

Savanna woody regeneration in response to different treatments of herbivory and fire

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ABSTRACT

Woody regeneration is one of the fundamental processes responsible for structuring savanna systems. Herbivory and fire are two primary drivers of woody structure, and therefore also woody regeneration. Regeneration responses of woody species to savanna controlling factors can be examined and explained by using the combined competition-based and demographic bottleneck model. Woody encroachment has received increasing attention in savanna system dynamics since savannas are considered vulnerable to encroachment. Woody species can broadly be categorised as encroachers, which are considered as species with the ability to outcompete other life forms when disturbances occur, and non-encroachers, which are considered more desirable. The savanna demographic bottleneck model has not yet been applied to these two woody functional groups separately. This could bring insight into woody encroachment and to what extent it can be controlled by herbivory and fire without negatively affecting non-encroacher species.

The main aim of this study was to test the effect of herbivory and fire (presence and release thereof) on woody regeneration of both encroacher and non-encroacher woody species across a small-scale (139 ha) heterogeneous landscape in a riparian semi-arid savanna ecosystem. The specific objectives were to (i) describe and compare dominant woody families and species and basic PFtraits of the woody layer across different treatments of herbivory and fire (presence and exclusion), (ii) evaluate the effects of herbivore exclusion on woody species assemblages, (iii) evaluate the effect of herbivory and fire on woody species abundances, and (iv) evaluate the effect of herbivore and fire presence and exclusion on woody community and population demography and stability. Woody species assemblages referred to the statistically tested woody species composition in the specific treatment and woody communities is the group of woody species within the borders of the herbivore or fire treatment. The broad hypothesis states that the exclusion of both herbivory and fire from a semi-arid savanna ecosystem will enhance regeneration and recruitment of woody species.

The study was conducted at the Nkuhlu long-term exclosures situated in the southern parts of Kruger National Park, South Africa. The exclosures are divided into different treatments of herbivory and fire. Herbivore treatments consist of a fully fenced exclosure (designed to exclude all mammalian herbivores larger than a hare); a partial exclosure (designed to exclude elephant, but also excludes giraffe due to their body height) and a control site (exposure to all large mammalian herbivores). Each herbivore treatment was divided into a fire-exposed and fire-excluded area by means of a fire break. Woody individuals were sampled inside permanently marked plots located on transects initiating in the riparian vegetation zone (close to the Sabie River), extending across the sodic midslopes to the crest (uplands).

Results from the floristic analyses indicated that 13 years of excluding herbivory and fire was long enough to initiate changes in abundance of dominant families and plant functional types, and excluding herbivores also changed species composition. Herbivores played an important role in structuring the woody layer, although fire had much less effects on woody regeneration than was expected in this savanna type. Woody species abundance results indicated that herbivore activity negatively impacted recruitment of both encroacher and non-encroacher species, with effects differing between the two groups. Herbivore effects were also evident in community and population demography. Herbivores managed to suppress regeneration of key encroacher species, except for *Dichrostachys cinerea*. Key non-encroacher species differed in their response to herbivore activity, with some indicating demographic resistance to herbivore pressure.

Key words: recruitment; encroachers; non-encroachers, recruitment bottleneck, elephants, mesoherbivores.

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CHAPTER 1

Introduction

1.1 Background and rationale

Savanna vegetation structure is characterized by a continuous herbaceous layer and discontinuous woody layer (Knoop & Walker, 1985). The complex co-existence between these two layers has been of interest for savanna ecologists over many years (Walter, 1971; Scholes and Archer, 1997; Higgins *et al.*, 2000; Bond *et al.*, 2003; Scholes *et al.*, 2003; Sankaran *et al.*, 2004). Savannas are heterogenous systems (Ben Shahr, 1996) that function at alternating stable states (Illius & O'Connor, 1999; Briske *et al.*, 2003; Gillson, 2004; Sankaran *et al.*, 2005) in response to various factors controlling the transition from one stable state to another. These factors include climate variability, geological substrate, herbivory and fire (Skarpe, 1991; Van de Koppel & Prins, 1998; Van Wilgen *et al.*, 2000). These factors act together to shape savanna ecosystems, depending on the specific characteristics of the area.

The Kruger National Park (KNP) is one of the largest protected areas in southern Africa shaped by interconnectivity between climate, soil, fire and herbivory. The park hosts a great diversity of large mammalian herbivores and is subjected to fire events. In 2001, long-term research exclosures were constructed along two of the large rivers in KNP, the Letaba and Sabie Rivers respectively, which provided the opportunity to study temporal and spatial responses of savanna vegetation structure to herbivory and fire exposure, as well as the effect of their exclusion from the system (O'Keefe & Alard, 2002). Research exclosures in the southern part of the KNP along the Sabie River, expand across a small-scale heterogenous savanna landscape (Siebert & Eckhardt, 2008; Siebert *et al.*, 2010), typified by different soil types along a riparian topographic sequence (often referred to as the catena), which hosts a unique vegetation structure. These exclosures, i.e. the Nkuhlu exclosures site, provide unique opportunities to study vegetation dynamics in response to herbivory and fire across a typical granitic landscape catena.

Woody encroachment are considered a concern to savanna systems due to its negative effects on the system. These negative effects include disruption in ecosystem functioning through altering soil carbon storage (Berthrong *et al.*, 2012), inhibiting ground water recharge (Gray & Bond, 2013), affecting tourism (Gray & Bond, 2013), lowering grazing potential (Angassa & Baars, 2000) and affecting biodiversity (Ratajczak *et al.*, 2012), therefore research on this topic is important. Woody encroachment is not only a concern for

private landowners but also for conservationists, which has led to extensive research on potential drivers of woody encroachment and suitable management practices for conservationists within southern African savannas. Woody encroachment have been identified as a consequence of the tree-grass 'balance' being disturbed (O'Connor *et al.*, 2014), with the disturbance leading to an increase in woody biomass, stem densities or woody cover in an ecosystem (Stevens *et al.*, 2016). Savannas are particularly vulnerable to woody encroachment (Parr *et al.*, 2014), and changes in the factors controlling savanna vegetation structure, i.e. climate, soils, herbivory and fire, are responsible for woody encroachment (O'Connor *et al.*, 2014). Recent research suggested that increasing atmospheric CO₂ levels should also be considered as a primary determinant and global driver of woody encroachment (Bond & Midgley, 2012).

Savanna woody structure (i.e. composition, abundance and height class distribution) is primarily determined by the ability of woody species to regenerate, despite interactions with factors controlling savanna systems. Regeneration is therefore defined here as the process through which one (established) generation of woody plants is replaced by the following generation (Harper, 1979). During the regeneration process, woody seedlings grow past the sapling phase (juveniles) to get established (adult). This is referred to as woody recruitment (Harper, 1979). Savanna woody recruitment is best studied when all life stages are considered, in other words from seedlings to established trees, to identify specific demographic stage alterations which ultimately determine future woody structure.

Regeneration responses of woody species to the most common savanna ecosystem drivers, i.e. herbivory and fire in combination with different soil types, can be examined by using a combination of assumptions and mechanisms from the competition-based and demographic bottleneck models (February & Higgins, 2010; O'Connor *et al.*, 2014). These models are commonly used to describe the tree-grass co-existence in savanna ecosystems (O'Connor *et al.*, 2014). The competition-based models refer to competition for nutrients, water and space between woody and herbaceous species (Walker & Noy-Meir, 1982; Walter, 1971). The demographic bottleneck models consider the variability of climate and disturbance, i.e. herbivores and fire, on growth and recruitment (Higgins *et al.*, 2000). When combining these two models (Sankaran *et al.*, 2004), one can predict that the herbaceous layer can directly or indirectly create demographic bottlenecks for woody plants, by (i) outcompeting woody seedlings, 'trapping' them within a high herbaceous biomass, which leads to (ii) high intensity fires that inhibit woody seedlings to grow past the 'fire trap'. Another factor which can be combined with the demographic bottleneck model is the browse trap. This is where

woody plants are directly severely utilized by browsing herbivores, inhibiting them to grow past a certain height, keeping them within the 'browse trap'.

By applying these savanna models to the woody layer across the Nkuhlu exclosures, insight could be gained on the specific effect of presence or absence of herbivores (especially mega-herbivores) and fire on regeneration of woody species in a semi-arid savanna ecosystem. Novel insights will include the specific effects on encroachers and non-encroachers.

Woody structure can be altered through 'trapped' woody individuals inside a demographic bottleneck. These changes can occur as a result of alteration in woody abundances (Higgins *et al.*, 2000; Staver *et al.*, 2009; Gandiwa *et al.*, 2012; Sankaran *et al.*, 2013) and size-class distribution (Condit *et al.*, 1998; Riginos, 2009; Kambatuku *et al.*, 2011; Holdo *et al.*, 2014; Vadigi & Ward, 2014).

Woody structure is therefore regulated by numerous environmental factors, although it is still unclear how these factors affect woody species with different ecological adaptations, e.g. encroacher species versus more desirable non-encroaching species. When discerning between these two functional groups and disentangling effects of different herbivores (meso- and mega-herbivores) and fire on these species, insight could be gained on woody encroachment in savanna systems. The demographic models has not yet been used to examine responses of encroachers and non-encroachers to herbivore and fire manipulations. These results could be used to aid management practices on controlling encroacher species without negatively affecting the desirable non-encroaching species.

1.2 Objectives

The main objective of this study was to test the effect of herbivory and fire (presence and absence thereof) on woody regeneration (recruitment and rejuvenation) of both encroaching and non-encroaching woody species across a small-scale heterogeneous landscape along a riparian semi-arid savanna ecosystem.

The specific objectives were to:

- Describe and compare frequency of dominant woody families (and species) and ratio's of basic plant functional types of the woody layer across different treatments of herbivory and fire (presence and release thereof) for seedlings and established woody individuals between 2002 and 2015 (Chapter 5).

- Examine and evaluate the effect of herbivore exclusion on woody species composition for both seedlings and established species between 2002 and 2015 (Chapter 5).
- Examine and evaluate the effect of herbivory and fire presence and absence on woody seedling and established woody individual abundances between 2002 and 2015 (Chapter 6).
- Examine and evaluate the effect of herbivore and fire presence and absence on woody community and population demography and stability (Chapter 7).

1.3 Hypothesis

The exclusion of both herbivory and fire from a semi-arid savanna ecosystem will enhance woody recruitment.

1.4 Dissertation layout

The layout of this dissertation conforms to the guidelines set for a standard dissertation by the North West University. However, the format was slightly adjusted in the respective results chapters to facilitate later manuscript preparations. Each results chapter therefore includes a short introduction, a description of methods specifically relevant to the research question addressed in the chapter, a description of the results and a discussion. A total of eight chapters are included, with a single reference list for all cited research at the end of the dissertation. A brief description of each chapter is provided below.

Chapter 2: Literature review

Literature relevant to the research topic is provided in this chapter. This includes a brief background on the Savanna Biome and short discussions on drivers of savanna structure and regeneration, as well as potential threats with special emphasis on bush encroachment.

Chapter 3: Study area

The study area, i.e. the Nkuhlu long-term research exclosures site, is described in terms of its locality, history, climate, geology, soil, topography, and vegetation.

Chapter 4: Materials and Methods

The experimental design and sampling approach is explained in this chapter. An overview of statistical analyses is provided, although analyses relevant to specific objectives are discussed in detail in the respective chapters.

Chapter 5: Floristic changes in response to herbivory and fire

This chapter serves as an introduction to the floristics of the study area. Floristic responses to the different herbivore and fire treatments are presented based upon dominant plant families, species and basic plant functional types. Both seedlings and established woody individuals were considered in analyses. The effects of herbivore exclusion on woody species composition were also evaluated. This was done to compare effects of mega-herbivore (elephant and giraffe) exclusion opposed to the exclusion of all mammalian herbivores.

Chapter 6: Woody abundance changes across herbivore and fire treatments

Changes in abundances of seedlings and established individuals of the (i) complete, (ii) encroacher, and (iii) non-encroacher woody communities were tested and evaluated across the different herbivore and fire treatments.

Chapter 7: Demography of the woody community after 13 years of herbivore and fire manipulation

In this chapter, the demography and stability of woody communities and pre-selected key encroacher and non-encroacher species were studied separately to evaluate the woody community structure after 15 years of herbivore and fire manipulations.

Chapter 8: Conclusions

The main findings are discussed and linked to the hypotheses tested (regarding each results chapter). Recommendations for future studies on regeneration of the woody layer in semi-arid savanna ecosystems are provided.

CHAPTER 2

Literature review

2.1 Savanna vegetation structure and dynamics

Savannas are widely defined as tropical or near-tropical seasonal ecosystems consisting of a continuous herbaceous layer, dominated by grass, and a discontinuous layer of trees and/or shrubs (Frost *et al.*, 1986; Skarpe, 1992; Mucina & Rutherford, 2006; Van As *et al.*, 2012). Savanna ecosystems are dynamic in their vegetation structure and species composition, which change in response to biotic disturbances and various interactions between organisms and their abiotic environment (Skarpe, 1991; Van de Koppel & Prins, 1998; Van Wilgen *et al.*, 2000). On the African continent, many different types of savannas exist. These include edaphic savannas, climatic savannas and disturbance-based savannas. Different formations of savannas ranging from shrubby grasslands to open woodlands exists with the primary drivers of vegetation structure differing between them. The savanna type under investigation in this dissertation is a disturbance-based savanna driven primarily by disturbances such as herbivory and fire as well as soil-characteristics.

2.1.1 Plant-plant interactions

In savanna ecosystems, the most apparent plant-plant interaction is between trees and herbaceous plants (Scholes & Archer, 1997; Sankaran *et al.*, 2004). The dominance of the one life form over the other is largely dependent upon geographical location, but also on specific environmental conditions, such as rainfall, soil type, soil nutrients, atmospheric CO² levels and frequency of herbivory and fire (Van As *et al.*, 2012).

