig. 1.2.1)

The 2010 aerial photographs and LiDAR data was collected and processed by Southern Mapping Company. The photos were rectified using an automated procedure, and the LiDAR points were processed using Precise Point Positioning (PPP) and a Digital Elevation Model (DEM) at one metre resolution was created from last-return points (Lefsky *et al.* 2002). From the DEM I extracted a Relative Elevation Model (REM) relative to the main river channel (min -3m, max 8m).

### 1.5.2 Field data collection

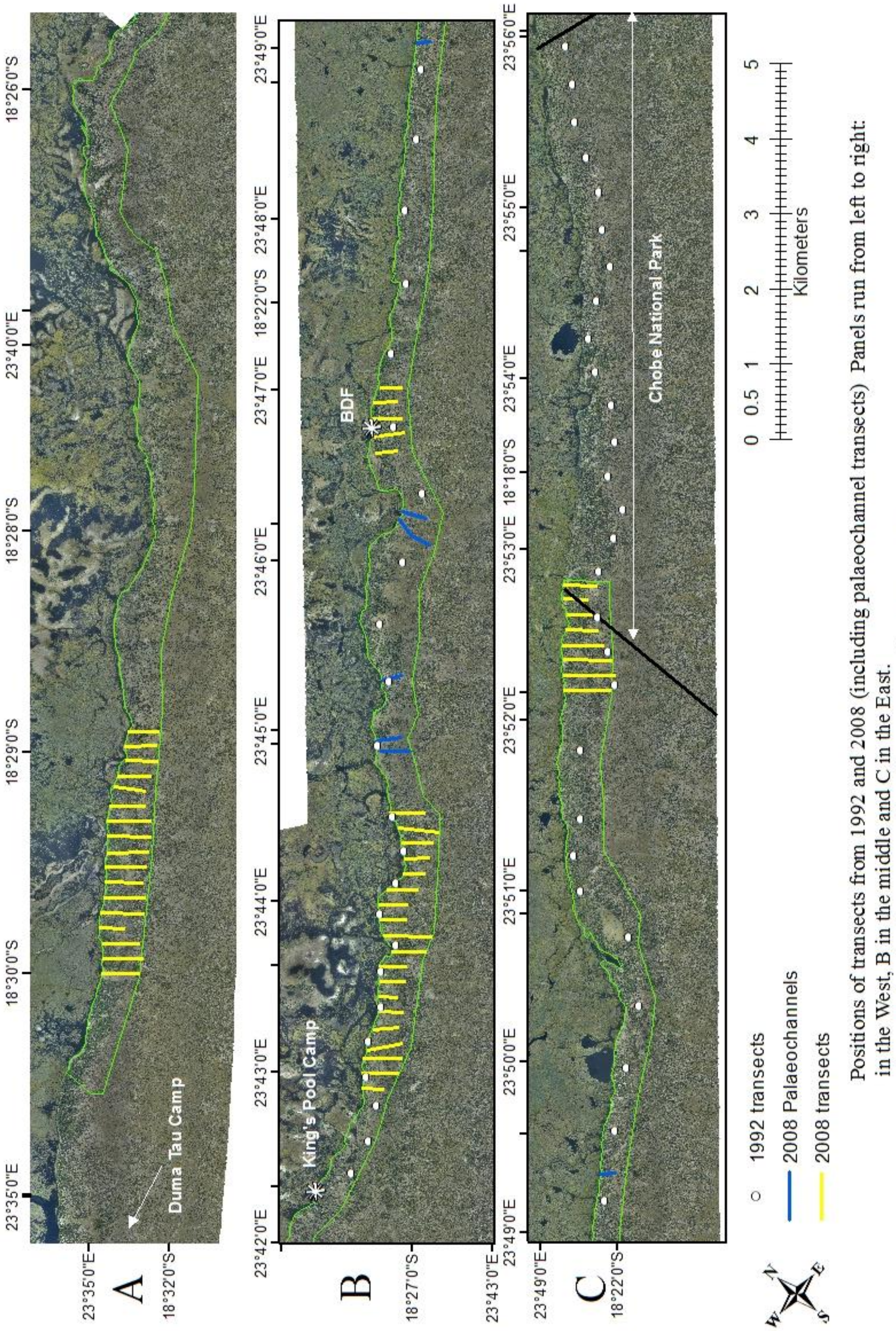
Vegetation field data was collected in transects traversing the riparian woodland. Wackernagel's study was based on field data collected in October 1991- January 1992 (for brevity referred to as the 1992 survey) from regular transects across the riparian zone from the eastern border of the Chobe National Park (CNP) Linyanti section, westwards towards King's Pool Camp (KPL). Transects were spaced every 1 km except for the two end sections where transects were 500m apart to sample high disturbance areas (Fig 1.6). 1992 transect positions were recorded as distances starting from the CNP cutline along the main road in set distances. I located the approximate positions of the transects on the 1992 aerial photograph by tracing the outline of the main road as a polyline the 1992 aerial photograph in ArcMap 9.2 and placing points according to the interval specified by Wackernagel (1993).

I followed up on this study in the wet seasons of Dec 2007/Jan 2008 and Nov/Dec 2008 (referred to as the 2008 survey in the text). I stratified the 2008 transects based on tree mortality (three regions of high mortality, one of low,) which I extracted from digital colour aerial photographs (1:10000) from 1992 and 2001. Three areas of high tree mortality were found (Appendix 1.3.1), two of which corresponded to the high disturbance areas intensively sampled by Wackernagel (1993) (near CNP and KPL). The 2007/2008 transects were grouped in these two areas, plus the additional area to the east of DT not covered in the 1992 survey (Fig. 1.6). An additional group of transects was placed around BDF (Fig. 1.6) representative of a lower density of dead trees. Palaeochannels were also visible from the aerial photographs and we placed transects on these to assess whether the lower relative elevation would have any difference to seedling abundance (Fig. 1.6). From the high-resolution 2010 REM I discovered that a major palaeochannel also ran through the BDF transects (Appendix 1.3.1).

The 2008 transects were placed every 200m apart. Transects (both 1992 and 2008) ran perpendicular to the river from river edge, across the riparian belt, to the mopane zone indicated by the increased prevalence of *C. mopane.* In 1992, transects were not of fixed-width but used distance-based sampling to estimate nearest neighbour density using the ‘T-Square Method’ (Byth 1982). Because of an overestimation bias in this distance-based density estimation method (discussed in Appendix 4.1), in 2008 we opted to survey fixed-width belt transects. The 2008 belt transects were 10m wide for riparian canopy tree species, excluding the most common tree *C. mopane*, which was sampled in a 5m width, as were all shrub species.

For both 1992 and 2008 surveys all living and dead plants above 0.5m were identified to species level (unidentified species were recorded as such and identified to genus level where possible). The height and basal stem diameters were recorded in classes: Four height classes (0.5-1m, 1-2.5m, 2-5-10m, >10m) and size basal stem diameter classes (<1.9cm; 2-3.9cm; 4-9.9cm; 10-19.9cm; 20-50cm; >50cm) were used. All shrub species as well as the common *C. mopane* were only surveyed by height. Elephant impact was grouped by high and low impact categories. A high elephant impact category was trees which had over 50% bark circumference removed and/or with the main stem broken (or pushed over) or over half of the side stems broken (heavy pollarding). Trees that had recovered from old elephant impact, either by resprouting a main stem or bark recovery were noted separately.

Seedlings (plants less than 0.5m in height) were not surveyed in 1992. In 2008 I surveyed seedlings using square metre quadrats placed at a sampling point every ten metres along each transect. I also included the 4 neighbouring quadrats to each side of the original sample point to increase the sample size to a total of 5 square metres per every sampling point. We estimated aerial cover percentage (to the nearest 5%) of seedlings for each square metre and per each shrub and tree species. The aerial cover of each seedling species was then totalled per transect ($m^2$), as well as the proportion of total area sampled covered by seedlings.



Positions of transects from 1992 and 2008 (including palaeochannel transects) Panels run from left to right: in the West, B in the middle and C in the East.
The 2000 ha riparian zone outlined in green. Scale = 1: 60 000

**Figure 1.6** Transect positions from 1992 and 2008. The 2008 transects around Chobe National Park and King's Pool Camp are in regions of intensively sampled 1992 transects. An extra set of transects was sampled to the east of Duma Tau corresponding with a high density of dead trees here (Appendix 1.2.1).

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## 1.7 Appendices

**1.1 Published paper in *Pachyderm* 47:18-25**

**1.2 Selected photographs of the Linyanti riparian woodland**

**1.3 Key Maps**

**Appendix 1.1 Published paper in *Pachyderm* 47:18-25**

## RESEARCH

# Elephants and riparian woodland changes in the Linyanti region, northern Botswana

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## Abstract

The decline of woodlands as a result of elephant disturbance is of much concern for biodiversity conservation in Africa. Northern Botswana supports the largest elephant (*Loxodonta africana*) population and highest local density levels near rivers during the dry season. We describe changes in structure and composition that have occurred in the riparian woodland flanking the Linyanti River, from unpublished reports, theses and our recent observations. There has been a progressive reduction in representation of the two most common *Acacia* spp. as a result of mortality to canopy trees, largely from felling and bark removal by elephants. However, both arboreal species show little regeneration, apart from localized seedlings. Other canopy tree species are less susceptible to damage, but also show a lack of saplings. A dense shrub understorey has developed since 1992, dominated by *Combretum mossambicense*, a species not utilized by elephants although browsed by ruminants. The patchy woodland decline and advancing shrubbery, plus contrasting recruitment patterns of canopy trees versus shrubs, suggest that factors besides elephants—such as climate—might also be involved in woodland change. The study we have initiated will interpret the potential consequences of these changes for woodland biodiversity, building on the spatio-temporal record provided by aerial photography.

**Keywords**
Botswana, Linyanti, elephant impacts, *Loxodonta africana*; plant biodiversity; riparian vegetation, regeneration

## Résumé

Le déclin de la savane boisée par suite aux perturbations de l'éléphant est sujet de beaucoup de soucis en ce qui concerne la conservation de la biodiversité en Afrique. Le Botswana du nord abrite la plus grande population d'éléphants (*Loxodonta africana*) et les plus hauts niveaux de densité locale près des rivières pendant la saison sèche. Nous décrivons les changements dans la structure et la composition qui se sont produits dans la savane boisée riveraine au bord du fleuve Linyanti, d'après les rapports inédits, les thèses et nos observations récentes. L'on a constaté une réduction progressive dans la représentation des deux spp *Acacia* les plus communs suite à la mortalité des arbres à voûte, due en grande partie au terrassement et à l'enlèvement des écorces par les éléphants. Cependant, les deux espèces arboricoles montrent peu de régénération, à part des semis localisés. D'autre espèces d'arbres à voûte sont moins susceptibles au dégât, mais aussi montrent un manque de jeunes arbres. Un sous-étage d'arbrisseaux denses s'est développé depuis 1992, dominé par

*Combretum mossambicense*, une espèce non utilisée par les éléphants bien que broutée par les ruminants. Le déclin de la savane boisée inégale et les arbrisseaux qui avancent, en plus des configurations contrastées de recrutement d'arbres à voûte contre des arbrisseaux, suggèrent que d'autres facteurs à part les éléphants - tels que le climat - pourraient aussi être impliqués dans le changement de la savane boisée. L'étude que nous avons commencée interprétera les conséquences potentielles de ces changements pour la biodiversité de la savane boisée, en se basant sur les données spatio-temporelles fournies par la photographie aérienne.

## Introduction

The consequences of high elephant abundance for vegetation structure and composition, and hence overall biodiversity, are of major concern in conservation (Cumming et al. 1997; Western and Maitumo, 2004; Kerley and Landman 2006; Owen-Smith et al. 2006). The transformation of the riparian woodland adjoining the Chobe River in northern Botswana to a shrub-land punctuated by the trunks of dead trees has been presented as an example of the kind of situation to be avoided elsewhere. However, following a comprehensive assessment, a team comprising both Norwegian and local researchers could not find any adverse consequences of the drastic vegetation changes for animal abundance or diversity, apart from a decline of bushbuck (Addy 1993; Skarpe et al. 2004).

Extremely high elephant concentrations have also developed further upstream along the Linyanti River. Local density estimates during the dry season have increased from 2.8 elephants per km$^2$ in 1974 (Sommerlatte 1976) to 12 per km$^2$ in 1987 (Spinage 1990), and while the regional density recently is 4.2 per km (DWNP 2006), it is estimated that local densities in the riparian fringe reach over 20 elephants per km$^2$ (pers. obs.). However, once the rains arrive these animals disperse widely through northern Botswana and northwards via the Caprivi Strip of Namibia into Angola (Chase and Griffin 2003). The total elephant population currently exceeds 130,000 within an overall range covering 125,000 km$^2$ (Blanc et al. 2007). A process of woodland conversion is in progress within the Linyanti river-front, offering the opportunity to understand the mechanisms and project the likely end state and consequences for regional biodiversity conservation. Several surveys of the vegetation there have been undertaken, but the results are contained in unpublished reports or theses and thus have not been widely disseminated. We have initiated a detailed investigation of the vegetation changes that have been and are occurring with regard to assessing the implications for plant biodiversity. Hence this article is a summary of what has been documented by past studies and what we observed during our visit to the region at the end of 2006.

## Study area

The Kwando River arises in the Angola highlands and flows south-east along the border between northern Botswana and the Caprivi Strip of Namibia to the east of the Okavango River. When it reaches a fault line the river takes a right angle bend and flows east-north-east along the fault line as the Linyanti River, which forms the border between Botswana and Namibia (Fig. 1). This river then enters a swamp region and emerges as the Chobe River. Apart from a narrow area, most of the Linyanti region lies to the west of Chobe National Park, and is managed as a concession (NG 15), previously for hunting and currently for photographic safaris.

Because the terrace follows the fault line south of the river, the riparian woodland on the Botswana side, which is the focus of our study, occupies a fairly narrow region of only a few hundred metres wide. The prevalent tree species include *Acacia nigrescens, A. erioloba, Berchemia discolor, Diospyros mespiliformis, Garcinia livingstonei, Ficus* spp., *Combretum imberbe*, with the predominant shrubs being *Croton megalobotrys, Combretum mossambicense, Philenoptera nelsii* and *Dichrostachys cinerea*. Further south *Colophospermum mopane* woodlands and shrub-lands become predominant on the relatively thin layer of Kalahari sand overlying basalt. Fires have evidently penetrated the riparian zone in the past, from the presence of burnt stumps, but apparently not over the past decade or longer due to the lack of standing grass by the later part of the dry season.

## Past studies

The earliest survey of the area by Sommerlatte (1976) during 1973-74 was focused on the 8.5 km region of the Linyanti river-front within Chobe National Park. Overall the density of trees taller than 3 m was 105 per ha, of which *Acacia* spp. constituted 38%. However,

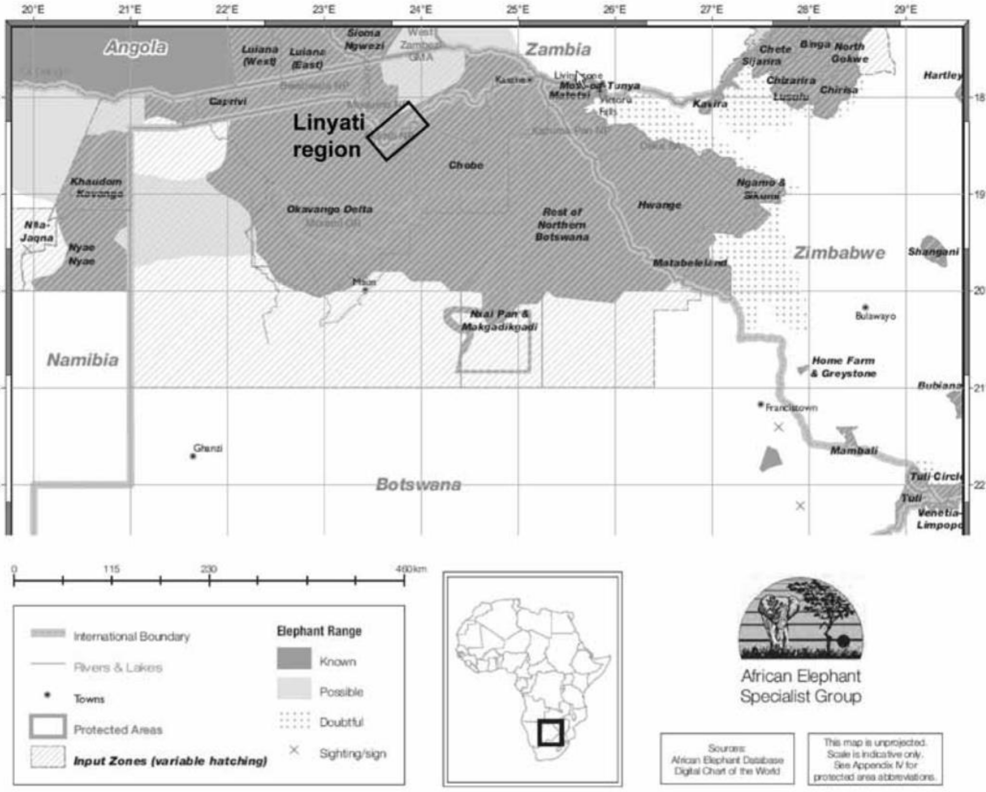

Figure 1. Map of elephant range in northern Botswana showing the Linyanti region (box) on the Botswana– Namibia border. Source: Blanc et al. 2007.

*Acacia* spp. amounted to only 16.5% of the regeneration layer, with *A. erioloba* poorly represented. From the proportion of dead trees, Sommerlatte estimated an annual loss of 7% of the trees, mostly from the regeneration layer, mainly as a result of uprooting or debarking by elephants. He expressed concern that the recruitment was inadequate to maintain the *Acacia* woodland component. Both *Combretum elaeagnoides* and *Baphia massaiensis* were recorded in the shrub layer.

Wackernagel (1992) conducted a detailed survey of the state of the riparian woodland along transects perpendicular to the river spaced 0.5–1 km apart spanning a 35 km section of the Linyanti riparian woodland. He estimated the total density of trees greater than 20 cm in stem diameter to be around 200 per ha, and summed the density of all woody plants taller than 0.5 m at about 1500 per ha. However, 60% of the *A. erioloba* trees >50 cm in stem diameter and half of the *A. nigrescens* in this size class were dead, while in the 20-50 cm diameter class, fewer than 10% of plants of these two species survived. The representation of *A. erioloba* in the canopy tree layer had declined from 54%, as recorded by Sommerlatte (1976), to 26%. Other tree species showed far lower mortality losses than did these two *Acacia* species. In the shrub or sapling size class, *D. cinerea* showed a mortality loss of around 50%, but very few *A. erioloba* or *A. nigrescens* plants occurred in diameter classes <20 cm. All canopy tree species were poorly represented in the scrub layer <4 cm in stem diameter, with the shrubs *C. mossambicense, D. cinerea* and *C. megalobotrys* predominant. All three of these species were more abundant than was evident at the time of Sommerlatte's survey.

Further, Wackernagel noted that not all tree deaths could be ascribed to elephant damage through felling or bark removal, documenting wind

Figure 2. Remains of a former grove of *Acacia erioloba* trees.

throw as an additional contributing factor. He also found that the strong visually evident patchiness in elephant damage occurred at a smaller scale than the 1 km gap between his transects. Apart from this, only a weak spatial pattern was evident with lower levels of tree damage around the Botswana Defence Force camp and in the region of the Linyanti Explorations Camp. During May 1992 aerial photographic documentation of the state of the riparian woodland was undertaken, obtaining a true-colour mosaic covering the complete 40 km extent of the river front at a scale of 1:10,000.

A further survey by Coulson (1992) in March 1992 encompassed a section of the Kwando River as well, but included only trees (standing or fallen dead as well as alive) greater than 30 cm in stem diameter at breast height. Of 2995 trees recorded, 42.5% were dead. Individual tree species showing high mortality included *Acacia erioloba* (two-thirds dead, most of which appeared recently killed) and *A. nigrescens* (almost 50% dead, mostly recently killed), largely through bark removal. Much lower mortality was recorded for *Philenoptera capassa* (14% dead), *Combretum imberbe* (12% dead) and *C. hereroense* (3% dead). Spatially a higher proportion of trees were dead along the Linyanti River than elsewhere. However, only in a small proportion of cases could tree mortality be ascribed definitely to elephant damage. Elephants were considered to have killed 19% of *A. erioloba* (with 0.7% killed by fire) and 16% of *A. nigrescens* trees, with undetermined or other agents, such as wind, responsible for the remainder. A surprisingly high level of damage apparently caused by wind was noted.

In June 2001 repeat aerial photography was undertaken covering the same area as Wackernagel's (1993) study. Bell (2003) analysed the changes that had taken place in the canopy tree layer (>5 m height), finding an overall net loss of 10.3%, equivalent to an annual rate of 2%. Mortality appeared to be concentrated in the height range 5–13 m, with *A. erioloba* and *A. nigrescens* showing the greatest loss. However, tree felling was patchily concentrated within cells less than 200 m in diameter. The photographs also revealed the widespread prevalence of a dense shrub layer that had not been clearly evident in the 1992 photographs.

## Recent observations

During a survey between December 2006 and February 2007 we counted 400 living and dead trees and shrubs in a series of 10–m wide belt transects (unpublished results). From this preliminary investigation and observations throughout the woodland, we noted that only around a third of the large trees of *A. erioloba* and *A. nigrescens* remained alive. The remainder were present as either standing trunks killed by bark removal or felled logs (Fig. 2).

Large specimens of other canopy trees such as *Diospyros mespiliformis* and *Combretum imberbe* showed relatively little damage, because their bark is resistant to removal. Few saplings below 3 m in height were observed, and those present showed much damage through branch or main stem breakage. Some small regenerating plants below 0.5 m in height of *D. mespiliformis* were found, especially on termite mounds, and we observed localized concentrations of small *A. nigrescens* and *C. imberbe* plants. Among sub-canopy trees, almost all *Combretum hereroense* plants had been reducing to coppiced stumps (Fig. 3), compared with 65% of plants showing heavy damage in 1992, with a similar pattern shown by *Peltophorum africanum*. Localized stands of *Terminalia sericea* also existed mostly in the form of resprouting stems. *Croton megalobotrys* showed much less damage and appeared to have increased in abundance.

A dense understorey of *Combretum mossambicense* shrubs had expanded over much of the study area from the east (Fig. 4), while clumps of *Diospyros lycioides* also seemed to be expanding. *Philenoptera nelsii* appeared to have maintained its local prevalence, while *Dichrostachys cinerea* had been reduced mostly to small plants, including seedlings, as well as root sprouts. These shrubs showed an abundance of small size classes from seedlings upwards. The *Colophospermum mopane* trees growing along the margin of the riparian fringe also showed an abundance of all size classes, despite evidence of much damage to stems as well as bark removal and felling by elephants.


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Figure 3. Shoot regeneration on *Combretum hereroense* stump.

## Discussion

Our recent observations coupled with earlier surveys indicate a progressive reduction of both *Acacia* spp. formerly prevalent in the riparian woodland. Nevertheless, a number of mature trees still remained standing, particularly of *A. nigrescens,* too large to be felled and resistant to further bark removal because of the way their bark has healed over past damage. In contrast, *A. erioloba* seemed less able to regrow bark following its removal by elephants. The standing mature trees continue to produce seeds. However, the lack of any plants in recruitment stages, apart from local patches of *A. nigrescens* seedlings, portends a continuing decline by these tree populations. A similar lack of small specimens of these species was also recorded by Wackernagel (1992), suggesting that this pattern has persisted for 15 years. Since elephants generally only seek out plants taller than 0.5 m (Jachmann and Bell 1985; Mwalyosi 1990), the absence of regeneration suggests the involvement of some other factor, perhaps a persistent desiccation of soil water hindering seedling establishment. It cannot be ascribed to browsing pressure by impala, identified as a major factor along the Chobe River (Skarpe et al. 2004), because impala numbers were low in 1991 and are still only moderate in the Linyanti riparian zone


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Figure 4. Dense stand of *Combretum mossambicense* plus *Philenoptera nelsii* shrubbery.

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Figure 5. Elephant bull feeding amid tall trees of mainly *Diospyros mespilliformis* in the section of the Linyanti riparian woodland near a Defence Force camp.

(2006 regional density: 0.3 impala/km compared with 0.9 impala/km along the Chobe river-front (DWNP 2006)). It seems that most of the decline in the canopy trees between 1992 and 2001 recorded by Bell (2003) was of these two *Acacia* spp. The continuing decline during this period was slow because most trees in the vulnerable size classes had been felled or debarked by elephants prior to 1992. In contrast to the Chobe river-front region, *A. tortilis* is mostly absent from the Linyanti riparian area, and *A. luederitzii* localized in its presence.

Mature *Diospyros mespiliformis* and *Combretum imberbe* are too large to be felled by elephants and have bark that is more resistant to stripping by elephants, and are therefore not directly threatened. A tall shady woodland where these two species predominated remained in the vicinity of the Botswana Defence Force camp, along a dry palaeo-channel (Fig. 5). However, apart from localized patches of small *C. imberbe* seedlings, both species showed very little recruitment. Furthermore, damage by elephants to regenerating stages could curtail plant growth towards canopy height. A similar lack of recruitment by these canopy dominants was documented by Wackernagel (1992). The level of elephant impact on smaller tree species had progressed since 1991 such that almost all specimens of *Combretum hereroense*, *Peltophorum africanum* and *Terminalia sericea* had been reduced to stump coppice. However, these species seemed able to survive in this state, at least for several years.

The dense spread of *Combretum mossambicense* in the shrub layer is reminiscent of an alien plant phalanx, and appears to have developed largely since the 1991 survey by Wackernagel and the time when the 1992 aerial photographs were taken. *C. mossambicense* appears to be unpalatable to elephants, although readily eaten by browsing ruminants (Makhabu 2005). Two other shrubby species have apparently also increased in prominence, although to a more localized extent: *Diospyros lyciodes*, which likewise appears to be little utilized by elephants, and *Croton megalobotrys*, browsed by elephants in the dry season. *Dichrostachys cinerea* has been almost eliminated as a shrub, but persists as root coppice plus abundant seedlings. It had appeared as abundant as *C. mossambicense* in the scrub layer at the time of Wackernagel's survey, while Coulson (1992) also noted dense stands of *D. cinerea* in the area.

It seems evident that a process of woodland conversion is under way, portending the elimination of *Acacia* spp. and gradual decline of other canopy trees due to the paucity of recruitment. This trend suggests the eventual replacement of the woodland by a shrub layer consisting largely of species not eaten by elephants, although palatable to other browsers, paralleling the changes inferred along the Chobe river-front. Elephants are clearly the prime agents of mortality among the larger trees through bark removal, although additional tree felling by wind-throw is often observed following storm events. Elephants are evidently contributing to the suppression of recruitment into the tree layer by retarding the growth of plants in the sapling stage. Carbon fertilization from increased atmospheric $CO_2$ cannot be ruled out as a factor promoting the invasion by shrub species commonly possessing large underground storage tissues (Bond and Midgely 2000).

However, the extreme lack of canopy species in the seedling or small scrub stage cannot be ascribed to elephants, and other factors seem to be at work. The drying of the swamp on the Caprivi side and apparently reduced flow of the Linyanti River, suggest that a general desiccation in soil moisture may be inhibiting seedling establishment (de Vries et al. 2000; Ringrose et al. 2007). Nevertheless, neither the expanding shrub species nor *C. mopane* shows this limitation. *C. mopane* is recognized as a species adapted to hot, dry conditions in its distribution. There is evidence that tree establishment may take place only at intervals of several decades or even centuries in semi-arid woodlands, while sufficient soil moisture persists long enough to enable seedlings to establish sufficient rooting depth to survive subsequent dry periods (Young and Lindsay 1988).

Our study will focus on establishing spatial variability in the patterns of change shown, particularly with regard to finding localities where tree regeneration may be evident. We will also seek evidence for past vegetation changes from the pollen preserved in former drainage channels or sumps. It has been postulated that the *Acacia* woodland along the Chobe River established during a period towards the end of the 19th century after elephants had been wiped out by human hunting and browser numbers were reduced to low levels by the rinderpest panzootic that spread through Africa around that time (Walker 1986; Skarpe et al. 2004). However, the large *A. erioloba* and *A. nigrescens* trees that were formerly a feature of sections of the Linyanti riparian zone appear to be much older than a century, suggesting that other climatic factors may underlie their establishment. McCarthy et al. (2000) assembled evidence suggesting an 80-year periodicity in water flow in the region. Projecting forwards, the dense shrub layer of species unpalatable to elephants may provide a nursery environment where canopy tree seedlings can eventually establish without being so apparent to elephants (Howe and Miriti 2000; Sharam et al. 2006), but the species benefiting from such conditions are unlikely to be light-demanding *Acacia* spp., although seedlings of species such as *D. mespiliformis* and *G. livingstonei* have been observed under shrubs.

Our study area represents some of the most extreme elephant densities, and hence impacts on vegetation, found anywhere in Africa, but at this stage we cannot make any definite projections about the ultimate consequences for plant diversity in this region. Extrapolating current trends suggests progressive biodiversity loss, but we are aware that ecological processes do not proceed along linear trajectories. Spatial variation in impacts can be to the ultimate benefit of species diversity through benefitting different species in different regions. Much will depend on how the elephants respond to the changing conditions brought about through their impacts, and on how changing climatic conditions influence river flow and soil moisture regimes in the region.

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## **Appendix 1.2:** Selected photographs of the Linyanti woodland

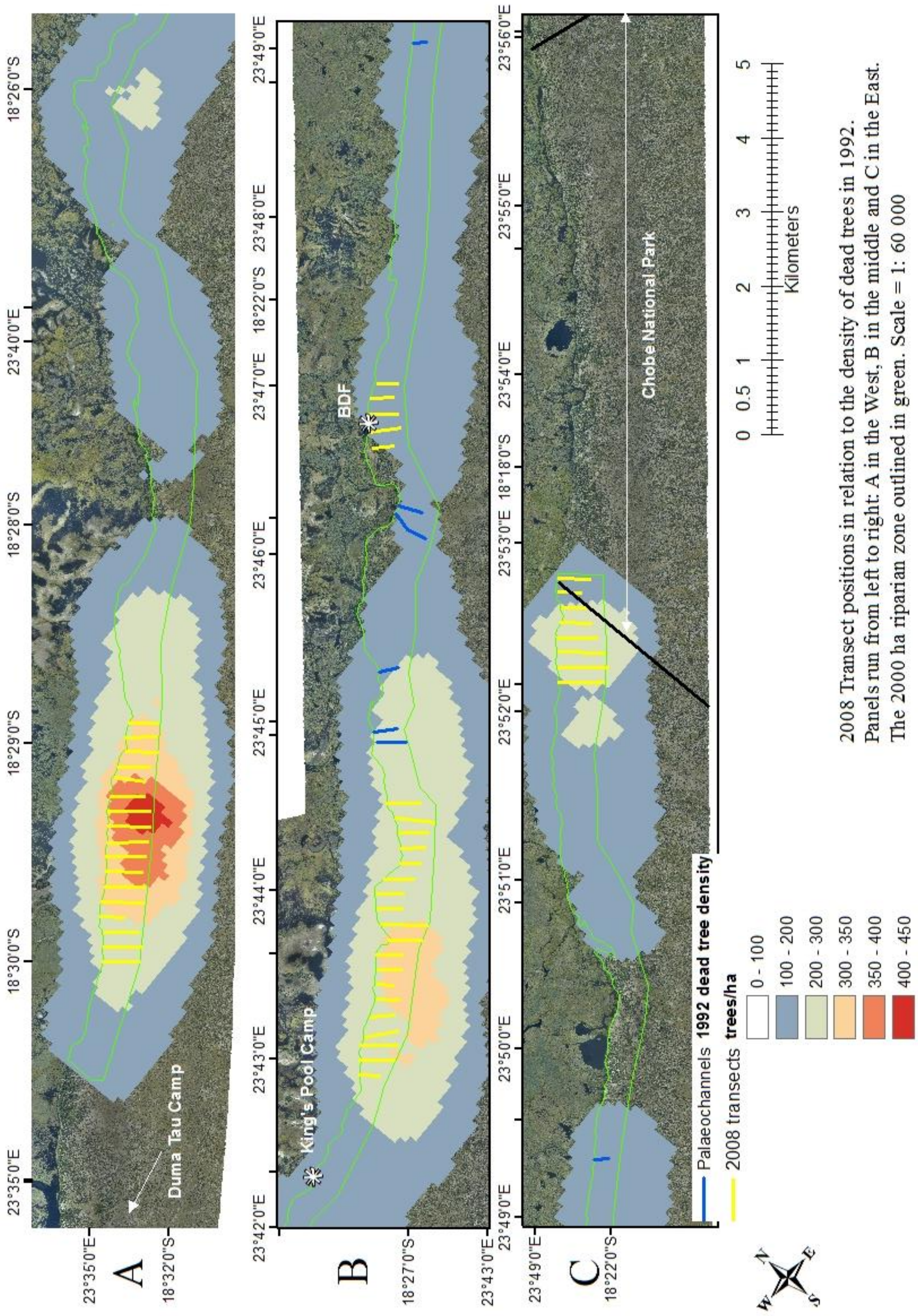
**Appendix 1.2.1** View of the Linyanti woodland from the Linyanti River showing standing and prostrate dead trees as well as living canopy trees with an understory shrub layer composed of *Croton megalobotrys* and *Diospyros lyciodes* near the river bank, and other shrub species further back. Photo taken December 2008.

**Appendix 1.2.2** View from the river towards the Botswana bank showing the dense line of living canopy trees which still remain along the river bank in some areas. Photo taken November 2008.

**Appendix 1.2.3** Photograph of an *Acacia luederitzii* pushed over by elephants and bark-stripped. This was one of the larger individuals observed to have been pushed over. Photo taken May 2010

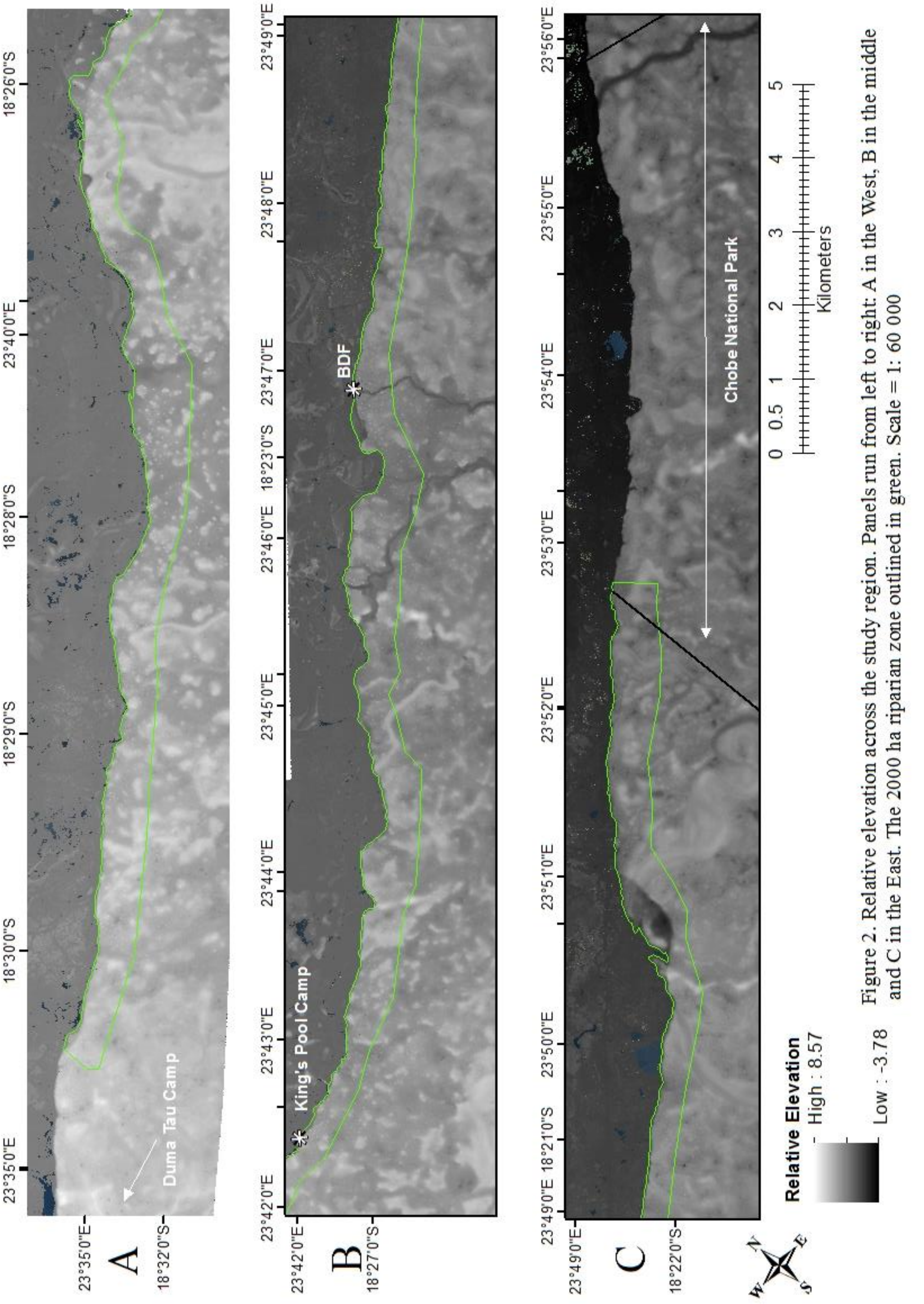
**Appendix 1.2.4** A remnant living *Acacia erioloba* tree in a grove of dead Acacia and Terminalia sericea trees, near King's Pool Camp. Photo taken May 2010.

## Appendix 1.3: Key Maps



2008 Transect positions in relation to the density of dead trees in 1992.
Panels run from left to right: A in the West, B in the middle and C in the East.
The 2000 ha riparian zone outlined in green. Scale = 1: 60 000

**Appendix 1.3.1** Map of the 2007/2008 transects stratified to reflect the density of dead trees extracted from earlier aerial photographs (only the 1992 dead tree density is shown here).



**Appendix 1.3.2** Map showing relative elevation (from the 2010 LiDAR DEM) of the riparian area. Note Palaeochannels visible around BDF surveyed in 2007/2008.

# CHAPTER TWO

# Patch dynamics of disturbance: elephant-mediated impacts on riparian woodland in northern Botswana

**Keywords:** Chobe National Park, clustering, DBSCAN, disturbance, elephants, heterogeneity, hierarchical patch dynamics paradigm, Linyanti, riparian woodland, shifting mosaic, tree mortality

## 2.1 Abstract

The Hierarchical Patch Dynamics Paradigm provides a conceptual framework for assessing how disturbances modify the spatial structure of a landscape. Disturbances create, modify, and occlude patches within a landscape leading to increased heterogeneity over time and space if a mosaic of patches is maintained. Unlike forest gap-dynamic studies, it is difficult to delineate discrete disturbance patches in savanna woodlands and there have been few attempts to test patch dynamics theory in disturbance-driven savannas. Here, we present a novel clustering technique (DBSCAN), to delineate patches of high disturbance in a riparian woodland subject to intensive elephant impacts. We were able to track patch dynamics across 2000 ha over 18 years using three sets of high resolution aerial photographs and determine mortality rates within patches and the matrix. Patches were highly dynamic over the period, as small patches appeared, grew and coalesced over time to produce patches of disturbance which were over 1 ha in size. Total patch area increased over the period from 6% to 23% as a result of increased mortality in the inter-patch areas. The current dead tree appearance rate was 0.28 trees.ha.yr$^{-1}$ which was not much higher than background tree death rates, suggesting tree death was slowing. Our results suggest that elephants can cause massive tree mortality (up to 50%) and create large patches of dead trees, but spatial heterogeneity was still maintained in spite of this and patches constituted only 23% of the landscape in 2010, though they were increasing. Fragmentation of the landscape by disturbance patches was evident, but there were still large areas that remained without disturbance patches. We foresee disturbance patch growth declining in the future due to the prevalence of resistant tree species in the remaining woodland and due to a lack of tree recruitment.

## 2.2 Introduction

### 2.2.1 Patch dynamics of disturbance

Disturbances are discrete events that change the structure and composition of vegetation through mortality of functionally dominant organisms (White & Jentsch 2001). Disturbances may be characterised by three defining aspects 1) intensity, where for example a stronger windstorm would fell more trees per area; 2) extent- a larger spatial effect creates bigger disturbed areas; and 3) frequency- a high return rate of windstorms would regenerate more area in the disturbed state or retard recovery (Pickett & White 1985a). These three aspects are linked to the Intermediate Disturbance Hypothesis (IDH) which states that at some intermediate level of intensity, extent or frequency, disturbance is most likely to maximise diversity because it allows both pioneering and less common species to coexist (Connell 1978; Fox & Connell 1979). For example, a forest that is subject to rare or low intensity windstorms would not open up many canopy gaps, and the forest would be dominated by mature stands of trees with little regeneration leaving only the most resilient species. Conversely, severe or frequent disturbances could lead to a forest dominated by open patches of pioneering species, with few mature stands. Recently the IDH has been criticised for its lack of empirical support in fluctuating environments (Fox 2013). Instead, new studies show that even very large disturbances do not cause a decline in diversity within a system, but create spatial heterogeneity, often at multiple scales (Turner 2010). This new evidence argues for an increased focus on the spatial effects of disturbance within a Hierarchical Patch Dynamics Paradigm (HPDP) (Wu & Loucks 1995). The HPDP takes non-static properties of ecosystems into account and provides for the description of how disturbances can cause patch changes in time and space (Gillson 2004a; b).

Patches are relatively discrete spatial units differing from their surroundings (Wiens 1976; Kotliar & Wiens 1990). Patches can thus be defined at multiple scales such as an area of dense seedling regeneration, a gap in a closed canopy forest, or a vegetation type in a landscape. Spatial patchiness may be quantified in terms of composition (patch types and their relative abundance), and spatial configuration measures which include size, shape, and contrast (Wu & Loucks 1995). Patches are created, maintained and occluded by different disturbance regimes, resulting in a mosaic of different patches in different stages (of active disturbance and recovery) interacting with each other (Turner 2010). The shifting mosaic steady state concept (Bormann & Likens 1979) states that a landscape composed of individual patches in different stages of succession (or disturbance) over time leads to enhanced heterogeneity (Pickett & Cadenasso 1995). Patches can create a directional landscape change where a patch type increases to dominate the area resulting in increased homogeneity, or heterogeneity can be maintained by a shifting mosaic pattern where the spatial configuration of patches change over time, but the relative amount of patches remains relatively constant (Pickett & White 1985b; Wimberly 2006; Turner 2010).

Measuring the dynamics of disturbance patches has rested on the delineation of gaps which exist as discrete entities only within a closed canopy. For example, recent studies within boreal forest systems have documented patch dynamics of disturbance by mapping discrete canopy gaps and quantifying their appearance, movement, growth, and decline (Hytteborn & Verwijst 2014). The authors found that spatially delineated gaps present in the boreal forest were mostly small at the onset (less than 100 $m^2$, in supplementary material) and that patches were more likely to grow and coalesce over the time period of 54 years, than were new disconnected patches to emerge. This patch growth led to the situation that gaps were increasing at higher rates than filling (with forest regeneration), leading to increased openness within the forest. They also went on to highlight the importance of a mixture of different gap sizes as large gaps were more likely to lead to regeneration than smaller gaps which closed more slowly, suggesting this was due to less root space competition in larger gaps (Hytteborn & Verwijst 2014). The delineation of similar disturbance patches in savannas is difficult due to the intrinsic lack of closed canopies. It is unknown whether similar dynamics of disturbance patch formation, growth and movement exist in savanna woodlands which have a discontinuous canopy.