Tree-grass co-existence in savanna ecosystems is regarded as unstable. Four models were summarized by House *et al.* (2003) to explain how these two life forms co-exist: (1) Niche separation, where woody and herbaceous plants occupy different regions in space (i.e. preferential access to deep soil water by woody plants versus shallow soil water use by grass); (2) Balanced composition, where intraspecific competition dominates over interspecific competition; (3) Competitive exclusion, where the system is eventually driven to a relative stable state and where one life form, for a short time, dominates and virtually eliminate the other until disturbances with greater effect prevent maintenance of this domination; (4) Multiple stable states, where the spatial and temporal heterogeneity of

resource availability and disturbance is incorporated into equilibrium models so that contrasting tree-grass ratios might exist for a given site at various times.

New explanations arose during recent years to explain the co-existence of trees and grasses. These explanations recognised the effect of disturbances, i.e. herbivory, fire and climatic variability, on the dynamic nature of tree-grass coexistence (Menaut *et al.*, 1990; Jeltsch *et al.*, 1996, 2000; Higgins *et al.*, 2000; Gardner, 2006; Van Langevelde *et al.*, 2011). These disturbances impact on the main or 'superior' life form at the given time, which create opportunities for the competitive 'inferior' life form to establish and persist (Warner & Chesson, 1985). The disturbance-based explanation of tree-grass co-existence is underlain by two different arguments for the dynamics (Sankaran *et al.*, 2004), which include (i) non-equilibrium dynamics (Higgins *et al.*, 2000; Gardner, 2006), and (ii) disequilibrium dynamics (Menaut *et al.*, 1990; Jeltsch *et al.*, 2000). These two paradigms consider that savannas are continually in transition with disturbances and temporal resource availability maintaining the transitional state (Van Langevelde *et al.*, 2011). The disequilibrium argument states that a system is prevented to reach an equilibrium state due to effects of disturbances, whereas the non-equilibrium argument ignores the existence of any equilibrium positions (Van Langevelde *et al.*, 2011). The non-equilibrium dynamics model only considers the effect of disturbances on tree recruitment, stating that inter- and intra-life form competition do exist but is assumed to have a minor effect on tree:grass ratios compared to climatic variability (Van Langevelde *et al.*, 2011). The disequilibrium dynamics assume that competition between trees and grasses occurs at all life stages in the particular environmental conditions, and internal drivers (disturbances) such as herbivory and fire prevent dominant vegetation structure and composition transitions (Van Langevelde *et al.*, 2011).

Scheiter & Higgins (2007) proposed a model that explains tree-grass co-existence by identifying above- and belowground competitive factors. These factors take in consideration the consequences of competition for multiple resources. Aboveground competition exists for light and belowground for water, rooting space and nutrients (Scheiter & Higgins, 2007). Herbivory and fire were identified as the main attributes to affect aboveground biomass. It was stated that tree-grass coexistence could only be achieved if belowground competition (roots) are held below a certain threshold and aboveground competition for light is low (Van Langevelde *et al.*, 2011).

High herbaceous biomass can suppress or inhibit tree establishment, but evidence exists that tree establishment can be facilitated by, for example, other trees (Holmgren *et al.*, 1997; Ludwig *et al.*, 2004) or even grasses (Brown & Archer, 1989; Davis *et al.*, 1998; Anthelme &

Michalet, 2009; Van Langevelde *et al.*, 2011). This facilitation effect is especially true for stressful environments (Brooker *et al.*, 2008).

2.1.2 Plant-herbivore interactions

African savannas are known for its rich diversity of large mammalian herbivores. Savanna vegetation has co-evolved with these animals, which led to certain adaptations from both sides (Charles-Dominique *et al.*, 2016). This includes the functional relationship between the development of spinescent trees in the presence of herbivores, especially of medium-sized social mixed-feeders (Charles-Dominique *et al.*, 2016). Herbivory was responsible for the formation of structural defences in multiple woody lineages (Charles-Dominique *et al.*, 2016).

More adaptations in woody plants to repel or prevent herbivory include (Van As *et al.*, 2012): (i) formation of leaf tannins (Scogings *et al.*, 2011), (ii) leaf shedding during dry seasons (Owen, 1978), and (iii) deep root system development to prevent uprooting (Du Toit *et al.*, 2014).

Interactions between trees and herbivores have led to niche diversification between the two groups. Several processes have been identified that could be involved in this niche diversification: (i) separation in height niches, where herbivores have different feeding strategies depending on their body size (Wilson & Kerley, 2003) and vertical separation in spines on plants match the herbivore body sizes present (Burns, 2014); (ii) niche specialisation, mammals likely to browse more have narrow muscles, longer tongues, and prehensile lips, allowing them to browse spiny plants better than grazers (Shipley, 2007); (iii) segregation of niches in time for trees, with impacts from browsers varying in season and between deciduous and evergreen trees (Bryant *et al.*, 1992; Massei *et al.*, 2000). This niche-diversification across evolutionary time also contributed to the diverse nature of African savannas (Skarpe, 1992).

African savannas have a long history of large herbivores shaping plant communities and maintaining landscape and species diversity (Guldemand & van Aarde, 2008; Levick & Rogers, 2008; O’Kane *et al.*, 2011; Scogings *et al.*, 2012; Van Coller *et al.*, 2013). For example, trees are attractive structural elements for a variety of small and large mammals, adaptation in seed dispersal and scarification, and animals are potential drivers of the spatial patterning of woody species. Increasing megaherbivore densities, particularly elephant may result in loss of woody cover, species richness and healthy regeneration (Whyte *et al.*, 2003; Western & Maitumo, 2004; Guldemand & Van Aarde, 2008; O’Connor, 2010; Asner &

Levick, 2012; Gaugris *et al.*, 2014; De Boer *et al.*, 2015). Significant negative elephant impacts include damage to large trees by debarking them, pushing the entire tree over, or by tearing of leaves and branches (Scholes *et al.*, 2003). Other smaller bodied herbivores also have substantial effects in changing savanna vegetation structure (Moe *et al.*, 2009; O'Kane *et al.*, 2012). This is done through direct consumption of grass and woody species, especially seedlings, or indirectly through trampling.

2.1.3 Plant-fire interactions

Fire-maintained savannas first appeared in the late Miocene, millions of years after mammals dominated savannas (Charles-Dominique *et al.*, 2016). These dyotrophic fire-dominated savannas are characterised by seasonally humid and nutrient-poor environments (Lehmann *et al.*, 2011; Charles-Dominique *et al.*, 2016). Fire has been considered as an ecosystem management tool for bush encroachment, especially in savanna conservation areas. The woody component can directly (direct consumption of woody biomass) or indirectly (clearance of herbaceous biomass to create establishment gaps for woody seedlings) be influenced by fire (Bond & Keeley, 2005; O'Connor *et al.*, 2014). The effect of fire on savanna woody plants is often species-specific (Bond *et al.*, 2001; Zida *et al.*, 2007). This was observed in studies that reported that *Sclerocarya birrea* individuals with a height less than 2m were negatively affected by fire (Jacobs & Biggs, 2001), whereas individuals of *Dichrostachys cinerea* and *Vachellia gerrardi* were negatively affected in the height classes less than 3m and those with a height greater than 3m were unaffected (Jordaan, 1995).

Trees have developed mechanisms to tolerate fire disturbances, for example, resprouting (López-Soria & Castell, 1992) by using stored reserves. Resprouting involves further growing after fire has caused damage to the tree. This mechanism enables trees to be resilient to fire disturbances. The ability of trees to reprot after a fire disturbance depends largely upon tree size (height). If a tree is unable to reach above a certain height before a fire disturbance, it have a higher chance to get killed.

A common feature within fire exposed savannas is the 'fire-trap', which creates a recruitment bottleneck for woody species (Higgins *et al.*, 2000). The 'fire-trap' inhibits woody seedlings/saplings to grow above a certain height (3 m). This may lead to a decline in woody cover over long-term periods.

2.1.4 Plant-soil interactions

Soil characteristics within a savanna can alter vegetation composition (Scholes & Walker, 1993; Levick *et al.*, 2010; Colgan *et al.*, 2012). The Kruger National Park consists of a heterogeneous landscape due to its geology. The granite/gneiss landscape in the southern parts of the park (at the Nkuhlu enclosure site) resides in rapid transitions between dystrophic and eutrophic environments, creating distinct vegetation zones. These zones are situated on the catena which initiate close to the Sabie River (riparian) and extend across the midslopes (sodic) to the crest. Rainfall commonly interacts with changes in topography to influence soil development. Clay particles are carried downslope, leaving the crest with sandy, nutrient-poor and well-drained soils, and the low-lying areas (riparian) with moist, nutrient-rich clayey soils (Scholes & Walker, 1993; Khomo *et al.*, 2011). In the riparian bottomlands, a low percentage of rock cover is found (<5%) and the vegetation structure is characterised as moderately closed to closed woodland (Siebert & Eckhardt, 2008). The mid-slopes (sodics) are also characterised with low percentage rock cover (5%) but with moderately open vegetation structure (Siebert & Eckhardt, 2008). On the crest, a higher percentage rock cover (5-10%) is found and the vegetation structure is a moderately closed shrubland/savanna (Siebert & Eckhardt, 2008). These changes in soil characteristics and rock cover across the catena influence vegetation composition. The catena can therefore be identified as one of the major determinants of savanna vegetation patterns within a landscape (Milne, 1947; Morison *et al.*, 1948; Fraser *et al.*, 1987; Baldeck *et al.*, 2014).

2.2 Regeneration of woody species

Regeneration can be defined as the process through which one generation of plants are replaced by a following generation (Harper, 1979). Through this process, various interactions may influence the recruitment process. Recruitment is the developing process of a woody plant from a seedling, past the juvenile stage, to form an adult tree (Harper, 1979).

The seedling stage of woody plants can be considered as the most vulnerable life stage and therefore also the most important stage (Hoffmann, 1999; Higgins *et al.*, 2000; Roques *et al.*, 2001). If the seedling can survive in its immediate environment despite various biotic and abiotic influences, the plant will be able to grow and get established in that specific area. In theory this is a simple concept to understand, but in nature, this process is rather complex due to complex interactions between numerous environmental factors.

Among the various factors that affect regeneration of woody plants in savanna ecosystems are herbaceous competition (especially grass), herbivory, and fire. The herbaceous layer is known to have competitive effects on woody regeneration specifically on the seedling stage (Riginos, 2009; Vadigi & Ward, 2014). This is where competition for nutrients, water and space plays an important role in woody establishment (Riginos, 2009; Kambatuku *et al.*, 2011; Vadigi & Ward, 2014).

Herbivory through grazing and browsing may affect woody recruitment either directly through consumption of woody plants, or indirectly by relieving grass competition and suppressing smaller herbivore effects, for instance by rodents and insects. In their study, Goheen *et al.* (2004) found evidence of large mammalian herbivores to facilitate and enhance seedling establishment by suppressing smaller herbivores such as rodents, insects, etc. Grazing herbivores may also reduce competition between woody species and the herbaceous layer by creating space for woody establishment and growth (Kambatuku *et al.*, 2011). Herbivory may also have negative impacts on woody establishment by direct tree utilisation (Moe *et al.*, 2009). Elephants have received considerable attention in African savanna ecosystems due to their apparent destructive feeding behaviour. Limited knowledge exist of their effects on woody seedlings. It has been suggested that smaller bodied mammals, such as impala could also be responsible for changes in woody structure (Belsky, 1981; Sharam *et al.*, 2006; Moe *et al.*, 2009; O’Kane *et al.*, 2012). Moe *et al.* (2009) and O’Kane *et al.* (2012) found a positive relationship between increasing densities in impala and larger impacts in terms of increasing mortalities of woody recruits. Lagendijk *et al.* (2015) suggest that elephants can possibly enhance woody regeneration through displacement of meso-herbivore activity.

Fire is considered a fundamental determinant of savanna vegetation structure through its impact on regeneration. In the seedling stage, woody individuals are most vulnerable to damage from fire (Harrington *et al.*, 1991; Casillo *et al.*, 2012; Joubert *et al.*, 2012; Taylor *et al.*, 2012) due to their thin bark, lack of carbon storage (Casillo *et al.*, 2012; Joubert *et al.*, 2012; Midgley, 2010), and exposure to high temperatures in the fire zone fuelled by the dry grass biomass (Miranda *et al.*, 1993). This imposes disruption in the recruitment process of these individuals (Harrington *et al.*, 1991; Casillo *et al.*, 2012; Joubert *et al.*, 2012; Taylor *et al.*, 2012). This is one of the reasons why fire has been considered a tool for managing woody encroachment (Lohmann *et al.*, 2014). By killing woody individuals in their seedling stage, less woody species will be able to grow into mature adult trees (Zida *et al.*, 2007).

2.2.1 Models that explain regeneration of woody species

Sankaran *et al.*, (2004) suggested that the tree-grass co-existence may be explained by combining the competition-based and demographic bottleneck models. Therefore, the dominance of the 'strongest' life form is explained through a close interaction between competitive exclusion and top-down controls, such as herbivory and fire, which cause a demographic bottleneck for woody recruits through suppressive effects on seedling growth (Riginos, 2009; Vadigi & Ward, 2014).

Walter (1971) introduced the two-layer hypothesis in the co-existence of the grass and woody layer in savanna ecosystems. This hypothesis states that woody and grass species occupy different soil layers, with roots growing much deeper (Walter, 1971). More recent studies contradicted this hypothesis (Riginos, 2009; February & Higgins, 2010; Tedder *et al.*, 2012, 2014; Wakeling *et al.*, 2015) with a new concept that although woody roots can grow deeper than roots of grass, they still directly compete with each other for nutrients (Cramer *et al.*, 2007, 2009, 2012; Bloor *et al.*, 2008), water (Gordon *et al.*, 1989; Weltzin & McPherson, 1997; Davis *et al.*, 1999; Picon-Cochard *et al.*, 2006) and space (McConnaughty & Bazzaz, 1991, 1992; Casper & Jackson, 1997) in the upper soil layer. This is however dependent on the involved species (both grasses and woodies), life history stages, soil properties and climatic conditions (Kambatuku *et al.*, 2013; Ward *et al.*, 2013). The grass layer commonly outcompetes woody seedlings, which inhibits their establishment and imposes a demographic bottleneck in their recruitment (Bond, 2008; February *et al.*, 2013; Wakeling *et al.*, 2015).

In grass-dominated ecosystems, woody individuals (less than 3 m in height) that fail to escape the fuel-zone are commonly believed to either be killed by hot burns, especially seedlings, or suppressed in terms of growth. This phenomenon is referred to as the 'fire-trap' which may lead to a recruitment bottleneck (Higgins *et al.*, 2000; Bond *et al.*, 2005). This means that fire disturbance is stage-structured by affecting saplings and not trees (Higgins *et al.*, 2000; Hanan *et al.*, 2008; Staver & Levin, 2012; Staver & Bond, 2014).

Analogous to that of a fire-trap is the browse trap created by chronic herbivory (Fornara & Du Toit, 2008; Staver *et al.*, 2009). To date, the understanding of herbivory effects on savanna systems has been vague (Bond & Keeley, 2005; Staver & Bond, 2014) although herbivory effects are in many respects similar to that of fire. The recruitment process of woody plants are suppressed by constant browsing at a specific height, and only when the pressure is reduced, the juvenile trees can grow into large trees (Prins & Van der Jeugd, 1993; Holdo *et al.*, 2009; Staver *et al.*, 2009). The juvenile trees can therefore be referred to

as being in a browse-trap. These two disturbance traps also differ in some respects. The fire-trap is considered an episodic disturbance, while herbivory is more continuous. It is rather the release from herbivory that is considered as an episodic event (Young, 1994; Holdo *et al.*, 2009). The browse-trap is also considered to be species specific, suggesting that woody species may be trapped in different size-classes depending on their forage preferences by different herbivores (Wigley *et al.*, 2014).

2.2.2 Savanna woody floristic changes driven by herbivory and fire

Savannas first began to spread across Africa in the Miocene, with herbivory and fire regarded as determinants of its spread. Mammal-dominated savannas predate fire-dominated savannas by millions of years (Charles-Dominique *et al.*, 2016). These two determinants of savanna structure seem to favour contrasting savanna environmental settings: herbivore-dominated (eutrophic) savannas are associated with nutrient-rich environments and fire-dominated (dystrophic) savannas with nutrient-poor environments (Scholes, 1990; Lehmann *et al.*, 2011; Hempson *et al.*, 2015). The evolutionary history of African savannas suggests that savanna vegetation is to some extent adapted to the presence of both fire and large herbivores and that the release of these factors from savanna ecosystems could lead to environmental changes. Herbivores do not only shape vegetation structure, but may also be considered as an important driver of species composition changes. It is suggested that palatable species are more likely to get browsed upon than unpalatable species. Regeneration of unpalatable woody species is therefore expected to be stronger than palatable species in the presence of herbivores, depending on the frequency and intensity of browsing pressure (Fornara & Du Toit, 2008). Herbivore exclusion could also cause changes in species composition through the removal of selective browsing pressure (Wiseman *et al.*, 2004; Fornara & Du Toit, 2008; Barton & Hanley, 2013; Gauris *et al.*, 2014), and therefore benefit recruitment of palatable woody species.

2.2.3 Savanna woody structure changes driven by herbivory, fire and the herbaceous layer

Studies on variability of woody abundances in savanna ecosystems revealed that demographic bottlenecks contribute to explaining patterns observed in vegetation structure. Staver *et al.* (2009) found that reduction in herbivore activity led to the escape of trapped seedlings (in the browse-trap), which resulted in an increase of adult tree abundances. This

was also observed by Gandiwa *et al.* (2012) who stated that it is fundamental for woody seedlings to escape fire- or browse-traps to increase in relative abundance. This phenomenon was also reported by Wakeling *et al.* (2011) and Hartnett *et al.* (2012). Increase in woody abundances after herbivore exclusion further demonstrated the ecological effects of browse-induced demographic bottlenecks (Sankaran *et al.*, 2013).

Woody abundance responses can also be species or functional trait specific. In their study, Fornara & Du Toit (2008) found that selective browsing reduced local abundances of palatable woody species, while unpalatable woody species abundances increased and eventually dominated. Species such as *Senegalia nigrescens* are adapted to browsing and their abundances did not decrease in heavily browsed sites in the study of Fornara & Du Toit (2008). Fire disturbances responsible for creating demographic bottlenecks in the form of a fire-trap are known to especially affect woody seedlings in savannas (Higgins *et al.*, 2000; Higgins *et al.*, 2007). Trapped seedlings cause a decrease in woody cover (Bond *et al.*, 2005; Sankaran *et al.*, 2005) by preventing adult tree establishment (Hoffmann, 1999; Higgins *et al.*, 2000) and therefore decreasing adult tree abundances.

The release of herbivores and fire from a system causes an increase in herbaceous biomass (Van Coller *et al.*, 2013). The herbaceous layer acting as a recruitment filter (Riginos, 2009; Vadigi & Ward, 2014) can therefore suppress seedling establishment, leading to changes in woody structure.

Demographic bottlenecks can also alter size-class distribution of plant species. Size-class distribution, which is a measure of demography or population structure, is commonly used to evaluate regeneration success and population or community stability within a specific environment (Shackleton, 1993; Mwavu & Witkowski, 2009; Venter & Witkowski, 2010; Byakagaba *et al.*, 2011; Shackleton *et al.*, 2015). The distribution of woody size-classes should reveal an inverse J-shaped curve when graphically displayed. This curve indicates that most individuals are located in the first size-class and the successive size-classes are monotonically declining. Woody individuals can be divided into size-classes according to diameter at breast height (DBH) (Baker *et al.*, 2005; Coomes & Allen, 2007; Wang *et al.*, 2009) or based on their crown height (Pellew, 1983; Holdo *et al.*, 2014).

Woody demography analyses highlight specific effects of environmental variables, such as herbivory and fire on size-class distribution. However, the seedling size-class is mostly affected by herbaceous competition (if herbaceous biomass is high), which inhibit woody growth past seedling stage (Eckhardt *et al.*, 2000; Riginos, 2009; Kambatuku *et al.*, 2011; Vadigi & Ward, 2014). Herbivory, by browsers, creating browse-traps, and fire-traps created

by fire exposure are identified to cause alteration in especially the sapling size-class distribution (1-3 m in height) of a woody population (Holdo *et al.*, 2014; Wigley *et al.*, 2014). These demographic bottlenecks ultimately cause variation to a normal inverse J-shaped population (Silvertown, 1992; Oliver & Larson, 1990; Condit *et al.*, 1998; Wilson & Witkowski, 2003; Mwavu & Witkowski, 2009; Holdo *et al.*, 2014). Demographic bottlenecks in size-class distribution analyses can be identified by a sharp drop in woody abundance between size-classes (Lykke, 1998), for instance where significantly more seedlings than saplings are recorded (Prior *et al.*, 2009), or where size-classes are missing. This can be linked to the specific environmental conditions to determine what the causes for the bottlenecks are.

2.3 Woody encroachment

Encroachment by woody species result in an increase of woody biomass, stem densities or woody cover, which is a growing problem in savanna ecosystems (Roques *et al.*, 2001; O'Connor *et al.*, 2014; Parr *et al.*, 2014; Stevens, *et al.*, 2016) and is considered one of the top three apparent rangeland problems in South Africa (Hoffmann *et al.*, 1999). Woody encroachment may have numerous negative effects on the environment. A combination of all these factors can accelerate woody encroachment. For example, an ecosystem subjected to high grazing levels will cause reduction in fire frequency and intensity, which will promote woody encroachment by releasing woody recruits from competition with the grass layer (O'Connor *et al.*, 2014). The rising atmospheric CO₂ concentrations will increase woody growth through improved water usage (Polley *et al.*, 1997; Leaky *et al.*, 2009) as well as increased rates of carbon uptake. This would extend the growing season and growth rates of woody species, which will increase woody cover (Bond & Midgley, 2000; Hoffmann *et al.*, 2000; Kgope *et al.*, 2010; Stevens *et al.*, 2016). Therefore, woody encroachment is a consequence of the tree-grass 'balance' in savannas being disturbed (O'Connor *et al.*, 2014).

Encroachment is likely to occur in woody communities containing a high abundance of nitrogen-fixing woody plants, for example, woody species from the family Fabaceae (Stevens *et al.*, 2016). Where these species dominate in combination with increased atmospheric CO₂ concentrations and/or reduction in drought stress, the community is likely to display a rapid increase in woody biomass over time. This is because nitrogen-fixing species can match elevated photosynthesis rates by producing more nitrogen-fixing tissues

(Leakey *et al.*, 2009; Rogers *et al.*, 2009) which maintain high nitrogen-fixation rates (Rogers *et al.*, 2009).

Rates of woody encroachment have allegedly accelerated during recent years (Buitenwerf *et al.*, 2012; O'Connor *et al.*, 2014). Encroachment has for a long time been limited in relatively pristine, large natural ecosystems, such as the Kruger National Park. These areas provide habitat for a complex faunal diversity (meso- and mega-herbivores) and fire has been used as a management tool for most of the last 120 years (Govender, 2003). The removal of elephant from savanna ecosystems have been identified as a significant cause of woody encroachment in Africa (Guldemond & Van Aarde, 2008). This is because free-ranging elephants which controlled encroachment where they roamed, have been removed from many parts of Africa and are now only present in conservation areas (Owen-Smith, 1992). Therefore, the presence of elephant is suggested to control woody encroachment to some extent (Stevens *et al.*, 2016) through limiting woody cover (Guldemond & Van Aarde, 2008).

CHAPTER 3

Study area

3.1 Locality

The study was conducted at the Nkuhlu long-term research exclosures in the Kruger National Park, South Africa (Figure 3.1) which comprise 139 ha of semi-arid savanna. It is situated approximately 18 km south of Skukuza along the Sabie River ($24^{\circ}59'10''\text{S}$ $31^{\circ}46'24.6''\text{E}$).

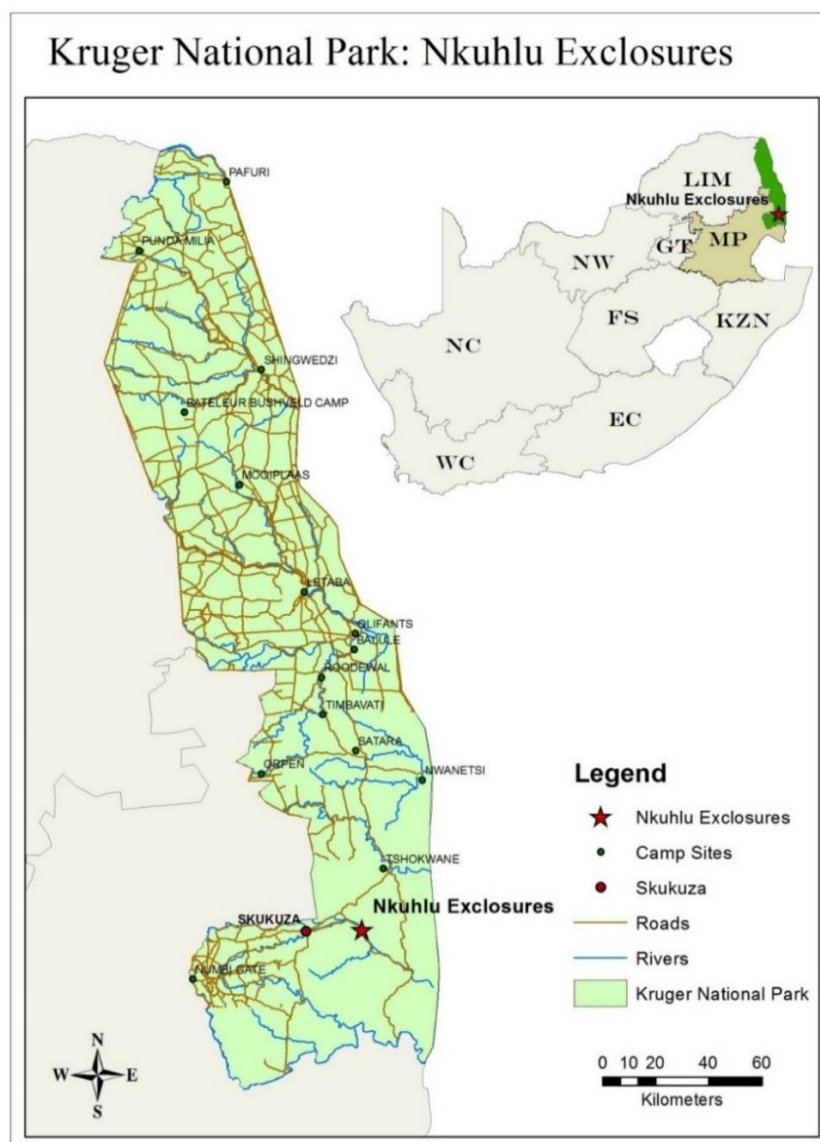


Figure 3.1: Location of the Nkuhlu exclosures research site in the Kruger National Park, South Africa.