Pollen evidence from savannas has supported a shifting mosaic driven by disturbance at the local scale where patches shift between woody and grassland phases, but the total number of patches in each phase remains stable over a long time period (Gillson 2004a). Previous analyses of spatial pattern of tree mortality in savannas has been limited to the finding that treefall (as measured by tree height decrease from LiDAR data) was significantly clustered within *Acacia* and *Combretum* dominated river catchments in Kruger National Park (KNP) using Ripley's K statistic (Levick & Asner 2013). Ripley's K statistic (Ripley 1976) measures how dispersed or clustered a pattern is but still pares the spatiotemporal data down to an overall distribution for the landscape, and does not allow for the measurement of patch dynamics.

The spatial analysis of disturbances in savannas has been restricted to square lattice (Schertzer, Staver & Levin 2014) or moving window (Meyer *et al.* 2007) methods which define patches by calculating density in a regular grid. This does not enable the measurement of dynamics of observation-based patches with no a-priori assumptions of size or movement. Square lattice models also cannot reveal important information on the shape and sizes of patches (Li 2000). Ripley's K statistic and square lattice models also do not allow us to distinguish pattern from noise: for example delineating a localised patch of dense tree mortality caused by a disturbance agent such as fire, amongst scattered dead trees in a savanna. Savannas are driven by disturbances such as fire and herbivory at a range of scales (Gillson 2004a). Given the potential importance of tree mortality in creating heterogeneity in savanna woodlands, there has been little attempt to analyse the clustering of dead trees in savannas within a patch dynamics paradigm. Remotely sensed time-series imagery provides data across large spatial scales needed to investigate disturbance dynamics in savannas, providing we can measure tree mortality at a landscape scale. LiDAR (Light Detection and Ranging) data provides an opportunity to measure the spatial patterns of treefall in savannas by height change (Levick & Asner 2013; Asner *et al.* 2015).   The limitation is that LiDAR surveys are recent tools and lack the long-time scales necessary for patch dynamics to be measured (Gillson 2004a).  We need a new method of measuring disturbance patches within a noisy environment which provides the ability to delineate and track patches over time and space and with no a-priori assumptions of patch size, shape or movement.

### 2.2.2 Elephants as selective disturbance agents in savannas

Fire has been recognised as the prime disturbance agent in modifying the spatial structure of savannas (Bond & Keeley 2005; Levick, Asner & Smit 2012; Scholtz *et al.* 2014; Schertzer, Staver & Levin 2014) where trees are kept in a 'fire trap', but there is increasing evidence of the role megaherbivores have in structuring ecosystems through large tree mortality, and often synergistically with fire impacts (Moncrieff, Kruger & Midgley 2008; Asner & Levick 2012). Africa is unique in having a comparatively intact Pleistocene megafaunal assemblage (Owen-Smith 1987), where megaherbivores impacts are able to change ecosystem structure and composition (Bakker *et al.* 2016; Malhi *et al.* 2016).   Fire differs from mammalian disturbance in that it destroys vegetation irrespective of species-based traits like forage quality (Bond 2005) but is structurally selective as it can kill fire-sensitive savanna trees within the 'fire trap' below about  3m (Higgins, Bond & Trollope 2000). In savannas, fire has minimal impacts on the mortality of taller trees, and does not usually kill canopy trees (Higgins, Bond & Trollope 2000; Staver *et al.* 2009; Sankaran, Augustine & Ratnam 2013).  Severe wind disturbance by comparison kills the largest crowned canopy trees (Ulanova 2000) and lightning strikes can cause mortality of tall trees (Spinage & Guinness 1971).  Porcupines (*Hystrix africaeaustralis*) are able to kill selected species of large trees through basal debarking, often in combination with fire as they tend to expose the heartwood

(Thomson 1975; Yeaton 1988). Similarly, tree-piping by termites in Australian savannas can indirectly lead to mortality of larger trees by making them more vulnerable to fire (Werner & Prior 2007). Riparian trees are also subject to death by flooding or drought events (Tafangenyasha 1997; O'Connor 2010). Elephants are the only disturbance agent in savannas that can kill savanna trees across a landscape in a range of sizes from seedlings by uprooting (Barnes 2001), to canopy riparian trees by debarking (Midgley, Balfour & Kerley 2005; Staver *et al.* 2009; Chafota & Owen-Smith 2009; Owen-Smith & Chafota 2012).

Elephants are highly selective agents of disturbance (Owen-Smith & Chafota 2012), preferentially feeding on species of *Acacia* and species from the *Combretum* and *Terminalia* genera (Ben-Shahar 1993; Skarpe *et al.* 2004; Owen-Smith & Chafota 2012); and *Colophospermum mopane* (Ben-Shahar 1993, 1996; Styles & Skinner 2000; Hartnett *et al.* 2012). Elephants impact plants by toppling or uprooting smaller trees, and debarking large trees (Midgley et al. 2005, Kerley et al. 2008 and references therein). There is increasing concern that where large concentrations of elephants impact tall trees these trees can decline, often through the synergistic effects of fire (Druce *et al.* 2008; Asner *et al.* 2009; Helm 2011; Shannon *et al.* 2011; Vanak *et al.* 2012; Levick & Asner 2013; Levick, Baldeck & Asner 2015). Where preferred forage species like acacias are abundant and spatially concentrated, elephant impacts may remain localised. This would form localised patches of high disturbance in a heterogeneous landscape. However, if elephant impacts are sufficiently intense, the abundant species may decline, leading to disturbance spreading onto more scattered trees, and spatial heterogeneity may decline.

Additionally, elephants are distinct disturbance agents in their spatial spread as they are intelligent, far roaming megaherbivores (van Aarde *et al.* 2008) which show complex habitat selection in a spatial hierarchy. At large spatial scales elephants are constrained by distance to water (Owen-Smith, 1988), but at smaller spatial scales they select for vegetation characteristics (Cushman, Chase & Griffin 2005; de Knegt *et al.* 2008) such as high cover (Harris *et al.* 2008). By comparison, smaller herbivores such as impala (Skarpe *et al.* 2004) or nyala (Lagendijk, Page & Slotow 2012) concentrate in relatively smaller areas where they may exert effects on vegetation structure through seedling predation (Moe *et al.* 2009, 2014). Smaller herbivores can also show spatial selection based on specific predation risk (Valeix *et al.* 2009), whereas elephants are mostly not affected by this 'landscape of fear' (but do show an avoidance of human settlements (Harris *et al.* 2008)).

In an already patchy landscape like savannas, the spatial spread or selectivity of a disturbance agent plays a large role in the disturbance effect on heterogeneity. Wind and flooding disturbances are fairly limited in their extent, while fire and elephants can disturb a much larger area. Fire has an effect on spatial dynamics by causing disturbance of fairly contiguous patches of susceptible vegetation in a nearest neighbour fashion (Schertzer, Staver & Levin 2014). Fire spread tends to stop at the edges of patches (for example where a shrub patch meets a tall tree patch, but when an area of flammable vegetation is burning, fire will tend to spread across the entire patch (Peterson 2002). Flooding, which results in tree death from bank degradation or inundation, is a disturbance agent with constrained spatial effects limited to depressions or river proximity (Spinage 1990; O'Connor 2010). The spatial effects of wind-throw in African savannas are poorly understood, as their relative disturbance effect is eclipsed by fire and large herbivores (Baxter & Getz 2005; Staver *et al.* 2009). However studies from temperate forests have shown that wind storms (not including tornadoes) affect isolated wind-susceptible trees, particularly when they are on the edges of dense patches, as opposed to causing patch blow-down (Belsky & Canham 1994; Ulanova 2000).

Elephants are unusual disturbance agents in their spatial spread as they can target individual favoured trees within a matrix of neglected species (unlike fire), or across a contiguous patch of preferred trees (unlike wind). Elephants can also cross patch boundaries easily, and skip neighbouring patches, and the spatial effects of this over a period of time are unknown. Following a study of episodic severe impact by elephants, Chafota and Owen-Smith (2009) hypothesized that elephant disturbances to canopy trees that are spatially concentrated while sufficiently widely spaced in time could lead to a mosaic of patches in different phases of recovery. This would ultimately enhance heterogeneity. Models have shown that at higher herbivore densities, herbivores are forced to be less selective and this results in the vegetation becoming spatially more homogenous (de Knegt *et al.* 2008). It is unknown if there is a threshold at which elephant disturbance of trees also declines at lower tree densities, as susceptible and preferred species decline, or if they continue to cause mortality of trees at high rates, and perhaps this is reflected in increased rates of tree death outside of original focal patches.

### 2.2.3 Elephant impacts in northern Botswana

Several studied have detailed dramatic canopy tree disturbance by elephants in the Linyanti riparian woodlands of northern Botswana (Sommerlatte 1976, Ben-Shahar 1993, Wackernagel 1993, Bell 2003). The Linyanti woodland presents an unparalleled opportunity to study the effects of elephants as disturbance agents in relative isolation, as fire is largely excluded due to fuel-load trampling by the large concentrations of herbivores. Additionally, human impact has largely been excluded due to the absence of any appreciable human settlements since the late 1800's due to tsetse fly diseases (Sommerlatte 1976). In the early 1980's the Savuti Channel, the eastern border of our study region, stopped flowing (Walker; In: Lewin 1986), compressing elephants along the perennial Linyanti-Chobe River system, and resulting in tremendous localised densities and impacts.

Our study is based on an exceptional record of vegetation change for nearly 20 years driven by extreme elephant concentrations. Two previous studies in the Linyanti area (Wackernagel 1993; Bell 2003) form the foundation for our long-term study. Wackernagel (1993) surveyed elephant impacts on living and dead trees along 35km of riverfront and estimated the spatial scales of elephant impact. He found that elephant impact was patchy across the riparian woodland but found very weak environmental relationships with patchiness (Wackernagel, 1993). In a follow up study of canopy tree loss from aerial photography over the period 1992-2001, Bell (2003) found that there were localised areas of high tree mortality in the Linyanti woodland, with these cells as large as 200m x 200m (4ha) in size.

Bell (2003) found a very low recruitment of canopy trees (0.7 %) resulting in a net loss of canopy trees at 1.8% per annum from 1992 to 2001. Skarpe et al. (2004) suggest that whilst the Chobe riverfront has experienced a disappearance of riverine Acacia woodlands, these woodlands were probably a transient effect of low densities of large herbivore following rinderpest in 1896/97 and elephant extirpation for ivory shortly before that. This historical context is important when considering contemporary changes.

### 2.2.6 Aims

Our aims were (1) to gain a better understanding of spatial heterogeneity changes caused by tree mortality by quantifying the rates and spatial patterns of dead tree appearance and (2) also assess whether a shifting patch mosaic of disturbance exists or if there is a directional shift to a landscape dominated by patches of intense disturbance.

To determine whether spatially distinct disturbance patches were present, we hypothesised that: (1) dead trees would be clustered spatially across the landscape, and that (2) patches of disturbance exist that would have higher rates of dead tree appearance compared to inter-patch areas. To assess the consequences of patchy disturbance for spatial heterogeneity we further hypothesized that (3) the inter-patch dead tree appearance rates would increase as evidence of elephants spreading their impacts but that (4) there would be evidence of a shifting mosaic where disturbance patches increase and decline but remain spatially localised and the total area of disturbance would remain similar; and lastly heterogeneity would be enhanced if (5) patches intensified in disturbance (dead trees.ha$^{-1}$) and a variety of patch sizes remained.

## 2.3 Methods

### 2.3.1 Study area

Botswana has the largest contiguous African elephant population in the world, upwards of 134 000 ((Blanc *et al.* 2007). Extremely high local elephant densities have been recorded for northern Botswana, and in particular for the Linyanti strip where elephant densities of 12 elephants.km$^{-2}$ were recorded in the late 1980's (Spinage, 1990), when conditions were exceptionally dry. In 1992 the dry season density of elephants in the Linyanti area was documented in excess of 4 animals.km$^{-2}$ (Coulson 1992). Following dispersal to neighbouring countries like Angola, and regionally within northern Botswana following a wet period, elephant densities in 2010 were recorded at 2.35 elephants.km$^{-2}$ (Chase 2011).

The Linyanti River forms the northern most boundary of Botswana with Namibia's Zambezi Region (ex Caprivi Strip) (Chapter 1 Fig. 1.4). The Linyanti River arises from the Kwando River in the Angolan Highlands, and becomes the Chobe River further eastward, before it flows into the Zambezi River. As the Kwando River flows SSE, it hits a fault line and takes a right angle bend flowing ENE, creating a steep terrace on the Botswana bank, and the Linyanti swamps on the Namibian side. Except for the narrow western corner of Chobe National Park (CNP), most of the Linyanti riparian region lies in a private photographic safari concession (NG15, Chapter 1 Fig. 1.4) currently leased by Okavango Wilderness Safaris (www.wilderness-safaris.com). Rainfall takes place in the summer months between November and April and the MAP for 92 years is 557.6mm at the nearest weather station at Kasane (NOAA, 2014). The hottest month, October has a mean daily maximum temperature of 39°C and mean daily minimum of 14°C, with the coldest, July experiencing a mean maximum of 30°C and minimum of 4°C (Aarrestad *et al.* 2011).

### 2.3.2 Aerial Photograph analysis of dead trees

Three time sets, spanning 18 years, of digitized colour aerial photograph mosaics were used: 1992 and 2001 (25cm pixel size) and 2010 which comprised a photo mosaic (15cm pixel size) as well as a LiDAR data set. The earlier aerial photographs were georeferenced, georectified and mosaicked by the authors, whilst the 2010 data was processed by the supplier (Southern Mapping Company).

The riparian zone was bounded in ARCmap 9.2 using the 2010 river shore edge and the Mopane/Riparian transition edge which was defined by the main vehicle track traversing the woodland. The riparian area common to all three aerial photo time sets encompassed 2000 ha in the form of a long narrow strip, 38km long and between 250 and 800m wide.

Our measure of disturbance was the appearance of dead trees as opposed to the disappearance of living trees, as dead trees were clearly visible in the colour aerial photographs (see appendix 2.1) and it was hard to distinguish individual living tree canopies from each other. Recent studies have used the change in height from lidar data to indicate treefall (Levick & Asner 2013) but this requires time-series lidar data which we did not have. The dead trees also provide prior disturbance patterns (pre-1992) over which period changes from 1992 to 2001 and 2001 to 2010 could be viewed.

At the scale of our photographs, we were able to manually mark dead trees creating shapefiles in ArcMap 10.0. We were also able to distinguish between felled, and standing dead trees (seen as leafless tree skeletons). Coppicing trunks, seen as green lengths of felled trees, were excluded as they may grow into shrubs or trees again. We marked each felled dead tree as a line (for newly felled trees we only marked the main trunk, and not any large side stems) and a point for each standing dead tree (See Appendix 2.1 for an example of the method). The standing dead tree points were placed where the tree shadow met the base of the trunk at the point on the ground. Where standing dead trees emerged above shrub cover, we marked the lowest point of the shadow. This enabled us to track trees over time as some standing dead trees fell over. For clustering analysis we combined felled and dead trees into a point shapefile and used the mid-point of each felled tree line to convert to a Spatial Point Pattern (SPP).

As each year’s dead trees were marked and counted independently, we used an overlay function with a 3m buffer (to account for any shift in mosaic triangulation) to select trees common to different years. We could then distinguish dead trees which had appeared since the previous photo (new mortality) from dead trees which had persisted from earlier. Five datasets were then created (1992, 2001, 2010 cumulative dead trees; 2001 new, 2010 new dead trees).

The 2001 aerial photos, flown in the early morning, were blemished by many shadows, hiding felled trunks and standing trunks resulting in an undercount of dead trees. We attempted to reduce this undercount by retrospectively examining the 2001 photos with the 2010 mortality overlaid to scrutinise any old missed disturbance mortality and update the 2001 datasets accordingly. After this, we estimated the remaining undercount bias by sampling 20 ha in detail to count missed dead trees by comparing the photos to the much sharper 2010 photos. The bias in 2001 dead tree numbers was estimated at 30% or 3 in 10 trees missed from critically examining a 20 ha area. Thus the change between 2010 and 1992 dead trees will be emphasised, as the accuracy of total population counts is more reliable for these years. With a lack of fire, dead trees persisted in the system but there were some trees which decayed and were not recounted (see Appendix 2.1 for an example) and we used the comparison between all three time sets to ensure that trees that disappeared were not missed. Small dead trees (<5m) may not have been counted as they were obscured by shrubs, or missed by our manual method.

The landscape-scale density of dead trees was calculated as the total count per each time set divided by the study area of 2000ha. The change in cumulative density between years divided by the time interval (9 years) gave cumulative dead tree appearance rate (trees.ha$^{-1}$.yr$^{-1}$) assuming no disappearance.

### 2.3.3 Clustering methods

To study the spatial patterns of disturbance requires a measure of patches of disturbance with no a-priori assumptions of the shape and structure of patches. This enables the patches to be quantified in terms of proportional size of disturbed area. Estimation of the frequency of disturbance requires us to be able to count patches, and view them over time, as new patches of disturbance develop, and older patches grow or decline. To estimate the intensity of the disturbance, we need a measure of disturbance intensity in patches and in the matrix and track that intensity over time. Clustering algorithms provide promise in this regard.

There are numerous cluster analysis algorithms available, and most fall into four distinct categories: 1) Connectivity-based or hierarchical clustering (Gower & Ross 1969) uses distance functions to recognise close objects as being more related than further ones, with single-linkage analysis the most popular, but generally inferior to later methods; 2) Centroid-based clustering has become popular, especially the k-means algorithm, though its biggest drawback is that the number of clusters (k) has to be specified in advance, and it is biased to produce similarly sized clusters (Dufrêne & Legendre 1997), limiting its application in patch dynamics studies; 3) Distribution-based clustering methods (see Legendre and Legendre 2012) define clusters as objects belonging to the same statistical distribution. They are commonly used in savanna ecology, for example in clustering Kalahari vegetation (Scanlon *et al.* 2007), but strong assumptions are placed on the data by the type of distribution used, and requires strong statistical knowledge; 4) Density-based clustering has emerged recently, having foundations in the computational data mining field. Density- based methods employ an algorithm to search for regions of high density, based on a fixed threshold value (Birant & Kut 2007). The most common algorithm used is DBSCAN (Density-Based Spatial Clustering of Applications with Noise) (Ester *et al.* 1996). DBSCAN uses two parameters: a radius value Eps (ε) based on a user-defined distance measure, and the value MinPts which is the minimum number of points to constitute a cluster within the Eps radius. Thus the algorithm defines clusters by “density-reachability” (points farther than a given distance) and points in sparse areas are considered to be noise. This presents a leap from other clustering methods, as it is data driven, and not reliant on an underlying imposed distribution, or neighbouring distance. It is therefore able to produce clusters of arbitrary shape in a noisy environment, does not require a predetermination of cluster numbers, and can work with very large databases (Birant & Kut 2007). Despite these obvious linkages to patch determination and spatial ecology, one of the few instances we found of DBSCAN used in ecology was a study of the dispersal of Afrotropical ducks (Cumming, Gaidet & Ndlovu 2012). Very recently it has been recognised as a tool to map discrete tree canopies from LiDAR (Tao *et al.* 2015). DBSCAN has the advantages of being scalable, hierarchical, and able to produce patches of different sizes. It is also applicable in a GIS workspace, allowing for explanatory analysis with environmental variables, and can produce a sample, exchangeable output such as a shapefile. This is advantageous because clusters can be viewed by non-clustering experts and easily compared to other regions or studies.

### 2.3.4 Quantifying patch dynamics

The extent of dispersion or clustering of dead trees was determined by Ripley’s K analysis (Ripley 1976) in ArcMap on each of the dead tree datasets. Ripley’s K determined deviation from Complete Spatial Randomness (CSR). A starting distance of 5m from each point, with 100 distance bands of 10m was specified, with the default value of 9 Monte Carlo permutations creating a confidence envelope (~90%) for the observed pattern. Evidence of a clustered or dispersed spatial pattern was given where the observed K deviated from this envelope. The boundary correction method, necessary for the long narrow study region, was set to simulate outer boundary values.

DBSCAN was then used for clustering the dead trees. The mortality shapefiles for each year were imported into R (2.13.2; R Development Core Team, 2011) as a spatial point pattern (SPP) using the package spatstat (Baddeley and Turner (2005)). DBSCAN was executed using the package fpc

(Hennig, 2010). The code is available in Appendix 2.2. A patch was defined as a minimum of ten dead trees (minPts) as representative of intense mortality in a small area. This number is based on Bell's (2003) finding that the range of dead tree appearance between 1992 and 2001 was 0 - 18 trees per each 4ha plot. Because we were interested in smaller-scale patchiness than that explored by Bell (2003), we selected 10 trees, representing the approximate mean value of dead trees appearing in high mortality areas. We performed a sensitivity analysis by keeping minimum points set at 10, and varied Eps (search radius) from 15 to 50 Ɛ (see Appendix 2.3 for details). Because we were interested in detecting sensitive changes in growth or decline of patches, we chose an Eps of 36. Larger search radii tended to produce very large patches, which were not as sensitive to change in size over time, whilst smaller radii produced a large amount of very small patches (Appendix 2.3). Each output .csv file was imported into ArcMap and viewed in the landscape comparing the resultant polygons for size, number, placement, and total area.

From DBSCAN, a .csv file of cluster number per each dead tree point was imported back into ArcMap, and converted into a shapefile with cluster number as an attribute. The minimum bounding geometry tool in ArcMap10 was then used to create convex hull polygons of each numbered cluster, and cluster 0 (ie non-clustered points) was then excluded. Area was calculated for individual polygons for each year. Overlapping areas 1992-2001 and 2001-2010 were added as separate polygons using the intersect tool in ArcMap10 and area calculated. The algorithm did create a few clusters (34 out of 1099 total) containing less than 10 minimum points and these artefacts were deleted from final analysis.

By scanning the aerial photographs at a resolution of 1:5000 with overlaid mortality and overlapping polygons for each time step, patch change was quantified using the patch fate definitions in Table 2.1. A frequency table of polygon number and corresponding area per definition was compiled and summary statistics of number, mean patch size and total patch coverage was calculated for patch growth, persistence and decline. Intensity (dead trees.ha$^{-1}$) was calculated for each patch. Disturbance rates (new disturbance.ha$^{-1}$.yr$^{-1}$) were compared between patches and the inter-patch matrix by dividing the number of trees per area covered per year. In order to evaluate the change in intensity (dead trees .ha$^{-1}$) and size of patches over time, we produced histograms of proportional frequency (%) of the number of patches by groups of dead tree density (dead trees.ha$^{-1}$) and by patch size. These histograms were statistically compared using multiple pairwise Kolmogorov-Smirnov tests in R.

**Table 2.1** Definitions of patch fate dynamics of disturbance patches determined by viewing overlapping polygons from 1992 to 2001 and 2001 to 2010. (T1 represents an earlier time period, and T2 the next time step)

| **Dynamic** | **Fate** | **Description** |
|---|---|---|
| **Persist** | Static | Polygons have less than 15% change in area or displacement |
| **Growth** | Expand | Polygons increase by >15% area |
| | Coalesce | Two or more polygons increase by being bound by a single polygon at T2 |
| | Shift | Polygons which increase density by one or more T2 polygons appearing as neighbours (within a distance of 100m) |
| **New Patches** | Colonize | T2 polygons that are not associated with T1 polygons, and emerge in an area not covered previously |
| **Decline** | Shrink | Polygons which decrease by >15% area |
| | Fragment | Polygon splits into 2 or more smaller T2 polygons |
| | Disappear | Polygon disappears from that area |
| **Reappear** | Reappear | T3 polygons which disappear at T2 but re-emerge in the same area as T1 |

## 2.4 Results

### 2.4.1 Are dead trees clustered spatially across the landscape?

Dead tree density increased from 6.85 trees.ha$^{-1}$ in 1992 to 11.92.ha$^{-1}$ in 2010 (Table 2.2). Felled trees were twice as common as standing trunks in 1992 and 2010. In 2001, felled trees were only 1.2 times more common than standing trees (7891 to 6725), likely as a result of the undercount in 2001 dead trees. The overall mortality difference between the 2010 and 1992 counts was used to represent rate of change of dead trees (losses and gains), calculated at 0.28 trees.ha$^{-1}$.yr$^{-1}$ (Table 2.2). The rate of new dead tree appearance increased over the period to 0.86 trees.ha$^{-1}$.yr$^{-1}$ for 2001-2010. The production of new standing dead trees decreased by nearly 40% from 3.05 to 1.88 trees.ha$^{-1}$ between the two time periods.

**Table 2.2** Comparison of dead tree abundance (n) and density (in brackets dead trees.ha$^{-1}$) in the riparian zone (2000 ha) depicting cumulative dead trees, and new dead tree appearance

| | 1992 | 2001[a] | 2010 |
|---|---|---|---|
| Cumulative felled dead trees | 9078 (4.54) | 6725 (3.36) | 16504 (8.25) |
| Cumulative standing dead trees | 4619 (2.31) | 7891 (3.95) | 7343 (3.67) |
| Cumulative total dead trees | 13697 (6.85) | 14616 (7.31) | 23847 (11.92) |
| Dead tree density change (trees.ha$^{-1}$) | | 0.46 | 4.61 |
| Average dead tree rate of change (1992-2010) (trees.ha$^{-1}$.yr$^{-1}$) | | | 0.28 |
| New felled dead trees | | 4355 (2.18) | 11847 (5.92) |
| New standing dead trees | | 6103 (3.05) | 3758 (1.88) |
| New total dead trees | | 10458 (5.23) | 15605 (7.80) |
| New dead tree appearance rate (trees.ha$^{-1}$.yr$^{-1}$) | | 0.58 | 0.86 |

[a] 2001 likely represents undercounts, particularly of felled trees- see text for details

Dead trees from all three years showed a significant spatial clustering pattern up to a distance of about 600m (Observed K). None of the datasets showed dispersion at any distance. (Fig. 2.1)

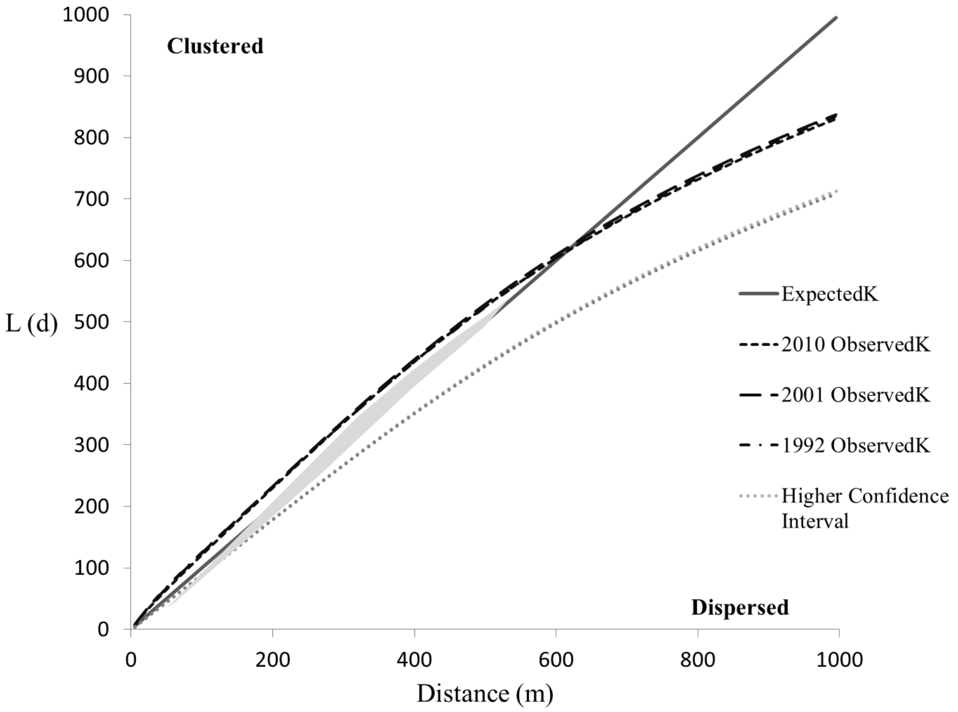


**Figure 2.1** Multi-distance spatial clustering (Ripley's K) of disturbance per year over the 2000ha study area. The confidence interval is provided by Monte Carlo permutations. Values above the solid line represent significant clustering. Observed values for each year fall along the same curve.

### 2.4.2 Dynamics of dead tree patches

The DBSCAN algorithm produced a clustering proportion of 37% of all dead trees in 1992, which increased to over 60% in 2010 (Table 2.3). The total area covered by patches was initially a small proportion of the landscape (6.5% in 1992) but tripled by 2010 to 23% of the total area. There was large increase in dead tree production in 2010 (2010 new) and these patches were high in both total area covered by patches (161.11 ha), mean polygon size and also in intensity of patches. This resulted in a doubling of patch size (average patch size in 2010 was over 1ha) and the largest range in patch sizes seen throughout the time period (the largest patch over 50ha in size).

The disturbance intensity (density of dead trees) was much higher in patches compared to inter-patch areas (8 times higher in 1992 and 5 times higher in 2010) (Table 2.3) Patch intensity appeared to decline over the period leading to a negative disturbance rate (density of dead trees appearing per year) (Table 2.3) but patches expanded more than 3 times in area between 1992 and 2010, so in fact more dead trees appeared in patches.

**Table 2.3** Summary of patch structure over the time period. Cumulative patch datasets refer to patches extracted from the total counts of dead trees in that year, whereas new patch datasets are the dead trees remaining after dead trees which persisted from the previous time step were removed.

| | **1992 Cumulative patches** | **2001 Cumulative patches** | **2010 Cumulative patch** | **2001 New patches** | **2010 New patches** |
|---|---|---|---|---|---|
| Total number of patches (n) | 190 | 213 | 324 | 111 | 222 |
| Mean patch size (range) (ha) | 0.68<br>(0.09- 5.47) | 0.76<br>(0.08-10.55) | 1.42<br>(0.04-52.63) | 0.47<br>(0.11- 3.45) | 0.72<br>(0.06- 14.26) |
| Total area of patches (ha) (% of sample area) | 130.0<br>(6.50%) | 162.4<br>(8.12%) | 460.6<br>(23.03%) | 52.0<br>(2.60%) | 161.1<br>(8.05%) |
| Mean dead trees per polygon (range) | 26.73<br>(10-163) | 27.56<br>(10-265) | 45.94<br>(10-1410) | 19.24<br>(10-110) | 26.39<br>(10-326) |
| % dead trees clustered | 37.08% | 40.18% | 62.41% | 20.42% | 37.55% |
| Patch disturbance intensity (dead trees.ha$^{-1}$) | 39.58 | 36.51 | 32.62 | 41.42 | 36.66 |
| Inter-patch disturbance intensity (dead trees.ha$^{-1}$) | 4.57 | 4.73 | 5.73 | 4.26 | 5.27 |
| Patch disturbance rate (dead trees.ha$^{-1}$.yr$^{-1}$) | | -0.34 | -0.43 | | |
| Inter-patch disturbance rate (dead trees.ha$^{-1}$.yr$^{-1}$) | | 0.01 | 0.11 | | |

Inter-patch dead tree appearance rates increased ten times over the time period (Table 2.3) which is substantial considering the inter-patch area only declined 1.2 times from 1992 to 2010. This meant that the difference between disturbance intensity in patches and inter-patch areas declined.

### 2.4.3 Is there evidence of a shifting mosaic as patches increase and decline but total patch area remains similar?

Areas of dense dead felled and standing trees were already apparent in the 1992 aerial photograph (Fig. 2.2 top) and the movement and increase or decline of patches of dead trees could be clearly tracked over the time period (Fig. 2.2 bottom).

Patches were dynamic over the time period, with patches increasing via new colonization, or growth by expansion, shifting (lateral movement) or coalescing into larger patches. Some patches also declined, but these made up a smaller proportion of total patch area (the 1992-2001 decline should be interpreted with caution as it likely reflects the 2001 undercount). Total patch area however increased 3.5 times from 1992 to 2010 (Table 3), and mostly as a result of small neighbouring patches coalescing to form large patches (>10 ha) between 2001 and 2010 (Fig. 2.3 B, C).

A greater number of new patches colonized the area than increased by expanding, shifting or coalescing (Fig. 2.3 A) although the difference was small in the first time period. The average size of new patches was small and remained constant at 0.4 ha compared to patches which grew (1.6 ha in the first period and 4.1 ha in the second as an average of all increasing patches) (Fig. 2.3 B). The total area contributed by new colonizing patches was much smaller than that of increasing patches (a half of increasing patches in the first period and a quarter in the second).

Coalesced patches contributed half of the total area of disturbance patches in 2010. So whilst many small (<0.5ha) patches colonized new areas, and this increased between time periods, these colonizing patches were overwhelmed in proportional coverage by old patches that expanded. In 2010 new colonising patches totalled 81.1 ha (Fig. 2.3 C), which was only 4% of the total area. Most of this intense disturbance increase was as a result of the coalescing of older patches and the total area of new disturbance patch appearance was constant over the time period (Fig. 2.3 C) suggesting the rate of new disturbance patch appearance had decreased.

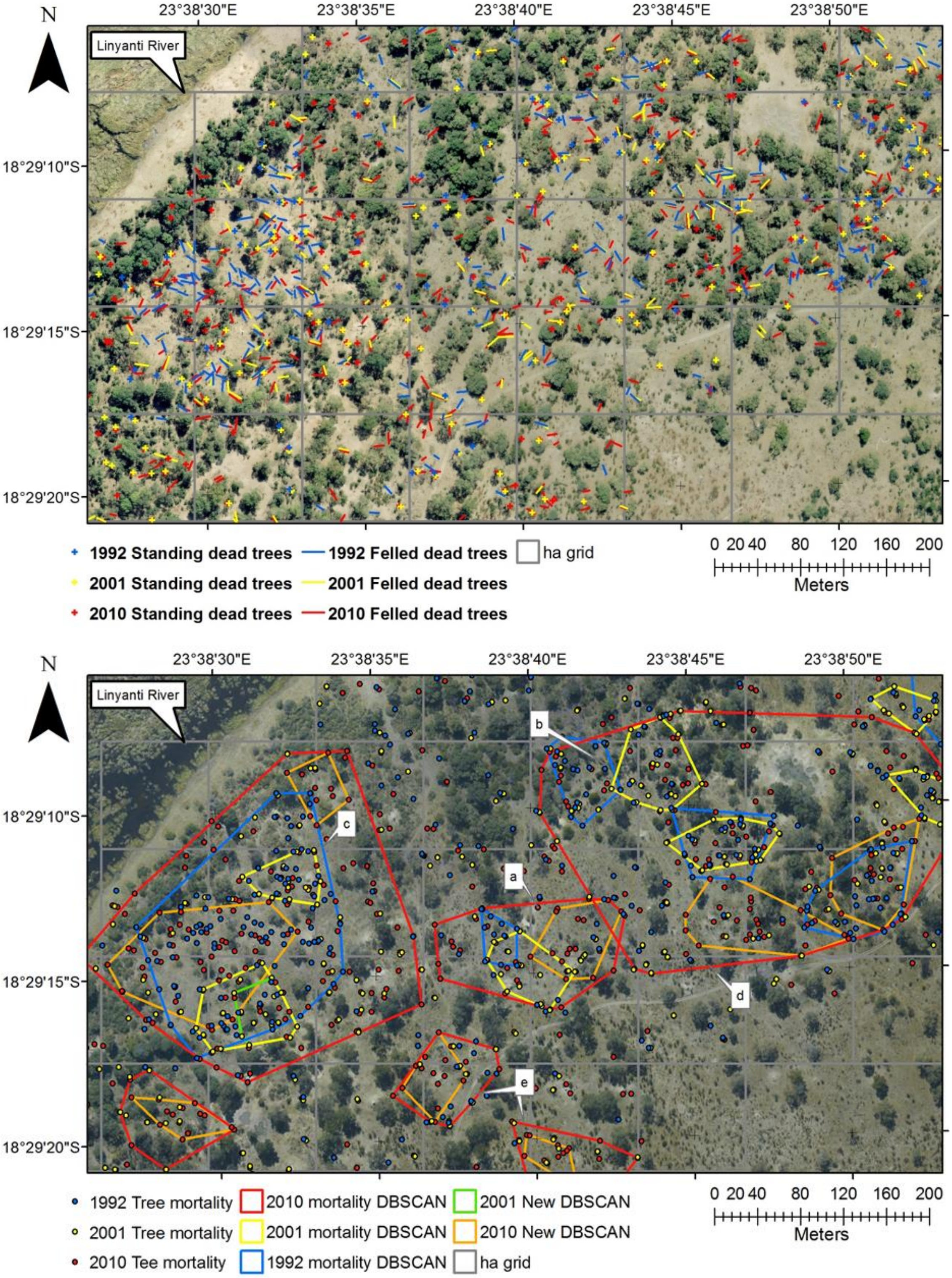


**Figure 2.2** Patchy tree disturbance superimposed on the 1992 aerial photograph (top) and for the same area of the 2010 aerial photograph showing DBSCAN-produced patches for each year (bottom). Scale = 1:3000. The position of future dead trees (2001, 2010) can be seen on markers overlaying canopies in 1992 (top). DBSCAN disturbance polygons (bottom) illustrate how patch dynamics can be measured over time (bottom). Some patches grew through expansion (patch a: 2001-2010); or lateral shifting to a neighbour (patch b: 1992-2001); whilst other fragmented into smaller patches (patch c: 1992-2001). New mortality in 2010 coalesced smaller patches into one big patch (patch d: 2001-2010); or appeared as new patches (e).

Patches also declined, through fragmentation, shrinking, and disappearing where dead trees either disappeared from decay or were obscured by shrub increase in those areas. Decline of disturbance patches was mostly by fragmentation where 5 patches broke up in 2001 forming 11 new smaller patches in 2010 with a total patch area of 12.7 ha (Fig. 2.3 C). We disregarded the large proportion of patches that disappeared between 1992 and 2001 due to the undercount in 2001. Between 2001 and 2010 a greater number of small patches disappeared (19 patches totalling 4.7 ha disappeared) as dead trees decayed or were replaced by patches of shrub obscuring felled trees. Disturbance patch size increased from a mean of 0.68 ha in 1992 to 1.42 ha in 2010 (Table 3). Fragmentation into small new patches was therefore not occurring to the same degree as growth of patches forming contiguous areas of intense disturbance patches in the matrix.

Very few patches remained static to persist with less than 15% area change (6 patches in 1992-2001 totalling 2.1ha and 7 patches in 2001-2010 totalling 0.8ha) (Fig. 2.3A,C). This shows that intense disturbance patches were highly dynamic in this landscape.

When viewed over the entire landscape, the pattern of the shift towards large coalesced patches between 1992 and 2010 becomes clear (Fig. 2.4). The main concentration of disturbance patches in 1992 was to the east of King’s Pool Camp (Fig. 2.4 panel B), and by 2010 these coalesced to form very large patches (up to 50ha in size). The increase in number of small patches by 2010 was pervasive from DT eastwards to BDF, but between BDF and CNP there were large areas which were not covered by disturbance patches.

Even though the total area of disturbance patches only increased by 16.5% over the period. there is also evidence of landscape fragmentation where inter-patch areas have become increasingly small and isolated (Fig. 2.4). Large tracts (up to 70 ha) in size of inter-patch areas still exist, particularly in the NE of the study region (Fig. 2.4).

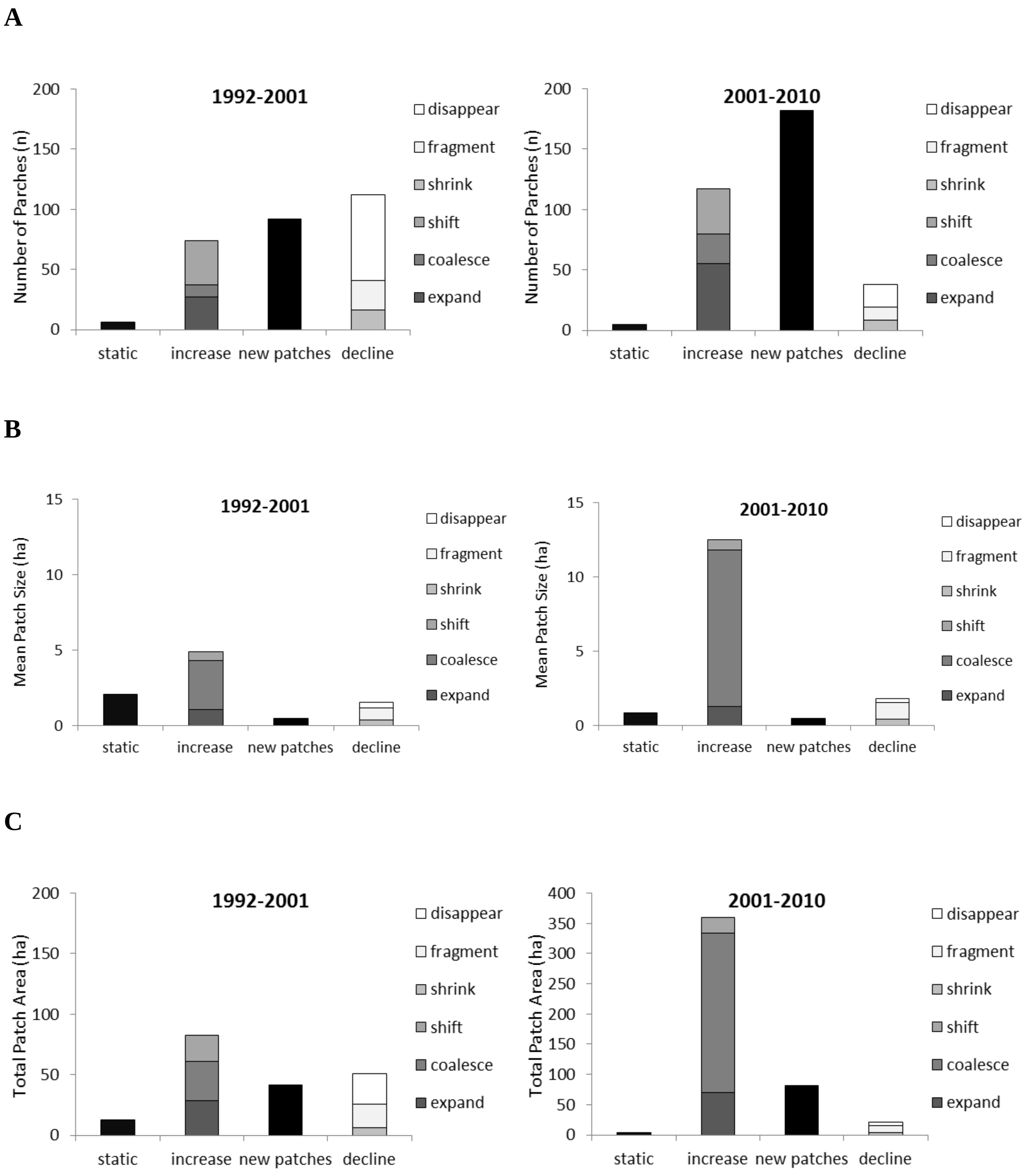


**Figure 2.3** Dynamics of patches through various fates of remaining static, increasing (via expanding, coalescing and shifting), new patch appearance, and decline (via shrinking, fragmenting and disappearing: for A) Number of patches; B) Mean patch size and C) Total patch area for 1992-2001 (left hand panels) and 2001-2010 (right hand panels). For panel C, the 2001-2010 y-axis is 2x that of 1992-2001

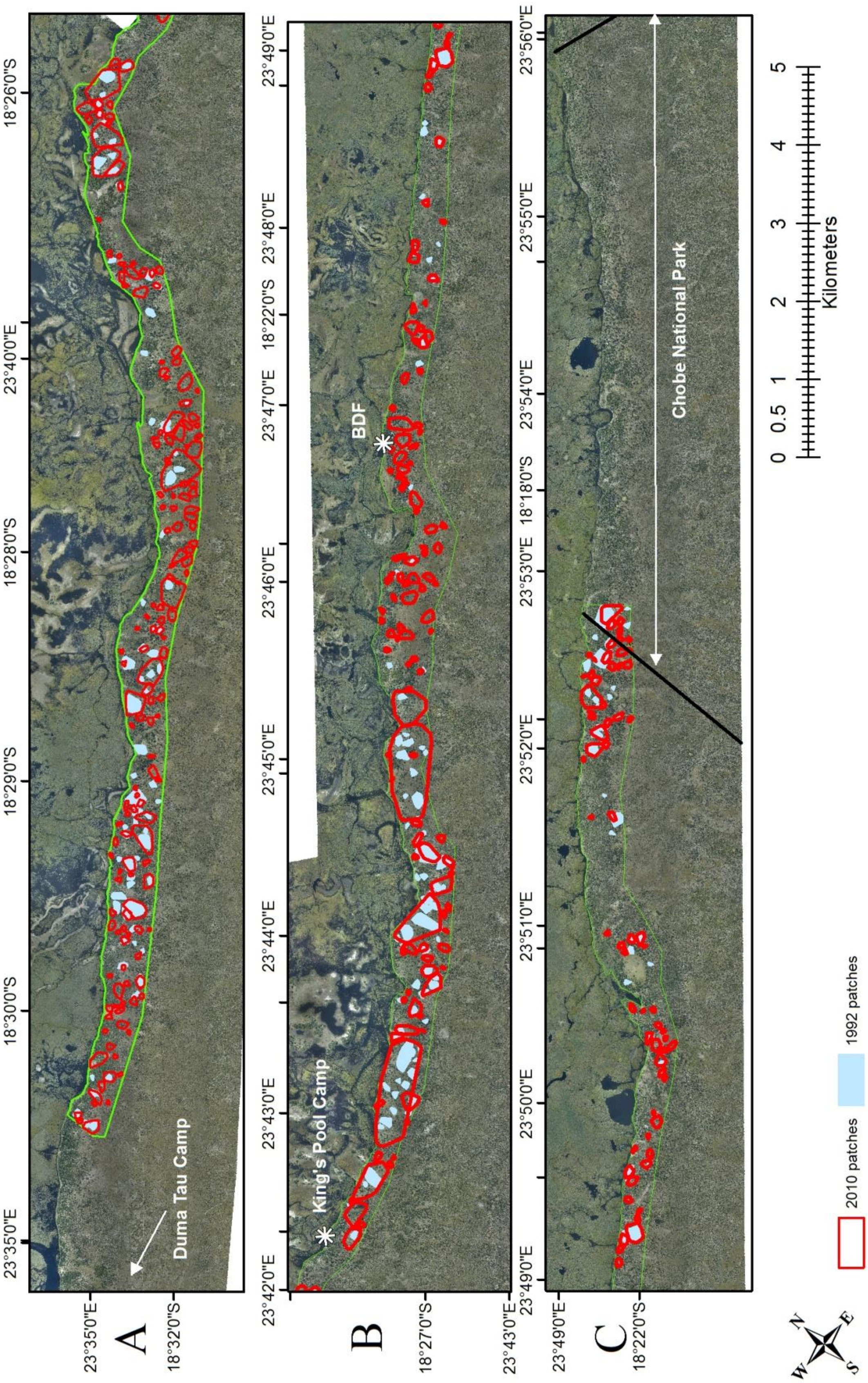


**Figure 2.4** Patch dynamics of disturbance patches from 1992 to 2010 across the 2000ha study region (outlined in green). Panels run from left to right with A in the West, B in the middle and C in the East. Scale = 1: 50 000.