3.2 History

The Nkuhlu exclosures were constructed shortly after the large flood event in 2000 to evaluate the natural restoration of a semi-arid savanna riparian ecosystem. In addition to flood response, the research exclosures were designed to test the combined effects of herbivory and fire on vegetation structure, composition and diversity to provide research-based evidence for the development or adjustment of management policies in the Kruger National Park (O'Keefe & Alard, 2002). The exclosures are intended to be monitored for at least 25 years (starting in 2002). By using this data, insight could be gained on key ecological processes that would otherwise be difficult to obtain (O'Keefe & Alard, 2002).

General research objectives were provided in 2002 by O'Keefe & Alard (2002) for specific studies which needed to be done at the exclosures. The following research questions have been formulated: (i) how do herbivory and fire change the vegetation pattern? (ii) How do herbivory and fire affect the regeneration of vegetation following a major flooding event? (iii) How do herbivory and fire affect seed dispersal, seed germination, and then seedling survival? and (iv) What effect do animals have on the physical and biogeochemical features of the landscape?

Throughout recent years (from 2002 until 2015) several vegetation studies have been conducted at the Nkuhlu exclosures, which include a vegetation and floristic description of the exclosures (Siebert & Eckhardt, 2008), responses of woody vegetation to exclusion of large herbivores (Scogings *et al.*, 2012), stem growth of woody species (Scogings, 2011), secondary metabolites and nutrients of woody plants in relation to browsing intensity (Scogings *et al.*, 2011), herbaceous species diversity patterns across herbivory and fire treatments (Van Coller *et al.*, 2013; Van Coller & Siebert, 2015), deciduous sapling response to season and large herbivores (Scogings *et al.*, 2013), landscape scale effects of herbivores on tree fall (Asner *et al.*, 2012). No studies on woody plant species regeneration has been conducted at this particular study site.

3.3 Herbivore community

The area in and around the study site (exclosures) are rich in a diversity of herbivores. Most common species found in the area and surrounding areas are elephant (*Loxodonta africana*), impala (*Aepyceros melampus*), warthogs (*Phacochoerus africanus*), rhino (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), hippo (*Hippopotamus amphibious*), buffalo (*Syncerus*

caffer), zebra (*Equus quagga*), and blue wildebeest (*Connochaetes taurinus*) (Reardon, 2012).

3.4 Climate

The study area is characterised as a semi-arid savanna (Sankaran *et al.*, 2005) with a mean annual precipitation average of 561 mm (as measured at Skukuza) (<http://www.sanparks.org/parks/kruger/conservation/scientific/weather>). Two distinct seasons characterise the area, which include a hot, wet, growing season from October to April (summer), and a cool to warm, dry period from June to August (winter) (Williams *et al.*, 2009; Scogings *et al.*, 2012). The Skukuza region is generally frost-free, with temperatures ranging from minimum means of $\pm 6^{\circ}\text{C}$ in June, July, and August to maximum mean temperatures of above 32°C in December, January and February (Gertenbach, 1983).

3.5 Geology, soil and topography

The study site is mainly underlain by Archean granite and gneiss (Gertenbach, 1983), which is characterised by a typical Lowveld savanna granitic toposequence with a unique vegetation composition at each catenal position (see 3.5). The site varies in altitude from 210 m above sea level at the lowest catenal position (i.e. the riparian bottomlands) up to 235 m on the upland crests (Siebert & Eckhardt, 2008). The soil is in general shallow with a few rock patches on the upland areas, but deeper in bottomland areas where there is an accumulation of clay and minerals (Gertenbach, 1983). On the mid-slopes (sodics), hyper-accumulation of exchangeable sodium occurs as a result of reduced hydrolic conductivity (Khomu & Rogers, 2005). This is due to the release of sodium from granite as the parent geology (Khomu & Rogers, 2005). In 1972, Harmse & Van Wyk identified Mispah and Glenrosa as the main soil types. Other soil types located at the Nkuhlu exclosures across the landscape (from bottomlands to uplands) include Oakleaf in the riparian, mainly Montagu on the sodics and Glenrosa/Mispah and patches of Clovelly on the crest (Siebert & Eckhardt, 2008).

3.6 Vegetation

The study site falls within the Lowveld Bioregion and forms part of the Granite Lowveld vegetation type (SVI 3, Mucina & Rutherford, 2006). The vegetation of the surrounding area of the Nkuhlu exclosures is classified as 'Thickets of the Sabie and Crocodile Rivers' described by Gertenbach (1983) and the vegetation type as the *Acacia* (*Senegalia*) *nigrescens* - *Combretum apiculatum* association. The dominant woody species of the Sabie River granitic landscape include *Combretum apiculatum*, *Grewia bicolor*, *G. flavescens*, *Dichrostachys cinerea*, *Euclea divinorum*, *Terminalia prunioides*, *Spirostachys africana*, *Vachellia* (*Acacia*) *grandicornuta* and *Senegalia* (*Acacia*) *nigrescens* (Gertenbach, 1983).

Siebert & Eckhardt (2008) described the vegetation of the Nkuhlu exclosures as a patchy mosaic, within a relatively small, spatially restricted, heterogeneous landscape. The exclosures consist of five main plant communities, which include ten sub-communities and few small-scale variations, all of which are linked to a specific catenal position (riparian, sodic and crest (Figure 3.2)) (Siebert & Eckhardt, 2008). Diagnostic woody species in the riparian zone include *Flueggea virosa*, *Gymnosporia senegalensis*, *Peltophorum africanum*, *Euclea divinorum*, *E. natalensis*, *Combretum hereroense*, *C. imberbe*, *Phyllanthus reticulatus*, *Spirostachys africana*, *Kigelia africana* and *Bridelia cathartica* (Siebert & Eckhardt, 2008). In the sodics *Vachellia grandicornuta*, *Rhigozum zambesiaceum*, *Pappea capensis*, and *Adenium multiflorum* are the diagnostic, whereas *Senegalia nigrescens*, *Dichrostachys cinerea*, *Combretum hereroense*, *C. apiculatum*, *C. zeyheri*, *Sclerocarya birrea* and *Vachellia exuvialis* dominate the crest of this granitic landscape (Siebert & Eckhardt, 2008).

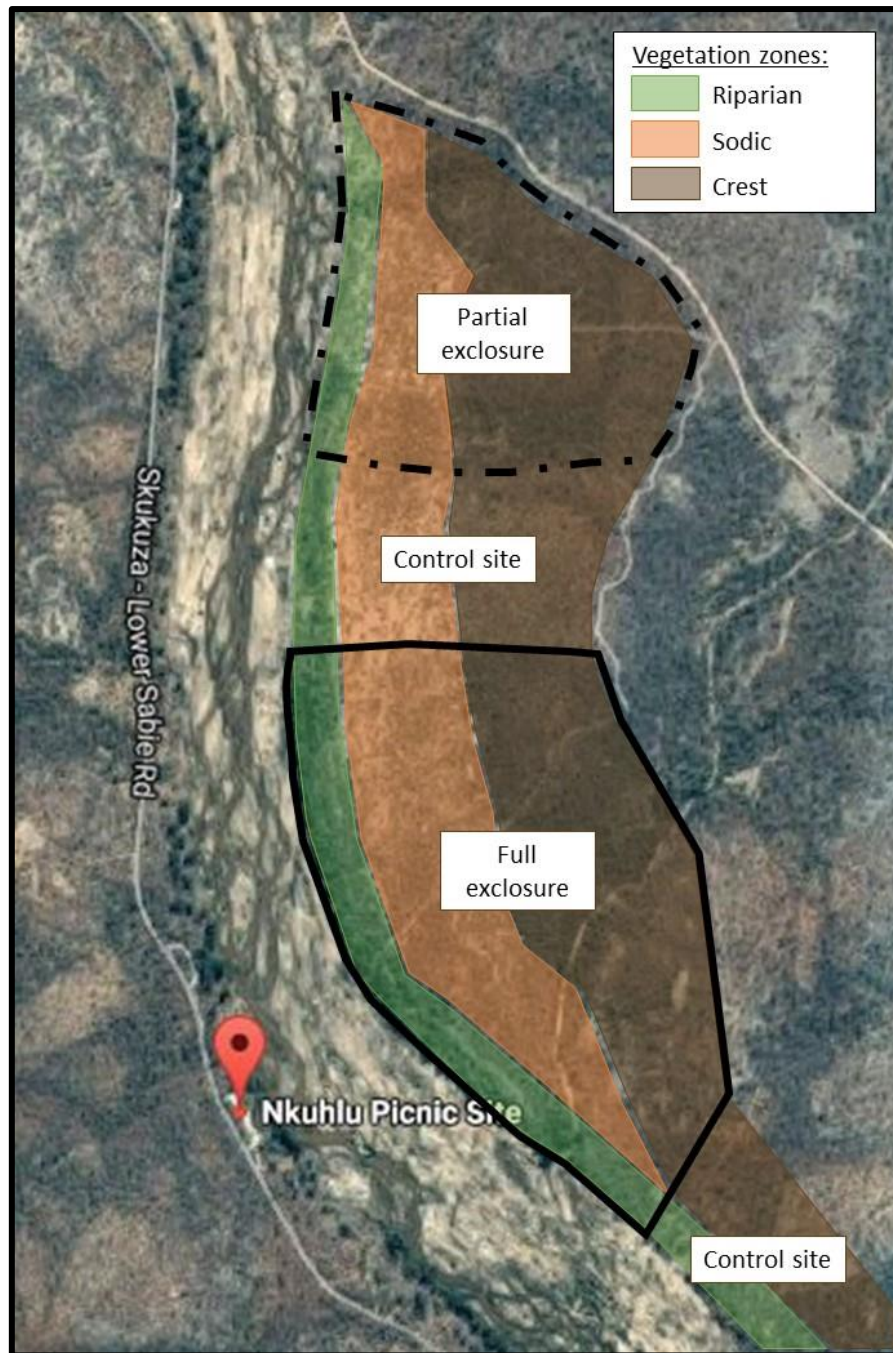


Figure 3.2: Aerial image (Google Maps, 2016) of the Nkuhlu exclosures study site overlain by the herbivore treatments, which illustrate the position of the broader vegetation zones (Riparian, Sodic and Crest) across the topographic sequence. More detail on the herbivore treatments will be provided in Chapter 4.

CHAPTER 4

Materials and methods

4.1 Experimental design

The Nkuhlu long-term research exclosures are divided into different treatments of herbivory and fire (Figure 4.1). The herbivory treatments consist of the following: (1) fully fenced exclosure (designed to exclude all mammalian herbivores larger than a hare) (Figure 4.2a); (2) partial exclosure (designed to exclude elephant, but also exclude giraffe due to their body height (Figure, 4.2b); and (3) a control site, which allows for access by all large mammalian herbivores. To test the effect of fire on vegetation structure and diversity, each herbivore treatment site was subdivided into a burn and a no-burn block, separated by a fire break (O'Keefe & Alard, 2002). Fire as a treatment conforms to fire management of the area, which allows natural fires within the broader management unit to enter the fire treatments, but excluding them from the no-burn blocks. The last fire treatment was applied in 2012. Permanent transects were placed within each herbivore and fire treatment, and extend from the Sabie River riverbank across the granitic toposequence, i.e. from the alluvial bottomland (riparian zone) across the seepline (sodic zone) to the coarse sandy upland (crest zone). Along these transects, fixed 200 m² plots were permanently marked with steel rods and positioned with the longest side (20 m) parallel to the river. These plots were used as replicates in the analysis of the data.

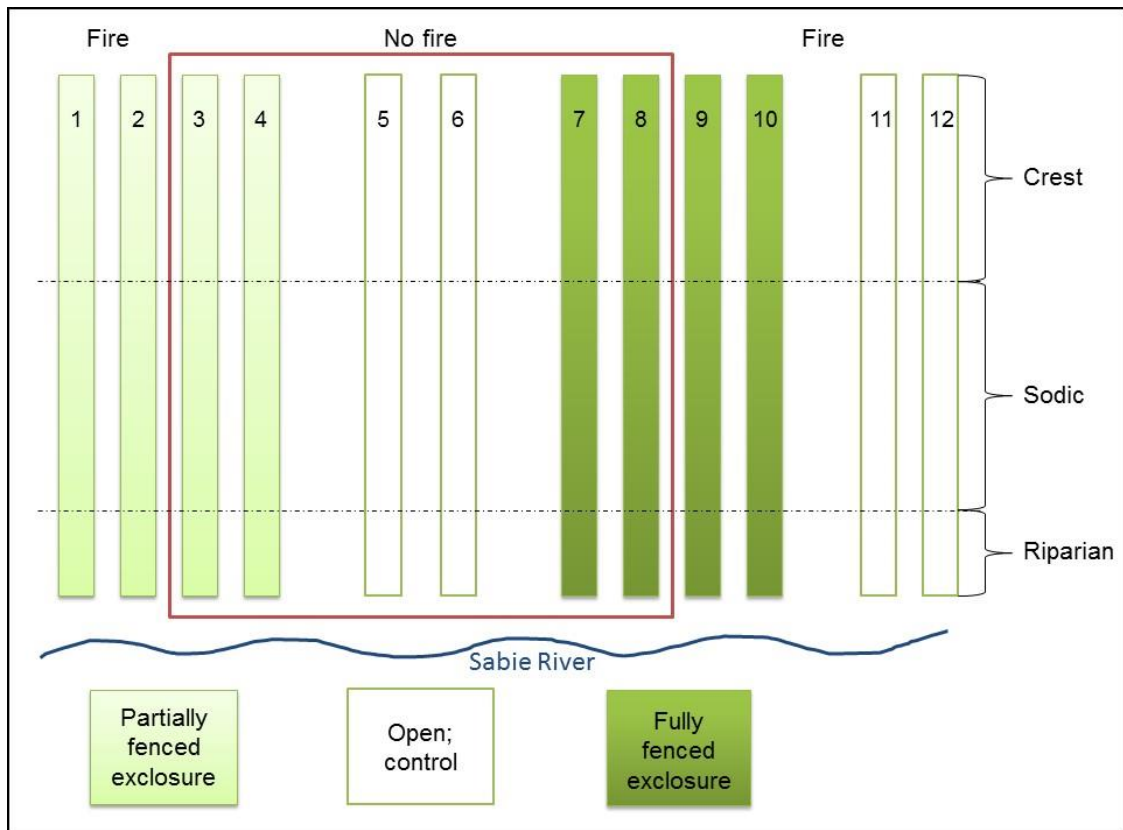


Figure 4.1: Graphic representation of the experimental design of the Nkuhlu long-term research exclosures (adapted from Van Coller *et al.*, 2013).

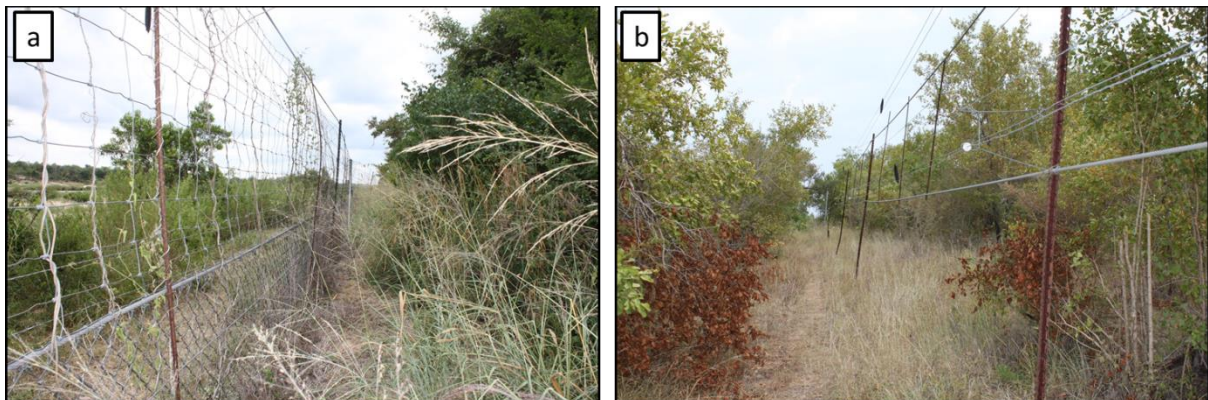


Figure 4.2: The fully fenced (a; right side of the fence is inside the exclosure) and partially fenced (b; right side of the fence is in the exclosure) exclosures which represent the herbivore treatments at the Nkuhlu exclosures

4.2 Data sampling

Data sampling was done according to standardized protocol designed by O'Keefe & Alard (2002). First data were sampled by SANParks in 2002 and in 2015 a group from the North West University, Potchefstroom sampled the data.

Two brightly coloured 30 m ropes were extended around the corners of the fixed 200 m² plots to clearly mark the sampling plot. All woody individuals of size >10 cm in height and rooted inside a plot were identified up to species level, counted and various measurements were recorded per individual (see below for details). Where it was not clear what constitutes an individual inside a clump of vegetation with multiple stems or whether stems are a result of vegetative reproduction, stems further than 0.5 m apart were treated as different individuals (O'Keefe & Alard, 2002).

For each woody individual canopy height was measured using a measuring pole marked at 0.5 m intervals. Basal diameter of each individual was measured using a calliper (for stems <10 cm in diameter) or a measuring tape (for stems >10 cm in diameter). Basal diameter was measured at 5 cm aboveground. The basal diameter of multi-stemmed species were measured for all stems.

Woody individuals were divided into two life stages: seedlings or established trees and shrubs. Seedlings and saplings were not differentiated, but lumped into a single seedling category. The term 'seedling' in this particular study refers to all woody individuals with a height between 10 cm up to 1 m, with a basal diameter of less than 1 cm. Established individuals represents shrubs or trees with a canopy height of over 1 m and basal diameter larger than 1 cm. If basal diameter was above 1 cm and height less than 1 m, the individual was regared as an established tree or shrub.

A woody population in this study represent all individuals from the same species inside a specific treatment. A community in this study represent all woody and shrub individuals from the different species inside the specific treatment.

All woody species recorded in the study site were classified as either encroachers or non-encroachers (Wiseman *et al.*, 2004; Gaugris *et al.*, 2014). Encroachers are considered the 'increasers' of woody plants because they are the first to increase in the presence of disturbances and the non-encroachers are classified as the 'decreasers', usually unable to tolerate disturbance (Moe *et al.*, 2009).

4.3 Data analyses

Data analyses were performed to test the effect of (i) catenal position, (ii) herbivore treatment, and (iii) fire treatment, on the structure and composition of the whole woody community as well as for encroacher and non-encroacher woody species. A summary of the analyses is presented below. Please note that a detailed account of statistical analyses is provided within each of the corresponding chapters.

Chapter 5: Floristic analyses based upon multi-dimensional ordinations were done to assess species composition changes. A description of the dominant families, species and basic plant functional types (eg. growth form, deciduousness, palatability, and encroaching ability) of the woody plants is presented. Comparisons between woody species composition among seedlings and established trees and shrubs were made through the application of Non-Metric Multidimensional Scaling (NMDS) in Primer 6 (Clarke, 1993). Significant differences in species assemblages were determined through the application of a One-way ANOSIM (in Primer).

Chapter 6: Linear modelling (Hancock & Meuller, 2010) was used to compare the responses of woody abundances (seedlings and established individuals respectively) across different treatments of herbivory and fire, as well as across vegetation zones between 2002 and 2015. Interaction effects were tested for herbivore treatments, fire treatments and the vegetation zones between 2002 and 2015. Effect sizes (Ellis & Steyn, 2003) were used to test for significant temporal changes in woody abundances within herbivore and fire treatments.

Chapter 7: The demography of woody species was analysed by using size-class distributions (SCD's). Woody individuals were grouped into 6 size-classes based upon their canopy height (i.e. ≤ 1 m; $>1-2$ m; $>2-3$ m; $>3-4$ m; $>4-5$ m; >5 m). SCD's were graphically displayed for visual comparisons. Ordinary Least Square Linear regressions (Hutcheson, 2011) were performed on the size-class distributions to determine the slope significance. The Permutation Index (Wiegand *et al.*, 2000) was used to evaluate the deviation of the community or population from a monotonic decline. Simpson's Index of Dominance (Wiegand *et al.*, 2000) measured the evenness of size-class occupation. Population stability was evaluated by using quotient analyses (Shackleton, 1993).

CHAPTER 5

Floristic changes in response to herbivory and fire

5.1 Introduction

The Nkuhlu exclosures site is characterised by a rich woody diversity in co-existence with a herbaceous layer dominated primarily by grass, but rich in forb species (Siebert & Scogings, 2015). Studying the floristic composition of an ecosystem is often neglected, although it often reveals important knowledge on changes that can not always be depicted from structural data analyses. Note that this chapter serves only as an introductory chapter on woody regeneration and therefore the results of the floristics and plant functional types are not discussed but only described.

Several studies have indicated that herbivore and fire effects on trees are species specific (Levick & Rogers, 2008; Wigley *et al.*, 2014). Whether herbivore and fire effects can be linked to changes in dominant woody families are relatively unknown. Plant functional traits have become a major research topic in savanna vegetation studies (De Deyn *et al.*, 2008; Hoffmann *et al.*, 2012; Clarke *et al.*, 2013). Therefore, basic plant functional traits were also considered to test for trait dominance changes over time across herbivore and fire treatments.

African savanna flora evolved in association with herbivores and fire for millions of years (Charles-Dominique *et al.*, 2016). Therefore, it is predicted that herbivory and fire exclusion from a savanna ecosystem will lead to changes in dominant woody families and traits. This chapter will test whether 13 years of herbivore and fire exclusion is long enough to reveal any changes.

Herbivore activity or exclusion may cause changes in woody species composition (Levick & Rogers, 2008; Barton & Hanley, 2013). Herbivores can negatively impact recruitment of woody species, resulting in unsuccessful regeneration. This can especially be true for more palatable woody species, which are more likely to get browsed upon, while unpalatable species can grow into established size-classes (Fornara & Du Toit, 2008). It is predicted in this descriptive chapter that seedling and established communities will differ in species composition when comparing the two communities where herbivores are present and the absence of herbivores will cause similarity in seedling and established community composition.

5.2 Methods

A detailed description of the experimental design and woody data sampling approach is provided in Chapter 4 (Materials and Methods). Each recorded woody individual (seedling or established tree) was identified up to species level and then assigned to its plant family according to Germishuysen & Meyer (2003). Each herbivore and fire treatment was assessed in terms of dominant families and species in the seedling and established communities separately. This was done to test whether 13 years of herbivore exclusion (either exclusion of only mega-herbivores or exclusion of all herbivores) or fire treatments affected dominant families and species for seedlings and established community respectively.

The dominant species were further assessed in terms of their basic plant functional types to test whether herbivore and/or fire treatments caused changes in trait dominance between 2002 and 2015. The traits that were evaluated included (i) encroacher or non-encroacher, (ii) growth form, i.e. tree, shrub or liana, (iii) single- or multi-stemmed, (iv) deciduous or evergreen, and (v) palatable (commonly browsed upon) or unpalatable (not preferred by browsers). These plant functional types were assigned to the species based on expert knowledge and literature (Germishuysen & Meyer, 2003).

Statistical analyses were not done for the dominant families and plant functional types, since a detailed account was considered beyond the scope of this study. Differences in the percentage contribution based on individual abundances by each dominant family and ratio's between dominant traits were used to test whether treatments of herbivory and fire affected floristic dominance over time. Results of herbivory effects on dominant families and traits were displayed for both 2002 and 2015, while results of fire effects were only provided for 2015. This is because significant patterns between fire and no-fire treatments were only revealed in the 2015 community. The 2002 results are provided in Appendix B.

Woody species composition was analysed to test effect of sampling year (between 2002 and 2015) as well as for effects within the same year between seedlings and established individuals in herbivore exclusion treatments. The 2002 dataset (abundance per plot per treatment) was used as a control treatment where species composition was a result of herbivore presence, while the 2015 dataset (abundance per plot per treatment) was used as the variable explaining the effect of herbivore exclusion on species composition. These analyses were performed for the full and partial exclosures only because it addressed the specific objective to determine the effect of herbivore exclusion (either all herbivores or only mega-herbivores) on woody species composition. Analyses on species composition were

performed through the application of Non-Metric Multidimensional Scaling (NMDS) in Primer 6 (Clarke, 1993). The data was fourth-root transformed to reduce weighting of the more abundant species, while not losing information on their relative abundances (Clarke, 1993; Scogings *et al.*, 2012). Bray-Curtis similarity resemblance measure was used, with 50 restarts. These procedures were followed for both the seedling and established woody data sets - firstly analyses were done between years to test temporal effects on seedling and established species composition in the herbivore exclusion treatments, followed by a combined analysis of seedlings and established trees of the 2002 and 2015 data sets (respectively). This was done to test for differences in species composition between the two life stages within each year. Each vegetation zone hosts its own unique vegetation composition (Siebert & Eckhardt, 2008) and therefore species assemblage changes were also tested across the different vegetation zones (i.e. riparian, sodics and crest) for both seedlings and established individuals between 2002 and 2015.

One-way ANOSIM (in Primer 6) (Clarke, 1993) was applied to the species assemblage datasets to test for significant differences in species composition between woody seedlings and established community in 2002 and 2015. Bray-Curtis coefficient of similarity was used together with 9999 permutations of the data. The R-statistic was used to calculate significant differences in species assemblages in the ordinal space. R=1 indicate species assemblages between two groups were totally different and R closer to 0 indicate groups to be indistinguishable. For this experiment, R-values >0.3 suggest observed differences in woody species assemblages.

5.3 Results and discussion

5.3.1 Floristic changes

5.3.1.1 Responses to herbivore treatments

5.3.1.1.1 Herbivore presence; Control treatment:

Seedling dominant families did not change over time across any of the catenal positions, but changes did occur in the established community (Figure 5.1). These changes may be ascribed to continued herbivore activity in the control site. Euphorbiaceae replaced the frequently occurring Tiliaceae (*Grewia*) in 2015 in the riparian vegetation zone (Figure 5.1). In the sodic zone, herbivore presence favoured occurrence of Rubiaceae over the more palatable Sapindaceae (*Pappea capensis*) (Figure 5.1). The abundant species in the riparian

zone (*Bridelia cathartica*, *Flueggea virosa* and *Spirostachys africana*), which are all in the family Euphorbiaceae are less palatable than species from other families, such as Fabaceae species, but are known to be utilized by elephant and black rhino (Scogings *et al.*, 2011). Although *F. virosa* (Euphorbiaceae) is one of the top ten most browsed species in the study area, especially by elephants (Scogings *et al.*, 2012), results revealed that *F. virosa* remains under the most abundant riparian species in the presence of all herbivores. This suggests that *F. virosa* can tolerate elephant herbivory. Utilization of Tiliaceae (*Grewia* spp.) by herbivores is usually the same as that of *F. virosa* (Scogings *et al.*, 2012), but the *Grewia* spp. in this study were more suppressed by elephants. Elephants are likely to topple *Grewia* spp. or break their branches (Boundja & Midgley, 2010). Results suggest little floristic changes in crest vegetation zone over time.