### 2.4.4 Is there evidence of enhanced heterogeneity where patches intensify in disturbance and patch size remains varied?

There was no significant difference in the distribution of patch intensity over time (multiple pairwise KS tests), although only in 2010 were there patches with an intensity over 140 dead trees.ha$^{-1}$ (6 patches) (Fig. 2.5 A). The distributions of patch size over time also remained similar indicating that a variety of patch sizes remained over time (Fig. 2.5 B). The frequency of larger patches increased in 2010 and this was the only year to have patches larger than 10 ha (7 patches) (Fig. 2.5 B). There was no significant difference in patch size distributions between years (KS tests). Whilst the highest densities of dead trees and patch sizes were recorded in 2010, we can't conclude that contrast was enhanced by overall intensification, but a variety of patch sizes did remain (Figs. 2.4; 2.5B) .

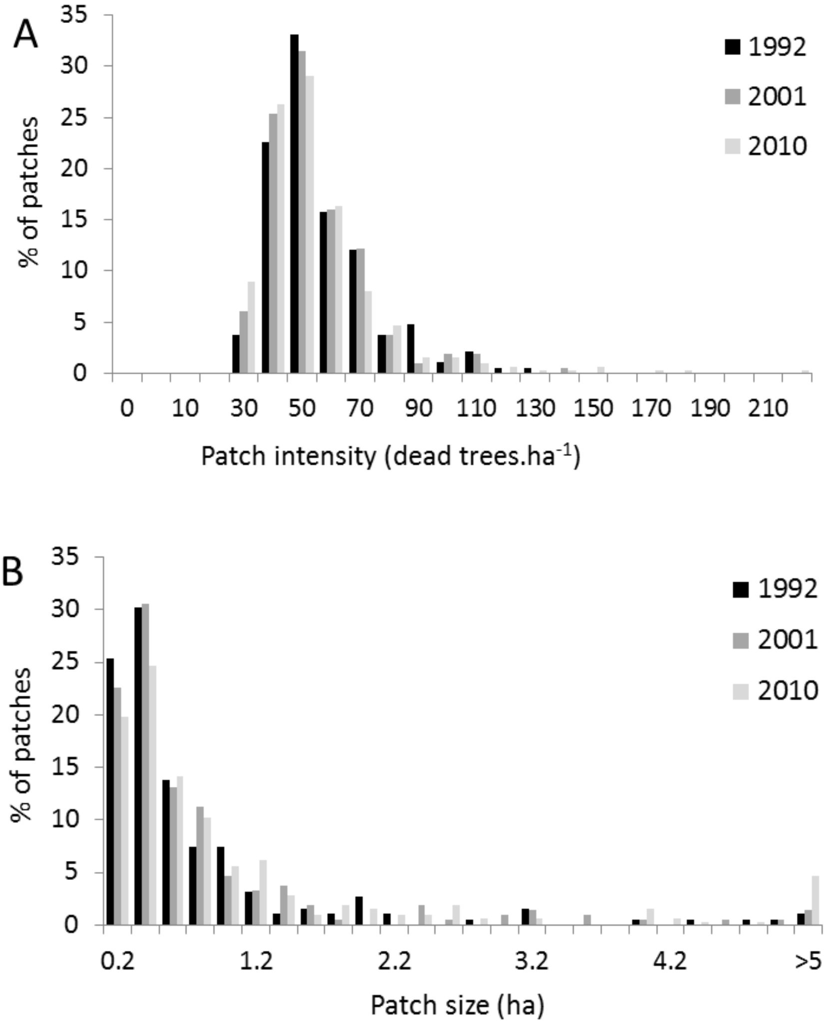


**Figure 2.5** Percentage of patches with A) different intensity classes (given as the density of dead trees per patch) and B) different size class (ha) for1992, 2001, and 2010 cumulative patches.

## 2.5 Discussion

### 2.5.1 Patch dynamics of elephant- mediated disturbance

We have found evidence of a dynamic system of patches of intense disturbance caused by elephant impacts (Chapter three) in the form of felled or standing dead trees. The patchy nature of intensive tree mortality is probably related to a patchy distribution of tree species. The majority of large (stem diameter >20cm) dead trees surveyed in a 2008 survey were of the two main acacia species (*A. erioloba* and *A. nigrescens*) which were found at a combined density of 18.7 ± 7 dead trees.ha$^{-1}$ (Chapter 3 Appendix 3.2) and were noted as occurring in groves.

The formation of patches of clustered dead trees in a savanna woodland landscape has important ecological consequences. Patches of concentrated large tree mortality represent larger changes in ecosystem structure and function than isolated tree falls would. Studies of large gap dynamics in northern hemisphere forests suggest these patches likely represent changed microclimate with increased solar radiation and soil temperatures (Prévost & Raymond 2012). In a semi-arid area this has important consequences for tree regeneration, favouring shade intolerant species, higher soil temperatures are likely to reduce the frequency of suitable germination episodes linked to periods of sufficiently high rainfall, although seedling establishment is enhanced through radicle extension rate (Stevens *et al.* 2014). A study of mortality of Australian acacias suggest that important nutrients such as organic matter, total N, total S and available P remain at elevated levels in the soil after tree death compared to open areas (Facelli & Brock 2000).

Disturbance patches increased at a rate of 0.9% of the total area per year to constitute 23% of the landscape area by 2010. There was no evidence of shifting steady-state mosaic system where disturbance patch area increased and declined but overall disturbance area remained constant (Turner 2010). Instead, tree mortality appeared to increase across the landscape, and spread mostly outside of patches, where inter-patch dead tree appearance rates increased 10 fold over the time period, despite the shrinkage of inter-patch areas which decreased 1.2 times over the same period. Small new patches of disturbance appeared in the inter-patch areas and over time this resulted in existing patches coalescing. By comparison, the rate of dead tree appearance inside disturbance patches remained more or less constant (the actual rate slowed over time (-0.38 trees.ha$^{-1}$.yr$^{-1}$) but measured for an increasing area).

If we take total area coverage as our measure, the overall pattern was one of growth in size of existing patches, and not the appearance of new patches, which is similar to a pattern of gap dynamics found in boreal forests (Hytteborn & Verwijst 2014). Whilst the total area of new patches remained constant, many small new patches appeared between 2001 and 2010. The most interesting dynamics were seen in the mean size of patches of different fates (Fig. 2.3B) and illustrated in our conceptual diagram Figure 2.6. Small patches (<1ha) appeared, coalesced and expanded into medium sized patches. These medium-sized patches (1-2ha) were most likely to persist or coalesce into larger patches, and very large patches (>4ha) tended to fragment back into medium sized patches. This can be seen across the landscape (Fig. 2.4) where the largest patches in 1992 had coalesced to form huge patches in 2010. The apparent mechanism for the fragmentation of patches was due to shrub increase (Chapter 4). Either new shrubs obscured old felled dead trees or dead trees decayed and disappeared, which meant gaps between older disturbance patches formed over time. Our method of marking standing dead trees meant any new standing dead trees could clearly be seen above the shrub canopy (Appendix 2.1) and even with shrub increase would still be categorised as a disturbance patch. The scale of patchiness produced by DBSCAN matches that of Bell (2003) who suggested the scale of impact was as large as 4 ha the period 1992-2001.

Ultimately there was a directional shift to increased larger disturbance patches in the landscape, and greater landscape fragmentation where inter-patch areas became increasingly small and isolated (Fig. 2.4). Fragmentation can have negative effects on biodiversity due to a larger number of increasingly smaller suitable habitat sites for animals as well as increased edge effects which increases the time spent by a species in disturbed areas (Fahrig 2003). For birds that rely on high cover in particular this can be detrimental. However large areas not classified as disturbance patches (open areas or filled with either shrubs or canopy trees) remained throughout the period, particularly to the west of CNP (Fig. 2.4), which is probably due to the high proportion of the resilient *C. mopane* in this area (pers. obs.).

In a study of 0.06 ha plots along the Chobe Riverfront, Rutina and Moe (2014) could not find any evidence of increased habitat heterogeneity of living woody plants following elephant disturbance and suggested the scale of study was too small to pick up heterogeneity change. We have shown that patches of disturbance were as big as four ha (though most were below 1.2 ha) suggesting the scale of elephant-induced patchiness is much larger than previously thought and may not be tied to groves of acacia as we hypothesized.

Some patches declined or fragmented, where dead trees were no longer visible due to decay or becoming obscured by the pervasive shrub encroachment documented in Chapter Four. We did not measure rate of dead tree disappearance, but expect dead trees of most species such as the acacias to persist in the system between the time points captured by the photos. Work in the arid Negev desert suggests that acacia trees can remain standing for about 10 years after death (Ward & Rohner 1997). The rate of decomposition once fallen is not known. Dead logs of hard wood species such as *Combretum imberbe* have been shown to persist in the landscape for up to 90 years when fires are absent (Vogel & Fuls 2005). Whilst dead trees may have remained in patches which declined, the shift from a disturbance patch of clearly visible dead trees to shrub recruitment remains a functional patch shift. We did not observe any replacement of disturbance patches with living large canopy trees over the period, but did not test this directly.

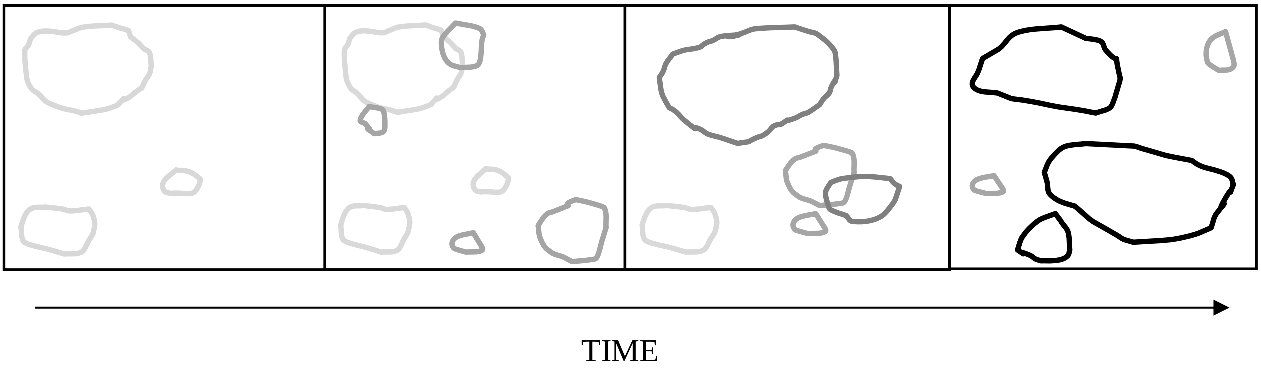


**Figure 2.6** Conceptual diagram of patch dynamics of intense elephant disturbance in the Linyanti woodland over time. Small patches appear and grow, with some disappearing (where standing dead wood decayed or was covered by shrub growth). Medium patches tend to coalesce, forming large patches which may decline by fragmentation. Scale approximately 4 ha for each square.

The shift to larger patches of disturbance may increase the chance of woodland regeneration. In a study of boreal forests Hytteborn and Verwijst (2014) found that larger forest gaps were more likely to be filled with regeneration, suggesting the mechanism for this was lower tree root competition in larger stands of dead trees. We suggest that fewer living trees in a large area potentially has less frequent visitations by elephants who move in the landscape in relation to forage and tree cover (de Knegt *et al.* 2008; Harris *et al.* 2008). Different sized patches are advantageous to different tree species having different light and nutrient requirements (Hytteborn & Verwijst 2014). The mixture of different sized disturbance patches evident in our study (Fig. 2.4) would also benefit a greater diversity of species.

Theoretical fragmentation studies have suggested whilst there is a nonlinear relationship between the availability of remaining habitat and the probability of species persistence (Harrison & Bruna 1999), species richness can decline when a threshold of about 20% of the original suitable habitat remaining, is reached (Fahrig 1998; Huggett 2005). Even with the increase in mortality over the time period, only 23% of 2000 ha was covered by intense disturbance patches in 2010, suggesting low fragmentation.  Contrast (intensity measured as the density of dead trees) within patches, and between patches and the matrix appeared to decline over the period. Contrast is an important measure of heterogeneity as contrasting composition of patches may support different ecosystem processes like regeneration or nutrient cycling (Cadenasso *et al.* 2003).

### 2.5.2 Disturbance rates at the landscape scale

We can calculate average proportional disturbance intensity measured as the density of dead trees in the landscape as a proportion of living trees calculated from transect surveys (Chapter 4). The density of living canopy tree species above 2.5m was calculated from transect data in 1992 and 2008 (Chapter 4) and represents the component of woodland which would leave large visible dead trees forming our dead tree dataset here. Dead trees as a proportion of remaining living trees was calculated as 9% for 1992 (6.85 dead trees.ha$^{-1}$ out of 74.5 trees.ha$^{-1}$ of living canopy trees taller than 2.5m) which increased to 42% in 2010 (11.92 dead trees.ha$^{-1}$ out of 28.19 (± 8.6 SE) living trees in 2008).  This is supported by our calculation that 50% of the tree population was dead in 2008 (Chapter 3).  This represents a considerable 4 fold increase of disturbance intensity from 1992 to 2008/2010. We do not think this suggests loss from compensatory recruitment, as we surveyed a distinct lack of saplings (Chapter 4) but rather a time-lag between elephant impact and tree death. Most impacted trees (90%) surveyed in 1992 had old impact, and only 1% had signs of new impact (Wackernagel 1993).  Some species were more resilient to elephant impact than others (the abundant *Acacia nigrescens* for example, can withstand repeated bark removal in comparison to the other abundant species *A. erioloba*).  Supporting this was the 40% decline in production of standing dead trees between the two time periods. Standing dead trees are likely to represent more recently ringbarked trees before they fall over whereas felled dead trees may have been killed a long time ago. Thus some of the large increase in dead trees and disturbance patches between 1992 and 2010 represents much earlier impact. By 2010 living canopy trees consisted mostly of resistant species (Chapter 3) and so we foresee patch growth slowing down in the future (Chapter 3).

Across several landscape types in the Kruger National Park, the areas outside herbivore exclosures experienced an average treefall rate of 1.27 trees.ha$^{-1}$.yr$^{-1}$ (measured by tree height change from lidar data) (Asner & Levick 2012). However when these authors examined two different river catchments,  they found extremely high rates of 3.8  and 2.1 trees.ha$^{-1}$.yr$^{-1}$ respectively and an estimated 5% annual adult tree mortality (Levick & Asner 2013). The background treefall rate in herbivore exclosures was around 0.19 trees.ha$^{-1}$.yr$^{-1}$ (Asner & Levick 2012). Although these rates were only measured over two years, they suggest that our gross dead tree increase rate of 0.28 $trees.ha^{1}.yr^{-1}$ is not much higher than a background rate, and it may be that elephant disturbance has reached an apex at 50% adult tree mortality. This was suggested by Wackernagel (1993) who found that 90% of elephant impact on living trees surveyed in 1991 was older than two-seasons. The cessation of water flow in the Savuti Channel in the early 1980's may have contributed to the historical high mortality pattern as elephants were compressed in a small area during a dry period. Elephants have become more dispersed in recent years, enhanced by exceptionally high rainfall since 2008 that has maintained upland ephemeral pans into the dry season (pers. obs.), the recommencing of the Savuti River flow, and the opening up of previously war-torn Angola to elephants (Chase & Griffin 2009).

## 2.6 Conclusion

The documentation of the dynamics of landscape systems in savannas is limited due to the heterogeneous spatial and structural template common in savannas (Levick & Rogers 2011). The exploration of patch dynamics in African savannas is extremely limited, and has relied on spatially explicit models (Wiegand, Saltz & Ward 2006); or theoretical models of large-scale changes between woody and grassy patches (Dean, Milton & Jeltsch 1999; Gillson 2004a; Meyer *et al.* 2007). We were able to delineate ecologically meaningful patches of intense tree disturbance and track the changes in patch dynamics through time using the novel density-based clustering method of DBSCAN. For the first time, spatiotemporal changes of disturbance patchiness has been analysed for intense elephant disturbance in a complex savanna.

Elephants have been considered as causing local landscape transformation through tree mortality (Tafangenyasha 1997; Western & Maitumo 2004; Rutina, Moe & Swenson 2005), and in a spatially explicit model de Knegt et al. (2008), found that high herbivore densities resulted in homogenisation of vegetation. Whilst the Linyanti woodland is shifting to pervasive tree mortality, a spatially heterogeneous patch structure still existed, and patches were dynamic and interacted with each other to grow, coalesce and fragment. The riparian woodland is also distinct from the upland savanna and broader scale patchiness was not tested. The rate of dead tree appearance was low compared to other areas suggesting the remnant trees were resistant to impacts, supported by our fieldwork data (Chapter 3). Turner (2010) found evidence that even very large disturbances do not homogenize the landscape, but rather that they create spatial heterogeneity, often at multiple scales. Our results suggest that even though disturbance patches increased as a result of increased mortality in inter-patch areas, patches themselves were clustered in parts of the landscape associated with increased fragmentation, while other areas had relatively few patches of disturbance (across time). A mixture of different sized patches with differing intensities was also maintained. Our results suggest that elephants can cause massive tree mortality (up to 50%) and create large patches of dead trees, but spatial heterogeneity was still maintained in spite of this and patches only constituted 23% of the landscape in 2010, though they were increasing. We foresee disturbance patch growth declining in the future due to the prevalence of resistant tree species in the remaining woodland. This highlights the importance of compensatory recruitment of canopy trees, which appears to be lacking in the riparian woodland.

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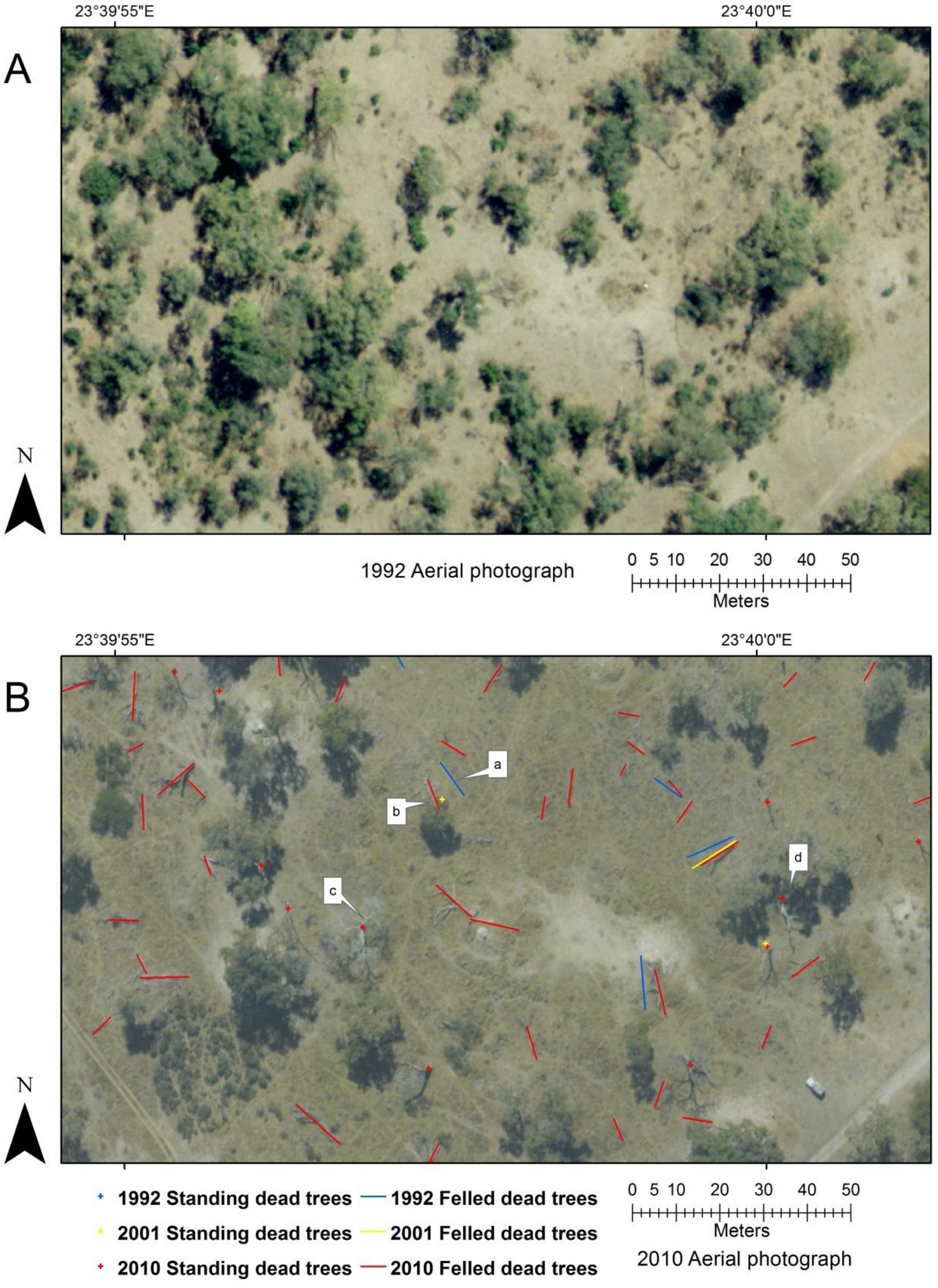
## 2.8 Appendices

2.1 Illustration of the method of manually marking dead trees from the aerial photographs

2.2 R code used for the DBSCAN method to extract high density patches from a spatial point pattern

2.3 Sensitivity analysis of DBSCAN search radius (ɛ) in clustering of dead trees



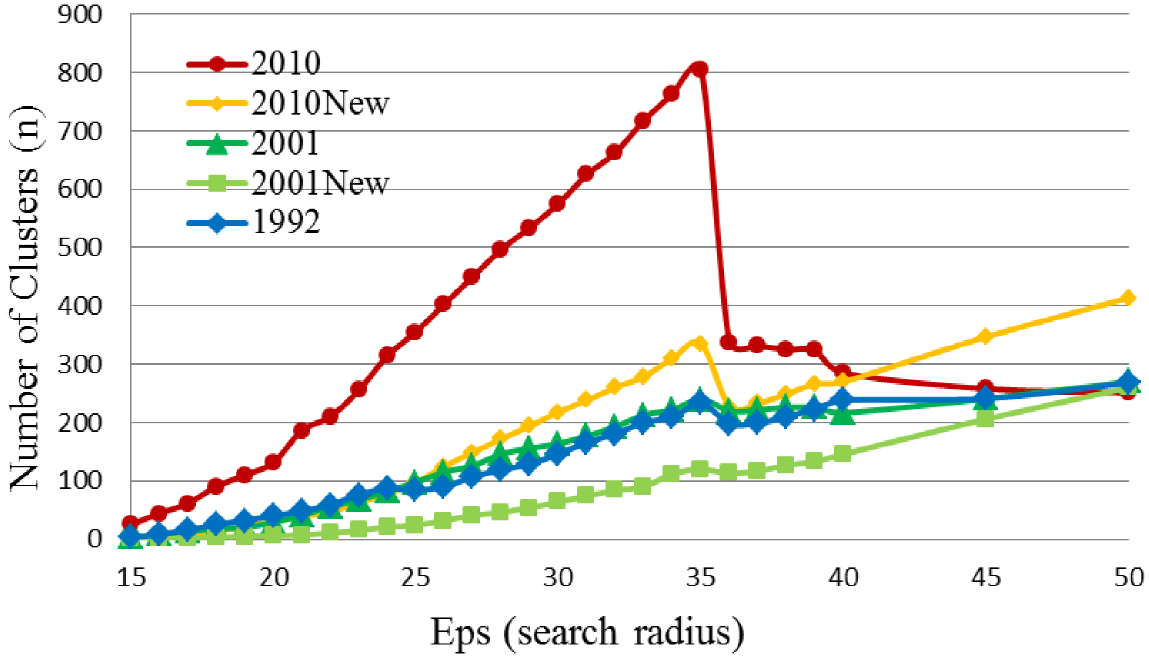
**Appendix 2.1** Illustration of the method of manually marking dead trees from the aerial photographs. Panel A is a sample of the aerial photo in 1992. Panel B is the same area in 2010 showing the marked dead trees (standing dead trees as dots and felled dead trees as lines) for all years where a) represents a dead felled log in 1992 which decayed to 2001 and was not remarked; b) a standing dead tree in 2001 which became felled in 2010; c) a newly dead standing dead tree in 2010; d) a dead tree emerging from a shrub understory. A landrover is visible in the bottom right corner of the 2010 image for scale.

## Appendix 2.2 R code used for the DBSCAN method to extract high density patches from a spatial point pattern “Mortx”

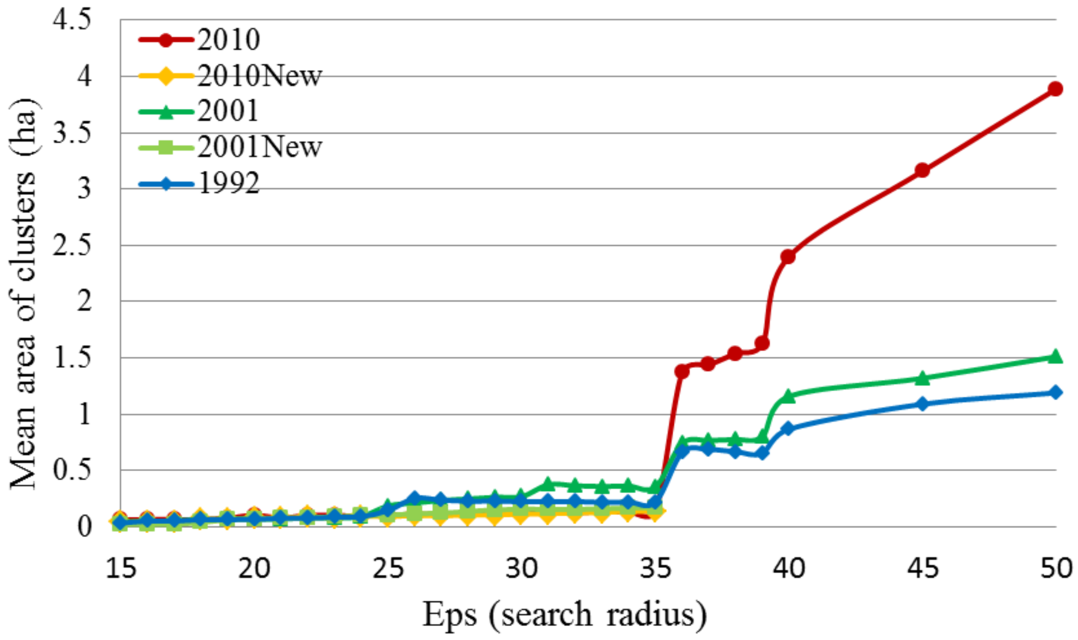
```
###load required packages###
    install.packages(mgcv, spatstat, maptools, sp, raster, rgdal, gpclib, spdep, spatial, fpc)
    require(mgcv, spatstat, maptools, sp, raster, rgdal, gpclib, spdep, spatial, fpc)
    spatstat.options(gpclib = TRUE)
###Import arcgis shapefile of mortality multipoint "mortx.shp"###
    mortx <- readShapePoints("mortx.shp")
###Convert shapefile tp planar point pattern for R###
    SP <- as(mortx, "SpatialPoints")
    mortx_ppp <- as(SP, "ppp")
###Create new matrix file of planar point pattern id, x-coordinates, y-coordinates###
    Mortx <- cbind(mortx_ppp$x, mortx_ppp$y)
    colnames(Mortx) <- c("x","y")
###Run DBSCAN on Matrix using Minimum number of points per cluster "MinPts", Search radius "eps" and showing all plots of the cluster process###
    d <- dbscan(Mortx,MinPts=10,eps=30,showplot = 2)
###bind the cluster number from each point to the matrix, renaming that column eps30###
    Mortx <- cbind(Mortx, d$cluster)
    colnames(Mortx) <- c("x","y","eps30")
###Export Matrix of ID, x-coordinates, y-coordinates, and cluster number for each point for each iteration###
    write.csv(Mortx, "C:/foldername/filename.csv")
###Add the csv file in ArcMap and then export it as a shapefile
```

## **Appendix 2.3** Sensitivity analysis of DBSCAN search radius (Ɛ) in clustering of dead trees

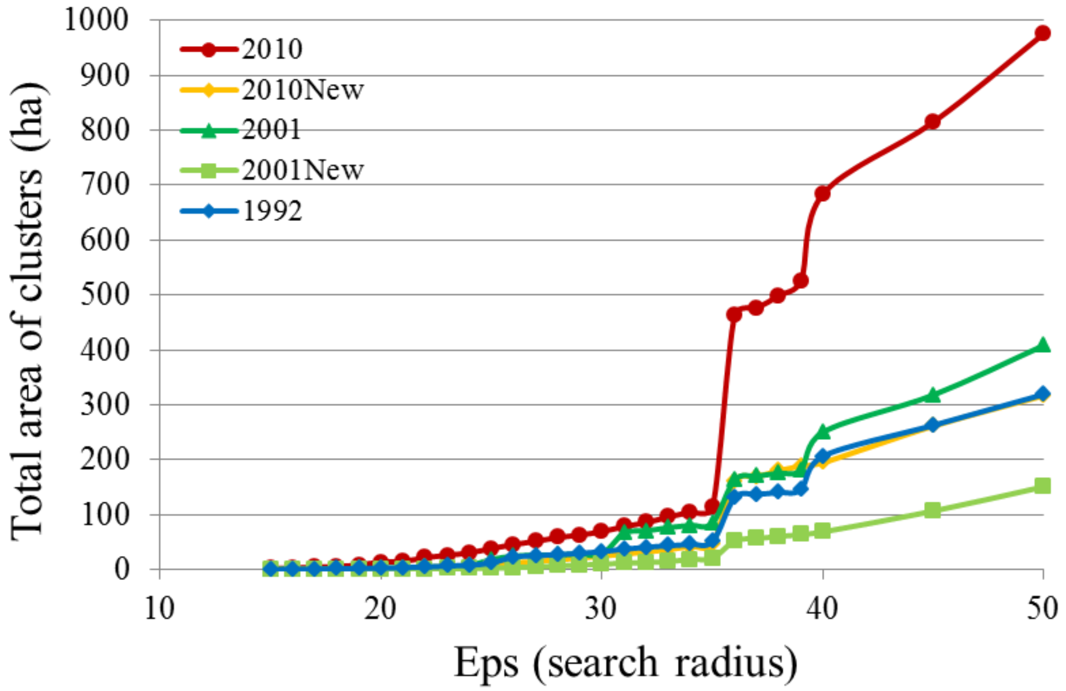
In order to establish the sensitivity of DBSCAN to various search radii Eps (Ɛ), we kept the minimum number of point at 10 dead trees, and varied Eps to determine at what distance neighbouring clusters merged as opposed to remaining discrete, which is what we would expect in a patchy environment of tree mortality. The sensitivity analysis of cluster number and area per Eps (Ɛ) search radius revealed that below a search radius of 35 Ɛ the mean size of clusters remained stationary, but patch number increased exponentially (Fig. 1). Above this threshold the smaller clusters started to coalesce and the number of clusters drops off, and at a distance of 40- 50 Ɛ the cluster numbers (Fig. 1) and mean cluster size (Fig. 2) tended to converge to a single point. This means that after 35 Ɛ the algorithm was more sensitive to bigger patches and could therefore detect coalescence, instead of just increasing number of patches. Above an Eps of 40, the total cluster size increased exponentially, especially for the 2010 data (Fig. 3). So between 35 and 40 Ɛ the algorithm was more sensitive to cluster size. We therefore chose 36 Ɛ as an appropriate search radius that did not form artificial large patches, but was sensitive to change in patch size.



**Appendix 2.3.1** Number of clusters produced by the DBSCAN algorithm for each year per each search radius (in 1 eps increments from 15 to 40 and then 5 eps increments to 50)



**Appendix 2.3.2** Mean area of clusters produced by the DBSCAN algorithm for each year (2010 on the right hand axis of larger scale) for each search radius.



**Appendix 2.3.3** Total area of all clusters per year produced by the DBSCAN algorithm per search radius.

# CHAPTER THREE

## Elephant-mediated compositional changes in riparian canopy trees over 17 years in northern Botswana

**Keywords**: Acacia, Chobe National Park, *Colophospermum mopane*, debarking, elephant impact, Linyanti, recruitment, regeneration, savanna woodland, selective disturbance, tree mortality, windthrow

## 3.1 Abstract

Savannas are disturbance driven systems where agents such as elephants (*Loxodonta africana*), through selective feeding on tree species and sizes, can change woody composition, often through the synergistic effect of fire. The Linyanti riparian fringe in northern Botswana represents a highly elephant impacted woodland where fire is largely excluded, and a valuable opportunity to assess decadal compositional changes caused by elephants. Following from a field survey in 1991/1992, we surveyed a sample of the woodland in 2008/2009, counting living and dead canopy tree species, level of elephant damage to each tree, as well as seedling abundance. We reconstructed the earlier pre-1992 woodland from living and dead trees and compared it to the composition and structure of the 1992 and 2008 woodland states. The woodland has seen dramatic compositional changes from an *Acacia-Colophospermum mopane* dominated tall tree woodland pre-1992 to a woodland in 2008 composed primarily of two resilient species (*C. mopane*, *Combretum hereroense*), and one avoided species (*Philenoptera violacea*). Through compiling Size Class Distributions where elephant impact was included, and logistic regression models of impact for each species, we found that elephant impact was likely the cause of this progressive woodland decline, although wind and senescence also contributed to large tree mortality. Elephants shifted their impact over time from preferred species that were easily ring-barked (*Acacia* spp., *Terminalia* spp.) to species more resistant to de-barking (*Combretum imberbe*, *Berchemia discolor*). The declining canopy tree species were represented in the seedling layer, but there was a recruitment bottleneck in the sapling stage. Low mortality rates suggest that a lack of recruitment and not mortality of large trees has driven the compositional shift in the woodland.

**Nomenclature:** All plant nomenclature follows Coates-Palgrave (2002)

**Abbreviations:** AIC = Akaike's Information Criterion; CCA= Canonical Correspondence Analysis; CNP = Chobe National Park; REM = Relative Elevation Model; DT = Duma Tau; GLM = Generalized Linear Model; KPL = King's Pool Camp; SCD = Size Class Distribution

## 3.2 Introduction

### 3.2.1 Disturbance in riparian woodlands

Savanna woody plant cover and composition is determined by both bottom-up factors such as soil and rainfall which determine Plant Available Moisture and Nutrients (PAM-PAN) and top-down factors of herbivory and disturbance (Walker & Langridge 1997; Sankaran *et al.* 2005, 2008; Bucini & Hanan 2007). Rainfall controls the upper limit of woody vegetation cover, and disturbances reduce woody cover below this upper limit (Sankaran *et al.* 2008). In the case of riparian systems, PAM is also dependent on groundwater recharge from the channel which is determined by rainfall in the river catchment.

Riparian woodlands are hotspots of biodiversity (Naiman, Decamps & Pollock 1993) and areas of the highest woody biomass in savanna landscapes (Colgan *et al.* 2012). They are also areas of high concentration of water-bound wildlife such as the African bush elephant (*Loxodonta africana* Blumenbach 1797) during the dry season. There is increasing concern for woody cover and compositional change in riparian areas and the knock-on effects for biodiversity (Smit & Ferreira 2010; O'Connor 2010; Levick & Rogers 2011).

Riparian woodlands are distinct features in savanna landscapes where large trees are key structural elements that provide resources such as shade, nutrients and nesting sites (Belsky 1990, 1994; Dean, Milton & Jeltsch 1999), enhance spatial heterogeneity (Manning, Fischer & Lindenmayer 2006), and provide essential forage for herbivores (Treydte, Riginos & Jeltsch 2010). Understanding the processes of turnover of canopy tree species (species which are capable of forming a riparian woodland) is therefore of particular importance (Ludwig, De Kroon & Prins 2008; Shannon *et al.* 2011; Asner & Levick 2012).

Riparian woodland composition can be altered by mortality of trees through flooding and drying through water table fluctuations (Tafangenyasha 1997; O'Connor 2010), and through disturbances from fire, herbivores and wind-throw. Disturbance from fire in riparian areas is fairly limited due to the low grass fuel load from grazing and trampling impacts of herbivore concentrations during the dry season (Plumptre 1993). Disturbance from herbivores takes place where the feeding habits of animals directly leads to plant death. This can be immediate when herbivores such as impala (*Aepyceros melampus,* Lichtenstein, 1812) consume seedlings (O'Kane *et al.* 2012), or delayed, where accumulated damage from debarking or stem breakage kills the tree. Porcupines (*Hystrix* *africaeaustralis*) have been noted as important debarking agents of certain tree species, leading to tree death, particularly when combined with fire (Thomson 1975; Yeaton 1988) but their pattern of debarking is distinguishable from that of elephants. Similarly, studies from Australian savannas have shown that tree-piping by termites may lead to the death of large trees when in combination with fire (Werner & Prior 2007). Megaherbivores are able to alter woody plant species composition by selectively impacting certain plant species (Owen-Smith & Chafota 2012; Bakker *et al.* 2016) and it is critical we understand the drivers and trajectories of compositional change in diverse riparian woodlands.

African elephants can kill plants by felling, pollarding, and uprooting smaller trees, and through bark removal (for reviews see Midgley, Balfour & Kerley 2005; Kerley *et al.* 2008) Elephants, unlike fires, are able to kill mature canopy trees through debarking, although intense windstorms and lightning may fell isolated large trees in savannas (Spinage & Guinness 1971; Williams & Douglas 1995). Elephant induced mortality of trees can affect savanna vegetation structure and composition at large scales (Barnes 2001b; Midgley, Balfour & Kerley 2005; Staver *et al.* 2009; Chafota & Owen-Smith 2009; Teren & Owen-Smith 2010; Owen-Smith & Chafota 2012). However little is known about long-term progressive effects of sustained elephant impacts on tree composition and woodland structure. This is mostly because it has been difficult to isolate and interpret elephant impacts separate from the additive and synergistic effects of fire (Moncrieff, Kruger & Midgley 2008; Chafota & Owen-Smith 2009; Shannon *et al.* 2011; Vanak *et al.* 2012), frost (Holdo 2007), and other herbivores (Skarpe *et al.* 2004; Makhabu, Skarpe & Hytteborn 2006; O'Kane *et al.* 2014) at the landscape scale. Most studies that incorporate the wide-spatial scales necessary for interpreting vegetation change are usually based on imagery (Mosugelo *et al.* 2002; Asner *et al.* 2015) and do not reveal compositional shifts.

Woody species that are capable of forming a canopy tree layer (hereafter referred to as trees) are distinct from subcanopy-forming shrub species that are fast-growing and kept within a fire and herbivore trap (below about 2.5 m) (Higgins, Bond & Trollope 2000; Zizka, Govender & Higgins 2014). Trees are capable of 'escaping' the browse and fire traps as tall adults, but are vulnerable as saplings (Neke, Owen-Smith & Witkowski 2006; Zizka, Govender & Higgins 2014). Here, we explicitly evaluate compositional changes affecting the riparian tree canopy rather than with structural changes in height and composition of the shrub layers (covered in Chapter 4).

Unlike most other disturbance agents, elephants are highly selective for plant species and sizes (Vesey- Fitzgerald 1973, Anderson & Walker 1974; Jachmann & Bell 1985; Kerley *et al.* 2008; Owen-Smith & Chafota 2012). Because of this, in woodlands where elephant impact is intense we would expect to see selected species and sizes decline while neglected species become proportionally more abundant (Bakker *et al.* 2016). Elephant impact can lead to tree death if it is severe enough; for example if a tree is ring-barked or if the main stem has been broken (uprooted) or snapped (pollarded). In addition to selection by elephants, compositional change can be driven by the differential responses of trees, as some species can recover bark following debarking events (Helm *et al.* 2011). Additionally, gaps created by the removal of selected or abundant species can be occupied by other previously minor species leading to woodland compositional turnover (Rutina & Moe 2014; Anderson *et al.* 2015; Bakker *et al.* 2016).

Within sub-Saharan Africa, elephants preferentially feed on species of *Acacia* (*A. erioloba, A. nigrescens, A. tortilis, A. xanthophloea*), species from the *Combretum* and *Terminalia* genera ((Ben-Shahar 1993; Skarpe *et al.* 2004; Owen-Smith & Chafota 2012); and *Colophospermum mopane* (Ben-Shahar 1993, 1996a; Styles & Skinner 2000; Hartnett *et al.* 2012). Wind and fire, by contrast, kill trees based on structural attributes like height and crown size, and not on palatability. Compositional shifts due to elephant disturbance are also likely to be related to woody species bark structure where greater mortality of trees with easily removed string bark (such as Acacias) may favour other groups with brittle bark which breaks off in small pieces (found in the Combretaceae) (Malan & van Wyk 1993).