5.3.1.1.2 Elephant and giraffe exclusion; Partial enclosure:

Changes in the floristics of the riparian zone were minor, opposed to more pronounced changes in the sodics zone. Dominance in abundance by seedlings from the Tiliaceae family (*Grewia* spp.) replaced *Rhigozum* spp. seedlings (Bignoniaceae), and the palatable *Pyrostria hystrix* (Rubiaceae) seedlings in 2002 were replaced by less palatable *Maerua parvifolia* (Capparaceae) in 2015 (Figure 5.2). These shifts in floristics of seedlings are suggested to be associated with an increased mesobrowser effect when elephants are excluded from the landscape (Fritz *et al.*, 2002; Valeix *et al.*, 2008; Hilbers *et al.*, 2015; Lagendijk *et al.*, 2015). In the established woody community of the sodic zone, there was a strong shift towards Fabaceae species dominance in the abundance of individuals in the absence of elephants (Figure 5.2), which suggests elephant control of Fabaceae species. The unpalatable *Euclea divinorum* (Ebenaceae) was no longer one of the most abundant species after 13 years of elephant exclusion (Figure 5.2). On the upland crest the *Grewia* spp. (Tiliaceae) became dominant in abundance in the established woody community (Figure 5.2), which suggest that elephants have suppressive effects on *Grewia* spp.

5.3.1.1.3 Total herbivore exclusion; Full enclosure:

The exclusion of all herbivores for 13 years had the largest effect on floristic abundance dominance of all herbivore treatments in both the seedling and established woody community. In the riparian zone, the plant families that dominated, in abundance, the seedling community in 2002 were totally different than the dominant abundances in 2015 (Figure 5.3). Fabaceae seedlings were replaced by Ebenaceae (*Euclea* spp.) (Figure 5.3). The appearance of *Jasminum fluminense* as a dominant abundant species in the seedling community in 2015 (Figure 5.3) illustrates the positive effect of herbivore exclusion on lianas.

Lianas are therefore suppressed by herbivores because when herbivores were excluded Lianas became more abundant. Herbivores, especially browsing herbivores, utilize plant material directly from or near trees and/or shrubs, therefore lianas are suppressed by herbivore activity either through direct utilization or trampling. Euphorbiaceae seedlings were replaced by Celastraceae (*Gymnosporia* spp.), which suggest stronger competitive ability of the latter to increased herbaceous biomass. However, in the established woody community, Euphorbiaceae appeared as a dominant abundant family to the expense of *Grewia flavescens* (Figure 5.3). In the sodic zone the more palatable Sapindaceae (*Pappea capensis*) seedlings appeared and the Capparaceae (*Maerua parvifolia*) disappeared as being dominant (Figure 5.3). In the established community, *Rhigozum* abundances increased in the absence of all herbivores, while Ebenaceae spp., which are usually associated with the sodic vegetation zone, became less abundant (Figure 5.3). In the crest zone, the dominant families changed only in the seedling community. Combretaceae seedlings were not listed as one of the top three abundant families and were replaced by Tiliaceae (*Grewia flavescens*) (Figure 5.3), which are probably more sensitive to herbivores and more tolerant to high herbaceous biomass competition.

In summary, less dynamic floristic changes occurred in the crest vegetation zone than in the riparian or sodic zones. The crest vegetation zone is considered as a dystrophic savanna and therefore less intense herbivore activity is expected. The eutrophic bottomlands (riparian and sodic vegetation zones) indicated the most floristic changes.

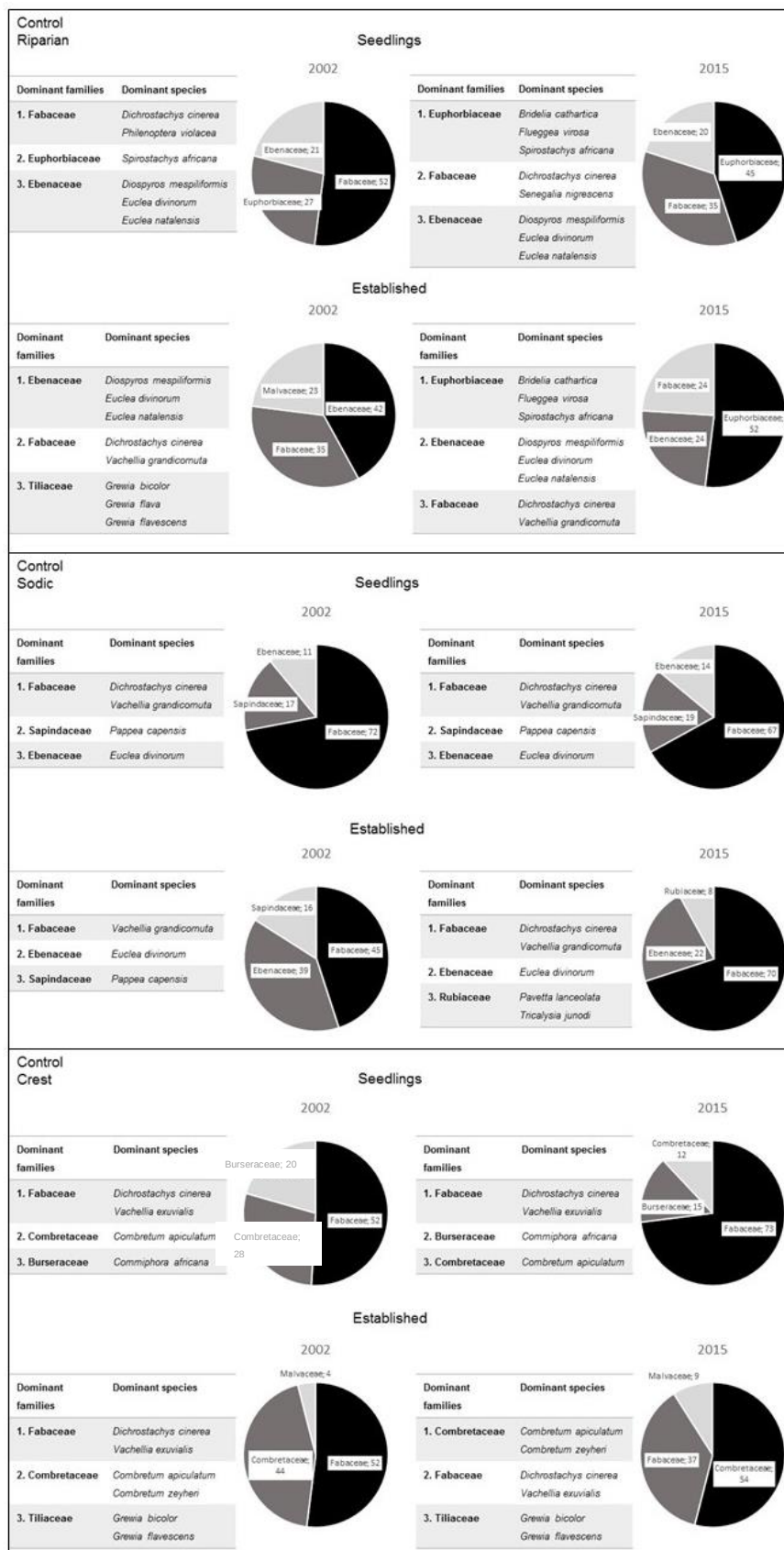


Figure 5.1: Top three dominant woody families (expressed as abundance in %) and species per year (i.e. 2002 and 2015) for both seedling and established communities for each vegetation zone (riparian, sodic, crest) of the control treatment.

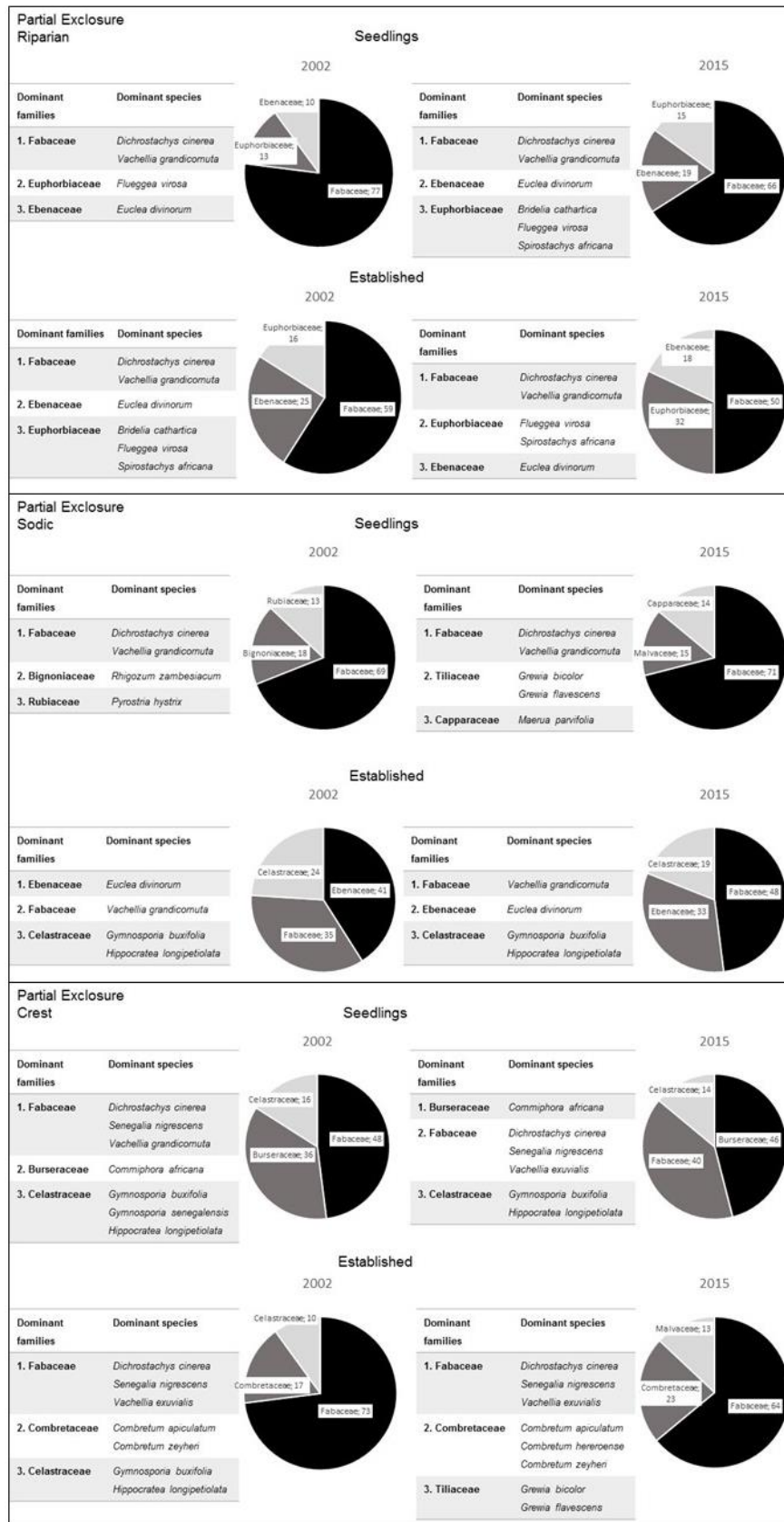


Figure 5.2: Top three dominant woody families (expressed as abundance in %) and species per year (i.e. 2002 and 2015) for both seedling and established communities for each vegetation zone (riparian, sodic, crest) in the partially fenced treatment.

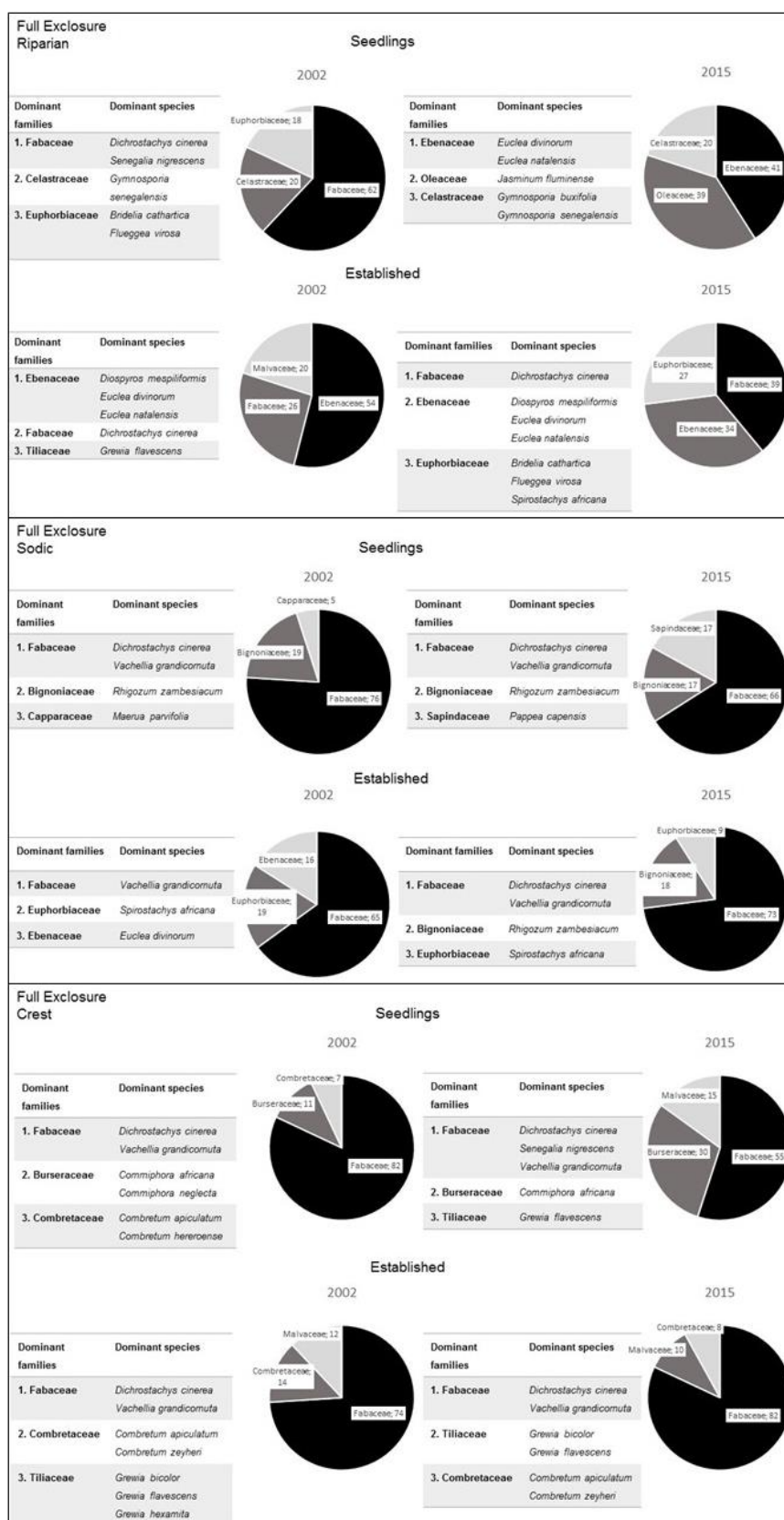


Figure 5.3: Top three dominant woody families (expressed as abundance in %) and species per year (i.e. 2002 and 2015) for both seedling and established communities for each vegetation zone (riparian, sodic, crest) in the fully fenced treatment.

5.3.1.2 Responses to fire treatments

5.3.1.2.1 Herbivore presence; Control treatment:

In the control site, only the riparian and the crest zone could be tested for fire effects since the sodic vegetation zone did not extend into the fire exposed area. Euphorbiaceae seedlings was most abundant in the riparian vegetation zone despite fire or no-fire treatments (Figure 5.4). Fire did not cause any remarkable changes in the woody seedling floristics on the crest zone (Figure 5.5). The established community responded to fire treatments when 2002 and 2015 communities were compared (Appendix B). Burseraceae (*Commiphora* spp.) were amongst the top three dominant families in 2002 but not in 2015, which indicated that *Commiphora* spp. are sensitive to fire exposure. *Grewia* spp. were dominant in fire exposed areas, but this could be due to low intensity (cold) fire, because adult *Grewia* spp. are usually more sensitive to fire.

5.3.1.2.2 Elephant and giraffe exclusion; Partial exclosure:

In the riparian vegetation zone, Fabaceae and Ebenaceae seedlings were most abundant despite fire exposure or absence of fire (Figure 5.6). In the sodic zone Tiliaceae and Capparaceae seedlings were more fire resistant than the palatable Boraginaceae (*Ehretia amoena*) and Celastraceae (*Gymnosporia buxifolia*) (Figure 5.7). No changes were observed in the riparian and sodic vegetation zones in the established community (Figure 5.6 and 5.7). In the crest zone, Tiliaceae (*Grewia* spp.) were more tolerant to fire than Celastraceae (especially the palatable *G. buxifolia* and *Hippocratea longipetiolata*) in both the seedling and established communities (Figure 5.8). No changes were observed within fire treatments between 2002 and 2015 (Appendix B).

5.3.1.2.3 Total herbivore exclusion; Full exclosure:

In the fully fenced treatment, the high herbaceous biomass (Van Coller *et al.*, 2013) was expected to have an impact on floristic composition and dominance of woody species due to the competitive exclusion effect. In the riparian zone, Ebenaceae was abundant in both the presence and absence of fire (Figure 5.9). Euphorbiaceae and Fabaceae seedlings indicated tolerance to fire while the absence of fire favoured Oleaceae and Celastraceae (Figure 5.9). In the sodic vegetation zone, Tiliaceae and Capparaceae seedlings were more fire resistant than the palatable *Rhigozum zambesiicum* and especially *Pappea capensis* seedlings, which are seemingly not fire resistant in their seedling stage (Figure 5.10). In the established community, *Grewia* spp. were more sensitive to fire than *Spirostachys africana* (Euphorbiaceae) and *Euclea divinorum* (Ebenaceae) (Figure 5.9). In areas where fire was

excluded, *Grewia* spp. dominated (Figure 5.9). *Rhigozum zambesiicum* was also dominant in the absence of fire (Figure 5.10). On the crest zone, Burseraceae family (*Commiphora africana*) responded negatively to fire exposure (Figure 5.11). *C. africana* is a low-growing species which usually remains within the fire-trap. Ebenaceae (*Euclea divinorum*) dominated in the presence of fire, but *Grewia* spp. dominated where fire was excluded (Figure 5.11). This suggests that *Grewia* spp. are sensitive to fire in their seedling stage. *Grewia* spp. in the established community were also sensitive to fire. The palatable Celastraceae family indicated tolerance to fire, but not during the seedling stage.

Fabaceae was the most successful family in this system because it was abundant in most of the treatments. This family also indicated most tolerance to fire. Fabaceae species are mostly palatable and therefore herbivores are expected to affect their abundance. It was however only in the riparian vegetation zone in the fully fenced enclosure (Figure 5.9) where Fabaceae was not listed as one of the top three abundant families in 2015.

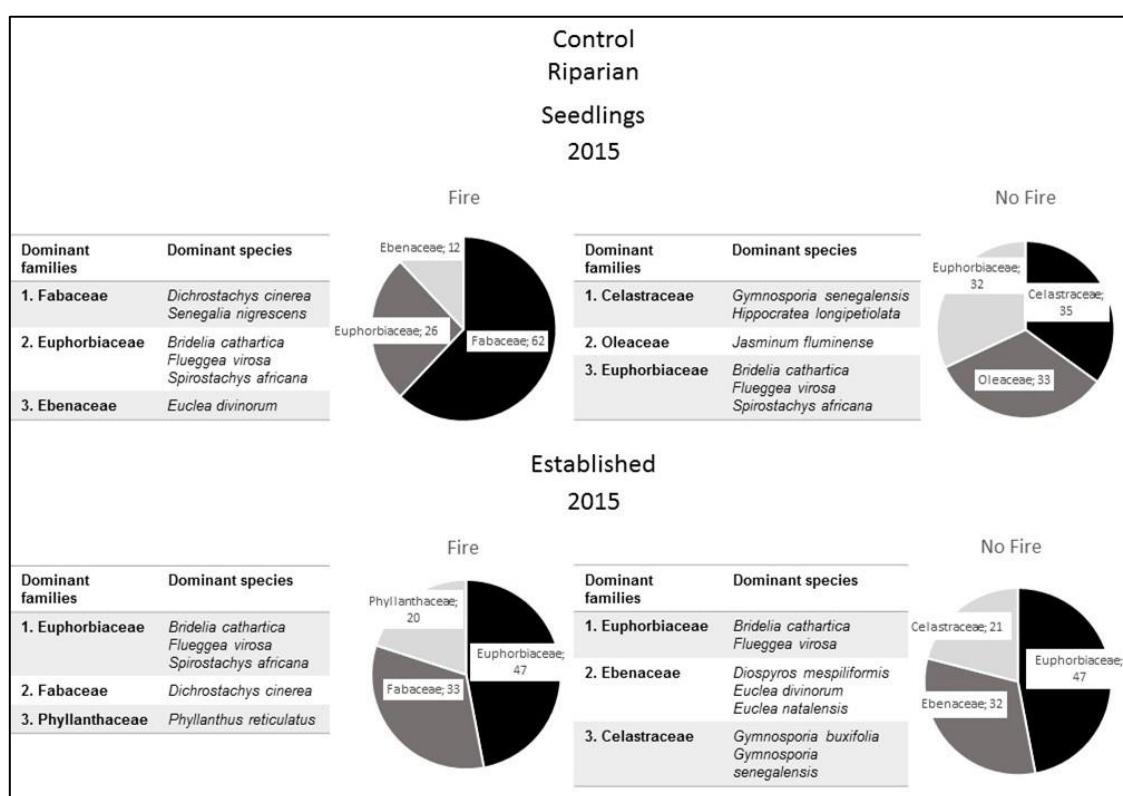


Figure 5.4: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the riparian zone of the control treatment.

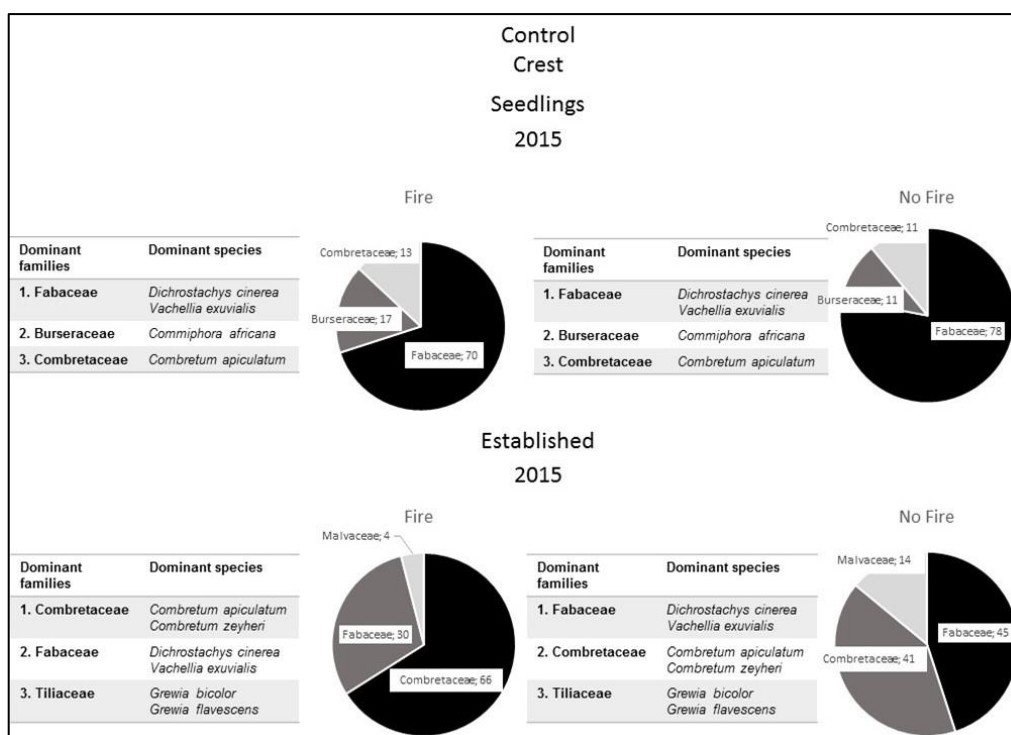


Figure 5.5: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the crest zone of the control treatment.

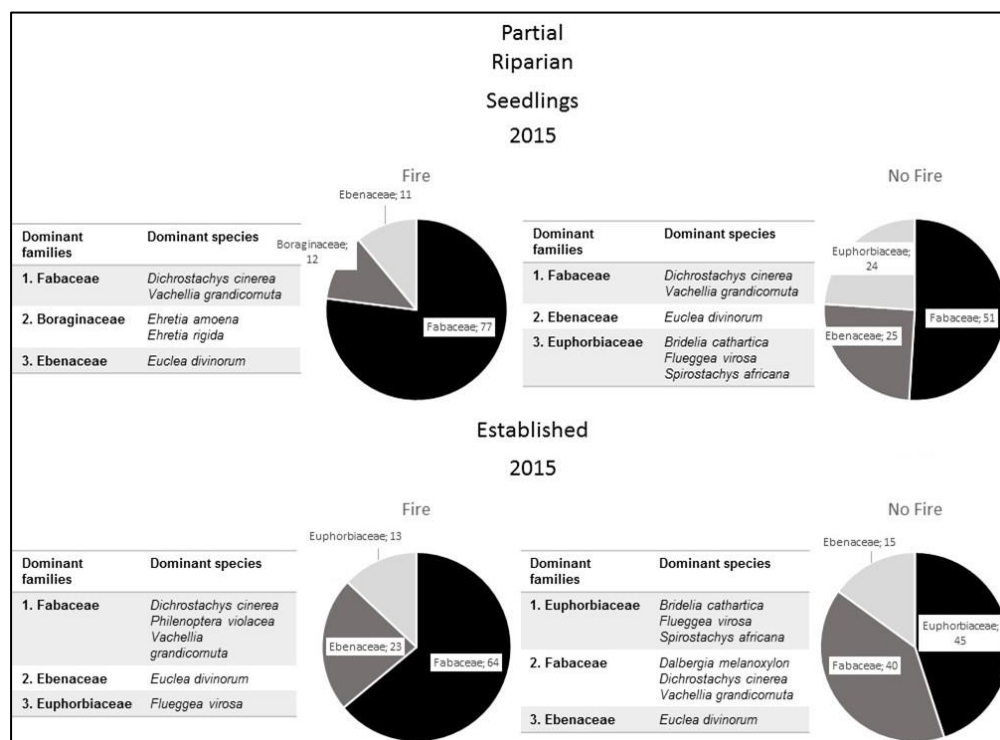


Figure 5.6: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the riparian zone of the partially fenced treatment.