### 3.2.2 Recruitment patterns in savanna woodlands

Studies of declining woodlands have commonly concentrated on mortality of large trees (by elephants and often through the synergistic effects of fire) (Helm 2011; Shannon *et al.* 2011; Vanak *et al.* 2012; Levick & Asner 2013; Levick, Baldeck & Asner 2014) and not on potential replacement of those trees from recruiting classes. Herbivore-driven bottlenecks arise through elephant-mediated selection in both sapling and seedling recruitment in the absence of significant fire disturbance. Only very rarely have compositional change studies taken a long-term view of disturbance-driven savannas concentrating on mortality and seedling regeneration of large trees (Moe *et al.* 2009). Studies of demographic bottlenecks are also limited (Higgins, Bond & Trollope 2000; Helm & Witkowski 2012; Sankaran, Augustine & Ratnam 2013; Anderson *et al.* 2015).

Savanna woodland tree species such as *Acacia erioloba* can live for centuries (Steenkamp *et al.* 2008) and seedling recruitment is dependent on appropriate soil moisture and temperature (Neke 2004; Midgley & Bond 2001). Episodic regeneration linked to rainfall in semi-arid savannas has been suggested for species such as the invasive *Acacia mellifera* in Namibia (Joubert, Smit & Hoffman, 2013) and *A. erioloba* in the Kalahari (Seymour, 2008). Episodic recruitment may also result from release from browsing pressure and fluctuations in elephant populations (Dublin, Sinclair & McGlade 1990; Prins & van der Jeugd 1993).

Elephants tend to concentrate their feeding on intermediate size classes and largely ignore small seedlings and plants less than 1m tall (Croze 1974; Pellew 1983; Jachmann & Bell 1985; Gadd 2002; Boundja & Midgley 2009). Chafota (2007) and Stokke and du Toit (2000) found that elephants concentrated their browsing within the height class 1-3m across the year in the Chobe river front. However for some species such as *Acacia* spp. elephants can search out and uproot even the smallest plants (Croze 1974; Barnes 2001a). These seedlings are also extremely sensitive to desiccation with no survival in dry years (Barnes 2001b) and it can be difficult separating causes of seedling mortality. In dry periods, germination under shading can increase seedling survival by reducing moisture loss (O'Connor 1995), but increase vulnerability to trampling and herbivory. Where elephants have removed the big trees, smaller seedling predators such as impala can prevent recruitment from seedlings as in the Chobe woodland (Skarpe *et al.* 2004, 2014; Rutina, Moe & Swenson 2005; Makhabu, Skarpe & Hytteborn 2006; Moe *et al.* 2009).

Elephant selection of certain size classes may lead to demographic bottlenecks of selected species, where recruitment into adulthood is prevented through mortality or continual pollarding and small trees are kept in a' herbivore trap' (Higgins, Bond & Trollope 2000). Tree species that can tolerate intense hedging through vigorous regrowth can form "browsing lawns" as displayed by *C. mopane* (Smallie & O'Connor 2000; Styles & Skinner 2000). But without mature trees producing propagules, there is a negative long-term effect on species persistence (du Toit et al. 1990, Fornara and du Toit 2007, Cromsigt and Kuijper 2011).

It has been hypothesised that the acacia woodlands along the Chobe River are a relic from the disturbances of rinderpest pandemic and ivory hunting (Walker, 1986; Skarpe *et al.*, 2004). Prior to the 19th Century, large concentrations of elephant in northern Botswana were noted by the earliest European explorers (Oswell, 1900 In: Meredith, 2001). During the19th Century elephant numbers were decimated by European and indigenous ivory hunters and by 1900 there were few remaining elephants in the northern areas of Botswana (Sommerlatte 1976; Campbell 1990; Vandewalle & Alexander 2014). Elephants numbers increased from about 1950 onwards (Vandewalle & Alexander 2014) and in 1963 spoor counts estimated about 500 elephants along the Chobe River (Child 1968) At the same time as elephants were extirpated, the rinderpest pandemic struck northern Botswana in 1895/1896, decimating ungulate populations such as buffalo (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), and bushbuck (*T. sylvaticus*) (Elephants were immune) (Caughley 1976; Walker In: Lewin 1986; Skarpe *et al.* 2014). With almost no browsers present, this probably resulted in an extreme recruitment event for trees.

There may also be longer term cycling of long-lived species. Evidence from archival records, field investigations and remote sensing also suggest there has been increased aridity over the past few centuries in northern Botswana (Ringrose *et al.* 2007; Hamandawana, Chanda & Eckardt 2008) and old acacia trees that are now senescing may be legacies of a much wetter past when elephants were more dispersed and recruitment chances were higher (Young & Lindsay 1988). The interplay between suitable regeneration conditions and seedling removal by herbivores can lead to episodic recruitment both in space and time (Skarpe *et al.* 2004; Wiegand, Jeltsch & Ward 2004), and may be reflected in long-term tree population demography.

Size Class Distributions (SCDs) have often been used to interpret the consequences of disturbance on tree recruitment and regeneration on demography (Fisher *et al.* 2011; Helm & Witkowski 2012). However, they are usually compiled irrespective of the health of trees, without distinguishing heavily damaged trees which may be dying. Additionally, authors have often interpreted inverse-J-shaped SCDs as indicative of ‘healthy agrading populations’ and J-shaped SCDs as representing ‘unstable’ or degrading populations (Jacobs & Biggs 2002; Helm & Witkowski 2012; Tsheboeng & Murray-Hudson 2013). Size Class Distributions as snapshots in time do not take long-term patterns of episodic recruitment (Moustakas *et al.* 2006) into account. There are also very few studies of the SCD of mortality (Shannon *et al.* 2008), and none where dead tree layer composition has been used to project historical conditions. Long term comparisons of SCDs are needed if we are to understand the consequences of demographic bottlenecks potentially caused by elephant impact.

Botswana has the largest contiguous African Elephant population in the world, upwards of 134 000 ((Blanc *et al.* 2007) and the Linyanti and Chobe Rivers are subject to extreme densities of elephants as they congregate along these perennial rivers in the dry season (April-October) (Skarpe *et al.* 2004; Chase 2011). This makes these riparian woodlands ideal study sites for investigating elephant impacts on composition and structure. A long term study of the Chobe riparian woodlands was undertaken but described changes in total canopy cover with no species information (Mosugelo *et al.* 2002) or broad shifts in composition of vegetation types (Skarpe *et al.* 2004, 2014). The transformation of the Chobe River woodlands was dramatic and by the early 2000s riparian woodland aerial cover had decreased from 60% to 30% over 36 years (Mosugelo *et al.* 2002).

Studies of compositional shifts resulting from elephants in other areas like Kruger National Park, have taken the form of exclosure studies (Wigley *et al.* 2014) with little information on long-term compositional change following disturbance. The Linyanti riparian woodland in northern Botswana represents an exceptional case to study severe elephant impact with historical data documenting the severity of the elephant impacts during this time (Coulson 1992; Wackernagel 1993; Ben-Shahar 1996b, 1998; Bell 2003). It also presents the opportunity of potentially separating elephant impacts from those of fire and smaller herbivores as fire is largely excluded and impala density is lower than that of Chobe (Chase 2011).

### 3.2.3 Research questions

The aims of this study were to determine compositional changes of canopy trees in the Linyanti riparian woodland, comparing field data from 1992 and 2008, and to assess the relative role of elephant impact, as well as the regeneration potential of the seedling and sapling layers. Towards these aims, our specific questions asked were: i) How has the composition of the woodland changed from pre-1992 to 2008? ii) Do the majority of dead trees show intense elephant impact? iii) Does the composition of the seedling and sapling layers allow for regeneration of the historical canopy woodland? iv) Is there evidence that canopy tree seedlings are limited to areas of higher moisture availability?

## 3.3 Methods

### 3.3.1 Study area

The Linyanti River forms the international border between northern Botswana and Namibia’s Zambezi region (previously Caprivi Strip), and has its sources in the Angolan highlands as the Kwando river, flowing SE before hitting a fault line and abruptly turning NE as the Linyanti River, before becoming the Chobe and Zambezi River downstream to the east (Chapter 1, Fig. 1.4). Except for the narrow western corner of CNP, most of the Linyanti riparian region lies within a photographic safari concession (NG/15, Chapter 1, Fig. 1.4.) currently leased by Okavango Wilderness Safaris (www.wilderness-safaris.com). On the Namibian side lie the Linyanti swamps of the Nkasa Rupara National Park (previously Mamili NP). Rainfall takes place in the summer months between November and April with a mean annual rainfall of 557mm (calculated for 92 years to 2014) at the nearest weather station at Kasane on the Chobe River, 140km away (NOAA 2014).

During the wet season elephants disperse to take advantage of ephemeral pans in upland areas. Local patterns of tree utilisation reflect this seasonality where elephants debark trees close to the river in the dry season and during the wet season forage on the mopane woodlands close to ephemeral pans (Fullman & Child 2012; Owen-Smith & Chafota 2012). Elephant density is seasonally extremely high in the study region of NG/15 (a survey area of 1232 km$^2$) where a density of 2.35 elephants.km$^{-2}$ was recorded during the dry season of 2010 (Chase 2011). These high densities have persisted since the 1980s where 12 elephants.km$^{-2}$ in 1000 km$^2$ of the Linyanti-Kwando area was recorded in the dry season of a 1987 survey (Spinage 1990)). Impala have been reported at lower densities in the Linyanti woodland compared to the Chobe riparian area (1.32 impala.km$^{-2}$ in a survey area of 1232 km$^2$ compared to 2.75 impala.km$^{-2}$ in a survey area of 1320 km$^2$ along the Chobe River (Chase 2011)). We observed very few other potential seedling browsers (steenbok, duiker, bushbuck)in the Linyanti and so do not consider these important disturbance agents.

The riparian woodland on the Botswanan side is a narrow (~100-200m wide) strip of mixed woodland occurring on a terrace above the river with no deep alluvium, backing on to vast mopane (*Colophospermum mopane)* woodlands. All plant nomenclature follows Coates-Palgrave (2002) and we have persisted in using the *Acacia* genus name as it represents a cohesive group in our compositional analyses. Soil conditions along the Linyanti riparian fringe differ from those along the Chobe River as there is a fault terrace on the Botswana side, instead of the Chobe alluvial terrace (Skarpe *et al.* 2014). Soils on the riparian terrace are broadly described as Vertic-Mollic Gleysols (FAO, 1990), but spatial variation in soil properties is seen by the presence of numerous palaeochannels as well as calcrete outcrops. Little is known about the soil distribution along the Linyanti but it appears that the soils are consolidated Kalahari sand mixture overlaying basalt bedrock that represent downwash from inland catena rather than being derived from flood deposits. Little is known about the hydrology of the Linyanti system but flooding takes place towards the alluvial fans of the Linyanti swamps on the Namibian side (Cronberg *et al.* 1995; Haddon & McCarthy 2005). Trees on the Botswana side are elevated above the river level and not subject to flooding.

There are few records of historical vegetation composition along the Linyanti apart from a survey conducted in 1966-1967 by Child (1968) and one in1973-74 by Sommerlatte (1976). In the 1960's the Linyanti riparian woodland was described as acacia riparian forest composed of *Acacia erioloba* and *A. nigrescens* interspersed with open woodland and shrubland (Child, 1967). Sommerlatte (1976) identified two main vegetation types along the Linyanti, dominated by either *C. mopane* or *Acacia* spp (*A. nigrescens, A. erioloba, A. luederitzii*) depending on the soil type. *Acacia erioloba* dominated the acacia areas with a relative frequency of 54.2% in the tree layer (>3m in height) and 8.3% in the shrub layer (<3m in height). Already in the 1970's there was concern over the lack of acacia regeneration and episodic recruitment was suggested (Sommerlatte 1976). Additionally Sommerlatte (1976) noted that the acacia stands along the Linyanti appeared very old. In the 1970's in the Linyanti area 29% of trees were already dead and 81.1% of total mortality was attributed to elephant impact (Sommerlatte 1976).

### 3.3.2 Field Data Collection

This long-term study is dependent on an earlier survey conducted by Wackernagel (1993) in the wet season of October 1991- January 1992 (for brevity referred to as the 1992 survey) and reported in an unpublished MSc thesis (Wackernagel 1993). Wackernagel surveyed vegetation composition, structure and impact along 35km of riverfront between the eastern boundary of Chobe National Park westwards to the King's Pool Safari camp (Chapter 1, Fig. 1.6). Wackernagel (1993) sampled regular transects every 0.5km along the main safari road on either end of the study region (high disturbance area) and every 1.0km in the middle section (lower disturbance area), giving a total of 50 transects .The 1992 study provides baseline data of compositional changes documented earlier by (Sommerlatte 1976). We located the approximate positions of the transects on the 1992 aerial photograph by tracing the outline of the main road as a polyline the 1992 aerial photograph in ArcMap 9.2. We placed points according to the interval specified by Wackernagel (1993) every 500m in the two high density areas at either end of the 1992 study region, and every 1.0km in between (Chapter 1, Fig 1.6). In our follow-up-study in the wet seasons of Dec 2007/Jan 2008 and Nov/Dec 2008 (referred to as the 2008 survey in the text) we repeated this survey. Because we were interested in areas of high tree mortality, we used digital colour aerial photographs (1:10000) of the study area from 1992 and 2001 to divide the 2008 sampling area into high tree mortality areas by manually marking every dead tree and running a density kernel function in ArcMap 9.2. Three areas of dense tree mortality were found (Chapter 1, Appendix 1.3.1) and surveyed in 2008: one in the west of the study area (but not covered in the 1992 survey) near Duma Tau Camp (DT) (17 transects), one 10km east, on the eastern side of King's Pool Camp (KPL) (18 transects) (and intensively covered in 1992) and the last in the eastern side of the study area around the CNP/NG 15 cutline (also intensively sampled in 1992) (Chapter 1 Fig.1.4. Map of Transects). Additionally, 6 palaeochannels visible from the photographs and 5 transects around the Botswana Defence Force (BDF) camp were surveyed as they represented potentially lower elephant impact/higher soil moisture than the high impact transects. In each of our survey areas in 2008, transects were placed every 200m apart, giving a total of 55 transects. The DT transects were not included in the analysis comparing the 1992 and 2008 composition to reduce spatial variability, but were included in comparing the 2008 seedling, sapling and tree compositional similarity.

Transects (both 1992 and 2008) ran perpendicular to the river from river edge to mopane zone indicated by the increased prevalence of *C. mopane.* In 1992, transects were not of fixed-width but used distance-based sampling to estimate nearest neighbour density using the T-Square Method (Byth 1982). In 2008 we opted to survey fixed-width belt transects which increased the number of transects we could survey but meant that density estimates of compositional change could not easily be compared between surveys. Instead we opted for describing proportional abundance changes. Each belt transect in 2008 was 10m wide for riparian canopy tree species and 5m wide for *C. mopane*. The 2008 transect start and end points were determined in the field with a GPS and used to calculate the length of each transect. For the 2008 survey we calculated the density of all species and sizes across the survey area.

All dead and living trees above 0.5m in height were identified by species, and their height (in metres) and basal stem diameter (in centimetres) recorded. Species of dead trees were identified from bark, cambium, root, and branching morphology as well as colour. If a species was unknown, it was marked as such, with some only being identified to the genus level. We used consistent stem diameter size classes from 1992 in 2008, giving six classes: <1.9cm; 2-3.9cm; 4-9.9cm; 10-19.9cm; 20-50cm; >50cm. Note that only plants taller than 0.5m were surveyed for this study. In 2008, for time constraints we surveyed the abundant *C. mopane* by height only, in four classes: <1m, 1-3m, 3-10m, >10m. Rare acacias were lumped into one group (*Acacia* spp.) which included *A. luederitzii* (the most common of the group), and the more localised *A. caffra* and *A. schweinfurthii*. *Combretum hereroense* was apparently incorrectly identified as *C. molle* in some cases in the 1992 survey and these two species were combined for the purposes of analysis.

Elephant impact was recorded by percentage of main stem circumference stripped of bark and number of stems (main or side stems) broken. A high elephant impact category was trees which had over 50% bark circumference removed and/or with the main stem broken (or pushed over) or over half of the side stems broken (heavy pollarding). Trees that had recovered from old elephant impact, either by resprouting a main stem or bark recovery were noted separately.

Fire is a rare event in the riparian zone, and we documented zero extensive fires and only six documented localised (<1km$^2$) single fire events between 2001 and 2016 across the 2000ha study region from MODIS data (NASA FIRMS 2016). No transects in 2008 were located in fire-affected areas. Disturbance from wind-felling could only be positively identified following chance severe storms which occurred during both field seasons. Trees that were identified as having severe impacts from other agents of mortality such as wind, fire, termites were grouped as ‘other impact’. If the damage to trees was not positively identified (for example on very old decayed dead trees), this was noted as unknown damage. Although some dead trees may have decayed over time, with the lack of fire dead wood remains on the ground for some time (felled trunks visible in 1992 aerial photographs were resampled in photographs 18 years later (Chapter 2)).

Seedlings (plants less than 0.5m in height) were not surveyed in 1992. In 2008 we surveyed seedlings using square metre quadrats placed at a sampling point every ten metres along each transect. The quadrat was flipped on each of its edges to include 4 neighbouring quadrats to increase sample size to a total of 5 $m^2$ per every sampling point. We estimated the aerial cover percentage (to the closest 5%) of seedlings for each square metre and per species. The aerial coverage of each seedling species was then totalled per transect ($m^2$), as well as the proportion of total area sampled covered by seedlings. We compared the aerial coverage of seedlings (<0.5m) to the densities of saplings (>0.5m in height, <10cm stem diam.) and canopy trees (>10cm stem diam.) for the 2008 survey. We used density instead of proportional abundance to reflect actual regeneration capacity from seedlings and saplings. Density was calculated from a total area covered by transects of 23.91 ha. We compared the density of saplings to trees for the most common species using a paired t-test to establish if recruitment potential from saplings exceeded the current adult density. We only used those species with a minimum of ten sapling/tree observations (transects).

To evaluate the effect of increasing aridity on regeneration, we used relative elevation above the main river channel as a proxy for available soil moisture. We produced a Relative Elevation Model (REM) relative to the main channel. The REM (min -3m, max 8m) was calculated from a 2010 LiDAR survey DEM (Digital Elevation Model). The ground DEM was a 1m rasterized layer of the ground returns from LiDAR flown in 2010. Ground validation of vegetation height for LiDAR was conducted at the same time as aerial data collection. LiDAR points were pre-processed using Precise Point Positioning (PPP). We used Zonal Statistics in ArcMap to extract the mean relative elevation values for each 10m wide belt transect. Whilst average REM values per transect are admittedly not able to account for microtopography such as small troughs, we felt that because some transects were placed directly along palaeochannels, and there is an east-west elevation gradient, using average REM values was a simple approximation of potential rooting soil moisture.

### 3.3.3 Data and statistical analysis

#### 3.3.3.1 Research question 1

To evaluate compositional changes, we projected the former state of the woodland prior to 1992, by combining living and dead canopy trees surveyed in 1992 and plotted a 3D chart of species and size class. We compared this to the state of the woodland by living trees in 1992 and 2008 by compiling two further 3D charts. We used descriptive statistics to evaluate proportional abundances in the canopy tree layer (trees >20 cm stem diam.) and for all sizes.

#### 3.3.3.2 Research question 2

To assess elephant impact on tree mortality we compared proportional abundance of high and low impact on living and dead trees between 1992 and 2008. We then compiled individual SCD's per species of living and dead trees, including proportional high elephant impact for both 1992 and 2008. Proportions were of total tree count per species per survey.

To determine the effects of agent and level of impact (high elephant, low elephant, other agent), size class and year (1992 or 2008) on the mortality of trees per species, we performed logistic regression models (GLMs) with the form:

$$P = \frac{1}{1 + e^{-(\beta_1 + \beta_2 X_2 + \ldots \beta_n X_n)}}$$

With $P$ being the probability of mortality, $X_2 - X_n$ being independent variables, and $\beta_1 - \beta_n$ being coefficients estimated from mortality data.

We produced GLMs for each species individually where the response variable was 0 if the tree was alive and 1 if the tree was dead. The independent variable size class was a categorical factor of six levels of stem diameter for all species except for *C. mopane* which had 4 bins of height classes. Because of complete separation occurring due to the overwhelming proportions of dead trees and/or high elephant impact, we fitted logistic regressions using Firth's (1993) maximum likelihood bias-reduction method. This was done in R (version 2.15.3; R Core Team (2013)) using the package brglm (Kosmidis, 2013) where fitting took place on iteratively updated pseudo-data which the package calculated to mimic the behaviour of the input responses and totals. Our R code is presented in Appendix 3.1.

The response variable was tree mortality (binomial 0 = a living tree, 1 = a dead tree) and all explanatory variables were categorical: 1) impact (with 3 levels- high elephant impact used as a reference level; low elephant impact; and impact by other or unknown agents); 2) size classes (6 levels of stem diameter size classes with the smallest- 0-2cm used as a reference); 3) Year (1992 vs

2008); 4) the 2-way interaction between impact and year and 5) the 2-way interaction between impact and size class and 6) the 3-way interaction of impact, year, and size class For *C. mopane* the size classes are instead given in four levels of height: 1-3m, 3-10m, >10m, with 0-1m height used as the reference.

For each model we calculated percentage explained variation by McFadden's pseudo $R^2$ ($R^2$ = 1- null deviance/ residual deviance). We performed model selection by manual backwards stepwise selection using Akaike's Information Criterion (AIC). Model selection details are given in Appendix 3.1. The use of AIC in model selection of penalized likelihood models is controversial as AIC was developed under the assumption that estimation is by maximum likelihood (MLE) which is violated by using Firth's penalized likelihood in brglm, but we noted Kosmidis (2013) comments that the modified-scores approach (of brglm) is equivalent to maximum likelihood as the MLE is asymptotically unbiased.

We selected the best model for each species based on ΔAIC rank by progressive backwards stepwise elimination of 10 candidate models from all interactions to single factor models: 1) all interactions: ~impact * size class * year; 2) excluding the 3-way interaction; 3) excluding the 2-way interaction impact * year; 4) excluding the 2-way interaction impact * size class; and 5) only single terms: ~impact + year + size class; 6) excluding year: ~impact + size class; 7) excluding size class: ~impact + year; 8) only ~impact; 9) only ~size class; 10) only ~year (Appendix 3.1). We chose the most influential explanatory variables for each best model based on variable estimates and standard errors.

#### 3.3.3.3 Research questions 3 and 4

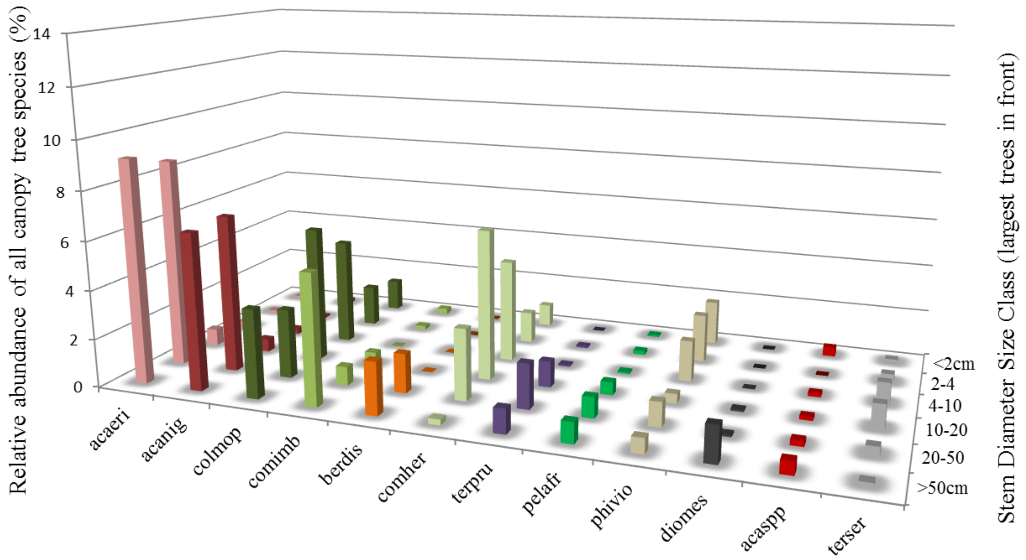
Compositional recovery potential of the canopy was assessed by comparing the proportional contribution of canopy tree species in the tree (>10cm stem. diam.), and sapling layers (<10 cm stem diam.) by percentage density (trees.ha$^{-1}$)) and compared to the seedling layer (percentage total seedling foliar cove (m$^2$). To determine the environmental variables that influence canopy tree seedling distribution in 2008, we performed a CCA (Canonical Correspondence Analysis) in CANOCO 4.5 using the coverage (m$^2$) of the 11 most common canopy tree seedling species per each of the 55 transects. The environmental variables used were: 1) the density of all living canopy trees, 2) the density of all dead canopy trees, 3) the density of dead acacia trees, 4) the density of all shrub species, 5) the density of *Combretum mossambicense* (the most common shrub which occurs in dense patches (Chapter 4)), and 6) average relative elevation (above the main channel) (REM). Down-weighting of rare species was allowed for, and forward selection by Monte Carlo tests (999 permutations) were used to select significant environmental variables ($p < 0.05$). The total variation explained by the CCA was calculated as a percentage of all canonical eigenvalues divided by the sum of all eigenvalues (Lepš and Šmilauer 2003).

## 3.4 Results

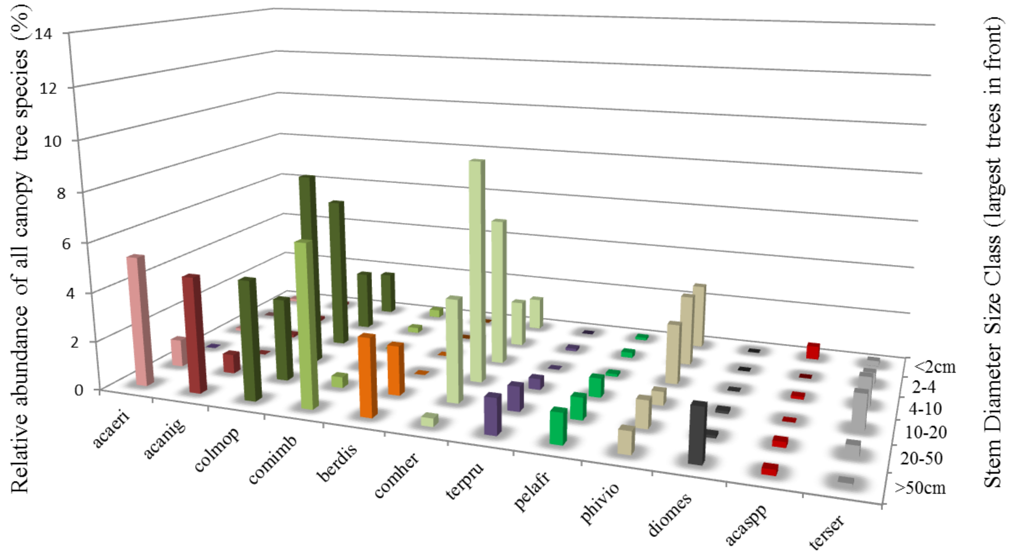
### 3.4.1 How has the composition of the woodland changed from 1992 to 2008?

By combining both living and dead trees surveyed in 1992, we recreated the historical pre-1992 compositional and structural representation of the woodland and compared it to the state of the woodland in 1992 and 2008 (Fig. 3.1). Tall canopy trees (trees over 20cm in diameter) prevailed in the recreated woodland prior to 1992, forming 60% of the woodland, but declined to 47% in 1992, and were further reduced to just 18% in 2008 (Fig. 3.1A). Two Acacia species that dominated the tall canopy layer (size classes 5 and 6: >20cm diameter) in the recreated pre-1992 woodland were *A. erioloba* (17.8%) and *A. nigrescens* (13.0%) (Fig. 3.1A). By 1992 (Fig. 3.2B) the canopy layer (trees >20cm diam.) was no longer dominated by the Acacias, but evenly spread amongst 6 species (*A. erioloba, A. nigrescens, C. mopane, C. imberbe, B. discolor, C. hereroense/ molle*) each of which contributed between 4.5% - 8.2% to this layer. Whilst the Acacias were still prevalent in the canopy layer in 1992 (around 6%) they were by then limited to only the largest trees (>50cm diam.) (Fig. 3.1B). The decline of large canopy trees had continued to 2008 (Fig. 3.1C). Large trees (>20cm diam.) of *A. erioloba* were extremely rare and *C. imberbe* had become the most common large tree (4.8%), followed by *D. mespiliformis* (2.8%), which was proportionally uncommon previously.

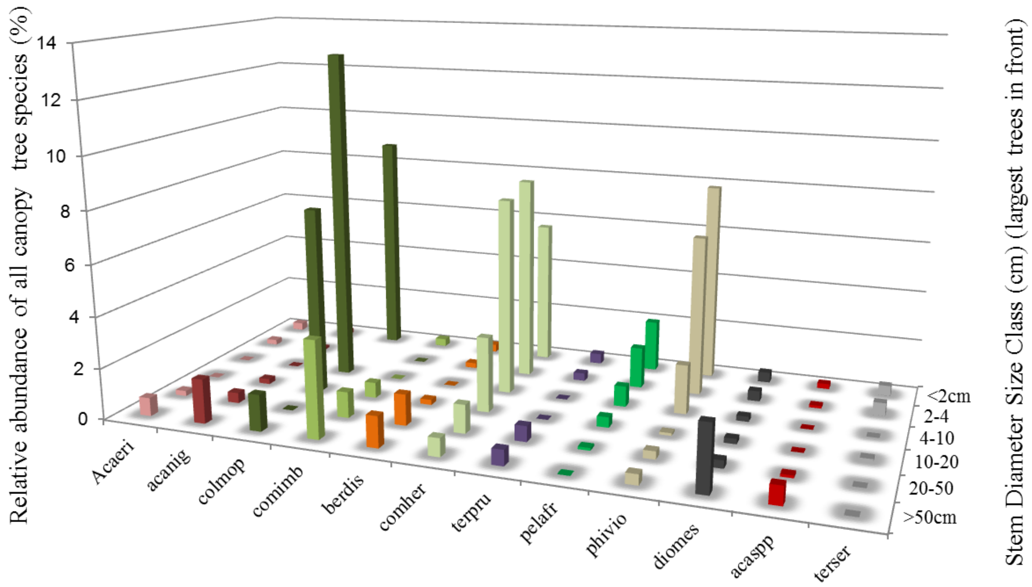
For all size classes, *C. mopane* was the most common tree pre-1992 at 20.0% of the woodland followed by *A. erioloba* (19%) and *A. nigrescens* (14%) (Fig. 3.1A). The combined *C. hereroense/molle* group was also very common in the woodland (15.8%) but concentrated in intermediate sizes. The remainder of the woodland composition was spread between 3 and 7% per species amongst *C. imberbe, B. discolor, T. pruniodes, P. africanum, P. violacea,* and *T. sericea* (*T. sericea* was mostly absent from the canopy sizes). *Diospyros mespiliformis* and the remaining *Acacia* species were relatively uncommon in the pre-1992 woodland recreation at less than 2%. In 1992, *C. mopane* remained the most common tree, increasing in proportion to 26.7% (Fig. 3.1B). *Combretum hereroense/molle* was the second most proportionally abundant woodland species (23%) followed by *P. violacea* (10.7%).



**A.** Reconstructed Composition Pre-1992 (living and dead trees in 1992)



**B.** 1992 Woodland Composition (Living trees 1992)



**C.** 2008 Woodland Composition (Living Trees 2008)

**Figure 3.1** Compositional changes in the woodland from **A:** a reconstructed historical composition of the woodland pre-1992 (derived from live plus dead trees in 1992); **B:** composition of the woodland in 1992 and **C:** composition of the woodland in 2008. Stem diameter size classes representing the tallest trees are in front. Values are percentage abundance of all trees per year. Species are ordered in abundance of the largest canopy trees (>20cm diam.) by projected pre-1992 dominance. Species codes are: acaeri *Acacia. erioloba*, acanig *Acacia nigrescens*, colmop *Colophospermum mopane,* comimb *Combretum imberbe*, berdis *Berchemia discolor*, comher *Combretum hereroense/molle*, terpru *Terminalia prunioides,* pelafr *Peltophorum africanum*, phivio *Philenoptera violacea,* diomes *Diospyros mespiliformis,* acaspp *Acacia* spp., terser *Terminalia sericea*. *C. mopane* is displayed in four height classes in 2008 (0.5-1m; 1-3m; 3-10m; >10m) because stem diameters were not measured for this most abundant species. The bars for *C. mopane* have been shifted to best fit the diameter ranges. Individuals less than 0.5m were excluded.

The decline of the two previously common Acacia species to around 6% of all trees was due to lack of any recruitment into smaller sizes (Fig. 3.1B). By 2008 (Fig. 3.1C), the Acacias had virtually disappeared from the woodland and there was a conversion from a tall canopy tree woodland to one dominated by small sizes and by only 3 tree species which together make up 75% of the woodland in 2008: the relative proportion of *C. mopane* had increased from 20.0% to 30.6%, followed by *C. hereroense* (26.6%) and *P. violacea* (16.9%), comprising mostly small plants.

### 3.4.2 Do the majority of dead trees show intense elephant impact?

A total of 1321 trees were surveyed in 1992 and 2121 trees in 2008. By 2008 the majority of the canopy was dead at 51% (n=1093) having escalated from 31% (n = 413 trees) in 1992. This indicates an annual mortality rate of 2% per year over all size classes. The majority of dead trees showed signs of severe elephant impact (over 50% stem circumference debarking or main stem breakage) for both surveys (Fig. 3.2). In 1992 most dead trees showed severe elephant impact (52% of dead trees n = 1321). By 2008 elephant-impacted dead trees increased to 62% (n = 2121) of dead trees exhibiting severe elephant impact.

The proportion of dead trees with indeterminate impact or signs of other disturbance agents (mostly wind with some trees showing fire scars) was almost as high as elephant impact in 1992 (13.3% of all trees) and this proportion stayed relatively constant in 2008 at 14.2%. Of this 14.2% in 2008, 4% were dead trees with signs of impact from other agents, excluding indeterminate impacts on old degraded stumps. Uprooting or main stem snapping from wind-storms was the most common other mortality agent with 26 trees (2.3% of dead trees) identified in transects in 2008 as being uprooted or snapped by wind in storms in the wet seasons of 2007/2008. These were all big trees (>20cm stem diam.). There was evidence of historical fires, but fire scars declined from 3% in 1992 to 0.7% of dead trees in 2008 and no evidence of recent fires was found in 2008. Other agents of mortality in 2008 were identified as strangler figs (2 trees, 0.18% of dead trees); termites (3 trees); or humans, where 12 trees (1.1% of dead trees) showed axe marks. Ten percent of dead trees in 2008 were very large dead trees found with no signs of impact, suggesting these trees had died from old age.

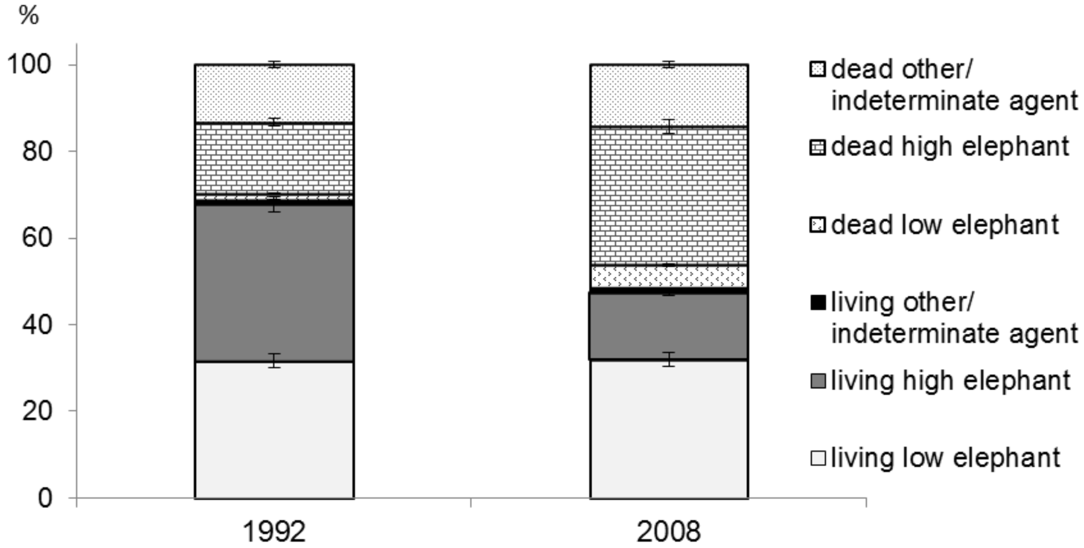
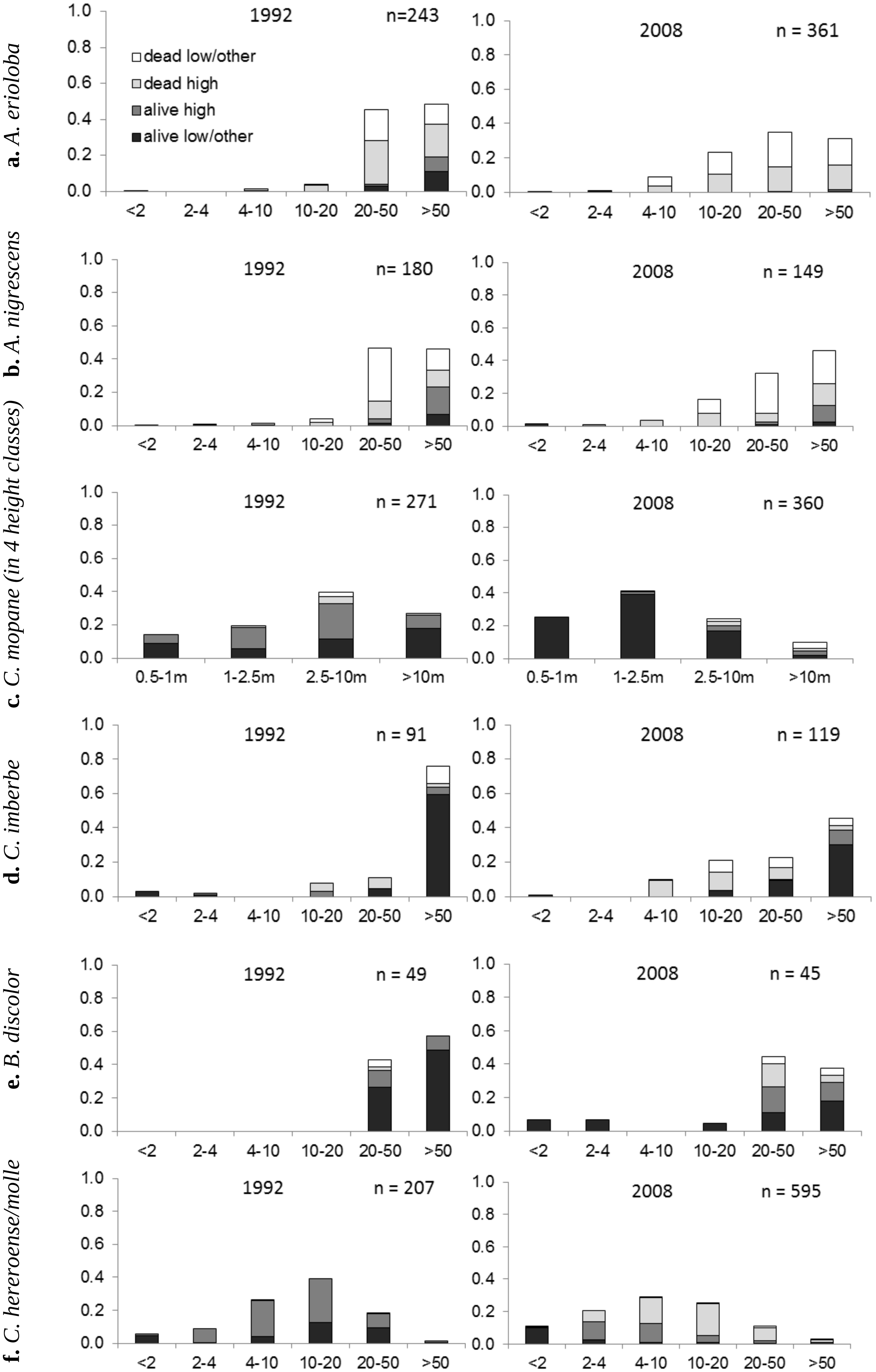


**Figure 3.2** Mean percentage ( ± SE) (of all trees per survey) of living (solid bars) and dead (stippled bars) trees surveyed with low and high elephant impact as well as impact from other (and unknown) agents for 1992 (left) (n = 1321) and 2008 (right) (n =2121)

The tree species known to be selected for by elephants (*Acacia spp., Terminalia spp., C. hereroense*) already showed pervasive high elephant impact on living trees in 1992, and tree death with little recruitment led to proportionally very few living trees left in 2008 (Fig. 3.3). The *Acacia* and *Terminalia* genera had the highest proportions (out of all trees) of high elephant impacted dead trees in 1992 (*A. erioloba* 47%, *A. nigrescens* 25%; *Acacia* spp. 29%; *T. prunioides* 28% (Fig.3.3). *Terminalia sericea* (Fig.3.3l) showed the highest proportion of living trees with high elephant impact in 1992 (85%) and by 2008 dead trees with high impact had increased to 42%. There was regeneration of *T. sericea* in 2008 (38% of all trees) but only the smallest plants (<4cm diam.) did not have high elephant impact. This pattern was also apparent for *C. hereroense* (plus *C. molle*) (Fig. 3.3f) which had a high percentage of elephant- impacted living trees in 1992 (66%) across all size classes, but by 2008 most of these trees had been converted to dead trees (52%) and only 14% of the trees surveyed were living with low elephant impact (Fig. 3.4). In 1992 27% of dead *A. erioloba* (Fig. 3.3a) trees displayed signs of impact from other and unknown agents which included 7 trees showing fire scars, and this proportion had increased to 41% (n= 148 trees) in 2008. Several instances of obvious axe-marks were encountered on very old, dead *A. erioloba* trees (4 out of 350 trees in the 2008 survey). Two *A. nigrescens* trees and one *C. imberbe* were surveyed with axe marks in 2008.

Other species also showed increases in elephant impact, both in proportion and amongst sizes. *Combretum imberbe* (Fig 3.3d) exhibited an increase in the proportion of dead trees with high elephant impact from 13 % in 1992 to 30% in 2008, but this was restricted to smaller size classes which weren't recorded in 1992. Only one *D. mespiliformis* (Fig. 3.3j) tree (<5% of the survey) displayed high elephant impact in 1992, but in 2008, this increased to 20% across more size classes. *Berchemia discolor* (Fig. 3.3e) had a high proportion of living trees with elephant impact in 1992 (18 %) mostly by debarking on the largest two size classes, which increased to 26% (n= 12) in the same sizes by 2008. *Peltophorum africanum* (Fig. 3.3h) had a very high proportion of living trees displaying high elephant impact in 1992 (66%) spread over all size classes, but with no highly impacted dead trees. By 2008, highly impacted dead trees totalled 28%, and all living trees over size class 2 had high elephant impact (20%), with the remainder (50%) being small established seedlings less than 4cm in diameter.

*Philenoptera violacea* (Fig. 3.3i) showed the most regeneration for both surveys with 73% of trees being less than 10cm in diameter in 1992, which increased to 94% in 2008. The majority of impact on living trees in 1992 and 2008 was on the smallest three size classes with little impact on the adult trees. *Colophospermum mopane* (Fig 3.3c) was the only species that displayed a reduction in impact on living trees from 47% in 1992 to just over 6% in 2008. The impacted trees had likely not been converted to dead trees as the proportion of dead impacted trees remained mostly constant at 4-6%. The intermediate size classes (1-3m and 3-10m height) accounted for the majority of high elephant impact in 1992 and 2008.


a. A. erioloba
1992
n=243
2008
n = 361
dead low/other
dead high
alive high
alive low/other
<2
2-4
4-10
10-20
20-50
>50
b. A. nigrescens
1992
n= 180
2008
n = 149
c. C. mopane (in 4 height classes)
1992
n = 271
2008
n = 360
0.5-1m
1-2.5m
2.5-10m
>10m
d. C. imberbe
1992
n = 91
2008
n = 119
e. B. discolor
1992
n = 49
2008
n = 45
f. C. hereroense/molle
1992
n = 207
2008
n = 595
0.0
0.2
0.4
0.6
0.8
1.0

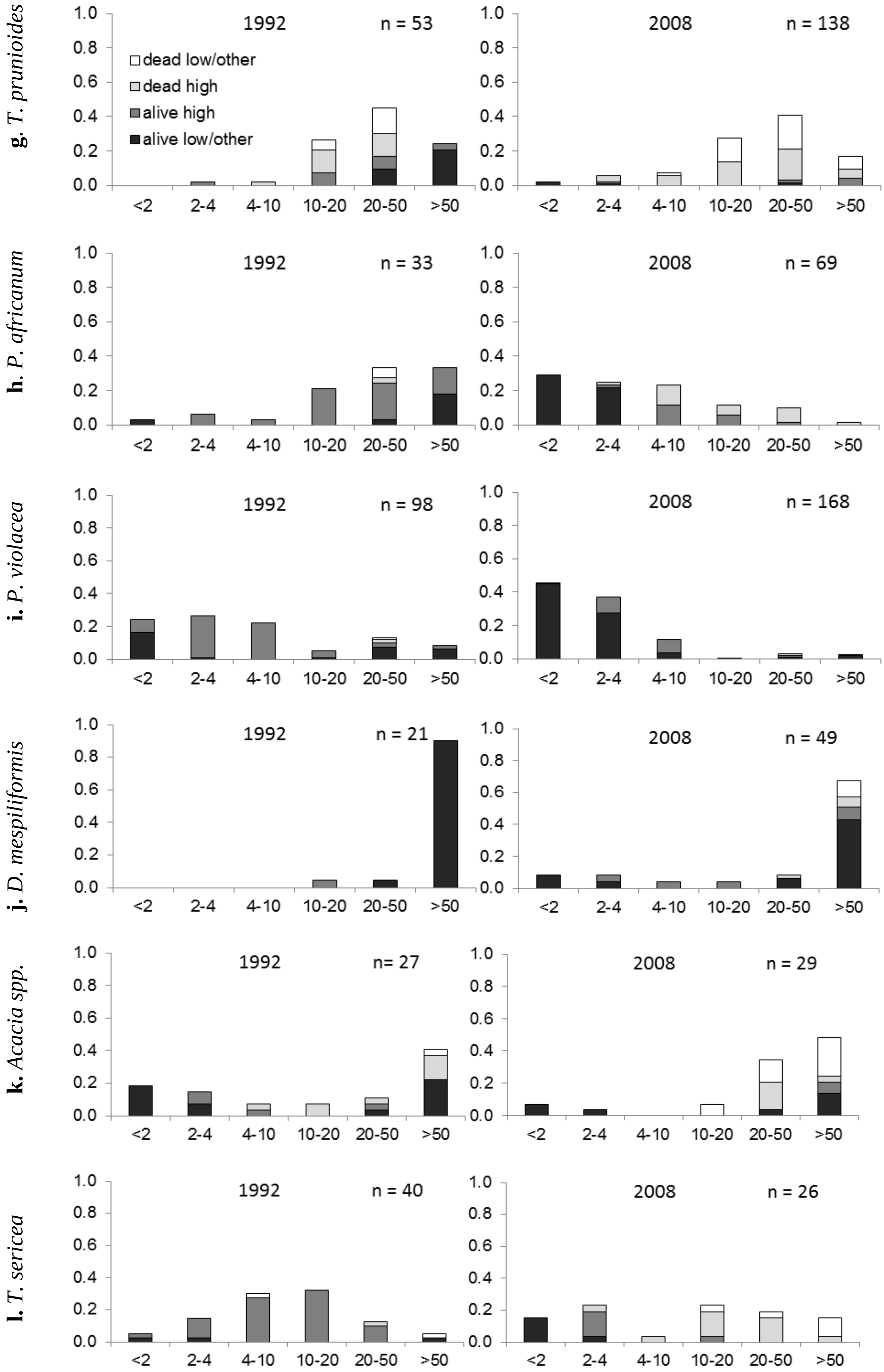

g. T. prunioides
1992
n = 53
dead low/other
dead high
alive high
alive low/other
2008
n = 138
h. P. africanum
1992
n = 33
2008
n = 69
i. P. violacea
1992
n = 98
2008
n = 168
j. D. mespiliformis
1992
n = 21
2008
n = 49
k. Acacia spp.
1992
n= 27
2008
n = 29
l. T. sericea
1992
n = 40
2008
n = 26
1.0
0.8
0.6
0.4
0.2
0.0
<2
2-4
4-10
10-20
20-50
>50

**Figure 3.3** Size class distributions (SCDs) (proportion of total abundance) and elephant impact on living and dead canopy tree species for 1992 (left) and 2008 (right). All graphs show basal diameter size classes (in cm) except for C. mopane which is in 4 height classes. Sample sizes of total count per species per year are included.

Our GLM showed that elephant impact was a significant factor in the mortality of most tree species (Table 3.1). The selected best models of tree mortality were found as either the single factor models or including the interaction between impact and year (Table 3.1). *Acacia erioloba, D. mespiliformis* and *P. violacea* were not included due to an absence of living trees (*A. erioloba*), or dead trees (*D. mespiliformis, P. violacea*) (Appendix 3.1). We selected the most influential predictors per each selected model by comparing estimates and SE, and presented these as bold in Table 3.1.

Out of nine canopy tree species analysed, seven species had dead trees related to high elephant impact (given as negative low elephant impact as high elephant impact was the reference level). Dead trees of *A. nigrescens* and *T. sericea* were associated with other agents of impact, whilst dead trees of *T. pruniodes* and *B. discolor* were associated with both high elephant impact and impact from other agents. For *B. discolor* the other agent was a windstorm in 2008 which killed four out of the 12 dead trees surveyed. The other agents of impact for dead *A. nigrescens* were noted as wind and fire (6 % of all trees), but the majority (43% in 1992 and 30% in 2008) of *A. nigrescens* were very old degraded trees with unknown agents of mortality.

All species except *A. nigrescens, Acacia spp.,* and *C. imberbe* showed increases in dead trees from 1992 to 2008, although elephant impact increase was only shown for *Acacia spp.* (Table 3.1). Dead trees were spread across most sizes for *A. nigrescens, Acacia* spp., *C. hereroense*, *T. pruniodes* and *T. sericea* but limited to the largest trees for *P. africanum* (>20cm diameter) and *C. mopane* (>3m in height) (Table 3.1). For *C. imberbe* mortality was associated with small sizes (4-10cm). *Colophospermum mopane* was the only species to show a decline in elephant impact in 2008 as a result of bark repair or main stem resprouting following pollarding to the extent that they were noted as ‘recovered trees’.

**Table 3.1** Logistic regression models for each species, of mortality of trees (0 = alive, 1 = dead) predicted by the categorical variables: impact[a]; year (1992 vs 2008); size class[b]; year[c]; and the interaction between impact and year. Values are given as variable estimates ± SE. Variables selected as most influential are in bold type. Variables marked with – refer to no data in that category, and *na* refers to variables which were not included in the best model[d]

| **Species** | Inter-cept | Mortality related to impact | | Increase in mortality in 2008 | Mortality related to stem diameter size classes | | | | | Elephant Impact * Year 2008 | Other impact * Year 2008 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Selected model given as tree mortality~… [c] | | Low elephant | Other agents | | 2-4cm | 4-10cm | 10-20cm | 20-50cm | >50cm | | |
| ***Acacia nigrescens***<br>~impact + year + size.class +impact*year | -2.93 ± 1.9 | -1.08 ± 0.6 | **3.44 ± 0.8** | 1.07 ± 0.3 | 2.02 ± 2.2 | **3.97 ± 2.1** | **5.87 ± 2.3** | **4.03 ± 1.9** | **2.6 ±1.9** | 1.32 ± 0.8 | **-2.49± 1.25** |
| ***Acacia spp.***<br>~impact + year + size.class +impact*year | -0.77 ±2.0 | **-3.76 ± 1.6** | 0.06 ± 2.4 | -0.53 ±1.2 | -0.89 ± 2.5 | 0.77 ± 2.4 | **3.05 ± 2.5** | **2.53 ± 1.9** | **1.81 ± 1.8** | **3.51 ± 1.9** | 0.12 ± 2.7 |
| ***Berchemia discolour***<br>~impact + year | -2.03 ± 0.8 | **-2.50 ± 0.9** | **3.74 ± 1.8** | **1.67 ± 0.9** | *na* | *na* | *na* | *na* | *na* | *na* | *na* |
| ***Colophospermum mopane***<br>~impact + year + size.class +impact*year | -4.04 ± 1.4 | **-1.26 ± 0.5** | 1.55 ± 1.0 | **1.33 ± 0.4** | 1.33 ±1.4[b] | **2.57 ± 1.4[b]** | **2.24 ± 1.4[b]** | - | - | **-2.32 ± 0.9** | 2.35 ± 1.8 |
| ***Combretum hereroense***<br>~impact + year + size.class | -7.39 ± 1.1 | **-1.86 ± 0.4** | 0.85 ± 0.9 | **5.12 ± 0.6** | **1.74 ±0.9** | **2.58 ±0.8** | **3.70 +-0.9** | **3.92 ± 0.9** | **2.90 ± 1.0** | *na* | *na* |
| ***Combretum imberbe***<br>~impact + size.class | 0.47 ± 1.7 | **-2.67 ± 0.5** | -0.40 ± 0.5 | *na* | -1.56 ± 2.7 | **3.53 ± 2.3** | 1.43 ± 1.7 | 1.08 ± 1.7 | -0.71 ± 1.7 | *na* | *na* |
| ***Peltophorum africanum***<br>~impact + year + size.class | -2.70 ± 0.85 | **-4.07 ± 1.49** | 2.25 ± 47.4 | **3.05 ± 0.9** | *na* | *na* | *na* | *na* | *na* | *na* | *na* |
| ***Terminalia pruniodes***<br>~impact + year + size.class +impact*year | -3.83 ± 1.9 | **-3.06 ± 1.5** | **2.00 ± 1.0** | **1.72 ± 0.6** | 2.46 ± 1.9 | **5.53 ± 2.4** | **4.86 ± 1.9** | **3.77 ± 1.8** | **3.49 ± 1.9** | **3.22 ± 1.6** | 0.34 ± 1.7 |
| ***Terminalia sericea***<br>~impact + year + size.class | -8.64 ± 2.8 | 1.98 ± 1.4 | **4.41 ± 2.9** | **4.71 ± 1.3** | 2.15 ± 2.2 | **6.31 ± 2.7** | **5.00 ± 2.5** | **7.50 ± 2.8** | **5.27 ± 2.6** | *na* | *na* |

[a] impact is of 3 levels- high elephant impact used as a reference level; low elephant impact; and impact by other agents

[b] 6 levels of stem diameter size classes with the smallest- 0-2cm used as a reference for all species except *C. mopane* where size classes given in four height classes.

[c] 1992 was the reference year.

[d] Details of model selection given in Appendix 3.1

### 3.4.3 Does the composition of the seedling and sapling layers allow for compositional recovery of the historical canopy woodland?

A total of 880 square metre quadrats were sampled for seedlings across the woodland, and seedlings only covered 361 $m^2$ (seedling foliar cover) with only 31% of those being canopy tree species, and the remainder shrub species. We have presented results of just tree species seedling abundance.

There was dissimilarity in proportional composition of tree, sapling and seedling stages for canopy tree species (Fig. 3.4). Surprisingly, there were numerous seedlings present for most canopy tree species that had showed large declines in the canopy layer over time (*Acacia erioloba, A. nigrescens*, *Acacia* spp., *C. imberbe, D. mespiliformis, T. pruniodes*), but there was little recruitment potential for these species shown by the sapling layer.

The most common species among trees and saplings, *C. mopane,* had a high representation in the seedling layer, but *C. imberbe* was the most common seedling surveyed (total coverage of ~33$m^2$ in 0.9ha sampled and found in 36 out of 55 transects). Even though the Acacias had almost no sapling classes (<0.2 trees.$ha^{-1}$), the group showed relatively high seedling abundance, with *A. nigrescens* the third most common seedling (total coverage 20 $m^2$ and found in 23 out of 55 transects). Adult (canopy tree) *A. nigrescens* trees had declined to 1.9 trees.$ha^{-1}$. *Acacia erioloba* also had an unexpectedly high seedling proportional contribution (total coverage 4.05$m^2$) although it was only found in a quarter of the transects. *Combretum hereroense* showed abundant recruitment from seedlings and saplings, but the majority of saplings showed severe elephant impact (Fig. 3.4). *Peltophorum africanum, P. violacea* and *C. mopane* were the only species surveyed which exhibited abundant seedling and healthy (low proportional impact) sapling stages.

Sapling density was significantly higher than canopy tree density for both *C. hereroense* ($t$ = 2.64, df = 44, P < 0.05) and *P.violacea* ($t$ =5.86, df = 48, P < 0.0001) but not for *C.mopane* ($t$ = 1.92, df = 45, P = 0.06).

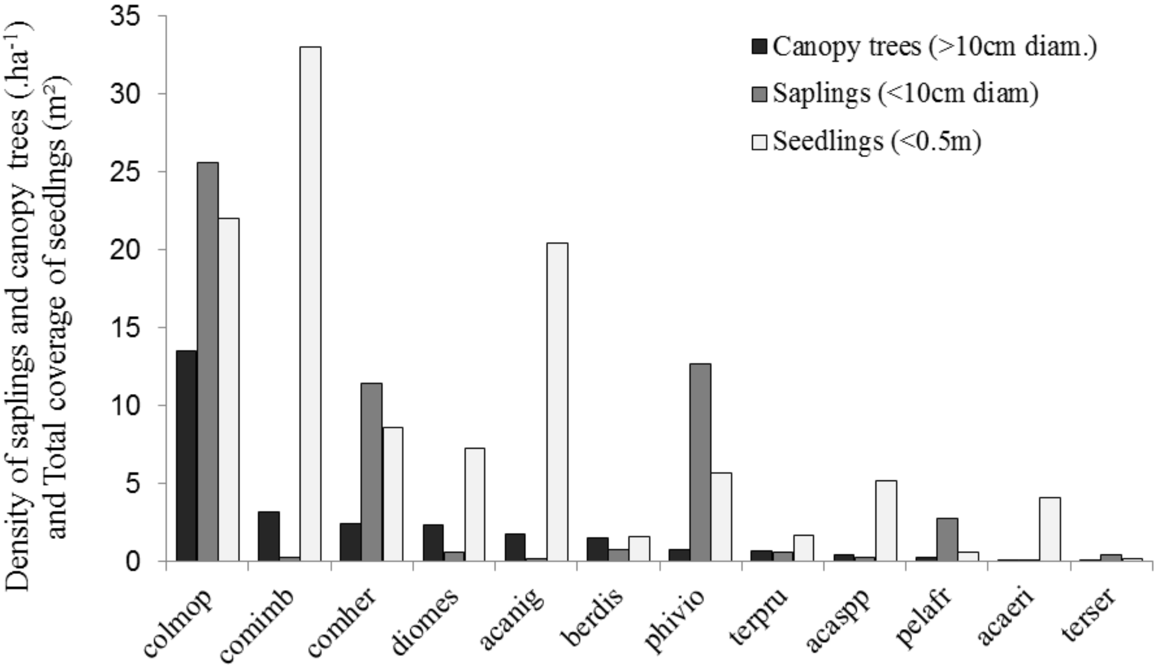


**Figure 3.4** Regeneration potential of canopy tree species in the 2008 survey by comparison of canopy trees (>10cm diameter, ( for *C. mopane* >3m height)), saplings (<10cm diameter, (for *C. mopane* 0.5-3m height)) and seedlings (<0.5m height). Saplings and canopy tree figures given as average density (trees.ha$^{-1}$) and seedling figures given as total aerial coverage (m$^2$). Species order is by descending canopy tree density. Species codes are: colmop *Colophospermum mopane*; comimb *Combretum imberbe*; comher *Combretum hereroense;* diomes *Diospyros mespiliformis;* acanig *Acacia nigrescens*; berdis *Berchemia discolor*; phivio *Philenoptera violacea*; terpru *Terminalia pruniodes*; acaspp *Acacia* spp.; pelafr *Peltophorum africanum;* acaeri *Acacia erioloba;* terser *Terminalia sericea*

We calculated the variation explained by the Canonical Correspondence Analysis (CCA) of canopy tree seedlings by environmental variables as the sum of all canonical eigenvalues as a percentage of all eigenvalues, which equalled 15.3%. Four environmental variables were significant ($p<0.05$) following Monte Carlo permutation tests, and we have included the nonsignificant ($p=0.1$) variable of shrub density (Fig. 3.5). The first two axes explained 20% of the variation. The density of dead trees did not emerge as a significant variable ($f = 1.35$, $p = 0.23$), but the density of dead *Acacia* spp. trees came out as a particularly strong correlate, although no species were associated with this axis in the biplot (Fig. 3.5). The density of all shrub species did not explain much of the species variation, but the unpalatable shrub species *Combretum mossambicense* (Chapter 4) was a significant environmental variable (Fig. 3.5). Seedlings of *A. nigrescens*, *B. discolor* and *P. violacea* were associated with high densities of *C. mossambicense* (and the correlated variable of dead acacia density). Saplings were strongly associated with high densities of tall trees, and not with shrubs as expected (Chapter 4). *Ficus spp., C. hereroense* and to a lesser extent *A. erioloba* seedlings were associated with high densities of large trees, but the seedlings of *T. pruniodes* and *A. luederitzii* were associated with high relative elevations, although *C. imberbe* was associated with low-mid relative elevations (Fig. 3.5). Seedlings of *D. mespiliformis* and *C. mopane* were not associated with any environmental variables.

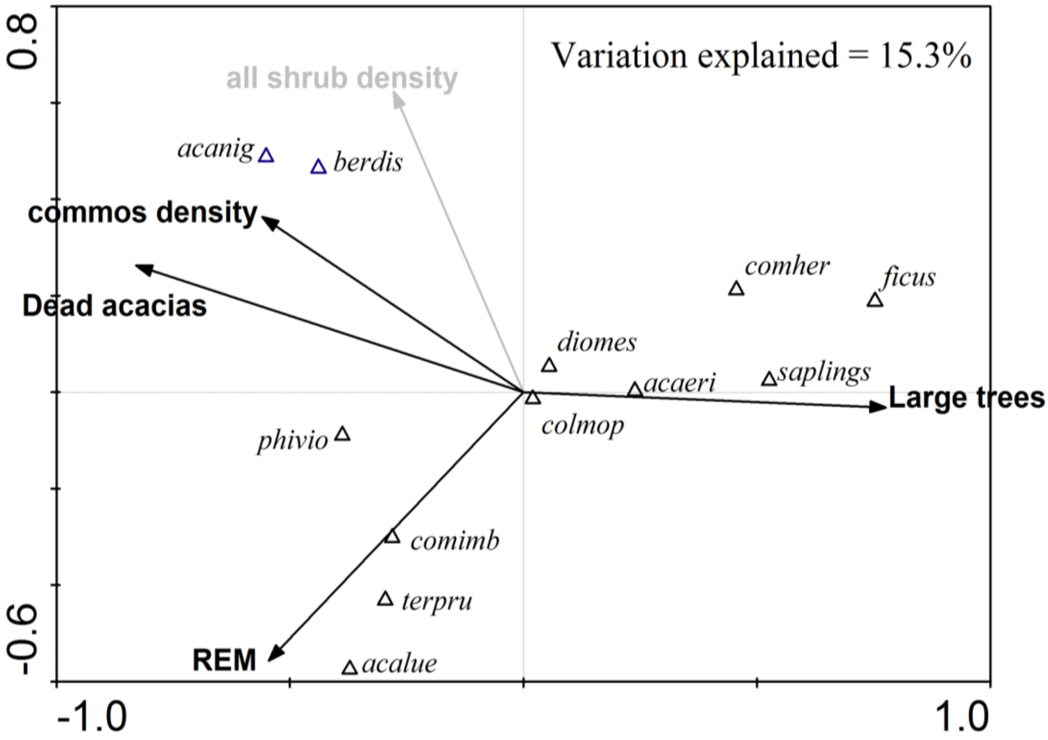


**Figure 3.5** Canopy tree seedling abundance (by species) and total sapling density (trees<10cm diam.) variation explained by a CCA biplot. Significant ($p<0.05$) explanatory variables of Commos density (Combretum mossambicense density); Dead Acacias (density of dead Acacia trees); Large trees (density of all species of large trees (>10cm diam.) and REM (Relative Elevation Model) displayed as bold axes. Non-significant environmental variable of Shrub density displayed as a grey axis ($p = 0.1$). Species codes are (clockwise): acanig *Acacia. nigrescens*; berdis *Berchemia. discolor*; comher *Combretum hereroense*; ficus *Ficus spp.*; acaeri *Acacia erioloba*; diomes *Diospyos mespiliformis*; colmop *Colophospermum mopane*; comimb *Combretum imberbe*; terppru *Terminalia pruniodes*; acalue *Acacia luederitzii*; phivio *Philenoptera violacea*.

## 3.5 Discussion

### 3.5.1 How has the composition of the canopy woodland changed over time?

The prior reconstruction (pre-1992) of the Linyanti woodland is consistent with historical descriptions of a riverine woodland composed primarily of *Acacia* spp. and *Colophospermum mopane* (Child 1968; Sommerlatte 1976). The acacias showed progressive declines from 35% of all trees pre-1992, to 13.6% in 1992 to finally just totalling 5% in 2008. *Acacia erioloba* has almost disappeared from the Linyanti, leaving few remnant large trees (only 10 trees >50cm diam. surveyed in 2008 with 5 of those showing extensive ringbarking). The other previously common acacia, *A. nigrescens,* has also declined to a density of less than 2 trees.ha$^{-1}$ (Fig. 3.4) by 2008, and three quarters of those exhibited high impact, mainly in the form of debarking (see Appendix 3.3.1).

The large tree canopy layer experienced persistent, large compositional changes over the last few decades. Together with *C. mopane*, the acacias were dominant large trees in our pre-1992 reconstruction, and following the decline of the acacias, with no recruitment, the composition became evenly spread between 8 species in 1992 (*A. erioloba, A. nigrescens, C. imberbe, B. discolor, T. sericea, T. pruniodes, P. violacea* and *P. africanum*). With continued decline of large canopy trees, by 2008, the woodland was dominated by small sizes of only *C. hereroense/molle* and *P. violacea*, with *C. imberbe* persisting in the tallest canopy layer.

There has not been a complete loss of tall trees, and the total large tree density (>20cm diam.) was 12 trees.ha$^{-1}$ (± 5 SE) in 2008 (Appendix 3.2). The composition has undergone major shifts from a woodland dominated by a few species in the pre-1992 reconstruction, to a woodland where composition was fairly even in 1992. By 2008 the woodland was again dominated by a few species. We expect the proportional composition of the canopy tree woodland to stabilise because the dominant species are either resilient to elephant impact in the case of *C. mopane* which can form coppiced 'browsing lawns' following intense elephant impact (Smallie & O'Connor 2000; Styles & Skinner 2000; du Toit & Olff 2014) or resistant to impact through being avoided (*P. violacea*) (Walker, Kinzig & Langridge 1999; Sasaki & Lauenroth 2011).

The mortality rate for our canopy trees (all sizes) was calculated as 2% per year. In his analysis of canopy tree disappearance from aerial photos between 1992 and 2001, Bell (2003) found a mortality rate of 1.85 % across the landscape from 1992 to 2001 from aerial photographs. Our mortality rate has not changed much from that of Bell (203) though it is slightly higher, probably due to the inclusion of smaller sizes of canopy trees which would not be visible at the aerial photograph scale. It is also surprisingly not much higher than the mean annual death rate of 1% without disturbances from herbivores or fire, found for *A. erioloba* over 53 years (with one site experiencing 2.9 %) (Moustakas *et al.* 2006). Considering the impact of elephants, our mortality rate is very low and suggests that mortality of canopy trees is not the only cause of the drastic decline of woodland species over the time period. Rather it points to a lack of replacement of canopy trees from recruiting size classes.

### 3.5.2 Are elephants responsible for the decline in canopy tree species?

The compositional shift was dependent on selectivity by elephants whereby some species were heavily targeted across all sizes (*Acacia spp., Terminalia spp.* and *Combretum hereroense*) as well as the tree response to impact where species like *A. nigrescens* appeared more resilient to debarking than *A. erioloba* (see Appendix 3.3.1) Some species were vulnerable only in certain sizes (large trees of *P. africanum* and *C. mopane* succumbed to severe bark stripping but smaller pollarded trees are able to resprout (Ben-Shahar 1996a; Smallie & O'Connor 2000; Styles & Skinner 2000). Species with rough bark which breaks off in smaller blocks and is harder to remove than stringy bark (Malan & van Wyk 1993; Coates-Palgrave 2002) such as *B. discolor, C. imberbe, D. mespiliformis* all had lower proportions of high elephant impact on canopy trees. Impact spread to even these species in 2008.

Elephants have been observed to seek out and repeatedly debark preferred species and sizes till they are completely ringbarked and die (Buechner & Dawkins 1961; Croze 1974; Gadd 2002). In Linyanti, preferred species from the *Acacia* and *Terminalia* genera have almost disappeared from the canopy layer (seedlings were found). The majority of dead trees showed severe impact either in the form of debarking or top-killing (Appendix 3.3.1). Elephant impact increased significantly on the rare *Acacia* spp. in 2008 as elephants sought out even the most scattered acacia trees. The diffuse effect of elephant impact to mortality across most sizes on the acacias, as well as *Terminalia* spp., and *C. hereroense,* supports our finding that these are the most selected and heavily impacted species in the woodland. For *C. imberbe* which is not easily ringbarked due to extremely brittle bark which is less likely to be removed in large pieces (Malan & van Wyk 1993), elephants impacted the smaller size classes by pollarding, killing these trees.

*Philenoptera violacea* had the lowest proportion of dead trees in both years. Although elephants debarked up to 5% of *P. violacea* trees in Kruger National Park, they were much more likely to pollard individuals or break branches to feed on the foliage (Scogings *et al.* 2012). We found the same pattern in our study where elephants pollarded very small individuals in 2008 but because of copious regeneration, the impacted proportion was still minor. There is some suggestion that the bark of this species is unpalatable and potentially poisonous (Coates-Palgrave 2002; O'Connor 2010) perhaps explaining why large trees were not commonly debarked in this study. This evidence suggests that this species could become increasingly dominant in the canopy tree layer.

The proportion of dead trees with indeterminate impact or signs of other disturbance agents was as high as elephant impact in 1992. This was due to two factors: a high proportion of very old dead trees which were degraded already by that time, and chance observation of the damage following a windstorm. Following a storm in January 1992, Wackernagel (1993) surveyed 26 uprooted trees following a single wind storm and determined that wind-felling was a significant disturbance agent in the Linyanti. Trees damaged by wind were also observed following two windstorms in the 2008 survey. Spinage & Guinness (1971) warn against ascribing all felling of trees to elephants, noting that lightning and wind-throw are significant agents of mortality. We found that felling by wind was an important contributor to canopy tree mortality in the Linyanti, but noted wind-felling only of big trees that are not vulnerable to felling by elephants. The relative contribution of wind mortality can only be quantified following chance events. Most of the wind-felled trees also displayed high elephant impact, and synergistic mortality from elephant damage weakening trees to be uprooted by wind needs to be quantified. Fire had not been completely excluded in the woodland as trees with old fire scars were encountered (3% in 1992 and 0.7% of trees in 2008); but with little recent evidence of fire, we can be confident that fire is not a major disturbance agent in the Linyanti woodland. We did not find any definite signs of basal ringbarking by porcupines but cannot discount mixed debarking by both porcupines and elephants on completely debarked trees. Senescence was also a contributor to large tree mortality where 10% of dead trees in 2008 had died without signs of any impact. Due to the lack of fire as a prevalent disturbance agent in the Linyanti, and because wind felling affects primarily the largest-crowned trees, the pattern of mortality occurring across sizes suggests elephants are the most plausible agent of mortality in the Linyanti, overlying natural senescence rates.

### 3.5.3 Are Acacias a relic of the past?

*Acacia nigrescens* mortality was not associated with elephant impact in our GLM, but rather with other and indeterminate agents. A large proportion (43% in 1992 and 30% in 2008) of dead *A. nigrescens* was noted as being very old and decayed. Wackernagel (1993) found that 90% of elephant impact on living trees surveyed in 1991 was older than two-seasons. This supports the hypothesis that these trees died well before 1992 and may have established at a time when conditions were more favourable for seedling recruitment. We cannot dismiss the hypothesis that the loss of mature acacias may be the result of an even-aged cohort established following rinderpest and elephant hunting for ivory (Young & Lindsay 1988). However, without dating the Acacias these are speculations beyond the scope of this study.

Additionally, anecdotal reports suggest that many of the large *A. erioloba* trees in the Linyanti area were ringbarked or cut-down during Tsetse Fly Control (TFC) operations in the 1960's and 1970's (Davies & Bowles 1976; M. Ives *pers. comm.*) This practice of bush-clearing was intended to eliminate the preferred habitat of *Glossina* spp. by removing shady trees (Davies & Bowles 1976; Hargrove 2003). Maps of bush clearing in northern Botswana (Davies & Bowles 1976 Map 1A) suggest this activity took place outside of our study area towards Kachikau. However we found several instances of obvious axe-marks on old, dead acacias in the Linyanti (see Appendix 3.3.2) that were too far away from any present day roads to have been cleared for road-making.

This evidence points to a general pattern of acacias being fast to disappear from a woodland, but also that they are potentially fast to re-establish when conditions are appropriate. The abundance of Acacia seedlings, relative to adult trees, surveyed in 2008 supports this hypothesis.

### 3.5.4 Is regeneration of the woodland prevented by elephants?

The Acacias showed unexpectedly high seedling abundance considering the high mortality of adult trees. It is possible that acacia seeds have been dispersed from elsewhere, as potential elephant-dispersal distances of *A. erioloba* have been predicted up to 50km in Kalahari Sands (Dudley 1999).

The regeneration layer contained seedlings of all canopy tree species preferred by elephants, suggesting that elephant impact has not led to a bottleneck of seedling establishment. Instead there was a distinct lack of saplings (<10cm stem diam.) apart from four species which were either resilient to elephant impact by resprouting vigorously, like *C. mopane, C. hereroense* and *P. africanum,* or mostly unpalatable like *P. violacea.* The saplings of sensitive species which were found such as *B. discolor* and *D. mespiliformis* showed signs of intensive elephant impact (see Appendix 3.3.4). This suggests a demographic bottleneck of seedling transition into the next size class. The most likely answer is that of mortality of seedlings. In the Chobe riverine woodland, high impala concentrations were found as the main mortality agent of tree seedlings, preventing woodland regeneration (Moe *et al.* 2009). However impala are found at much lower densities in the Linyanti (Chase 2011) and we hypothesize that elephants are mortality agents of seedlings in the Linyanti. Elephants were found to be the main mortality agent of *A. erioloba* established seedlings in the Savuti, where browsers such as impala only supressed growth (Barnes 2001a). Our observations were that impact on acacia seedlings was mainly by elephants (see Appendix 3.3.3), although this is impossible to test without controlled conditions excluding other potential seedling mortality agents such as rodents (Goheen *et al.* 2004). There was seedling recruitment into saplings of most canopy tree species in the fenced staff camps of Duma Tau and King's Pool (see Appendix 3.3.5) where all large herbivores were excluded (but mesoherbivores like impala occasionally enter). Further research is needed to determine the potential roles of elephants, impala, and other seedling mortality agents, on regeneration of the woodland.

Under current elephant pressure, the only woodland species that were showing healthy recruitment from both seedling and sapling stages were *C. mopane* and *P. violacea* (Fig.3.4). Whilst *C. hereroense* also exhibited an abundant sapling layer, the majority of these plants showed impact from elephants, and most of the plants surveyed were already dead (Fig. 3.3). If elephant impact were removed from the woodland, there would still be very little recruitment from saplings into the canopy layer for the majority of species due to missing small sizes. Only in the future, if seedling establishment conditions become favourable, and there were a long enough period with reduced elephant pressure, could the canopy tree species *C. imberbe, D. mespiliformis,* as well as the acacias, regenerate from the abundant seedling layer. However, we do acknowledge that our seedling survey was in a period of unusually high rainfall as the survey months (Dec 2007 and January, November and December 2008) had an average rainfall 3.5 times higher (1146 mm) than the mean annual rainfall (557mm MAP) for 92 years (Chapter 1). Seedlings were classified as plants below 0.5m but the majority were noted as newly established seedlings less than 10cm tall. Thus apart from *P. violacea* which showed abundant sapling recruitment in both surveys, canopy tree seedlings may have been unusually abundant in our 2008 survey Another seedling survey would be needed in a dry period to ascertain if all tree species are represented in the regeneration layer. There is evidence that elephants have recently been moving away from the Linyanti/Chobe riverfronts to previously unoccupied areas such as Angola (Chase & Griffin 2009) and that the population growth has stabilised (Chase 2011)). If this continues for an extended period, it may allow sensitive canopy trees to escape the ‘herbivore trap’

Whilst *C. imberbe* was well represented in the seedling layer, only 1 plant smaller than 10cm stem diameter was found alive in the 2008 survey, suggesting seedling recruitment is being suppressed. Because *C. imberbe* seedlings were associated with lower elevations, current available soil moisture conditions may not be favourable for seedling survival, limited by a trend of increased aridification in northern Botswana (Murray-Hudson, Wolski & Ringrose 2006; Ringrose *et al.* 2007). *Acacia nigrescens* and *B. discolor* seedlings, likely to be targeted by elephants, were associated with high densities of the shrub *C. mossambicense* (Fig. 3.5). Because elephants largely avoid this shrub (Chapter 4), it may function as a ‘nurse shrub’ (Olff *et al.* 1999; Riginos, Milton & Wiegand 2005; Smit *et al.* 2007) in protecting sensitive seedlings from elephant feeding.

Several established seedlings and saplings of *A. nigrescens, B. discolor, C. imberbe,* and *D. mespiliformis* were noted as occurring on termitaria refugia in the 2008 survey. Large termitaria built by *Macrotermes* are scattered throughout the woodland and can act as refugia for tall trees in disturbed landscapes, forming nutrient-rich islands and suitable germination sites (Joseph *et al.* 2011). Termitaria have the additional capacity in high elephant-density areas that often the slopes of the mounds are too steep for elephants to climb, protecting vulnerable tree sizes and species from elephant disturbance (Humphrey 2008) and allowing for future recolonization through seed reserves (Western & Maitumo 2004).

## 3.6 Conclusion

The canopy riparian woodland along the Linyanti has been subject to intense elephant disturbance with over 50% of canopy trees displaying severe elephant impact (more than 50% stem circumference bark stripping, or main stem breakage) in 2008. This has resulted in a compositional shift from a historical *Acacia-C. mopane* woodland to one composed of two resilient species which can resprout vigorously following disturbance: *C. mopane* (Smallie & O’Connor 2000; Styles & Skinner 2000) and *C. hereroense* (Neke 2004); and one largely neglected species: *P. violacea*. The preferred and susceptible acacias and terminalias have been reduced to scattered remnant trees, but have not disappeared from the woodland entirely, and were found in the seedling layer. The abundance of the highly resilient *Colophospermum mopane* in the Linyanti riparian woodland may have acted as a buffer against complete canopy loss as evident along the Chobe River (Aarrestad *et al.* 2014), but there is still a lack of recruitment of canopy tree species. We calculated a mortality rate of 2% p.a. which is not much higher than background mortality rates and suggests that a lack of recruitment, and not tree mortality has led to the woodland decline and compositional turnover.

Species which are in decline in the canopy layer were prevalent as seedlings, but there was a lack of most species in the sapling class, and there is evidence of an “elephant-trap” or ‘herbivore bottleneck’ (Levick, Baldeck & Asner 2014) preventing seedling recruitment. There has not been a complete loss of canopy trees, and refugia in space (like termitaria) and time (nurse shrubs) may enable the woodland to regenerate in the future (Bakker *et al.* 2016).

Our findings illustrate compositional turnover from many palatable acacia species to a canopy woodland dominated by a few resilient or unpalatable species.  The decline in common species potentially has the effect of enhanced compositional diversity and maintenance of ecosystem function as long as the minor species are functionally similar (Walker, Kinzig & Langridge 1999; Sasaki & Lauenroth 2011). However, we have shied away from using simple diversity indices as they do not provide information on ecosystem functional changes (Loreau 2010; Wang & Loreau 2016). Rather the replacement of palatable acacias with a few resilient species represents a loss in the diversity of functional types within the canopy tree layer (Mori, Furukawa & Sasaki 2013), if there is a continued lack of recruitment of seedlings.  Our results suggest elephants are able to drive a rapid change in composition (Bakker *et al.* 2016), but we found the canopy woodland had declined not only from elephant-mediated mortality of large trees but because losses were not being compensated by recruitment. Our study highlights the non-equilibrium dynamics of savannas over long periods (Sankaran, Ratnam & Hanan 2004; Gillson 2004; Sankaran, Augustine & Ratnam 2013), where elephants were able to shift the composition of a canopy tree woodland. We do however acknowledge that decadal time series data can illustrate disturbance patterns, but longer term insights into recruitment processes are currently lacking.

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## 3.8 Appendices

3.1 Model Selection by AIC of GLMs of mortality of trees by impact level, size class and year.

3.2 Table of density of living and dead canopy tree species in 2008 by stem diameter size class

3.3 Selected photographs of elephant impact and compositional changes in the woodland

## Appendix 3.1 Model selection

The R code for the full (null) model for each species was:

```
 model <- brglm(dead ~ impact * year * size.class, family = binomial(logit), data = x, method =
"brglm.fit", control.brglm = brglm.control(br.maxit=100))
```
[a]

[a] The term brglm.control(br.maxit=n) was used to control the number of iterations run to fit the model, where the default was 100, but we increased this to 10000 where model output detailed the iteration limit was reached.

**Table of model selection by AIC of binomial GLMs using the BRGLM function of mortality of trees by impact level, size class and over time. Highest ranking models in bold type.**

| **Model rank** | **Model Tree mortality~…** | **Number of parameters (K)*** | **Pseudo $R^2$ [b]** | **AIC** | **Delta AIC ($\Delta AIC_i$)** |
|---|---|---|---|---|---|
| ***Acacia erioloba*** n = 611 | | | | | |
| | Data unbalanced by lack of living trees. Living n = 70 Dead n = 541 | | | | |
| ***Acacia nigrescens*** n living =77; dead = 243 | | | | | |
| 5 | ~impact * size class * year | 23 | 27.70% | 270.56 | 15.76 |
| 2 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 15 | 29.35% | 257.08 | 2.26 |
| 3 | ~ impact + year + size.class + impact*size.class | 13 | 26.92% | 262.81 | 7.99 |
| 1 | **~ impact + year + size.class + impact*year** | **11** | **28.65%** | **254.82** | **0.00** |
| 4 | ~ impact + year + size.class | 9 | 28.29% | 256.71 | 1.89 |
| 6 | ~impact + size.class | 8 | 24.73% | 268.87 | 14.05 |
| 7 | ~impact + year | 4 | 20.29% | 280.01 | 25.19 |
| 8 | ~impact | 3 | 16.88% | 292.64 | 37.82 |
| 10 | ~size.class | 6 | 0% | 5274.4 | 5019.58 |
| 9 | ~year | 2 | 0% | 357.21 | 102.39 |
| ***Acacia* species** n living = 28; dead = 28 | | | | | |
| 9 | ~impact * size class * year | 19 | 25.81% | 74.19 | 11.89 |
| 7 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 15 | 23.65% | 70.24 | 7.94 |
| 8 | ~ impact + year + size.class + impact*size.class | 13 | 13.04% | 72.99 | 10.69 |
| **1** | **~ impact + year + size.class + impact*year** | **11** | **28.87%** | **62.30** | **0.00** |

| **Model rank** | **Model Tree mortality~…** | **Number of parameters (K)*** | **Pseudo $R^{2}$ [b]** | **AIC** | **Delta AIC ($\Delta AIC_{i}$)** |
|---|---|---|---|---|---|
| **Acacia species continued** | | | | | |
| 4 | ~ impact + year + size.class | 9 | 20.62% | 64.30 | 1.99 |
| 3 | ~impact + size.class | 8 | 20.12% | 63.82 | 1.52 |
| 2 | ~impact + year | 4 | 15.45% | 63.64 | 1.35 |
| 5 | ~impact | 3 | 11.78% | 65.96 | 3.66 |
| 6 | ~size.class | 6 | 14.92% | 66.07 | 3.78 |
| 10 | ~year | 2 | 3.19% | 75.74 | 13.44 |
| ***Berchemia discolor*** n living = 79; dead = 15 | | | | | |
| 8 | ~impact * size class * year | 14 | 24.54% | 74.22 | 22.95 |
| 7 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 12 | 29.10% | 69.28 | 18.01 |
| 6 | ~ impact + year + size.class + impact*year | 10 | 32.75% | 65.43 | 14.16 |
| 5 | ~ impact + year + size.class + impact*size.class | 10 | 30.67% | 64.41 | 13.14 |
| **3** | ~ impact + year + size.class | 8 | 34.50% | 60.55 | 9.28 |
| 4 | ~impact + size.class | 7 | 28.75% | 63.44 | 12.18 |
| 1 | **~impact + year** | **4** | **40.29%** | **51.27** | **0.00** |
| 2 | ~impact | 3 | 35.46% | 53.84 | 2.57 |
| 10 | ~size.class | 5 | 0% | 86.33 | 35.06 |
| 9 | ~year | 2 | 0.74% | 78.83 | 27.56 |
| ***Colophospermum mopane*** [a] n living = 572 dead = 59 | | | | | |
| 9 | ~impact * size class * year | 19 | 1.96% | 379.80 | 145.74 |
| 3 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 13 | 39.86% | 240.94 | 6.88 |
| 4 | ~ impact + year + size.class + impact*size.class | 11 | 37.89% | 245.48 | 11.42 |
| 1 | **~ impact + year + size.class + impact*year** | **9** | **40.81%** | **234.06** | **0.00** |
| 2 | ~ impact + year + size.class | 7 | 38.62% | 240.08 | 6.02 |
| 5 | ~impact + size.class | 6 | 36.88% | 246.09 | 12.03 |
| 6 | ~impact + year | 4 | 35.52% | 251.21 | 17.15 |
| 7 | ~impact | 3 | 33.43% | 258.88 | 24.82 |
| 8 | ~size.class | 4 | 12.92% | 334.41 | 100.35 |
| 10 | ~year | 2 | 0% | 395.81 | 161.75 |
| ***Combretum hereroense*** n living = 475; dead = 327 | | | | | |
| 10 | ~impact * size class * year | 28 | -1116.48 | 11950 | 11294.88 |
| 5 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 19 | 26.79% | 789.97 | 134.85 |

| **Model rank** | **Model Tree mortality~…** | **Number of parameters (K)*** | **Pseudo R$^{2\ b}$** | **AIC** | **Delta AIC ($\Delta AIC_i$)** |
|---|---|---|---|---|---|
| ***Combretum hereroense continued*** | | | | | |
| 4 | ~ impact + year + size.class + impact*size.class | 17 | 26.80% | 789.31 | 134.19 |
| 3 | ~ impact + year + size.class + impact*year | 11 | 27.17% | 780.1 | 124.98 |
| 1 | **~ impact + year + size.class** | **9** | **39.07%** | **655.12** | **0.00** |
| 7 | ~impact + size.class | 8 | 14.49 | 913.00 | 257.88 |
| 2 | ~impact + year | 4 | 31.70 | 735.34 | 80.22 |
| 8 | ~impact | 3 | 12.05 | 946.53 | 291.41 |
| 9 | ~size.class | 6 | 6.77 | 995.45 | 340.33 |
| 6 | ~year | 2 | 23.10 | 846.40 | 191.28 |
| ***Combretum imberbe*** living = 130 dead = 77 | | | | | |
| 6 | ~impact * size class * year | 22 | 42.15% | 173.25 | 7.05 |
| 4 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 17 | 41.90% | 169.11 | 2.91 |
| 2 | ~ impact + year + size.class + impact*size.class | 15 | 39.60% | 173.11 | 1.23 |
| 5 | ~ impact + year + size.class + impact*year | 11 | 39.98% | 167.43 | 6.91 |
| 3 | ~ impact + year + size.class | 9 | 39.15% | 168.25 | 2.05 |
| **1** | **~impact + size.class** | **8** | **39.84%** | **166.20** | **0.00** |
| 7 | ~impact + year | 4 | 29.77% | 188.38 | 22.18 |
| 8 | ~impact | 3 | 28.54% | 191.80 | 25.60 |
| 9 | ~size.class | 6 | 25.37% | 203.25 | 37.05 |
| 10 | ~year | 2 | 2.77% | 260.51 | 94.31 |
| ***Diospyros mespiliformis*** n= 70 | | | | | |
| | Data unbalanced by lack of dead trees. Living n = 61 Dead n = 9 | | | | |
| ***Peltophorum africanum*** n living = 64 dead = 23 | | | | | |
| 7 | ~impact * size class * year | 15 | 26.95% | 85.40 | 21.98 |
| 5 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 11 | 32.68% | 75.57 | 12.14 |
| 3 | ~ impact + year + size.class + impact*size.class | 10 | 33.95% | 72.99 | 9.57 |
| 4 | ~ impact + year + size.class + impact*year | 10 | 33.83% | 73.05 | 9.63 |
| 2 | ~ impact + year + size.class | 9 | 35.07% | 70.48 | 7.06 |
| 8 | ~impact + size.class | 8 | 9.23% | 90.34 | 26.91 |
| **1** | **~impact + year** | **4** | **37.91%** | **63.43** | **0.00** |
| 6 | ~impact | 3 | 17.28% | 82.00 | 18.57 |
| 9 | ~size.class | 6 | 7.00% | 90.40 | 26.97 |
| 10 | ~year | 2 | 1.62% | 95.35 | 31.92 |

| Model rank | Model<br>Tree mortality~… | Number of parameters (K)* | Pseudo $R^2$ [b] | AIC | Delta AIC ($\Delta AIC_i$) |
|---|---|---|---|---|---|
| ***Philenoptera violacea*** n = 266<br>Data unbalanced by lack of dead trees. Living n =261 dead = 5 | | | | | |
| ***Terminalia pruniodes*** n living = 42 dead = 151 | | | | | |
| 3 | ~impact * size class * year | 23 | 39.90% | 141.15 | 8.25 |
| 4 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 17 | 32.36% | 145.65 | 12.75 |
| 5 | ~ impact + year + size.class + impact*size.class | 15 | 30.03% | 148.39 | 15.49 |
| **1** | **~ impact + year + size.class + impact*year** | **11** | **35.99%** | **132.9** | **0.00** |
| 2 | ~ impact + year + size.class | 9 | 34.13% | 135.4 | 2.5 |
| 7 | ~impact + size.class | 8 | 17.66% | 163.70 | 30.80 |
| 6 | ~impact + year | 4 | 24.76% | 149.25 | 16.35 |
| 10 | ~impact | 3 | 8.81% | 179.37 | 46.47 |
| 9 | ~size.class | 6 | 10.12% | 178.73 | 45.83 |
| 8 | ~year | 2 | 10.58% | 176.97 | 44.07 |
| ***Terminalia sericea*** n living = 46 dead = 20 | | | | | |
| 8 | ~impact * size class * year | 22 | 48.22% | 71.82 | 29.63 |
| 6 | ~ impact + year + size.class + impact*year + impact*size.class + year*size.class | 17 | 56.72% | 59.39 | 17.20 |
| 2 | ~ impact + year + size.class + impact*year | 11 | 63.56% | 44.72 | 2.53 |
| 3 | ~ impact + year + size.class + impact*size.class | 15 | 61.37% | 53.48 | 11.29 |
| **1** | **~ impact + year + size.class** | **9** | **62.54%** | **42.19** | **0.00** |
| 7 | ~impact + size.class | | 12.34% | 71.76 | 29.57 |
| 4 | ~impact + year | | 34.94% | 53.94 | 11.75 |
| 10 | ~impact | | 5.11% | 74.76 | 32.57 |
| 9 | ~size.class | | 7.36% | 72.94 | 30.75 |
| 5 | ~year | | 25.48% | 58.91 | 16.72 |

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* K parameters are based on the number of predictor variables minus those not defined because of singularities (for example excluded size class levels due to no samples in those classes). [a] C.mopane size classes given in 4 levels of height. Significant size variable is 1-3m. [b] % variation explained by model is by McFadden's pseudo $R^2$ = 1-null deviance /residual deviance.

**Appendix 3.2 Table of density of living and dead canopy tree species in 2008 by stem diameter size class (1= <2cm, 2 = 2-4cm, 3 = 4-10cm, 4 = 10-20cm, 5 = 20-50cm, 6 = >50cm).**

| **Species** | **Size Class** | **Living Density ± SE** (tree.ha$^{-1}$) | **Dead Density ± SE** (tree.ha$^{-1}$) |
|---|---|---|---|
| ***A. erioloba*** | 1 | 0.18 ± 0.10 | 0 |
| | 2 | 0.12 ± 0.08 | 0.12 ± 0.13 |
| | 3 | 0 | 5.93 ± 0.42 |
| | 4 | 0 | 5.04 ± 0.82 |
| | 5 | 0.12 ± 0.10 | 7.49 ± 1.19 |
| | 6 | 0.42 ± 0.16 | 5.82 ± 0.89 |
| | Total | 0.83 ± 0.44 | 24.40 ± 3.46 |
| ***A. nigrescens*** | 1 | 0.12 ± 0.11 | 0 |
| | 2 | 0.06 ± 0.05 | 0 |
| | 3 | 0 | 0.30 ± 0.15 |
| | 4 | 0.12 ± 0.08 | 1.44 ± 0.37 |
| | 5 | 0.24 ± 0.12 | 2.64 ± 0.83 |
| | 6 | 1.02 ± 0.41 | 2.76 ± 0.75 |
| | Total | 1.56 ± 0.79 | 7.13 ± 2.11 |
| ***Acacia spp.*** | 1 | 0.12 ± 0.09 | 0 |
| | 2 | 0.06 ± 0.07 | 0 |
| | 3 | 0 | 0 |
| | 4 | 0 | 0.12 ± 0.06 |
| | 5 | 0.06 ± 0.055 | 0.42 ± 0.14 |
| | 6 | 0.42 ± 0.20 | 0.66 ± 0.19 |
| | Total | 0.66 ± 0.43 | 1.20 ± 0.40 |
| ***B. discolor*** | 1 | 0.18 ± 0.15 | 0 |
| | 2 | 0.12 ± 0.10 | 0 |
| | 3 | 0 | 0 |
| | 4 | 0.12 ± 0.20 | 0 |
| | 5 | 0.72 ± 0.25 | 0.48 ± 0.56 |
| | 6 | 0.72 ± 0.26 | 0.24 ± 0.15 |
| | Total | 1.86 ± 0.97 | 0.72 ± 0.72 |
| ***C. hereroense/molle*** | 1 | 6.72 ± 4.43 | 0.12 ± 0.19 |
| | 2 | 9.47 ± 4.58 | 4.92 ± 1.17 |
| | 3 | 9.11 ± 3.33 | 11.63 ± 2.76 |
| | 4 | 3.47 ± 1.17 | 14.51 ± 3.13 |
| | 5 | 1.32 ± 0.39 | 6.71 ± 1.90 |
| | 6 | 0.84 ± 0.32 | 1.08 ± 0.50 |
| | Total | 30.94 ± 14.24 | 38.97 ± 9.68 |

| **Species** | **Size Class** | **Living Density ± SE** (tree.ha$^{-1}$) | **Dead Density ± SE** (tree.ha$^{-1}$) |
|---|---|---|---|
| ***C. imberbe*** | 1 | 0.18 ± 0.10 | 0 |
| | 2 | 0 | 0 |
| | 3 | 0 | 0.84 ± 0.24 |
| | 4 | 0.36 ± 0.24 | 1.20 ± 0.38 |
| | 5 | 0.60 ± 0.23 | 0.84 ± 0.48 |
| | 6 | 2.22 ± 0.57 | 0.42 ± 0.31 |
| | Total | 3.36 ± 1.16 | 3.30 ± 1.42 |
| ***C. mopane*** | 1 | 10.31 ± 4.42 | 0 |
| (4 height classes) | 2 | 15.35 ± 6.08 | 0.12 ± 0.11 |
| 1= 0.5-1m, 2 =1-2.5m | 3 | 8.63 ± 2.37 | 1.80 ± 0.41 |
| 3= 2.5-10m, 4= >10m | 4 | 1.68 ± 0.68 | 2.28 ± 0.73 |
| | Total | 35.97 ± 13.50 | 4.20 ± 1.27 |
| ***D. mespiliformis*** | 1 | 0.24 ± 0.23 | 0 |
| | 2 | 0.24 ± 0.16 | 0 |
| | 3 | 0.12 ± 0.17 | 0 |
| | 4 | 0.12 ± 0.17 | 0 |
| | 5 | 0.18 ± 0.13 | 0.06 ± 0.32 |
| | 6 | 1.50 ± 0.58 | 0.48 ± 0.39 |
| | Total | 2.39 ± 1.46 | 0.54 ± 0.72 |
| ***Ficus spp.*** | 1 | 0.06 ± 0.04 | 0 |
| | 2 | 0 | 0 |
| | 3 | 0 | 0 |
| | 4 | 0.06 ± 0.10 | 0 |
| | 5 | 0.06 ± 0.11 | 0.06 ± 0.18 |
| | 6 | 0.12 ± 0.10 | 0 |
| | Total | 0.30 ± 0.36 | 0.06 ± 0.18 |
| ***G. livingstoneii*** | 1 | 0.06 ± 0.05 | 0 |
| | 2 | 0 | 0 |
| | 3 | 0 | 0 |
| | 4 | 0.06 ± 0.05 | 0.06 ± 0.18 |
| | 5 | 0.06 ± 0.10 | 0 |
| | 6 | 0.24 ± 0.37 | 0.06 ± 0.18 |
| | Total | 0.42 ± 0.58 | 0.12 ± 0.37 |
| ***P. africanum*** | 1 | 2.52 ± 2.15 | 0 |
| | 2 | 0.96 ± 0.90 | 0.06 ± 0.05 |
| | 3 | 0.48 ± 0.43 | 0.48 ± 0.24 |
| | 4 | 0.24 ± 0.23 | 0.24 ± 0.15 |
| | 5 | 0.06 ± 0.07 | 0.36 ± 0.36 |
| | 6 | 0 | 0.06 ± 0.08 |
| | Total | 4.26 ± 3.79 | 1.20 ± 0.90 |
| ***P. violacea*** | 1 | 4.62 ± 0.86 | 0 |
| | 2 | 3.72 ± 0.52 | 0 |
| | 3 | 1.14 ± 0.35 | 0 |
| | 4 | 0.06 ± 0.06 | 0 |
| | 5 | 0.18 ± 0.03 | 0.12 ± 0.05 |

|  |  |  |  |
|---|---|---|---|
|  | 6 | 0.24 ± 0.20 | 0 |
| **Species** | **Size Class** | **Living Density ± SE** | **Dead Density ± SE** |
| ***P. violacea*** | Total | 9.95 ± 2.05 | 0.12 ± 0.05 |
| ***T. pruniodes*** | 1 | 0.24 ± 0.14 | 0 |
|  | 2 | 0.18 ± 0.11 | 0.30 ± 0.13 |
|  | 3 | 0 | 1.14 ± 0.30 |
|  | 4 | 0 | 2.22 ± 0.53 |
|  | 5 | 0.36 ± 0.13 | 3.12 ± 0.87 |
|  | 6 | 0.36 ± 0.15 | 1.08 ± 0.41 |
|  | Total | 1.14 ± 0.54 | 7.85 ± 2.25 |
| ***T. sericea*** | 1 | 0.24 ± 0.28 | 0 |
|  | 2 | 0.30 ± 0.28 | 0.06 ± 0.09 |
|  | 3 | 0 | 0.06 ± 0.08 |
|  | 4 | 0.06 ± 0.04 | 0.30 ± 0.35 |
|  | 5 | 0 | 0.30 ± 0.21 |
|  | 6 | 0 | 0.24 ± 0.12 |
|  | Total | 0.60 ± 0.61 | 0.96 ± 0.87 |

## Appendix 3.3 Selected photographs of elephant impact and woodland composition

**Appendix 3.3.1** Photograph of an *Acacia nigrescens* showing intensive progressive debarking from very old (grey wood) to more recent (yellow wounds) and new (red wounds) with some wound recovery. Photo taken October 2009

**Appendix 3.3.2** Photograph of a dead *Acacia erioloba* which appears to have been cut down with an axe, possibly for bush-clearing as part of Tsetse Fly Control (TFC) operations in the 1950's and 1960's. Photo taken December 2008

**Appendix 3.3.3** Photograph of a deep-rooted *Acacia erioloba* seedlings showing repeated elephant impact. Photo taken December 2007

**Appendix 3.3.4** Photograph of a heavily impacted *Diospyros mespiliformis* sapling showing stunted growth.

**Appendix 3.3.5** Photograph of a *Diospyros mespiliformis* sapling growing in the fenced-off Duma Tau staff village. Photo taken October 2009.

# CHAPTER FOUR

# Megaherbivore-induced conversion of riparian woodland to shrubland along the Linyanti River, northern Botswana

**Keywords:** Acacia, African elephant, browsing lawn, Chobe National Park, *Colophospermum mopane, Combretum mossambicense*, debarking, elephant impact, Linyanti, *Loxodonta africana*, savanna woodland, selective disturbance, shrub encroachment, structural diversity, tree recruitment, tree mortality.

## 4.1 Abstract

One of the leading issues in ecology is the ability of megaherbivores to transform vegetation structure and ecosystem functioning by killing selected size classes. Elephants are an unusual disturbance agent as they are able to kill woody plants across all sizes from seedling to mature canopy tree. Here we report on the transformation of a riparian woodland caused by impacts from elephants (*Loxodonta africana*). We compared structural changes of tree and shrub species within a 45 km strip flanking the Linyanti River in northern Botswana between an earlier survey in 1991/2 and 17 years later in 2007/8. This area is subject to extreme elephant concentrations during the dry season, and fire is largely excluded due to trampling effects. We compared the density changes of tree (>2.5 m) and shrub or sapling (<2.5 m) stages. Tall (>2.5m) canopy tree density decreased by half between 1992 and 2008, representing an annual loss rate of 2.7% without replacement. Overall shrub density increased 2.5 times, while a single shrub species *Combretum mossambicense* increased five-fold to comprise 50% of the total woody plant density. This shrub encroachment wave was incipient in 1992 and by 2008 many of these plants had grown beyond 2.5 m in height, and there were few small plants <1m in height, suggesting the rapid encroachment had slowed. We propose that the spread of this shrub is due to its unpalatability by elephants, although we cannot rule out other potential drivers of increasing regional aridity or atmospheric $CO_2$. Our study documents how differential megaherbivore impact on woody vegetation can promote state transitions of tall canopy woodlands towards dense shrublands.

**Nomenclature:** All plant nomenclature follows Coates-Palgrave (2002)

**Abbreviations:** CCA= Canonical Correspondence Analysis; CNP = Chobe National Park; REM = Relative Elevation Model; DT = Duma Tau; KPL = King’s Pool Camp; SCD = Size Class Distribution

## 4.2 Introduction

### 4.2.1 Structural change in savannas

Savannas are mixtures of trees and grasses that cover over half the area of Africa (Scholes & Archer 1997), and are among the few places where megaherbivores persist in high abundances (Malhi *et al.* 2016). At a regional scale woody cover in savannas is determined by both precipitation determining the maximum limit, and disturbance by herbivores and fire reducing the cover below that maximum (Sankaran, Hanan & Scholes 2005). Within the variable woody component, structural diversity is determined by the relative proportions of shrubs reaching a maximum height of about three metres and canopy trees , reaching heights over 5m (and commonly up to 10m) (Zizka, Govender & Higgins 2014). Shrubs and trees have different architecture and life-history strategies where shrubs are generally contained within a fire and herbivore zone (Higgins, Bond & Trollope 2000; Higgins *et al.* 2007; Staver & Bond 2014) and trees are capable of ‘escaping’ the browse and fire traps as adults, but vulnerable as sapling recruits (Zizka, Govender & Higgins 2014). One of the leading issues in ecology is the ability of megaherbivores to transform vegetation structure (Bakker *et al.* 2016) by reducing woody cover and density (Levick *et al.* 2009; Asner *et al.* 2009), and forming browsing lawns (Cromsigt & Kuijper 2011; du Toit & Olff 2014) or grasslands (Dublin, Sinclair & McGlade 1990; Gillson 2004). These state transformations can also alter ecosystem functions such as fire regimes, and plant-animal interactions (Malhi *et al.* 2016).

A central theme in savanna ecology for decades has been the decline of large trees, without apparent replacement, through the effects of fire and elephants (Thomson 1975; Ben-Shahar 1998; Holdo 2007; Valeix *et al.* 2011; Shannon *et al.* 2011; Vanak *et al.* 2012; Helm & Witkowski 2013; Levick, Baldeck & Asner 2015). Tall canopy trees in savannas are keystone structures (Tews *et al.* 2004) that provide shade and scarce food resources (Belsky 1994; Treydte, Riginos & Jeltsch 2010) and are important for arboreal mammals, and birds (Jeltsch *et al.* 1996; Tews *et al.* 2004; Manning, Fischer & Lindenmayer 2006; Vogel *et al.* 2014). Herremans (1995) conducted a survey of birds in the Linyanti woodland and surrounding areas in 1991/1992 and found that woodland decline due to elephant impact did not significantly affect bird diversity, but rather altered bird species assemblages.

Disturbance plays a fundamental role in structuring savannas at different scales where variable tree cover (at a small-medium scale) is influenced by fire (Bond & Keeley 2005; Staver *et al.* 2009), and herbivory by elephants, and other herbivores (Caughley 1976; Jeltsch, Weber & Grimm 2000; Gillson 2004; O'Kane *et al.* 2014). Demographic bottleneck models (Higgins, Bond & Trollope 2000; Sankaran, Ratnam & Hanan 2004) suggest that disturbances such as frequent fire can prevent recruitment of trees into adulthood by top-killing saplings, resulting in either continual resprouting or mortality. Where fire is prevalent, a 'fire trap' can result where vegetation is kept below *c.* 2.5m in height through sustained top-kill by fire (Higgins, Bond & Trollope 2000; Levick, Baldeck & Asner 2015). In riparian zones where fire is limited due to the low grass fuel load by shading, (Pettit & Naiman 2007) grazing or herbivore trampling (Asner *et al.* 2009; Tjelele, Ward & Dziba 2015), tree demography is influenced by herbivores (Skarpe *et al.* 2004) or flooding and drought events (O'Connor 2010). Megaherbivores are able to transform vegetation by impacting selected woody plants and killing them.

### 4.2.2 Elephant selectivity for structure

African bush elephants (*Loxodonta africana*, Blumenbach 1797) can alter the structure of a savanna where they kill trees by uprooting, top-killing, and debarking (Barnes 2001; Midgley, Balfour & Kerley 2005; Staver *et al.* 2009; Chafota & Owen-Smith 2009; Teren & Owen-Smith 2010; Owen-Smith & Chafota 2012). Elephants are more selective for structure than fire as they tend to concentrate their feeding on intermediate size classes and often ignore small seedlings and plants less than 1m tall (Croze 1974; Pellew 1983; Jachmann & Bell 1985; Gadd 2002; Boundja & Midgley 2009). Chafota (2007) and Stokke and du Toit (2000, 2014) found that elephants predominantly concentrated their feeding within a narrow height range of 1-3m in the Chobe riverfront, northern Botswana. By comparison, fire tends to kill most plants below 3m (Higgins, Bond & Trollope 2000). Elephants are the main mortality agent of tall trees in savannas (with some contribution of wind (Chapter 3)) mainly through their ability to ringbark large trees (Guy 1976; Mwalyosi 1990; O'Connor, Goodman & Clegg 2007). If a plant species is not resistant to elephant topkill or pollarding, mortality of susceptible size classes can occur (Midgley & Bond 2001) keeping small trees in a herbivore 'trap' (Helm *et al.* 2011; Helm & Witkowski 2012; Staver *et al.* 2012; Clarke *et al.* 2013).

The 'elephant farming hypothesis' (Midgley, Balfour & Kerley 2005) suggests that elephants can modify vegetation structure, particularly of *Colophospermum mopane* ((J. Kirk ex Benth.) J. Kirk ex J. Léonard) woodland, so that browse height is lowered to one preferred by elephants (Guy

1976), but with no negative consequences for tree population persistence (Caughley 1976; Lewis 1991; Ben-Shahar 1996, 1998; Smallie & O'Connor 2000; Styles & Skinner 2000). Other browsers benefit from this hedging as available browse biomass is increased in a level accessible to mesoherbivores (Smallie & O'Connor 2000). Hedged mopane also has greater leaf nitrogen content (Kohi, Boer & Peel 2011) and flushes earlier, providing a key resource during the late dry season (Styles & Skinner 2000). Thus, elephants can form a 'browsing lawn' (for a review see Cromsigt and Kuijper 2011 and du Toit and Olff 2014) analogous to the grazing lawns of East Africa (Sankaran & McNaughton 1999). Makhabu and others (2006) found a similar pattern of elephant hedging of a variety of tree species in Chobe National Park which facilitated browsing by impala and kudu. There are indirect effects for other herbivores like impala which preferentially selected areas with high elephant impact which were associated with higher visibility, and probable predator avoidance (Valeix *et al.* 2011). There may be negative consequences for other tree species as the sustained high concentrations of impala along the Chobe riverfront have been implicated in suppressing tree regeneration by killing seedlings (Moe *et al.* 2009).

Elephant-mediated decline of mixed woodlands to shorter *Combretum* shrublands along the Chobe Riverfront led to increased dry-season browse availability for impala (*Aepyceros melampus*), and probably led to impala population increase (Rutina, Moe & Swenson 2005). However this may have feedback effects on woodland structure as the increase in impala has been implicated in seedling predation of sensitive tree species, repressing woodland regeneration (Moe *et al.* 2009, 2014). For most tree species the ability to compensate for elephant impact by resprouting is probably at the cost of compensatory regeneration (Neke, Owen-Smith & Witkowski 2006). This has been highlighted as a function of episodic recruitment (Midgley & Bond 2001; Moustakas *et al.* 2006; Helm 2011) where seedlings are only able to recruit into large size classes in exceptionally good rainfall periods and by escaping the browser trap.

### 4.2.3 Shrub encroachment in savannas

Another structural change in savannas which can potentially impact ecosystem functioning is woody plant encroachment, often by shrub species. Shrub encroachment is a global phenomenon, and well documented in sub-Saharan savannas (see reviews by Mitchard and Flintrop 2013 and O' Connor et al 2014) and is projected to continue with deleterious consequences for structural and compositional diversity (Midgley & Bond 2015). Shrub encroachment is defined as the increase in density, cover and biomass of indigenous woody or shrubby plants (Van Auken 2000). Woody encroachment (Buitenwerf *et al.* 2012; Mitchard & Flintrop 2013; Smit & Prins 2015) is synonymous with such terms as 'bush encroachment' (O'Connor *et al.* 2014); 'woody thickening' (Coetsee, Bond & February 2010; Bond & Midgley 2012) and 'thicket expansion' (Wigley, Bond & Hoffman 2010).

Woody encroachment is fuelled by both local and global drivers (Wigley, Bond & Hoffman 2010) and disentangling the relative causes is not easy. Local land use practices such as overgrazing remove the grass sward which can lead to shrub encroachment by limiting fires which allows woody plants to establish (Jeltsch *et al.* 1997; Roques, O'Connor & Watkinson 2001). Because fire is mostly excluded from riparian areas, the potential of shrub encroachment into riparian zones is high, but has often been overlooked.

However long term woody encroachment has been observed across different land-use types (Wigley, Bond & Hoffman 2010; Buitenwerf *et al.* 2012) and suggests a global driver such as increased atmospheric carbon dioxide ($CO_2$). Elevated $CO_2$ from greenhouse gas emissions favours $C_3$ woody plants over $C_4$ grasses (Kgope, Bond & Midgley 2010) with the added effect of allowing rapid growth of trees to escape the 'fire trap'(Bond & Midgley 2000). Evidence for elevated $CO_2$ driving woody encroachment in savannas is increasing, but has mostly been described for grass-dominated systems (Higgins, Bond & Trollope 2000; Bond & Midgley 2012; Higgins & Scheiter 2012).

High browsing pressure has been suggested as limiting shrub encroachment, but through the mechanisms of woody seedling predation by meso-herbivores or in combination with fire where browsing maintains woody plants in a fire trap (Roques, O'Connor & Watkinson 2001). The context of elephant effects on shrub encroachment has largely been that elephants are capable of preventing shrub encroachment through suppression of woody plant density (Levick *et al.* 2009; Staver *et al.* 2009; O'Connor, Puttick & Hoffman 2014; Daskin, Stalmans & Pringle 2015). Very rarely has the potential for shrub encroachment been linked to the action of large herbivores which remove large trees, providing gaps for colonisation. Downstream of the Linyanti River, on the alluvial terrace of the Chobe River, mixed woodland cover decreased from 60% to 30% over 36 years, with a converse increase of mixed shrubland cover from 5% to 33%, (Mosugelo *et al.* 2002). Elephants were suggested as the main cause of large tree death but seedling browsing by impala prevented recruitment (Skarpe *et al.* 2004, 2014b; Rutina, Moe & Swenson 2005; Makhabu, Skarpe & Hytteborn 2006; Moe *et al.* 2009). The mechanisms of the increase of shrub cover were less clear (Mosugelo *et al.* 2002).

To successfully document functional transformations of vegetation requires demonstration of a density change over time plus the ability to distinguish shrubs from tree saplings at species level. The most compelling studies of shrub encroachment in the presence of large herbivores have been of broad canopy cover changes (Eckhardt, Wilgen & Biggs 2000; Wigley, Bond & Hoffman 2010; Levick & Rogers 2011; Buitenwerf, Swemmer & Peel 2011), or spatially through exclosure experiments to infer large herbivore effects (Levick *et al.* 2009; Asner *et al.* 2009). Thus field studies which are at a fine enough spatial scale for species identification and over a long enough period to measure density changes are rare (Roques, O'Connor & Watkinson 2001). We also need additional evidence of the functional consequences of the demographic bottleneck of trees and shrubs at 2.5m. Because elephants are water-dependent, their greatest densities and effects can be seen around permanent water where the decrease in large trees or particular size classes may be as a result of loss of preferred species (Kalwij *et al.* 2010). This means that riparian woodlands are ideal systems to study the effects of elephants on vegetation structure. Riparian woodlands also stand out as areas of high structural diversity exhibiting the highest woody biomass (Colgan *et al.* 2012) and tallest trees (Levick & Rogers 2011) in the savanna landscape.

Analysing shrub encroachment in riparian areas where fire is largely excluded may present a valuable opportunity to distinguish local drivers such as disturbance from global drivers of increasing atmospheric carbon and climate change as fire is excluded, leaving only intense browsing as a potential local driver. In addition, elephant impacts are not homogeneous, as elephants are highly selective for species and sizes, and this affords the opportunity to study the spatial associations of increased shrubs with high elephant impact.

### 4.2.4 Questions

Our hypothesis for this study is that elephant impacts in the Linyanti riparian woodland have transformed the tall canopy tree woodland to a shrubland composed of shrub species. This hypothesis led to six questions: (1) Has the density of tall canopy tree species declined over the 17 years?; (2) Has the density of canopy tree saplings declined?; (3) Have shrub species increased in density over time?; (4) Does seedling composition suggest shrub species will continue to increase?; (5) Are high shrub densities associated with dead trees where elephants have created open gaps?; and (6) Do increasing shrub species show less impact from elephants than other shrub species?

## 4.3 Methods

### 4.3.1 Study Site

The Linyanti woodland is on the Botswana side of the Linyanti River, which forms the international boundary with Namibia's Zambezi Region (Chapter 1, Fig. 1.4). The riparian woodland lies in a private photographic concession area (NG/15), leased by Okavango Wilderness Safaris. The riparian zone on the Botswana side is a narrow strip (~100-200m wide) of mixed woodland on a terrace above the main channel. Inland of the riparian strip are vast *Colophospermum mopane* woodlands. The rainfall occurs in the summer months between November and April and the MAP for 92 years is 557.6mm at the nearest weather station at Kasane (NOAA, 2014).

Northern Botswana has an estimated elephant population of over 120 000 animals with a regional density of 1.75 km$^2$ (Chase 2011). In 1992 the dry season density of elephants in the Linyanti area was documented in excess of 4 animals.km$^2$ (Coulson 1992).  The population stabilised around 2004 (Chase 2011) with a recent dispersal of elephants into neighbouring Angola, Namibia and Zambia (Chase & Griffin 2009; Cushman, Chase & Griffin 2010).  The Linyanti and Chobe Rivers have been subject to extreme densities of elephants for decades as they congregate along these perennial rivers in the dry season (April-October). In a dry season survey of 1987 (Spinage 1990)) 12 elephants.km$^{-2}$ were recorded for the 1000 km$^2$ of the Linyanti-Kwando area.  During the dry season the vegetation close to the Linyanti and Chobe Rivers is subject to intense impacts, particularly debarking of trees (Ben-Shahar 1993; Wackernagel 1993; Teren & Owen-Smith 2010; Fullman & Child 2012; Owen-Smith & Chafota 2012).  During the wet season elephants disperse to take advantage of ephemeral pans in upland areas where they feed in mopane woodlands (Fullman & Child 2012).

Elephant density is seasonally extremely high in the study region of NG/15 (a survey area of 1232 km$^2$) where a density of 2.35 elephants.km$^{-2}$ was recorded during the dry season of 2010 (Chase 2011). For the same survey, the densities of other browsers were: 1.32 impala.km$^{-2}$; 0.09 giraffe.km$^{-2}$; and 0.05 kudu.km$^{-2}$ (Chase 2011).

Fire is a rare event in the riparian zone, with zero extensive fires and only six documented localised (<1km$^2$) single fire events between 2001 and 2016 across the 2000ha study region (NASA FIRMS 2016)

### 4.3.2 Field Data Collection

This is a long-term study which is dependent on an earlier survey conducted by Wackernagel (1993) in October 1991- January 1992 (for brevity referred to as the 1992 survey) (Wackernagel 1993). Wackernagel surveyed 35km of riverfront between the eastern boundary of Chobe National Park (CNP) (18.2702° S; 23.9365° E) westwards to the King's Pool Safari camp (KPL) (18.4370° S; 23.7079° E) by transects placed every 0.5km along the main safari road in both ends of the study region (high disturbance area) and every 1.0km in the middle section (lower disturbance area) (Fig. 1.6). We followed up on this study in the wet seasons of Dec 2007/Jan 2008 and Nov/Dec 2008 (referred to as the 2008 survey in the text). We stratified the 2008 transects based on tree mortality (three regions of high mortality, one of low, Fig. 1.6) which we extracted from digital colour aerial photographs (1:10000) from 1992 and 2001. We manually marked every dead tree in the photographs and ran a density kernel function in ArcMap 9.2 to extract regions of high and low tree mortality (Appendix 1.3.1). Our study area overlaps mostly with Wackernagel's, but excluded a portion of CNP (Fig. 1.6) and with the addition of an extra 19 transects to the far west of the study region around Duma Tau Camp (DT) (-18.5368° S; 23.5659° E) (Fig. 1.6). Two of our high-density regions (KPL and CNP) corresponded to the intensively surveyed transects in 1992, but the additional high mortality DT area was not surveyed in 1992 (Fig. 1.6). There were 50 transects in 1992 and 55 in 2008.

Transects (both 1992 and 2008) ran perpendicular to the river from river edge, across the riparian belt, to the mopane zone indicated by the increased prevalence of *C. mopane.* In 1992, transects were not of fixed-width but used distance-based sampling to estimate nearest neighbour density using the 'T-Square Method' (Byth 1982). Because of an overestimation bias in this distance-based density estimation method (Appendix 4.1), in 2008 we opted to survey fixed-width belt transects. The belt transects were 10m wide for riparian canopy tree species, excluding the most common tree *C. mopane*, which was sampled in a 5m width, as were all shrub species.

For both surveys, all living plants above 0.5m in height were identified by species, and their height and basal stem diameter recorded. We separated plants into two functional groups of shrub species and tree species based on architecture and height (Zizka, Govender & Higgins 2014). We separated species into tree and shrub groups based on architecture and known maximum height from the literature (Coates-Palgrave 2002). Shrub species were often (but not always) multi-stemmed, and formed the subcanopy of the woodland, whereas tree species were capable of reaching heights of 10m and greater, and formed the canopy of the woodland. All plants were placed into four height categories (0.5-1m, 1-2.5m, 2.5-10m, >10m) and later resampled into two groups- below 2.5m (saplings) and above 2.5m (trees). Shrubs were classed as woody species with a maximum height below the canopy layer of 10m. We counted individual plants instead of number of stems. For multi-stemmed shrubs, an individual plant was identified as a collection of stems sprouting from the same base, and for clonal plants a new individual was identified where we could clearly distinguish the basal shoot(s) from parent stock. We suspected that some *Combretum hereroense* plants were incorrectly identified as *C. molle* in the 1992 survey and combined these two species in our analyses for comparison with 1992 estimates.

Seedlings (plants less than 0.5m in height) were not surveyed in 1992. In 2008 we surveyed seedlings using square metre quadrats placed every ten metres along each transect. We included the 4 neighbouring quadrats of each side of the original sample point to increase sample size to a total of 5 square metres per every sampling point. We estimated aerial cover percentage of seedlings for each square metre and per each shrub and tree species. The aerial cover of each seedling species was then totalled per transect ($m^2$), as well as the proportion of total area sampled covered by seedlings.

Elephant impact on trees and shrubs was recorded by percentage of main stem circumference stripped of bark (for multi-stemmed shrubs this was 50% of all stems bark-stripped) and number of stems (main or side stems) broken. A high elephant impact category was plants which had over 50% bark circumference removed and/or with the main stem broken (or pushed over) or over half of the side stems broken (heavy pollarding).

All plant nomenclature follows Coates-Palgrave (2002) and we have persisted in using the *Acacia* genus name as it represents a cohesive group in our compositional analyses, and in comparing to the earlier survey.

### 4.3.3 Data analysis

To answer whether the density of tall canopy tree species had declined over the time period (question 1) we used descriptive statistics to compare the densities of tall canopy trees (>2.5m) between 1992 and 2008. The 1992 densities were calculated from distance sampling and the distance estimator ‘T-square’ (Byth 1982) which is described in Appendix 4.8.1. We used the 1992 densities reported in Wackernagel (1993) with a bias-correction factor of ¼ to compare to the later densities. This bias-correction factor was needed as the reported 1992 T-square densities were overestimated several-fold (Wackernagel 1993) as the T-square method has the explicit assumption that plants measured have a random spatial pattern (Clayton & Cox 1986). We approximated the bias-correction factor based on the comparative 2008 densities for tall (>2.5m) trees of *Colophospermum mopane,* an abundant species which we expected to have changed least in density, either up or down. For full explanation and calculations see Appendix 4.8.1. We realise that this bias-correction factor is an approximation but will enable comparisons for common species, and the bias is minimised where a species changes several fold in density, so where appropriate we have reported fold-changes instead of percentage changes. We compared the bias adjusted 1992 (Wackernagel, 1993) densities to those recorded in an unpublished report by Coulson (1992) (Appendix 4.8.1) and found that our calculations brought the densities in line with those recorded by Coulson, though they were probably still overestimated. We are confident that any fold-increases in density from 1992 to 2008 will be significant. For the 2008 densities we divided the number of plants surveyed by the area covered by the fixed-width transects (23.91 ha) and also calculated SE. To evaluate any disproportionate abundance of species in the additional set of transects around DT not covered in 1992, we compared the average density of each species between the different transect sections surveyed in 2008.

To assess potential transformation from woodland to shrubland (questions 2 and 3) we compared total shrub and tree densities between 1992 and 2008 for two height stages (<2.5m, >2.5m). To determine if the short tree layer (<2.5m) was composed of compensatory regeneration of saplings or hedging by elephant top-kill, we looked at species-specific changes in stage-class distributions over the time period and used elephant impact proportions from Chapter 3. We relied on descriptive statistics to compare numbers in 2008 against numbers in 1992 by stage class.

To assess regeneration potential from the seedling layer (question 4) we described seedling composition for 2008 by proportional abundance (of all seedlings surveyed) and further separated species into shrub and tree species.

We hypothesised that shrub species would colonise gaps created by elephant-induced tree mortality (question 5) and so we used dead tree density and other environmental variables in a CCA (Canonical Correspondence Analysis) of shrub density distribution using CANOCO 4.5. Our response variables were the density of the most common shrubs *Combretum mossambicense, Croton megalobotrys*, *Dichrostachys cinerea*, *Diospyros lyciodes* and *Philenoptera nelsii* across 55 transects. We further included the density of all species of shrubs and *C. mossambicense* by three size classes (0.5-1m, 1-2.5m, >2.5m) to evaluate the potential differences in distribution of seedlings and adult plants. We also included the seedling abundance per transect for *D. cinerea*, *C. mossambicense* and all shrub seedlings. Our environmental variables related to elephant impact were the densities of dead *Acacia* trees, all dead trees, and living trees in the four height classes.

We also included relative elevation as an explanatory variable in our CCA to evaluate the potential effect of available soil moisture on shrub density. We expected lower features such as palaeochannels to represent areas of higher water table access for roots. We produced a Relative Elevation Model (REM) relative to the main river channel (min -3m, max 8m). The REM was calculated from a 2010 LiDAR survey of one metre resolution DEM (Digital Elevation Model). We used Zonal Statistics in ArcMap to extract the mean relative elevation values for each 10m wide belt transect. Forward selection by Monte Carlo tests (999 permutations) was used to select significant environmental variables ($p < 0.05$). The total variation explained by the CCA was calculated as a percentage of all canonical eigenvalues divided by the sum of all eigenvalues (Lepš & Šmilauer 2003)

To assess whether increasing shrub species showed less elephant impact than other species (question 6) we compared proportional densities of severe impact on living shrubs (classified as over 50% stem(s) circumference ringbarked and/or where there was main stem breakage). For multi-stemmed shrubs the majority of stems had to be broken to be classified as severe impact. We categorised species as either increasers or not based on density changes and compared across the categories. We also included the proportion of severe impact of the only common dead shrub *D. cinerea.*

## 4.4 Results

### 4.4.1 Has the density of tall canopy trees declined?

Wackernagel (1993) surveyed a total of 4153 living plants, and identified 18 tree species and 17 shrub species, with an additional 7 unidentified shrub species (Appendix 4.2). The 2008 survey recorded 8865 plants with one new tree species record (*Acacia caffra*). Three shrub species were not recorded in the 2008 survey, and three species were only recorded in the later survey.

Both tree and shrub groups showed differences in structure from 1992 to 2008 (Fig. 4.1). For tall (>2.5m) canopy tree species, projected density had halved from an estimated 74 trees.ha$^{-1}$ in 1992 to 28.2 ± 8.6 (SE) trees.ha$^{-1}$ in 2008 (Fig. 4.2). Short (<2.5m) canopy tree density appeared to have increased slightly over the time period and was nearly double that of tall tree density by 2008 (Fig. 4.1).

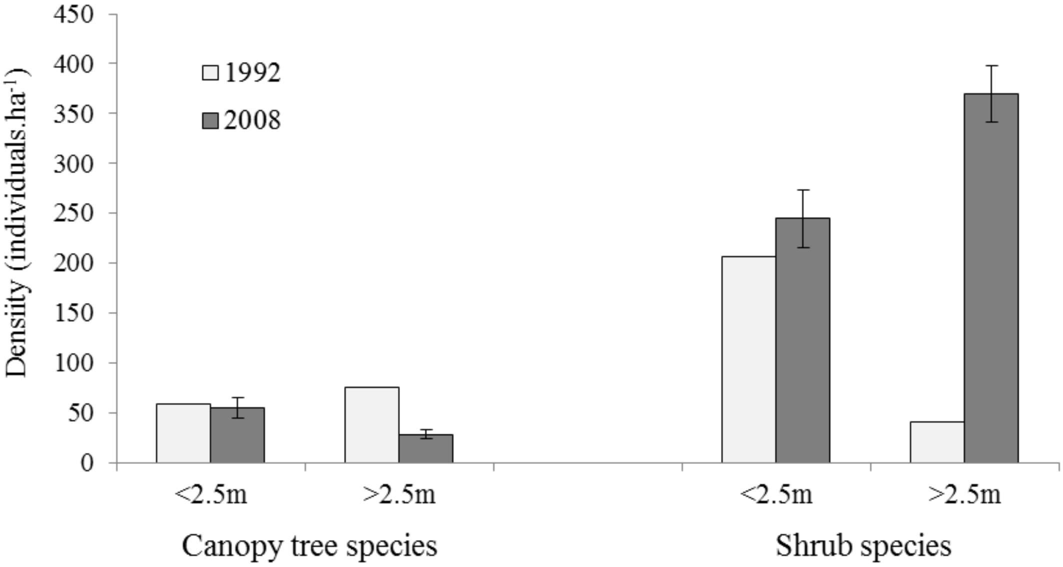

**Figure 4.1** Density comparison between 1992 and 2008, of short (>2.5m) and tall (>2.5m) plants classified as either canopy tree species or shrub species. Standard Error (SE) bars are included for the 2008 density estimates. 1992 figures have been projected based on a bias-adjustment factor of those presented by Wackernagel (for full details see Appendix 4.1)

The tall tree (>2.5m) densities of *C. hereroense, A. erioloba*, *A. nigrescens* and *T. pruniodes* declined most over the period (Fig. 4.2A) The apparent decline in tall trees density mostly ranged from 98% for *A. erioloba* which was previously the most common tall tree in 1992; to 47% for *P. violacea*. *Colophospermum mopane* had become the most common tall tree in 2008 at 13.1 (± 3.5) trees.ha$^{-1}$ (Fig. 4.2A). *Diospyros mespiliformis* tall tree density was higher in 2008, but as a result of a localised concentration of this species around BDF which was not intensively sampled in 1992.

### 4.4.2 Has the density of canopy tree saplings declined?

There was a generally low density of saplings where the density of most recorded species was less than 2.trees.ha$^{-1}$ (Fig. 4.2B). Saplings of all tree species declined in density except three (*C. mopane, P. africanum* and the uncommon *B. albitrunca*) (Fig. 4.2B). The apparent decline in density of saplings ranged between 75% (*A. erioloba*) and 90% (*T. sericea*) (Fig. 4.2B). Saplings of two species, *B. discolor* and *D. mespiliformis* were only recorded in the 2008 survey, probably as a consequence of a greater sampling area. *Colophospermum mopane* sapling density increased 1.5

times to 25.7 ± 4.1 trees.ha$^{-1}$ (Fig. 4.2B) which was responsible for offsetting the declines of other species in the sapling layer (Fig. 4.1). *Peltophorum africanum* was the only other sapling species to show an apparent increase in density (of 1.5 times).

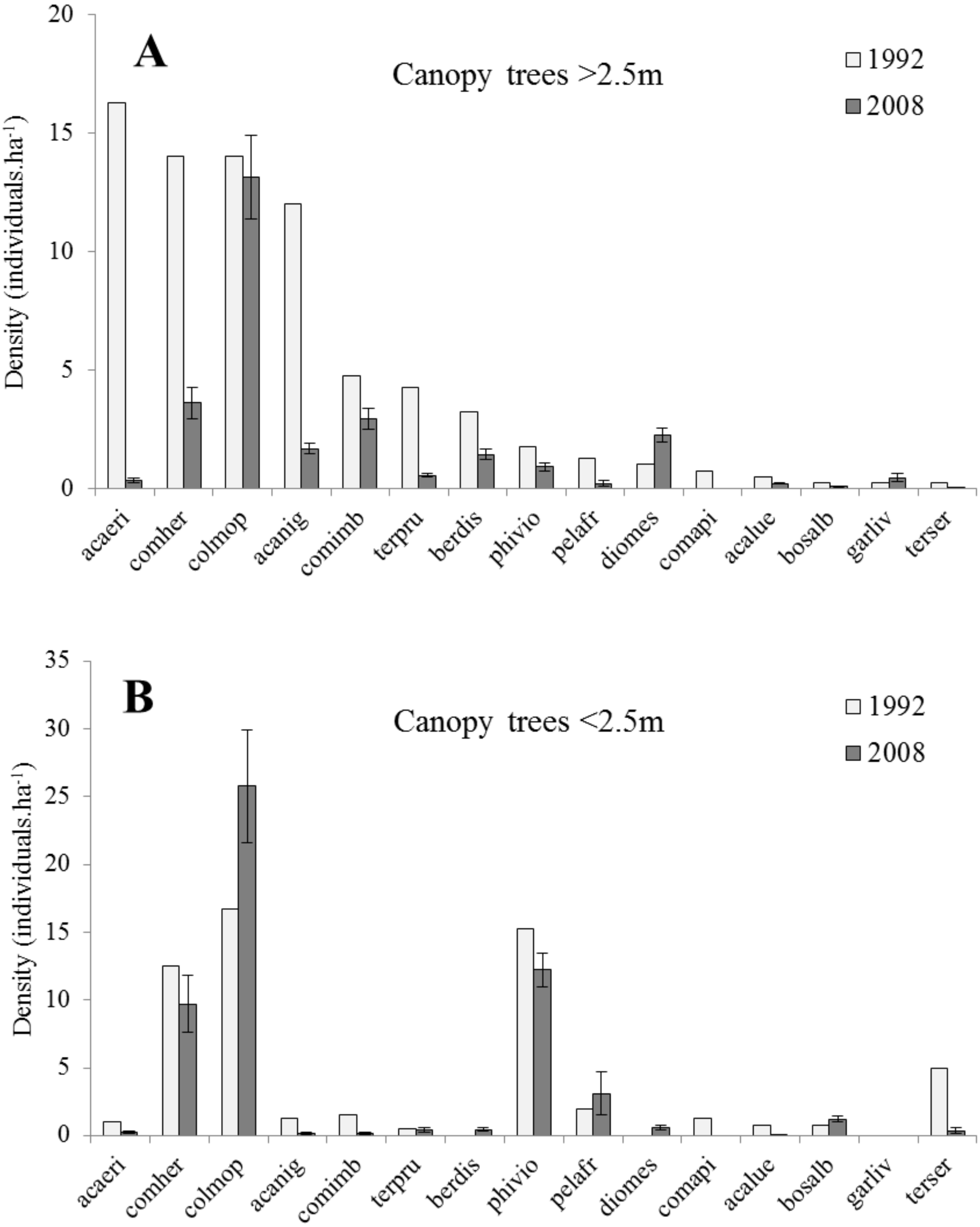

**Figure 4.2** Density comparison between 1992 and 2008 of the most common canopy tree species between A: tall canopy trees (>2.5m) and B: short saplings (>2.5m). Species are ordered in descending order of density of tall trees in 1992. Standard Error (SE) bars are included for the 2008 density estimates. Species codes are the first three letters of the genus and species names (listed in Appendix 4.2)

### 4.4.3 Have shrub species increased in density over time?

Shrub species were more abundant than canopy tree species in both surveys (1.8 times more abundant in 1992 and 7.4 times more abundant in 2008). The overall density of shrub species increased 2.5 times from 1992 to 2008 (Fig. 4.1). Shrub species in 2008 totalled a combined density of 614.3 (± 113.7 SE) individuals.ha$^{-1}$ (Appendix 4.2). The most dramatic change was the 10 times increase of tall shrub (>2.5m) density transitioning from the short shrubland of 1992 (Fig. 4.1). This dramatic shrub increase is due mainly to one species, *Combretum mossambicense*, which experienced a five-fold increase in density from 62.75 individuals.ha$^{-1}$ in 1992 to 348.2 (± 40.1 SE) individuals.ha$^{-1}$ in 2008 (Fig. 4.3). The density of this one species equalled the density of all other species combined at 349.7 (± 101.3 SE) trees.ha$^{-1}$ in 2008 (Appendix 4.2). The increase in *C. mossambicense* tall plants (>2.5m) increased 72 times as they transitioned from short plants surveyed in 1992.

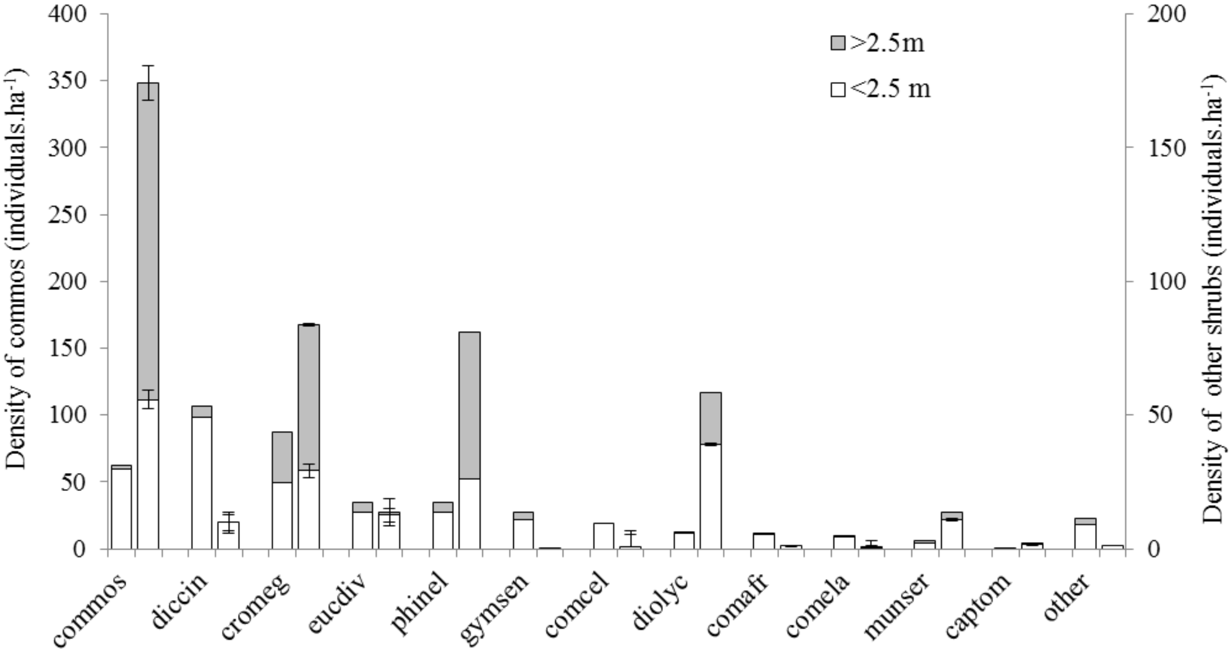

**Figure 4.3** Density comparison of the most common shrub species between short (<2.5m) and tall (>2.5m) individuals and over time where 1992 is on the left and 2008 on the right of every pair by species. Y-axis for *Combretum mossambicense* is on the left hand side and is 2x the y-axis for other species. Species are ordered in descending total density for 1992. Standard Error (SE) bars are included for the 2008 density estimates. Species codes are the first three letters of the genus and species names and listed in Appendix 4.2.

Most shrub species declined in density apart from *C. megalobotrys, P. nelsii, D. lyciodes,* and *M. sericea* (Fig. 4.3). *Croton megalobotrys* nearly doubled in density, also due to small plants transitioning to taller shrubs. There was a similar pattern for *P. nelsii* where most plants had become taller than 2.5m and increased nearly 5-fold overall. For *D. lyciodes* and *M. sericea,* the increase in density was mostly of small plants below 2.5m (Fig. 4.3). *Dichrostachys cinerea* declined most by over 80% from 1992 to 2008.

The SCD of proportional abundance of *C. mossambicense* reveals an interesting pattern of potential colonisation and plant growth in time (Fig. 4.4). Whilst *C. mossambicense* was a prominent feature in the woodland in 1992 (Fig. 4.3), the vast majority (85%) of plants were small recruits below 1m in height, with very few tall plants (only 6%) above 2.5m (Fig. 4.4). By 2008 the SCD distribution pattern had inverted where 70% of the plants were above 2.5m, but there very few (6%) small recruits (0.5-1m). This documents an incipient wave of encroachment in the woodland in 1992.

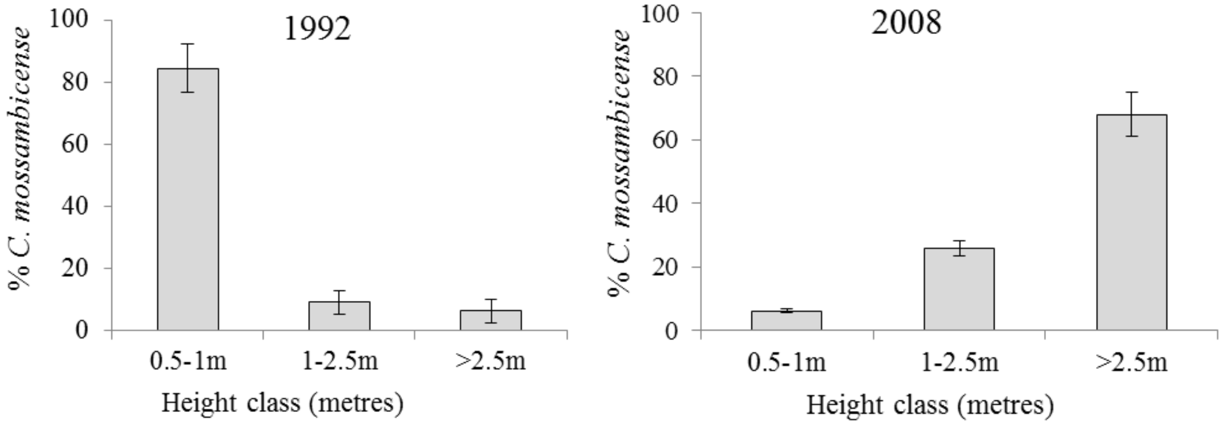

**Figure 4.4** Comparative Size Class Distributions of C. mossambicense for 1992 (left) and 2008 (right) by proportional abundance

### 4.4.4 Does seedling composition suggest shrub species will continue to increase?

The seedling layer in 2008 was dominated by *Dichrostachys cinerea* at 50% (182.7 $m^2$) of all seedling species abundance. Tree species such as *C. imberbe*, *C. mopane* and *A. nigrescens* formed the next most abundant seedlings (Fig. 4.5, Appendix 4.2). Shrub species altogether were represented in 70% of the seedling layer, but if we remove the influence of *D. cinerea*, canopy tree seedlings make up the majority of seedlings surveyed. Combretum *mossambicense* was prevalent at 5% of species but with only 17 $m^2$ (Appendix 4.2) covered by seedlings in the 8808 $m^2$ sample area, representing an occurrence proportion of 0.2% of area sampled. Out of 8808 plots, total seedling cover only contributed 4% of the total area sampled.

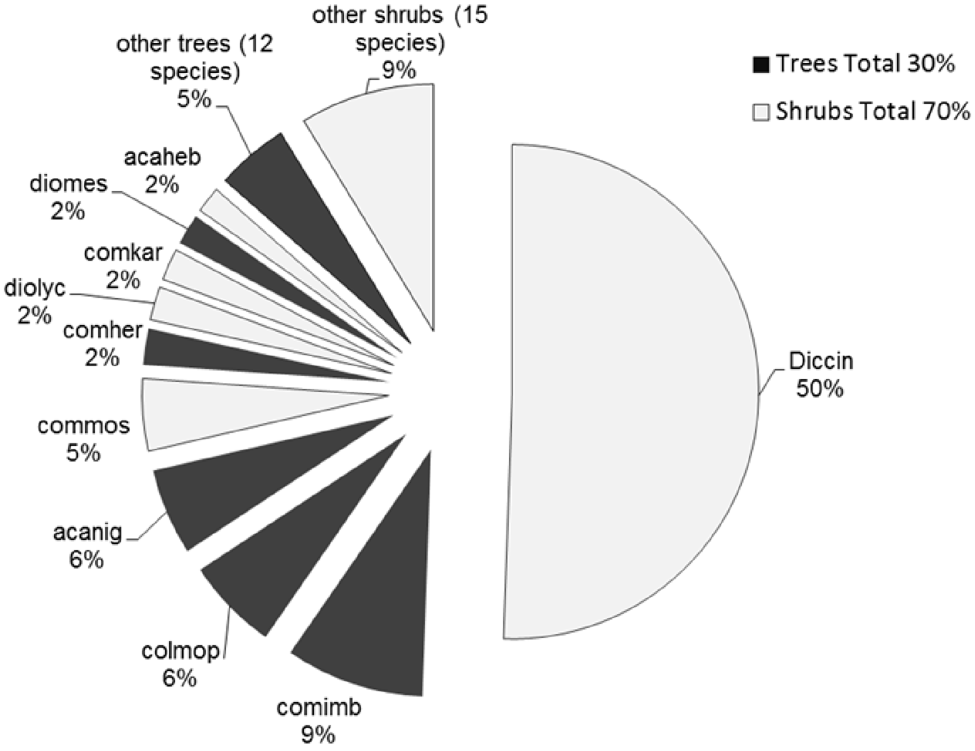

**Figure 4.5** Relative contribution of various tree and shrub species to the seedling layer (plants <0.5m in height), by total coverage ($m^2$) from the 2008 survey. Species contributing less than 2% are lumped into 'other'. Species codes are according to Appendix 4.2

### 4.4.5 Are high shrub densities associated with dead trees?

The most important environmental variables associated with the distribution of shrubs in our CCA were saplings (trees <2.5m) and the REM, with dead acacia density weakly influencing the distribution, and living acacia density not being influential and omitted from final analysis (Fig. 4.6). The density of large trees did not emerge as significant environmental variables for the distribution of shrubs. The density of saplings (trees 1-2.5m) explained 42% of the variation, established seedlings (0.5-1m) 35% and the REM 32%. The eigenvalue of the first axis was 0.069 and explained 66% of the variation of the species-environment correlations. The second axis eigenvalue was 0.062 and explained 51%. Seedlings of *D. cinerea* and all shrub species combined were not associated with any of the environmental variables used, but seedlings and tall (>2.5m) plants of *C. mossambicense* were associated with higher elevations. Small established seedlings (0.5-1m) of *C. mossambicense* were not associated with any of the environmental variables analysed. The density of *D. lyciodes* was associated with high densities of saplings (trees 1-2.5m), whilst *D. cinerea* shrubs were associated with high densities of dead *Acacia* trees. Relative elevation (REM) had an influential effect on the density of large shrubs of *C. mossambicense* as well as the density of *P. nelsii* (Fig. 4.6).

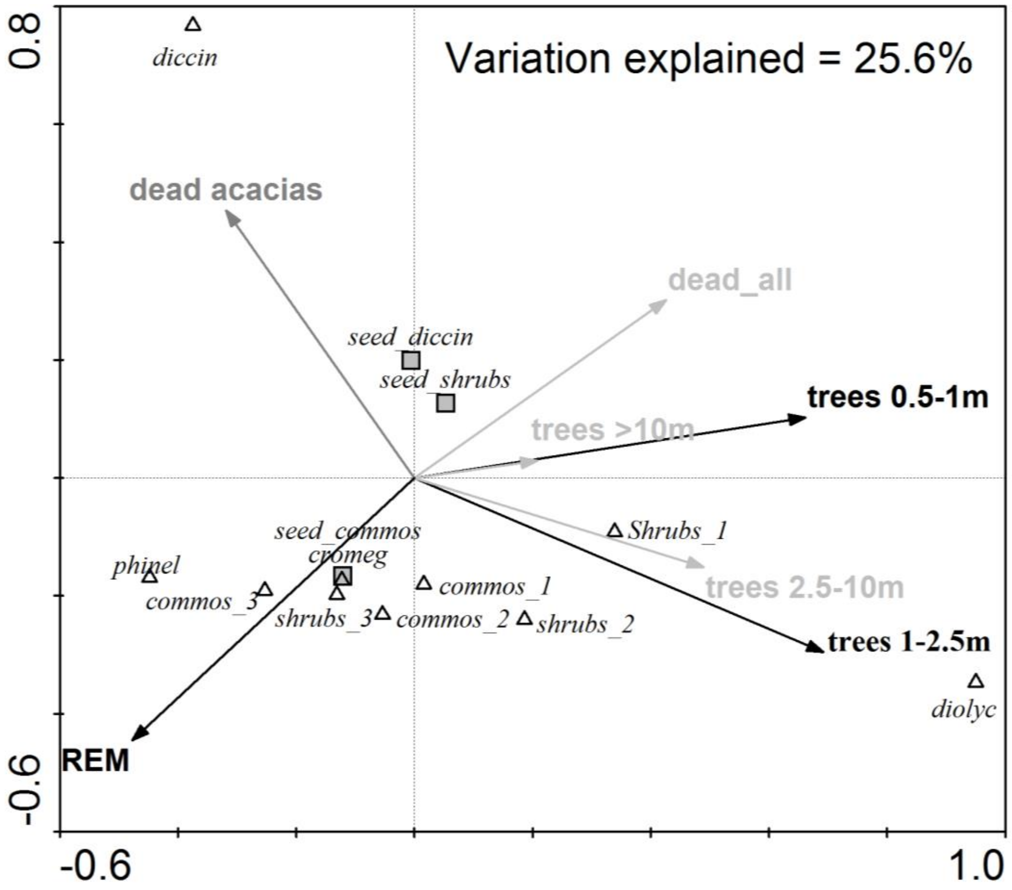

**Figure 4.6** Canonical Correspondence Analysis (CCA) Biplot of shrub density (open triangles) and seedling abundance (grey squares) explained by environmental variables. Black environmental variables significant at $p<0.05$; dark grey $p<1$; light grey not significant. Shrub density given as total density for dioyc, phinel, cromeg, and commos and density of commos according to 3 height classes: commos_1: <1m; commos_2: 1-2.5m; commos_3: >2.5m. All shrub species combined given in the same height classes. For species names see Appendix 4.2. Total explained variation was calculated as sum of all canonical eigenvalues as a percent of all eigenvalues.

### 4.4.6 Do increasing shrub species show less impact from elephants than other shrub species?

As expected, the shrub species that had increased most in density were subject to much lower prevalence of severe (fewer than 20% of plants for 1992) impacts (debarking, uprooting, pollarding) than shrub species which declined over the time period (Fig. 4.7). Interestingly, 16% of *C. mossambicense* plants showed high impacts in 1992 (Fig 4.7) where impacted plants (12% of all plants) were shorter than 1m (75% impact <1m). Only five plants (0.1%) of *C. mossambicense* were impacted in 2008 (Fig. 4.7). By contrast, shrub species which had declined over the period all showed much higher proportional impact with most of these species showing over 70% heavily impacted plants in 1992 (Fig. 4.7). *Dichrostachys cinerea* had declined most over the period (Fig.4.3), with 100% of dead plants in 1992 showing signs of high elephant impact. Impact proportions were higher in 1992 for all species.

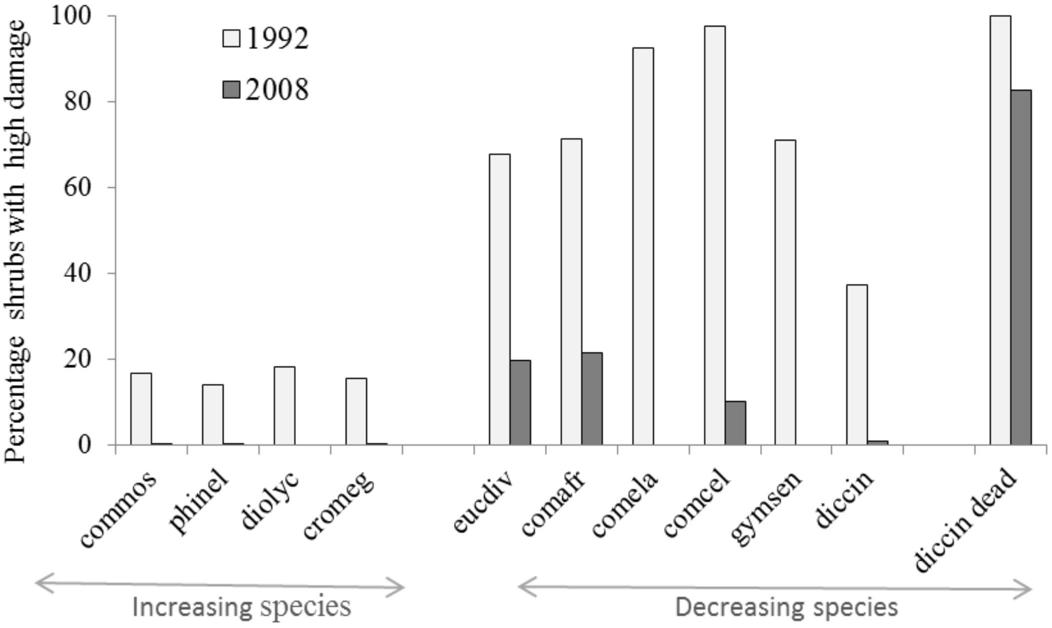

**Figure 4.7** Elephant impact on shrub species (% plants) for species which have increased in abundance, and species which have declined. All values given as a percentage of live shrubs with high impact, except for *Dichrostachys cinerea* (diccin) which has both living and dead proportions. Species order given by magnitude of change where commos shows the greatest increase, and diccin the greatest decline between 1992 and 2008. Species codes given in Appendix 4.2)

## 4.5 Discussion

### 4.5.1 Conversion of tall trees to short trees

We have documented a structural conversion of tall canopy trees to short trees as well as a functional conversion from canopy-forming tree species to shrub species. Tall canopy forming trees declined by 50 %, but there was no compensatory regeneration from saplings, as these also declined, apart from *C. mopane* which increased in the form of coppiced hedges (see Appendix 4.3.1). Tall trees have not however declined to the same extent as the Chobe riverfront where tree density can be as low as 0.15 ± 0.02 (SE) trees.ha$^{-1}$ (Rutina & Moe 2014).

Tall canopy tree (>2.5m) density declined at a rate of 3.6 % per year, which halved the density from 1992 to 2008.  The average rate for all sizes was 2.2 % suggesting tall canopy trees experienced higher rates of mortality. In Chapter 3 we used proportional abundance changes to calculate a mortality rate of 2 % which agrees with our findings here and supports our density calculations, validating our 4x density adjustment for 1992.  Bell (2003) analysed loss of canopy trees (trees noticeably above the shrub canopy of about 4m) from1992 and 2001 aerial photographs for the same study area. He found a loss rate of 1.85% per year. Our rate for the extended time period is twice that and may be as a result of covering a different height range. A background mean annual death rate (with disturbances from herbivores and fire excluded)  for *A. erioloba* in the Kalahari was calculated for over 53 years at around 1%, but could be as high as 3% for some sites (Moustakas *et al.* 2006). Our total loss rate of 2.2% is not much higher than this background mortality rate.

Tall trees of species known to be selected for by elephants, *C. hereroense*, *A. erioloba*, *A. nigrescens* and *T. pruniodes* (Chapter 3) declined most.  Two species of acacia were an important component of the tall canopy tree layer in 1992 and showed the most drastic declines with a 98% decline for *A. erioloba* and 86% for *A. nigrescens*. Around half of dead acacia trees in 2008 showed intense elephant impacts whilst others were thought to have died from natural senescence (Chapter 3). Other minor components of the tall tree layer which showed declines of over 75% (*Terminalia* spp., *P. africanum,* and *C. hereroense/molle*) also showed very high proportional elephant impact (Chapter 3). Elephant impact is therefore the most reasonable explanation for the decline in canopy trees as elephants debarked tall trees like the acacias, and pollarded and felled shorter trees like *C. hereroense* and *P. africanum* (Chapter 3).

By 2008 sapling (<2.5m) density was nearly twice that of tall trees, and this represents a stage conversion from adult trees to short trees trapped in the browse and fire zones. Saplings of all tree species declined in density except three (*C. mopane, B. albitrunca* and *P. africanum*) illustrating compensatory regeneration of saplings was not taking place.  *Colophospermum mopane* short trees (<2.5m) doubled in density to 25.7 ± 4.1 (SE) trees.ha$^{-1}$ in 2008, twice the density of the next most abundant sapling.  Elephants pushed over and pollarded intermediate sized trees (1-10m in height), which did not die, but recovered as a hedged coppice growth form (Midgley, Balfour & Kerley 2005; Cromsigt & Kuijper 2011) (See Appendix 4.3.1). This pattern of tall *C. mopane* tree conversion to coppiced logs extends beyond the riparian zone in the uplands of the Linyanti

(Mograbi 2011). This transformation to coppiced state potentially has both positive and negative consequences. If the ‘browsing lawn’ hypothesis holds for Linyanti as illustrated in other areas, available *C. mopane* browse quantity and quality will have increased for other browsers (Smallie & O’Connor 2000; Styles & Skinner 2000; Makhabu 2005b; du Toit & Olff 2014). However the general loss of tall canopy trees also has negative consequences for arboreal animals (Pringle *et al.* 2015), including bats (Fenton *et al.* 1998) and birds (Vogel *et al.* 2014). Birds in particular are more sensitive to structural changes than compositional shifts (Jeltsch *et al.* 1996; Tews *et al.* 2004; Manning, Fischer & Lindenmayer 2006; Sirami *et al.* 2009; Vogel *et al.* 2014). In their review of keystone structures Tews *et al*. (2004) described how large trees in savannas, but not saplings or thickets, create structural diversity for a number of animal species.

### 4.5.2 Shrub encroachment in the riparian woodland

The density of all shrub species and sizes increased 2.5 times over the period however the most dramatic result was the pervasive increase in density and size of one single shrub species, the shrub or scrambler *Combretum mossambicense,* which increased five-fold in density, from 1992 to 2008. By 2008 this one species came to constitute 50% of the total woody plant density, illustrating pervasive shrub encroachment (See Appendix 4.3.2). The increase in density and conversion of small to large shrubs represents an exponential growth rate of 10.5%. Even if the 4x adjustment factor in our density calculations is imprecise, the 10 times increase in *C. mossambicense* density is substantial. This approximately equals the highest rates of shrub encroachment (11.12% per year) presented in a meta-analysis of 16 situations of density-based shrub encroachment (O’Connor, Puttick & Hoffman 2014). Other shrub species also increased (*C. megalobotrys* and *D. lycioides*) but were commonly found along the marginal floodplain and may be tied to temporary river movement.

A similar structural shift from riparian woodland to shrubland was documented along the Chobe Riverfront, where elephants had killed the large trees which were replaced by *Capparis-Combretum* shrubland dominated by *C. tomentosa* as well as *C. mossambicense* (Skarpe *et al.* 2004; Rutina, Moe & Swenson 2005). *Combretum mossambicense* was the most abundant shrub in heavily disturbed Kalahari sand- alluvial sites, but at a lower proportion of 40% of relative abundance and evaluated for a small sample area of 0.48h (Rutina & Moe 2014). This fits with an earlier pattern reported by Simpson (1975) who noted locally dominant areas of *C. mossambicense* along the Chobe River. By contrast, in the Linyanti, this species was spread across the whole woodland as the only woody species to occur in 100% of transects in 2008. *Combretum mossambicense* is likely a previously undocumented encroaching species of shrub (for a review see O'Connor et al. 2014), which is widespread at low densities in southern Africa (Coates-Palgrave 2002).

*Combretum mossambicense* was noted as a 'particularly conspicuous' shrub in the early 1970's, but as *D. cinerea* contributed 80% of the total number of all shrubs, it remained a minor constituent of the woodland (Sommerlatte 1976). The SCD of *C. mossambicense* revealed a pattern of incipient encroachment where in 1992 the vast majority of plants (85%) were very small recruits below 1m in height, and by 2008, the population had transitioned to tall plants (>2.5m), and only 6% surveyed below 1m. Seedlings of *C. mossambicense* only occurred in about half the transects, further suggesting the spread had curtailed by 2008.

There are three potential main drivers of the encroachment of *C. mossambicense* in the woodland: 1) A global driver of enriched atmospheric $CO_2$ favouring the increase of fast-growing shrubs over trees; 2) Changes in climatic patterns regionally where increased aridity may favour shallow-rooted shrubs; or 3) A local driver of intense elephant disturbance driving shrub encroachment.

Without laboratory-based $CO_2$ experiments (Kgope, Bond & Midgley 2010) it is difficult to assess the potential of enriched atmospheric $CO_2$ as a driver of the shrub encroachment. In 2008 we observed that some plants of this species were spreading clonally via root suckers. Species with extensive root-suckering such as some variants of *D. cinerea* are expected to take greater advantage of elevated $CO_2$ as the extensive below-ground carbon sinks enable them to have higher rates of carbon assimilation (Buitenwerf *et al.* 2012) and therefore encroaching ability (Wakeling & Bond 2007).

Evidence from archival records, field investigations, and remotely sensed data suggest there has been increased aridity in the last few hundred years in northern Botswana (Ringrose *et al.* 2007; Hamandawana, Chanda & Eckardt 2008). We found that high densities of tall (>2.5m) *C. mossambicence* shrubs were weakly associated with higher relative elevations. This supports the hypothesis that this species favours high-lying and therefore drier conditions, but would require a study at a finer spatial scale to assess the potential of aridity as a driver.

Our hypothesis that shrub density, and particularly *C. mossambicense* density would be associated with gaps formed as a result of elephant-induced mortality of trees was not supported. The distribution of shrubs was not associated with the distribution of either living large canopy trees or dead canopy trees, as expected from a resource competition hypothesis.

The single most plausible driver of the extensive *C. mossambicense* encroachment is that of a 'browsing release hypothesis' (Lagendijk, Page & Slotow 2012; Staver & Bond 2014; Daskin, Stalmans & Pringle 2015) where *C. mossambicense* was allowed to spread because elephants do not feed upon it, but suppress other woody vegetation, conferring a competitive advantage on *C. mossambicense.* Whilst Guy (1976) reported that *C. mossambicense* was a highly selected forage species for elephants in *C. mopane* woodland the Sengwa Wildlife Research area in Zimbabwe, our own observations. and those of others (Makhabu, Skarpe & Hytteborn 2006; Stokke & du Toit 2014) were that elephants avoided this shrub. Only five plants (0.1%) of *C. mossambicense* were impacted in 2008 (Fig. 4.7) and four of these were pushed over. In 1992 12% of small (<1m) *C. mossambicense* were recorded with high impact, suggesting elephants find this plant palatable when young.

The reasons why elephants avoid *C. mossambicense* remain a mystery as they feed on other members of the *Combretaceae* such as *C. herereoense* to the extent of killing up to 50% of the population (Chapter 3). *Combretum mossambicense* is extensively browsed by other herbivores. Makhabu (2005) found that *C. mossambicense* contributed the majority of diet for kudu in both wet and dry seasons, impala in the wet season, and was the second most important browse species for giraffe, after *C. tomentosa. Combretum mossambicense* was also listed as an important dry season browse source for impala in the Sengwa area of Zimbabwe (Dunham 1980). In 2008 we observed a large proportion of tall *C. mossambicense* plants with extensive browsing of the top shoots from giraffe in particular (see Appendix 4.3.3). Even sable antelope (*Hippotragus niger*), a predominant grazer, was observed to browse on *C. mossambicense* in the dry season in the Okavango Delta (Hensman *et al.* 2012).

Makhabu (2005a) suggested that elephants were not discouraged from browsing *C. mossambicense* by chemical-herbivory related traits such as the concentrations of acid detergent fibre, carbon and nitrogen (Makhabu 2005a). The tannin concentration in mature leaves of *C. mossambicense* was reported in a low range of 1-14 mg TA.g$^{-1}$ (Skarpe *et al.* 2014a). However the tannin concentration of stems was not reported and it is possible that elephants are deterred by a higher concentration of chemical deterrents in the stems. Supporting this hypothesis was our observation that impacts were only reported in1992, and most (75%) of the impact was on small plants below one metre in height with very small stems. The hooks along the branchlets (Coates-Palgrave 2002) may in fact be elephant-specific defences as they ensure that when an elephant tries to strip leaves off a stem, the stem hooks and breaks off along with the leaves. Other browsers like giraffe or impala, are able to overcome this deterrent by stripping leaves off the stems (Appendix 4.3.3).

Several other minor shrubs also increased over the time period. The increased proportional abundance of *P. nelsii* in 2008 was likely as a result of the additional area surveyed in the west of the study region around Duma Tau Camp which was not covered in 1992. *Philenoptera nelsii* was the only species which was disproportionately more abundant in the additional DT area. This area has deeper sandy soils which favour a higher density of *P. nelsii*. Elephant impact was also were not observed on *Philenoptera nelsii*, although Ben-Shahar (1993) observed elephants utilising mature trees of this species. The pattern of increase of abundance of *Croton megalobotrys* is consistent with studies in the Chobe riverfront (Moe *et al.* 2009; Rutina & Moe 2014). *Croton megalobotrys* was an important contributor to diet for elephants in the dry season in the Chobe where elephants stripped the leaves leaving the shoots (Makhabu 2005b) but elephants are not known to debark this species (O'Connor 2010). *Capparis tomentosa* was relatively uncommon in the Linyanti woodland but appeared to be increasing (Appendix 4.2) and all plants larger than 1m showed signs of elephant impact. *Capparis tomentosa* dominates part of the Chobe riparian area (Mosugelo *et al.* 2002; Skarpe *et al.* 2004) and is also one of the most intensively browsed species that forms 5% of wet-season elephant diet (Makhabu 2005b).

*Dichrostachys cinerea* was the most abundant species in the seedling layer but had declined most out of all shrubs (Fig. 4.4), leaving a population of mostly small plants under 1m. A high proportion of large dead *D. cinerea* was recorded in both years and this was the only shrub species with significant mortality by elephants with all dead plants in 1992 showing high elephant impact. Historical records point to *D. cinerea* thickets as a prevalent under-canopy feature at Chobe (Simpson 1975) and this species remained prevalent to 2003, but only of small plants less than 0.5m tall (Skarpe *et al.* 2014b), which is consistent with our findings. This evidence suggests that *D. cinerea* was previously the dominant shrub but increased elephant densities now keep this species in a herbivore trap, and prevent it from increasing as found in other disturbed savannas like Kruger National Park (Buitenwerf *et al.* 2012). If elephant pressure was removed, we would expect *D. cinerea* to spread in the woodland. Impact on shrub species was higher in 1992 for all species, probably due to decompression of elephants in 2008, following a very wet period, and the opening up of other areas like the newly flowing Savuti Channel and increased movement to Angola (Chase & Griffin 2009).

Seedlings only covered 4% of sample plots illustrating an overall low occurrence of seedlings in the Linyanti woodland. This pattern of low seedling abundance and survival is common in savanna woodlands (O'Connor 1995; Barnes 2001; Neke 2004) and is likely as a result of episodic recruitment factors (Wiegand, Jeltsch & Ward 2004) and low abundance of seeds in the soil seed bank in general (Aarrestad *et al.* 2014). We would have expected higher seedling abundance as the seedling survey months (Dec 2007 and January, November and December 2008) had an average rainfall 3.5 times higher (1146 mm) than the mean annual rainfall (557mm MAP) for 92 years (Chapter 1). The high proportion of canopy tree seedlings relative to their abundance in the tree layer suggests there is potential for canopy trees to regenerate, provided conditions are right and the browse trap removed. Trees are producing seedlings, but they are not growing into the sapling stage (Fig. 4.2B) and we hypothesise elephants are the main agent of tree seedling mortality (Chapter 3). Shrubs were associated with small tree recruits (<1m) and saplings (>2.5m). The correlation between small tree recruits with high shrub density might be explained as unpalatable shrubs protecting localised palatable tree seedlings from herbivory acting as 'nurse shrubs' (Olff *et al.* 1999; Riginos, Milton & Wiegand 2005; Smit *et al.* 2007) (Appendix 4.3.4). This may eventually lead to regeneration if these trees can escape the browser trap, and alternate vegetation states of woodland- shrubland may occur over the long term (Bakker *et al.* 2016)

## 4.6 Conclusion

The Linyanti riparian woodland has undergone a structural and functional shift from a tall canopy tree woodland to a single shrub species dominated shrubland. The tall tree canopy woodland has thinned so that canopy trees above the bottleneck of 2.5m totalled 28.2 (± 8.6 SE) trees.ha$^{-1}$ in 2008. Tall trees have not however declined to the same extent as the Chobe riverfront (Rutina & Moe 2014). This state shift has been brought about by elephant impacts (Chapter 3) killing easily debarked canopy trees such as *Acacia* spp. and hedging plants of more resistant species like *Colophospermum mopane*. There was no evidence of compensatory recruitment of canopy trees. The formation of a potential *C. mopane* 'browsing lawn' may have positive consequences by increasing available browse quantity and quality for other browsers (Smallie & O'Connor 2000; Styles & Skinner 2000; Makhabu 2005b; du Toit & Olff 2014).

Secondly, and of more detrimental consequences for ecosystem functioning, shrubland has more than doubled in density in 2008, and was dominated by one species – *Combretum mossambicense*. This one species comprised nearly half of the total woody density by 2008, forming a dense screen of tall plants. This pattern of a shift from woodland to shrubland has been observed further downstream for the Chobe Riparian woodland. Mosugelo and others (2002) found a reduction in mature canopy woodland cover from 60% to 30% coupled with an increase in shrubland from 5%

cover to 33% over the period 1962-2008. This represents rates of change of around 0.8% per year for both woodland decline and shrub increase. Our results, whilst based on density and not cover, suggest a much faster state-change in the Linyanti where *C. mossambicense* increased at about 10% per year. This shrub encroachment wave was incipient in 1992 and by 2008 many of these plants there were few small plants <1m in height, suggesting the rapid encroachment had slowed. The shrub encroachment by *C. mossambicense* is best explained by the fact that elephants avoid feeding on this species (although other browsers do), in comparison to large declines seen in shrub species which are impacted by elephants such as *D. cinerea*. However, we acknowledge that a global $CO_2$ fertilisation driver may account for some shrub encroachment (Bond & Midgley 2000; Kgope, Bond & Midgley 2010). Our findings are important in understanding intense elephant impacts on structure and how elephant-mediated mortality of trees can open up unforeseen gaps for pervasive shrub encroachment. The state shift toward a shrubland has the potential to reduce biodiversity and resilience to further disturbance (Folke *et al.* 2004).

In conclusion, the extreme elephant concentrations in the Linyanti have impacted woodland structure through thinning of large trees and there is a demographic bottleneck of seedling recruitment into saplings, but the largest effect on structure is from shrub encroachment of a single species which elephants do not consume. A complete woodland transformation has not occurred and long-term dynamics may include alternate vegetation states where palatable tree species may regenerate under the unpalatable shrubs.

## 4.7 References

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## 4.8 Appendices

4.1 The Bias correction of the 1992 densities

4.2 Comparative densities of all species surveyed in 1992* and 2008 (± SE) by height, as well as 2008 occurrence and seedling abundance for 2008.

4.3 Selected photographs of structural changes and shrub encroachment in the woodland

## Appendix 4.1 The Bias correction of the 1992 densities

Wackernagel reported the calculated densities of individuals in the six size classes (Table 2.1) were positively biased and that the origin of the bias lay with the modification of Byth's (1982) adjusted T-square density method. The T-square method (described below) is a distance based method which explicitly assumes all species and size classes being sampled have a random spatial pattern. Because of the reality of clustering of trees (and in particular sizes) in the woodland, there was a severe overestimation of the density. Wackernagel stated the consequence of this was a several-fold underestimation of *x* (equation 1) and therefore a severe overestimation of *D* (equation 1).

The T-Square Method (Byth 1982) followed by Wackernagel (1993) is as follows: every 50m along a sampling line, a plant closest to the sample point *(P)* was located and the distance *x* measured in paces. From point *P* six nearest neighbouring plants in the opposite direction of the sampling line were located and the distance *z* measured in paces. Each of the $k^{th}$ nearest plants neighbouring plants were of each six basal stem diameter classes. The Density estimator is given as: (Byth 1982)

$$\hat{\bar{D}} = \frac{N^2}{\left(2\Sigma_{k=1}^{i} x\right)\left(\sqrt{2}\Sigma_{k=1} z\right)} \qquad (1)$$

Where $\hat{\bar{D}}$ is the Density estimator in a particular stem diameter class, *N* is the sample size, *x* is the distance from the point *P* to the $k^{th}$ nearest tree, *Q* and *z* is the distance from *Q* to the $k^{th}$ nearest tree in a direction away from *P*, that is the 'T-square' distance to the $k^{th}$ nearest tree from *Q* (Byth 1982; Clayton & Cox 1986).

For the 1992 density estimates we relied on those reported in Appendix Table 3 of Wackernagel (1993) (presented here in Appendix 4.2) as well as the raw 1992 count data and transformed the density to correct the over-estimation. We compared the reported 1992 density to the 2008 fixed-width density for tall (>2.5m) trees of *C. mopane*- an abundant species resistant to elephant impact which we expected to have changed least in density. The original reported density for *C. mopane* tall trees was 56 trees.ha$^{-1}$, whereas the estimated 2008 density was 13.13 ± 3.5 trees.ha$^{-1}$ (Table A1). We found that the 1992 overestimation was around a factor of four (4) (which brought the tall *C. mopane* density to 14 tree.ha$^{-1}$), and so we reduced the 1992 densities by this factor. We realise that this reduction factor is an approximation but we can draw heuristic comparisons at least for common species, and the bias is minimised where a species changes several fold in density.

Some densities in Wackernagel (1993) Appendix Table 3 were reported as <1 and we omitted these from calculation because we cannot make reliable estimates of their change over time. We removed one species (*Commiphora edulis*) which was reported in the thesis but not found in the raw data.

******We compared the bias adjusted 1992 (Wackernagel, 1993) densities to those recorded in an unpublished report by Coulson (1992). Coulson surveyed belt transects every 1km, corresponding with our study site, from the western border of Chobe National Park, along the Linyanti (classified as the Linyanti subsection) and extending westwards of our study site to the Kwando River (Selinda and Kwando sections). The most common tree and shrub densities were recorded, but only for plants with a minimum DBH of 30cm. This roughly equates to trees over 1m tall, using the regression model of stem circumference against height calculated for the Linyanti by Bell (2001). We compared our bias-adjusted 1992 densities to those calculated for selected tree species in Coulson’s Linyanti section (Table 20 in Coulson (1992)). Unfortunately *C. mopane* was not included in the selected species to contrast with our bias correction, but all other species were at similar (but higher) densities than our calculations, increasing confidence in our density estimates and change estimations (Appendix 4.2).

**Appendix 4.2** Comparative densities of all species surveyed in 1992 and 2008 (± SE) by height, as well as 2008 occurrence and seedling abundance for 2008. The 1992 Density is presented as both bias-adjusted figures used in the text and (in brackets) uncorrected original 1992 densities from Appendix Table 3 in Wackernagel (1993). Included for comparison are the 1992 densities reported by Coulson (1992)**

| | | **1992** | | | | **2008** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **Bias-adjusted (original from Wackernagel Appendix Table 3)** | | | **Coulson (1992)**** | **Density ± Standard Error (SE)** | | | **Occurrence** | **Seedling cover** |
| **Tree Species** | **Species code** | **<2.5m** | **>2.5m** | **Total** | **>30cm DBH** | **<2.5m** | **>2.5m** | **Total** | **% of transects** | **(m$^2$)[a]** |
| *Acacia caffra* | acacaff | | | | | 0.13 ± 0.05 | 0.17 ± 0.07 | 0.29 ± 0.12 | 12.7% | 0.35 |
| *Acacia erioloba* | acaeri | 1 (4) | 16.25 (65) | 17.25 (69) | 3.24 | 0.25 ± 0.10 | 0.33 ± 0.17 | 0.59 ± 0.27 | 23.6% | 4.05 |
| *Acacia luederitzii* | acalue | 0.75 (3) | 0.5 (2) | 1.25 (5) | | 0.08 ± 0.05 | 0.21 ± 0.07 | 0.29 ± 0.12 | 12.7% | 4.8 |
| *Acacia nigrescens* | acanig | 1.25 (5) | 12 (48) | 13.25 ( 53) | 3.60 | 0.17 ± 0.10 | 1.67 ± 0.43 | 1.84 ± 0.54 | 21.8% | 20.45 |
| *Adansonia digitata* | adadig | | | | | 0.17 ± 0.16 | 0 | 0.17 ± 0.16 | 5.5% | 0 |
| *Berchemia discolor* | berdis | 0 (<1) | 3.25 (13) | 3.25 (13) | 3.53 | 0.46 ± 0.19 | 1.42 ± 0.43 | 1.88 ± 0.63 | 56.4% | 1.6 |
| *Boscia albitrunca* | bosalb | 0.75 (3) | 0.25 (1) | 1 (4) | | 1.21 ± 0.40 | 0.08 ± 0.04 | 1.30 ± 0.45 | 29.1% | 0.95 |
| *Colophospermum mopane* | colmop | 16.75 (67) | 14 (56) | 30.75 (123) | | 25.77 ± 8.36 | 13.13 ± 3.50 | 38.90 ± 11.86 | 83.6% | 22 |
| *Combretum apiculatum* | comapi | 1.25 (5) | 0.75 (3) | 2 (8) | | | | | 0% | 0.2 |
| *Combretum hereroense*[b] | comher | 3.5 (14) | 3 (12) | 6.5 (26) | 7.87 | 9.41 ± 4.06 | 3.59 ± 1.27 | 13.00 ± 5.34 | | 8.75 |
| *Combretum molle*[b] | commol | 9 (36) | 11 (44) | 20 (80) | | 0.58 ± 0.25 | 0 | 0.58 ± 0.25 | | |
| *Combretum imberbe* | comimb | 1.51 (6) | 4.75 (19) | 6.25 (25) | 5.15 | 0.17 ± 0.12 | 2.93 ± 0.86 | 3.10 ± 0.98 | 52.7% | 32.95 |
| *Diospyros mespiliformis* | diomes | 0 | 1 (4) | 1 (4) | 4.93 | 0.59 ± 0.37 | 2.26 ± 0.57 | 2.84 ± 0.98 | 47.3% | 7.25 |
| *Ficus spp.* | Ficus | 0 | 0 (<1) | 0 | | 0.04 ± 0.03 | 0.21 ± 0.11 | 0.25 ± 0.15 | 10.9% | 2.2 |
| *Garcinia livingstonei* | garliv | 0 | 0.25 (1) | 0.25 (1) | 2.94 | 0 | 0.46 ± 0.31 | 0.46 ± 0.31 | 12.7% | 0.1 |
| *Peltophorum africanum* | pelafr | 2 (8) | 1.25 (5) | 3.25 (13) | 0.15 | 3.10 ± 3.10 | 0.21 ± 0.21 | 3.30 ± 3.37 | 5.5% | 0.55 |

| **Tree species** | **Species code** | **<2.5m** | **>2.5m** | **Total** | **Coulson (1992)** | **<2.5m** | **>2.5m** | **Total** | **% of transects** | **Seedling cover** |
|---|---|---|---|---|---|---|---|---|---|---|
| *Philenoptera violacea* | phivio | 15.25 (61) | 1.75 (7) | 17 (68) | 3.31 | 12.21 ± 2.42 | 0.92 ± 0.35 | 13.13 ± 2.78 | 81.8% | 5.7 |
| *Terminalia prunioides* | terpru | 0.5 (2) | 4.25 (17) | 4.75 (19) | 0.59 | 0.42 ± 0.26 | 0.54 ± 0.16 | 0.96 ± 0.43 | 27.3% | 1.65 |
| *Terminalia sericea* | terser | 5 (20) | 0.25 (1) | 5.25 (21) | | 0.38 ± 0.46 | 0.04 ± 0.03 | 0.42 ± 0.49 | 9.1% | 0.2 |
| *Z.iziphus mucronata* | zizmuc | 0 | 0 (<1) | 0 | 0.59 | 0.04 ± 0.05 | 0 | 0.04 ± 0.05 | 1.8% | 0.45 |
| All tree species | | 58.5 (234) | 74.5 (298) | 133.25 (532) | | 54.88 ± 20.68 | 28.19 ± 8.66 | 83.07 ± 29.35 | | 114.2 |
| **Shrub Species** | | | | | | | | | | |
| *Acacia hebeclada* | acaheb | 0 | 0 | 0 | 0 | 0.92 ± 0.92 | 0 | 0.92 ± 0.92 | 3.6% | 6.2 |
| *Baphia massaiensis* | bapmas | 0 (<1) | 0 (<1) | 0 | | | | | | |
| *Bauhinia petersiana* | baupet | 0.5 (2) | 0 | 0.5 (2) | | 0.08 ±0.10 | 0 | 0.08 ± 0.1 | 1.8% | 0 |
| *Boscia foetida* | bosfoe | | | | | 0.08 ± 0.21 | 0 | 0.08 ± 0.21 | 1.8% | 0.00 |
| *Capparis tomentosa* | captom | 0.5 (2) | 0 | 0.5 (2) | | 1.67 ± 0.75 | 0.42 ± 0.30 | 2.09 ± 1.06 | 29.1% | 0.4 |
| *Combretum celastroides* | comcel | 9.5 (38) | 0 | 9.5 (38) | | 0.92 ± 0.50 | 0 | 0.92 ± 0.50 | 18.2% | 5.8 |
| *Combretum collinum* | comcol | | | | | 0.08 ± 0.09 | 0 | 0.08 ± 0.09 | 1.8% | 0 |
| *Combretum elaeagnoides* | comela | 4.5 (18) | 0.25 (1) | 4.75 (19) | | 0.33 ± 0.21 | 0.08 ± 0.07 | 0.42 ± 0.29 | 5.5% | 0.8 |
| *Combretum mossambicense* | commos | 59.5 (238) | 3.25 (13) | 62.75 (251) | | 111.60 ± 14.34 | 236.67 ± 25.85 | 348.27 ± 40.19 | 100% | 17.05 |
| *Commiphora africana* | comafr | 5.25 (21) | 0 (<1) | 5.25 (21) | | 1.09 ± 0.89 | 0 | 1.09 ± 0.89 | 9.1% | 0.35 |
| *Commiphora karibensis* | comkar | 0 | 0 (<1) | 0 | | | | | 0% | 7.5 |
| *Croton megalobotrys* | cromeg | 24.75 (99) | 19 (76) | 43.75 (175) | 13.16 | 29.20 ± 5.67 | 54.54 ± 7.87 | 83.74 ± 13.54 | 90.9% | 3.85 |

| **Shrub Species** | | **<2.5m** | **>2.5m** | **Total** | **Coulson (1992)** | **<2.5m** | **>2.5m** | **Total** | **% of transects** | **Seedling cover** |
|---|---|---|---|---|---|---|---|---|---|---|
| *Dichrostachys cinerea* | diccin | 49.25 (197) | 4 (16) | 53.25 (213) | | 9.79 ± 6.39 | 0 | 9.79 ± 6.39 | 38.2% | 182.75 |
| *Diospyros lycioides*[c] | diolyc | 5.75 (23) | 0.75 (3) | 6.5 (26) | | 38.82 ± 11.75 | 19.49 ± 9.23 | 58.31 ± 20.99 | 8% | 7.95 |
| *Euclea divinorum*[d] | eucdiv | 13.5 (54) | 4 (16) | 17.5 (70) | | 12.63 ± 4.90 | 1.00 ± 0.55 | 13.64 ± 5.45 | 41.8% | 4.8 |
| *Gardenia ternifolia* | garter | 0 | 0 (<1) | 0 | | | | | | |
| *Grewia flavescens* | grewflav | 0.75 (3) | 0 | 0.75 (3) | | | | | | |
| *Gymnosporia senegalensis*[e] | gymsen | 10.75 (43) | 3 (12) | 13.75 (55) | | 0.08 ± 0.08 | 0 | 0.08 ± 0.08 | 1.80% | 5.35 |
| *Mundulea sericea* | munser | 2.25 (9) | 0.75 (3) | 3 (12) | | 10.96 ± 5.36 | 2.68 ± 1.51 | 13.64 ± 6.87 | 16.40% | 3.1 |
| *Philenoptera nelsii* | phinel | 13.5 (54) | 3.75 (15) | 17.25 (69) | | 26.27 ± 5.20 | 54.80 ± 10.17 | 81.06 ± 15.38 | 74.50% | 0.6 |
| *Rhus tenuinervis* | rhuten | | 0 | | | | | 0 | 0.00% | 0.3 |
| *Salvadora australis* | salaus | | 0 | | | 0.17 ± 0.12 | 0 | 0.17 ± 0.12 | 1.80% | 0.1 |
| Unknown 2 | | | | | | | | | | 0.5 |
| Spgg | | 1.75 (7) | 0.25 (1) | 2 (8) | | | | | | |
| spjj | | 0.5 (2) | 0 | 0.5 (2) | | | | | | |
| spll | | 1.5 (6) | 0.25 (1) | 1.75 (7) | | | | | | |
| spmm | | 0.75 (3) | 0 (<1) | 0.75 (3) | | | | | | |
| spnn | | 2 (8) | 0.5 (2) | 2.5 (10) | | | | | | |
| All shrub species | | 206.75 | 39.75 | 247.125 (988.5) | | 244.70 ± 57.58 | 369.68 ± 55.86 | 614.38 ± 113.174 | | 247.4 |

[a] Coverage of seedlings is calculated as total foliar percentage coverage from all $1m^2$ quadrats

[b] *Combretum hereroense* and *C. molle* were combined for analyses as there was some question of mixed identity in 1992

[c] We have interpreted the unknown shrub SPCC in 1992 as misidentified *Diospyros lyciodes* which was not recorded in Wackernagel (1993) but easily visible in large numbers in the 1992 aerial photographs and remained common through to 2008.

[d] SP03 in raw 1992 data corresponds with *Euclea divinorum* numbers reported in Wackernagel (1993) and has been renamed here as such.

[e] *Gymnosporia senegalensis* was recorded as the species complex *Maytenus heterophylla* in 1992

## Appendix 4.3 Selected photographs of structural changes and shrub encroachment in the woodland

**Appendix 4.3.1** Browsing lawn formed by elephants pollarding and felling tall *Colophospermum mopane* trees which coppices vigorously at a lower height. Photo taken December 2007

**Appendix 4.3.2** Dense screen of *Combretum mossambicense* under-canopy shrubs in the woodland. Photo taken December 2008

**Appendix 4.3.3** A giraffe feeding on *C. mossambicense* by stripping the leaves off shoots. Distinctive giraffe browse-line is evident as defoliated scrambling top shoots on the plants in the foreground and background

**Appendix 4.3.4** *Philenoptera violacea* seedlings growing undisturbed under dense *C. mossambicense* shrubs

# CHAPTER FIVE

## Elephants and Biodiversity: spatio-temporal dynamics of the Linyanti woodland, northern Botswana

## 5.1 Introduction

The aim of this study was to establish how the riparian woodland had been changed by elephant impacts and the consequences for biodiversity.
At the onset of this study there were four objectives:

5) To establish whether canopy tree disturbance is heterogeneous with respect to structure and composition
6) To establish whether shrub expansion is heterogeneous with respect to structure and composition
7) To establish whether tree regeneration is heterogeneous with respect to structure and composition
8) To evaluate the consequences of elephant impacts on canopy tree disturbance, shrub expansion and tree regeneration for structural and compositional diversity of the woodland

Following the findings from objective one that there was a progressive decline in canopy trees (discussed in 5.2), the focus shifted to establish the consequences of progressive disturbance for 1) compositional and 2) structural diversity. I will synthesise the main findings from each of the chapters of this thesis: 1) Spatial heterogeneity of canopy tree disturbance (Chapter 2); 2) compositional changes of canopy trees (including regeneration) following elephant impact (Chapter 3); and 3) structural changes following shrub expansion (Chapter 4).
Specifically, this concluding chapter sets out to:

- Evaluate the main findings of the study in the context of spatial heterogeneity change, compositional change, and structural change.

- Identify the limitations of each aspect of the study and remaining gaps in knowledge so as to make recommendations for future studies.

- Address the consequences of elephant impacts for biodiversity and identify the contribution made by this study to advance the current understanding of how elephants affect the biodiversity of savanna woodlands.

- Suggest management recommendations for elephant impacted woodlands in northern Botswana.

## 5.2 The spatial heterogeneity of canopy tree disturbance

In Chapter 2, I presented a novel method of delineating disturbance patches based on the spatial occurrence of dead trees based on marking dead trees visible in aerial photographs from 1992, 2001 and 2010. I found that there was a dynamic patch system, where patches of disturbance appeared, increased by expansion, coalescing and shifting, and also declined by disappearing, shrinking and fragmenting. Patches had higher rates of dead tree appearance compared to inter-patch areas. Disturbance patches increased in total area at a rate of around 1% of the total area per year to constitute 23% of the study area by 2010. The increase in area was mostly as a result of neighbouring patches coalescing following the increase of dead trees in the inter-patch area. Whilst some patches shrunk or were replaced by patches of shrub (dead tree density decreased due to felled trees being obscured by shrub growth), disturbance spread pervasively over time and overall structural heterogeneity shifted from a landscape with scattered small (<1 ha in size) patches of disturbance to a one where large areas (up to 50 ha) of the landscape were classified as disturbance patches. Even though large tracts of land not classified as disturbance patches remained throughout the period, there was evidence of fragmentation where inter-patch areas became increasingly small and isolated. Fragmentation can have a negative effect on biodiversity due to a larger number of increasingly smaller suitable habitat sites for animals (e.g. birds) (Fahrig 2003). This increase in greater areas of disturbance represents a state shift to decreased heterogeneity although the landscape was still patchy (Pascual & Guichard 2005). A decline in heterogeneity has important consequences for functional diversity as undisturbed patches provide different habitats and contribute different ecosystem processes such as nutrient cycling (Bowman, Facelli & Sinclair 2015), shade (Dean, Milton & Jeltsch 1999) compared to disturbed patches.

Previous analyses of spatial pattern of tree mortality (treefall as measured by tree height decrease from liDAR data) have been limited to the finding that treefall was significantly clustered within *Acacia* and *Combretum* dominated river catchments subject to elephant disturbance (Levick & Asner 2013). Given the potential importance of tree mortality in creating heterogeneity in savanna woodlands, there has been little attempt to analyse the clustering of dead trees in savannas within a patch dynamics paradigm. The spatial analysis of other disturbances has been restricted to square lattice (Schertzer, Staver & Levin 2014) or moving window (Meyer *et al.* 2007) methods which define patches by calculating density in a regular grid. This study is novel in the method of delineating irregularly shaped intense disturbance patches of different sizes with no a-priori assumptions of size, shape or movement. Additionally the density-based method was able to extract localised patches of disturbance within a noisy environment of scattered dead trees.

The average rate of dead tree appearance was calculated as 0.28 tree.ha.yr$^{-1}$, not much higher than the background treefall rate in herbivore exclosures of Kruger National Park around 0.19 trees.ha$^{-1}$.yr$^{-1}$ (in comparison the rate outside exclosures was 1.27 trees.ha$^{-1}$.yr$^{-1}$) (Asner & Levick 2012). This suggests elephant disturbance has reached a maxima at 50% mortality and the remaining trees are either resilient to impact or avoided (Chapter 3). I do not expect an increase in mortality rates of canopy trees. The slow mortality rate coupled with progressive decline suggests there was little recruitment into the canopy to replace the trees that were lost.

## 5.3 Compositional changes in the canopy tree layer

Chapter 3 reported the spread of elephant impacts on species and sizes of canopy trees and the resultant compositional changes. I chose to avoid using traditional species diversity indices like species richness due to the inherent lack of information contained in these simple indices for ecosystem functioning (Fleishman & Noss 2006) and their low applicability to the dynamic nature of savannas (Sankaran, Ratnam & Hanan 2004). Instead, I described the compositional changes and species-specific response to elephant impact. Compositional and functional diversity would be maintained if impacts were limited to abundant species which were functionally similar to less common species (sensu functional compensation (Mori, Furukawa & Sasaki 2013)). Functional compensation may take place, for example, if trees that provided abundant forage (e.g. acacias) were replaced by other palatable trees or if large shade tree species were likewise replaced by other canopy species.

Instead, there was a progressive decline of large canopy trees (>20cm stem diameter) and particularly in the relative abundance of the dominant acacias which declined from a proportional abundance of 30% in the reconstructed pre-1992 woodland to 12% in 1992 and just 4% in 2008.

An emerging concept in disturbance is the notion of ‘response diversity’ which describes the variation of responses to disturbance amongst species in a particular environment (Mori, Furukawa & Sasaki 2013). With regards to response to elephant disturbance, trees can be categorised into three main functional groups: 1) susceptible trees which are favoured by elephants and are easily killed: for example acacias with fibrous stringy bark prone to severe axial bark stripping (Malan & van Wyk 1993); 2) resistant species which may be rejected by elephants through chemical (Owen-Smith & Cooper 1987) or structural defences such as brittle bark which make them hard to ringbark (Malan & van Wyk 1993) or 3) resilient species which respond to pollarding and stem breakage by resprouting vigorously (Styles & Skinner 2000). With the acacias already reduced in abundance by 1992, elephant impact spread to other susceptible species such as *Terminalia sericea* and *T. prunioides* which were easily ringbarked. When these species declined between 1992 and 2008, impact spread to species with blocky bark which were more resistant to ringbarking such as *C. imberbe, Berchemia discolor* and *D. mespiliformis.* This illustrated a continual spread of impacts and mortality from abundant selected species, to less common but susceptible species and then to more resistant species. By 2008 the canopy tree species composition consisted mainly of two resilient species (*C. mopane* and *C. hereroense*) and one resistant species (*P. violacea*), the latter apparently unpalatable to elephants when mature (O'Connor 2010; Scogings *et al.* 2012; Viljoen *et al.* 2013). The abundant species *Colophospermum mopane* proved highly resilient to intensive elephant impact and instead of experiencing mortality from intensive impacts in 1992, responded by vigorous resprouting forming 'browsing hedges' locally which potentially are beneficial to other browsers (Smallie & O'Connor 2000; Styles & Skinner 2000; Hartnett *et al.* 2012).

If species that had declined from the canopy tree layer were represented in the sapling and seedling layers, then compositional replacement of the woodland would be possible and long-term compositional diversity could be maintained.

The seedling layer (plants below 0.5m) had high proportions of canopy tree species, and all but the rarest species were recorded (Chapters 3 and 4). The acacias were relatively abundant in the seedling layer at 26% of tree species. This suggests regeneration of the woodland is possible, and also that seed dispersal processes have not been negatively impacted by elephant impacts. By contrast, the sapling layer (0.5-2.5m) composition was limited to the few resilient (*C. mopane, C. hereroense*) and resistant (*P. violacea*) species and with the lack of saplings there appears to be a bottleneck of recruitment of seedlings into the next stage. The cause of this seedling-escape bottleneck could be due to three factors: 1) other browsers such as impala, as found for the Chobe Riverfront (Moe *et al.* 2009); 2) elephants as acacia seedling mortality has been documented (Barnes 2001a), or 3) insufficient soil moisture for seedling survival (Barnes 2001b). The density of impala in the Linyanti is much lower than that of Chobe (Chase 2011) suggesting seedling predation by impala is not the cause of the bottleneck. Soil moisture effects may have contributed to background seedling mortality as the 2007/2008 seedling survey was in a particularly wet period (Chapter 1) and seedling abundance in my survey may have been exceptionally high. However the vigorous growth of both seedlings and saplings in fenced-off camps (which allow some access to mesoherbivores) together with observed elephant impact on established seedlings outside of these exclosures suggests elephants are the main cause of this seedling recruitment bottleneck.

In this way, intensive elephant impacts can function similarly to fire disturbances, causing significant mortality of seedlings and preventing their recruitment. (Levick, Baldeck & Asner 2014). The implication of this is that elephants exert substantial selective pressure on a larger range of tree sizes than other disturbance agents (like wind or fire) from seedlings up to canopy trees.

## 5.4 Structural changes following shrub expansion

In Chapter 4 I examined the structural changes which took place following the canopy tree decline and replacement by shrubs. If evenly distributed densities of different sizes (tall and short trees), stages (seedlings, saplings, canopy trees) and growth forms (multi-stemmed shrub species vs. canopy-forming tree species) remained then there would be a variety of habitats for animal species and structural diversity would be maintained.

The main finding was that the tall canopy tree woodland was being replaced by dense and pervasive shrub encroachment, and mainly by one species- *Combretum mossambicense*. Whilst overall shrub density increased 2.5 times, *C. mossambicense* density increased five-fold, and by 2008 this single species constituted 50% of the total woody plant density. *Combretum mossambicense* was abundant in the shrub layer in 1992, but the population consisted mainly (80%) of very small plants less than one metre tall, but by 2008 a dense screen of tall shrubs (>2.5m) had formed. The rate of increase in density of *C. mossambicense* was very rapid within the context of documented shrub encroachments for southern African savannas (O'Connor, Puttick & Hoffman 2014). The most plausible hypothesis for the spread of this species is that it is unpalatable to elephants, although a wide variety of other browsers eat it. Elephant impact was recorded on the small plants in 1992, but there was no elephant impact recorded on the tall plants in 2008. My hypothesis is that there was a chemical deterrent in the stems which other browsers like giraffe were able to overcome by plucking leaves off the stems.

Other shrub species also increased to a lesser extent, but these were either regionally concentrated (*Philenoptera nelsii*) or common along the marginal floodplain (*Croton megalobotrys* and *Diospyros lycioides*) which would be tied to transient changes in flooding.

Evidence for elevated atmospheric $CO_2$ driving woody encroachment in savannas is increasing (Wigley, Bond & Hoffman 2010; Buitenwerf *et al.* 2012; Higgins & Scheiter 2012) as elevated $CO_2$ favours $C_3$ woody plants over $C_4$ grasses (Kgope, Bond & Midgley 2010). Elevated $CO_2$ also allows for rapid growth of woody plants (Bond & Midgley 2012) which may allow fast-growing shrubs to occupy available niches by outcompeting slower-growing tree species. A global driver of increased atmospheric $CO_2$ therefore cannot be ruled out. It follows then that if a $CO_2$ driver was established, then the shift to shrubland state may be of longer term consequence as shrubs out-compete slower-growing tree saplings. It also means that reduced elephant concentrations may not promote complete canopy tree regeneration.

There were also smaller structural changes within the tree layer. Tall (>2.5m) canopy tree density decreased by half between 1992 and 2008, representing an annual loss rate of around 3.6%. The average rate for all sizes was 2.2 % suggesting canopy trees experienced higher rates of mortality. The average rate of decline is also surprisingly not much higher than the mean annual death rate of 1% for *A. erioloba* over 53 years (with one site experiencing 2.9%) in an area where all disturbances from herbivores or fire were excluded (Moustakas *et al.* 2006). The density of saplings declined by 75% for all species, except *C. mopane.* Instead, *C. mopane* short trees (<2.5m) doubled in density to 2008 as a function of expansive coppice regrowth following elephant impact. It may be that this represents a ‘browsing lawn’ whereby available *C. mopane* browse quantity and quality will have increased in an accessible range for other browsers (Smallie & O’Connor 2000; Styles & Skinner 2000; Makhabu 2005; du Toit & Olff 2014). The increase in a palatable shrub has the potential to shift herbivore assemblages from grazers to browsers such as giraffe, as well as mixed-feeders like impala and mixed feeders.

## 5.5 Conclusion: What do we now know about how elephants affect biodiversity?

This study has attempted to address the question of how elephants affect biodiversity. Riparian woodlands are of particular concern in savanna ecology as they are biodiversity hotspots (Naiman, Decamps & Pollock 1993; Bennett, Nimmo & Radford 2014) and are important for water-dependent animals like elephants, particularly in the dry season. Measuring biodiversity change is not simple. Ecologists have moved away from traditional methods of measuring the number and type of organisms in species diversity indices (see review by Chiarucci, Bacaro & Scheiner (2011)) to measuring how ecosystem properties and processes change over time and space (Reiss *et al.* 2009; Loreau 2010). I have attempted to use this approach to advance understanding of how extremely high densities of elephant can affect spatial heterogeneity and the core attributes of biodiversity as defined by Noss (1990): compositional diversity, structural diversity, and by inference, functional diversity (Table 5.1).

Spatial heterogeneity shifted from a landscape with scattered small (<1 ha in size) patches of disturbance to one where large areas (up to 50 ha) of the landscape were classified as intense disturbance patches. Whilst the Linyanti riparian woodland shifted towards pervasive tree mortality, a spatially heterogeneous patch structure still existed, and patches were dynamic and interacted with each other to grow, coalesce and fragment. Large areas not classified as high disturbance remained throughout the period but there was evidence of fragmentation where inter-patch areas became increasingly small and isolated. Fragmentation can have a negative effect on biodiversity due to a larger number of increasingly smaller suitable habitat sites for animals (e.g. birds) (Fahrig 2003). Although the landscape was still patchy, this increase in greater areas of disturbance represents a state shift to decreased heterogeneity (Pascual & Guichard 2005). A decline in heterogeneity has important consequences for functional diversity as undisturbed patches provide different habitats and contribute different ecosystem processes such as nutrient cycling (Bowman, Facelli & Sinclair 2015), shade (Dean, Milton & Jeltsch 1999) compared to disturbed patches. It is unknown how the location of preferred species determines patchiness.

Whilst compositional diversity probably increased when the common acacias declined preceding 1992, there was a continued decline of other, less common species which has potential consequences for diversity. Large trees in savannas have important functions such as providing shade and browse (Belsky 1994) as well as nesting sites for raptors and vultures (Vogel *et al.* 2014). They also extract mineral nutrients from deep soil layers (Treydte *et al.* 2007) and improve grass forage quality under canopies (Belsky *et al.* 1993; Treydte, Riginos & Jeltsch 2010). The decline of large trees has not been to the same extent as that within the Chobe Riverfront (Rutina & Moe 2014) and there were still stands of large trees (>20cm diam.) (density =12 trees.ha$^{-1}$ (± 5 SE) (Appendix 3.8.2)) in the riparian zone in 2008. Tall trees were also present in the upland mopane area. These scattered trees are probably sufficient to provide for shade and nesting sites. Browse for other herbivores has probably increased due to the prolific coppicing of *C. mopane* and to a lesser extent *C. hereroense* and localised coppice patches of *P. africanum* as elephants have effectively lowered browse height.

Nutrient cycling is important for nutrient poor Kalahari sands. The conversion from woodland to shrubland and large disturbance patches has likely led to nutrient deficiencies in some patches. Whilst acacias are nitrogen-fixing legumes, their decline probably has no added consequences for nitrogen enrichment as there is evidence that N-fixers do not provide higher soil nitrogen than non-N- fixers (Belsky *et al.* 1993; Treydte *et al.* 2007).

The decline of the acacias in particular should be interpreted with caution, due to the hypothesis that they established in a recruitment event of low elephant numbers (following extirpation by ivory hunters), and low browser numbers (following rinderpest) (Skarpe *et al.* 2004). Additionally there is evidence that some acacias in the Linyanti were killed by human activity for tsetse fly control (Davies & Bowles 1976).

Savannas are non-equilibrium systems (Jeltsch, Weber & Grimm 2000; Gillson 2004) with episodic recruitment of trees (particularly of acacias) during extremely good rainfall periods, and with limited disturbance (Midgley & Bond 2001; Moustakas *et al.* 2006). Because canopy tree species were well represented in the seedling layer, recruitment of the canopy layer is possible. The largest threat to compositional and structural diversity appeared not to be the mortality of large trees, but rather the replacement of those trees by shrub species and not regeneration via tree saplings Mortality was not compensated for by recruitment as elephants removed saplings of all but the most resilient or resistant species. However the conditions that enable long-term regeneration of elephant-impacted woodlands, and the potential episodic conditions that enable regeneration, are still unknown. There were no extirpations of woody species, although *Acacia erioloba* had become extremely rare as canopy trees.

Rather, the main threat to biodiversity, at least in the short term, is from the pervasive and dense encroachment of a single shrub species. This represents a rapid structural and functional shift from woodland to shrubland and has potential consequences for ecosystem functioning (Eldridge *et al.* 2011) , biodiversity (Midgley & Bond 2015), and resilience (Folke *et al.* 2004; Mori, Furukawa & Sasaki 2013). According to the insurance concept of biodiversity, greater diversity within an ecosystem increases the system's resilience to disturbances (Loreau, Mouquet & Gonzalez 2003; Folke *et al.* 2004; Mori, Furukawa & Sasaki 2013). Ecosystem processes such as nutrient cycling, seed dispersal, carbon sequestration and cycling and ecohydrology are likely to be negatively affected by the woodland-shrubland transformation (Belsky 1994; Ludwig, De Kroon & Prins 2008; Treydte, Riginos & Jeltsch 2010; Rundel, Dickie & Richardson 2014), but only if this represents a permanent state shift. There was some evidence that this unpalatable shrub was protecting susceptible tree seedlings from elephant impact (Chapter four) and it may be that alternate states of canopy trees and unpalatable shrubs exist, which represents enhanced long-term functional diversity.

Many studies have suggested that woody density can only be suppressed by elephants when in combination with fire (Moncrieff, Kruger & Midgley 2008; Staver *et al.* 2009; Helm & Witkowski 2012) . My findings provide new insight into the ability of high elephant concentrations to suppress the woody composition of savannas.  Up until recently, the emphasis has been on climate and fire as the main regulators of woody vegetation (Higgins, Bond & Trollope 2000; Bond & Keeley 2005; Lehmann *et al.* 2011; Midgley & Bond 2015)  but this study supports increased awareness that large herbiovores can cause state shifts (Bakker *et al.* 2015).

Ultimately, answering questions of biodiversity change in non-equilibrium systems requires studies over long time scales and across large spatial extents to assess ecosystem-level effects. There have been other studies of elephant effects on structural diversity over large spatial extents (Asner *et al.* 2015), and over long time periods (Mosugelo *et al.* 2002), as well as inferring compositional changes following disturbance using spatially-stratified plots in contrasted disturbance areas (Rutina & Moe 2014; Wigley *et al.* 2014).  However, my study represents the first instance of a comprehensive analysis of structural, compositional and spatial heterogeneity changes over a long time period, relying on both large-scale remotely-sensed data, and species-level fieldwork data of seedling, sapling and canopy tree stages.

I can find no irreversible negative consequences for biodiversity in the long term. There have been shifts towards spatial homogeneity and a shrub-dominated state, but no functional transformations have occurred yet.

**Table 5. 1** Overview of elephant effects on woodland biodiversity with a focus on existing knowledge as well as new knowledge generated by this study, and their potential consequences for biodiversity

| Aspect of biodiversity | What is known | New findings from this study | Consequence for diversity | What is still unknown |
|---|---|---|---|---|
| **Spatial Heterogeneity**<br>**(Canopy tree disturbance over time and space)** | 1) Elephants can potentially increase heterogeneity by episodic disturbance to stands of trees[1].<br>2) Elephant-mediated tree-felling rates vary across broad landscapes[2]<br>3) Treefall is linked to large-scale geomorphological and edaphic patterns[3] | 1) Tree-felling rates vary across smaller scales within the riparian zone and dynamic patches of intense disturbance do exist.<br>2) Disturbance has spread pervasively over time and space as patches of dead trees coalesced | (1) Increase in fragmentation<br>(2) Shift towards increased homogeneity | 1) Relation of disturbance patches to acacia patches<br>2) The change in living tree patches and any correlated underlying environmental pattern<br>3) Wider scale patchiness of the Kwando-Linyanti System |
| **Compositional diversity**<br>**(Elephant effects on woody species)** | 1) Elephants are selective for certain species[4-8] which may decline, increasing the relative abundance of rare[9] or well-defended species[10] and potentially increasing compositional diversity through species turnover[11]<br>2) If abundant species decline, this can increase evenness and species richness[12]<br>3) Regeneration of trees is prevented mainly by smaller herbivores[13-16] | 1) Elephant impact spread from selected and vulnerable species onto other species, resulting in a decline of all canopy trees except for the most resistant or resilient species.<br>2) There was a lack of recruitment of canopy tree species<br>3) There is regeneration potential from seedlings but elephants are hypothesised to be the main mortality agent of seedlings exhibiting another browser-driven demographic bottleneck | (1) Decline of common acacias increased diversity<br>(2) Decline in response diversity as only resistant or resilient species dominate the canopy layer | 1) The long-term (>100ya) regeneration of elephant-impacted woodlands and species turnover<br>2) Episodic conditions enabling regeneration |
| **Structural diversity**<br>**(Elephant effects on woody sizes)** | 1) Elephants tend to concentrate impacts on intermediate size classes[3,6] which can result in a recruitment bottleneck[2] of reduced density and supressed recruitment into larger sizes[17-19]<br>2) Elephants can reduce the density of large trees by debarking[20,21] | 1) Elephants impact was highest on saplings within an 'elephant trap' but unpalatable shrub density increased within this zone<br>2) Elephants killed large trees by debarking but the dead tree appearance rate was not much higher than a background mortality rate without herbivores found in another study[25] | 1) Increase in available forage for other browsers due to the coppicing of *C. mopane*.<br>2) As long as some tall trees remain structural diversity is maintained | 1) The relative role of soil moisture availability on seedling mortality<br>2) The opportunity for woodland replacement of short-lived shrubs (alternative vegetation states) |
| **Functional diversity**<br>**(Ecosystem state shifts)** | 1) Elephants and fire together are capable of causing ecosystem state shifts from savanna woodlands to grasslands[22,23] or mixed shrublands[24] | 1) Elephants are causing a functional state shift from acacia woodland to shrubland.<br>2) There has been rapid and pervasive shrub encroachment of a single species which is unpalatable to elephants , but palatable to other browsers | (1) Negative consequences for functional diversity<br>(2) Potential changes in herbivore assemblage | (1) The influence of global drivers of increased atmospheric $CO_2$ and regional aridification |

[1]Chafota & Owen-Smith (2009); [2]Asner & Levick, (2012); [3]Asner, et al. (2015); [4]Ben-Shahar (1993); [5]Skarpe et al. (2004); [6]Owen-Smith & Chafota (2012); [7]Kerley et al. (2008); [8]Chafota (2007); [9]Scogings et al (2012); [10]Wigley et al (2014); [11]Guldemond & van Aarde (2007); [12]Svensson et al (2012); [13]Gadd (2002); [14]Boundja & Midgley (2009); [15]Shaw et al (2002); [16]Moe et al (2009); [17]Staver & Bond (2014); [18]Sankaran et al (2013); [19]Asner et al (2009); [20]Jacobs & Biggs (2002); [21]Shannon et al (2008); [22]Dublin et al (1990); [23]Gillson (2004); [24]Mosugelo (2002); [25] Moustakas et al (2006).

## 5.6 Limitations of the study and recommendations for further research

One of the potential limitations of the heterogeneity study is the novel nature of the patch delineation method. By defining patches by density of dead trees, (with no real alternative measure), one could argue that more patches would be defined simply as a function of an increase in spatially random dead trees. This would not be representative of a true patch mosaic system as there would be little difference in pattern between initial patches and inter-patch areas. There was however no real alternative measure of potentially patchy mortality. I also initially showed that dead trees were clustered in space, and that the rate of dead tree increase in patches was different to inter-patch areas. I believe that this method allows for an accurate representation of clustered dead tree patches as defined in a patch mosaic system. This method then has great advantages over square lattice or moving window methods as it identifies ecologically-relevant patches (of any point pattern process such as seedling dispersal, or shrub expansion) which can be tracked over time at a defined scale.

I did not measure the change in spatial pattern of patches of living trees, and because individual species-scale identification is largely not possible from the aerial photographs (Baldeck *et al.* 2014), the composition of disturbance patches is unknown. It may be that the initial patches of intense disturbance were simply stands of acacia trees. Future studies should examine the composition of disturbance patches and inter-patch areas.

My findings in Chapter three only represent a compositional shift between stages (seedling, sapling, canopy tree) for the transects surveyed, and I did not investigate spatial variation in seedlings in relation to patches of heavy and light impact. The seedling survey was conducted in a period of extremely high rainfall (Chapter 1) and it is hard to separate soil moisture effects from browsing in seedling mortality. Another seedling survey is recommended to assess seedling survival and elephant impacts on seedlings, particularly following the extremely dry year of 2015.

A palaeopalynology reconstruction to establish long-term woodland compositional change is recommended for further research. Using historical data in combination with contemporary studies can provide invaluable insight into the impacts of elephants on woody plant species composition (Bakker *et al.* 2015), particularly compositional changes related to elephant extirpation and rinderpest in the late 19th century. There is little knowledge of episodic conditions which enable regeneration in savannas (Bond, Smythe & Balfour 2001; Wiegand, Jeltsch & Ward 2004; Staver, Bond & February 2011) and historical reconstructions also help address the gap in knowledge of long term (>100 years) savanna dynamics. Recruitment opportunities may be much rarer than the 1-4 recruitment events per century hypothesized to be the minimum frequency to sustain populations of trees like acacias (Wiegand, Jeltsch & Ward 2004).

Only the structural aspects of shrub expansion were documented in Chapter four, and great opportunity for elucidating the drivers of shrub expansion lies in the analysis of the spatial aspects from the aerial photograph time-series. Examples from non-native shrub invasions into semi-arid riparian areas illustrate how invasions into treeless areas are often caused by disturbances or climate that remove what had been previous barriers to tree establishment such as ground water and nutrient availability (Rundel, Dickie & Richardson 2014). I did not find this pattern of *C. mossambicense* density association with dead trees, but this is likely due to the spatial scale of the transects.

The 1992 aerial photographs have fortuitously captured an incipient wave of shrub encroachment providing a dataset where the spatial aspects of encroachment may relate directly to the three hypothesised drivers of 1) elephant disturbance, 2) ground-water change, and 3) $CO_2$. I recommend that a study of the spatial dynamics of shrub encroachment can be used to evaluate the three potential hypothesized drivers where: 1) the elephant impact hypothesis would be supported if shrubs colonized open areas following tree mortality; 2) the increasing aridity hypothesis would be supported where shrub cover increased most at higher elevations as shrubs may better tolerate aridity than tree saplings; and 3) the global atmospheric $CO_2$ driver hypothesis would be supported if there are no obvious spatial patterns. An additional commission of aerial photography (with lidar data) by 2019 is recommended to enhance the dataset to 27 years. A new survey to document changes since 2008 would enable us to answer what follows shrub encroachment in a woodland.

The 1992 density was originally calculated for size classes of all combined transects across the study area and this meant that the raw transect data from 1992 could not be used in a spatio-temporal analysis.

Because this is the only dataset of its kind, representing time series of both large-scale remotely-sensed data, and species-level fieldwork data for elephant-impacted savannas over 17 years, all efforts to increase the data-set to ensure continuity must be made.

## 5.7 Management implications and recommendations

It must be explicitly stated that the management implications and recommendations hereof, are based on, and applicable to the Linyanti riparian woodland. Regional effects of elephants within the upland mopane areas, or within the larger Kavango/Kwando/Chobe system were not studied and I cannot draw management implications outside of the study region.

In Botswana's national elephant policy and strategy document of 2003 (DWNP 2003), three strategies were outlined to fulfil the objective set out to 'prevent, reduce or reverse unacceptable elephant-induced environmental changes'. These were:

Strategy one: "in some areas accept that changes to environment are of less importance than other issues regarding elephants (such as tourism)";

Strategy two: "bring impacts of elephant to within limits to acceptable change"

Strategy three: "protect samples of habitat types that are threatened by elephant to preserve parts of the original vegetation diversity and create a species bank for the future" (DWNP 2003). The applicability of each of these strategies to the Linyanti woodland is as follows:

The main economic function of the Linyanti riparian woodland is tourism, both public camping within the narrow strip of CNP, and the private safari camps of NG/15 and therefore there are reasons why strategy one would apply to this region. Tourism is seen as an important sector in the economy of Botswana, with a total contribution (both direct and indirect) of 8.5% of GDP in 2014, as well as providing 10.1% of total employment in 2014 (World Travel and Tourism Council, 2015). The conversion of woodland to *Combretum* shrubland is likely to benefit browsers such as giraffe and kudu, and potentially have knock-on positive effects for predators. In addition to the main tourist attraction of large herds of elephants, the increase in charismatic wildlife species like giraffe may help to offset the negative effects of reduced wildlife visibility within the dense shrub layer as well as the aesthetic consequences of the loss of large trees.

If strategy two were to be taken up, to curtail any negative consequences of elephants on riparian woodlands in open systems like northern Botswana would require either: 1) greatly reducing elephant densities,) or 2) ensuring broader-scale open movements within the Kavango-Zambezi (KAZA) Trans-Frontier Conservation Area TFCA. Density reduction in the form of culling is only a short-term solution, which may give rise to immigration and longer-term intensification of impacts (Aarde, Whyte & Pimm 1999; Gillson & Lindsay 2003), and has ethical considerations

(Lötter *et al.* 2008) but is in any case practically unfeasible for the massive and nomadic northern Botswana population of elephants. Lethal options of density control would also be undesirable in the Linyanti as this could result in international outcry which might negatively affect tourism (DWNP 2003).

Ensuring corridors where elephants can move away from the highly impacted Linyanti-Chobe systems will allow local elephant densities to fluctuate naturally through dispersal (van Aarde & Jackson 2007). This last option is probably the only long-term solution, if we are to allow for episodic recruitment and long-term cycling of savanna trees. The commencement of water flow in the Savuti Channel in 2008 since it stopped flowing in the early 1980's lowered elephant concentrations in the Linyanti (pers. obs.) and regeneration may be possible if it continues to flow for long enough. Within a larger system the KAZA TFCA may also provide for decompression of elephants in the Linyanti. Unfortunately, the KAZA TFCA, which is meant to link Botswana with Namibia, Angola, Zambia and Zimbabwe in a relatively open system, has largely been truncated with only 30km remaining open on the border and animal control fences across the Zambezi Region (Caprivi Strip) (Botswana Dept. of Environmental Affairs 2015). The flip-side of an increasing population of elephants in northern Botswana is that the areas on the Namibian side of the Linyanti woodland have the highest incidence of human-elephant conflict (HEC) (O'Connell-Rodwell *et al.* 2000). The incidences of HEC are likely to increase with decreased forage availability for elephants in the Linyanti and conservation efforts need to be directed to HEC mitigation.

Strategy three would be a viable, but short-term option for the Linyanti. The presence of dense saplings of sensitive canopy tree species in fenced off staff areas of Duma Tau and King's Pool suggests that human areas can function as botanical reserves (Lombard *et al.* 2001). Historically, human settlements along the river may have protected vulnerable species in areas of high elephant impact as has been postulated for marula (*Sclerocarya birrea*) in the Kruger National Park (Helm 2011). In this way, increasing permanent fenced exclosures like safari camps in the Linyanti may help vulnerable tree species to persist in the short term.

Ultimately, the only management strategy for relatively open systems is to accept elephant-induced changes, particularly given the declining populations (Wittemyer *et al.* 2014) of elephants in Africa, which badly need to be conserved. The relatively open system of the KAZA TFCA can allow for more natural impact mitigation by decompressing elephant populations (Aarde, Jackson & Ferreira 2006; van Aarde & Jackson 2007).

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