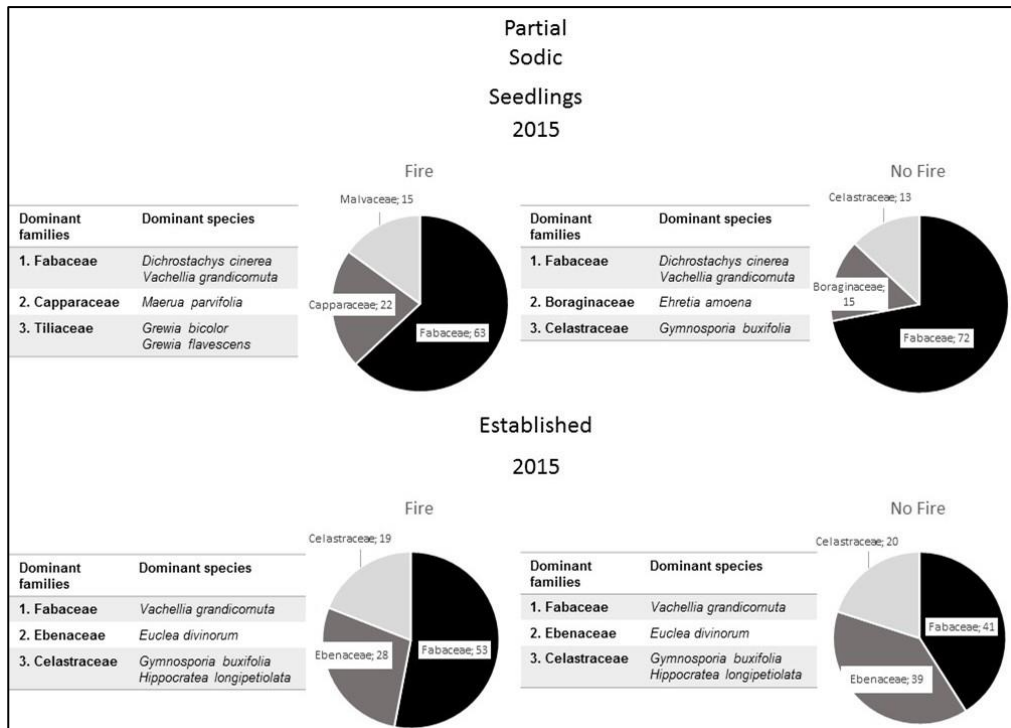


Figure 5.7: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the sodic zone of the partially fenced treatment.

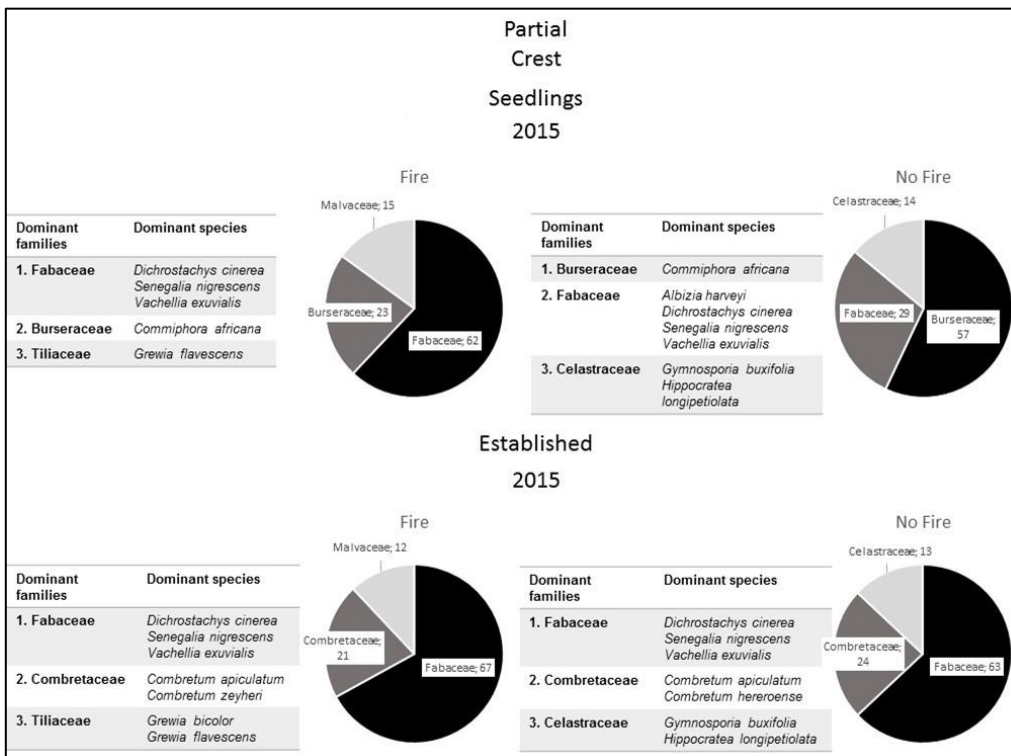


Figure 5.8: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the crest zone of the partially fenced treatment.

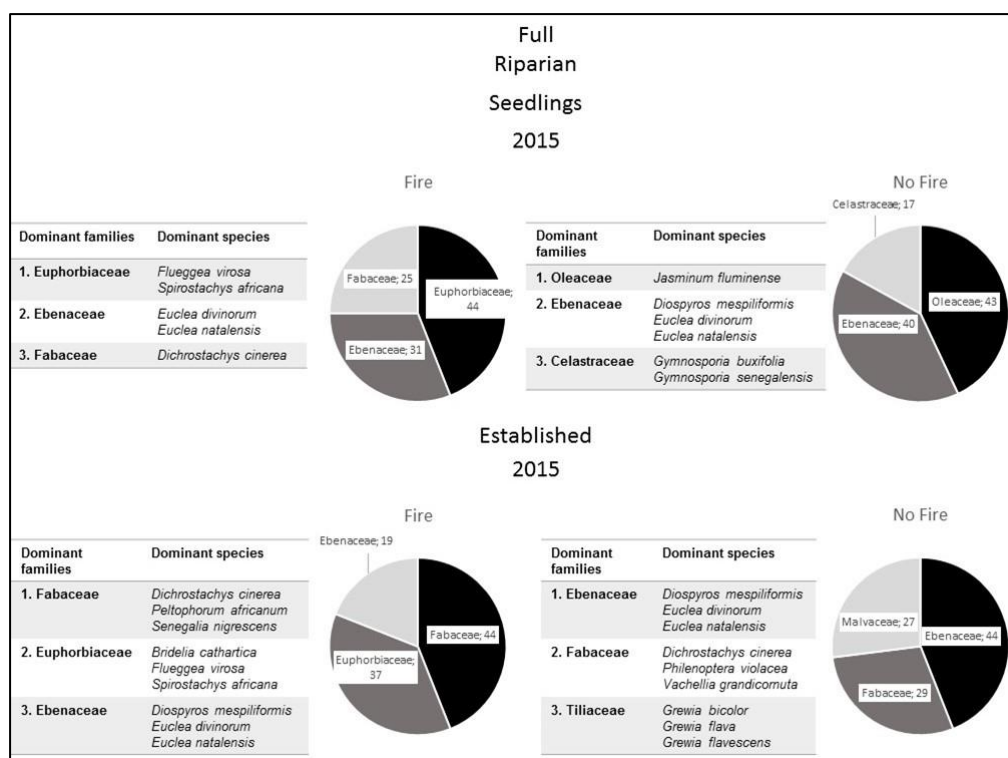


Figure 5.9: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the riparian zone of the fully fenced treatment.

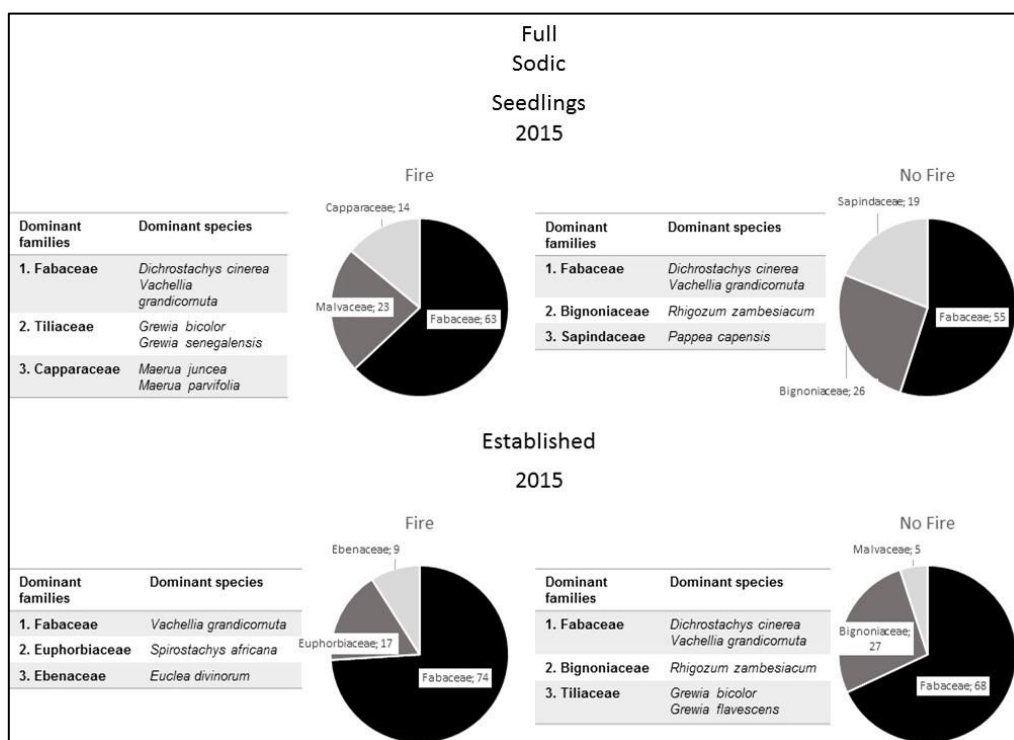


Figure 5.10: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the sodic zone of the fully fenced treatment.

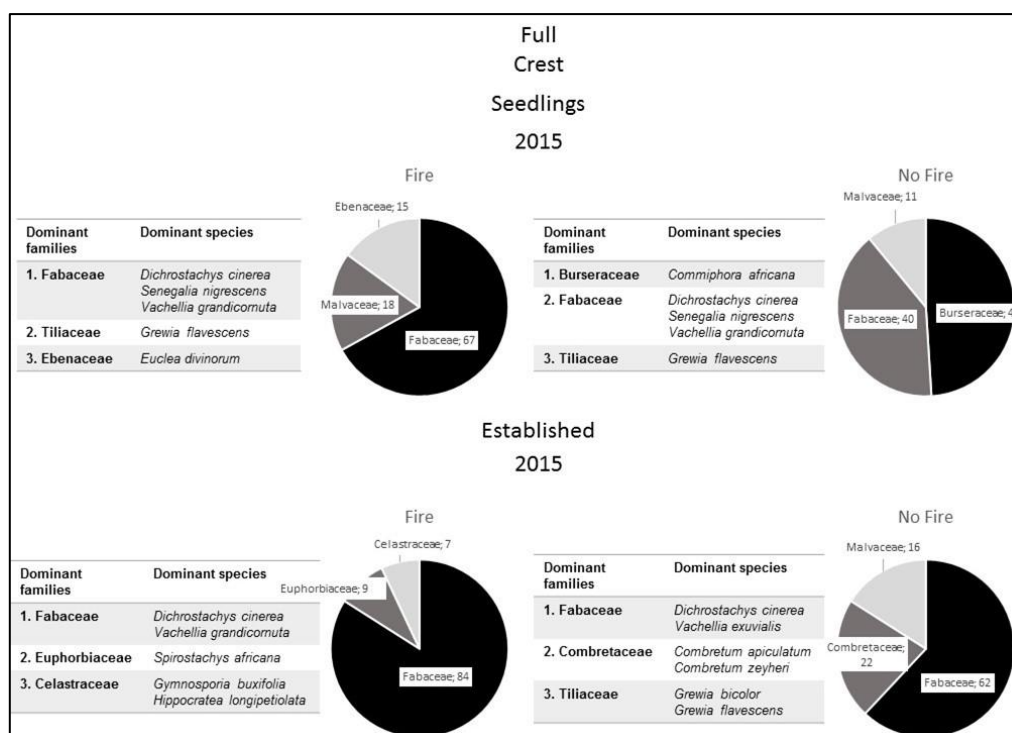


Figure 5.11: Top three dominant woody families (expressed as abundance in %) and species per fire treatment in 2015 for both seedling and established communities in the crest zone of the fully fenced treatment.

5.3.2 Basic plant functional type changes

5.3.2.1 Responses to herbivore treatments

The dominating functional types for the seedling community at the study site were palatable, deciduous, single-stemmed encroacher tree and shrub species. The established community was dominated by palatable encroacher multi-or single-stemmed shrubs.

5.3.2.1.1 Riparian zone; Seedling functional type changes

Little changes in dominant plant functional types were observed in the control site (Table 5.1). In the partially fenced enclosure, the ratio between encroachers and non-encroachers increased and the dominant growth form changed from single stemmed trees in 2002 to multi-stemmed shrubs in 2015 (Table 5.1). Dominance by deciduous and palatable species slightly decreased from 2002 to 2015. In the fully fenced enclosure, the ratio between encroachers and non-encroachers decreased, which suggests dominance of non-encroacher over encroacher species after 13 years of herbivore exclusion (Table 5.1). In 2015, shrubs and lianas became more dominant (Table 5.1). This was also observed in the appearance of Oleaceae family in 2015 (see section 5.3.1.1; Figure 5.3) Multi-stemmed

species dominated in 2002, but the dominance changed to single-stemmed species in 2015 (Table 5.1). A decrease in dominance by palatable species occurred between 2002 and 2015 (Table 5.1) where Ebenaceae family (*Euclea* spp.) became more dominant in the riparian zone of the fully fenced enclosure (see section 5.3.1.1; Figure 5.3).

5.3.2.1.2 Riparian zone; Established community functional type changes

The only remarkable change in plant functional types in the control site was the increased abundance of unpalatable over palatable species (Table 5.2). This could be explained by the changes in dominance from Ebenaceae and Fabaceae in 2002 to Euphorbiaceae and Ebenaceae in 2015 for the established woody community (see section 5.3.1.1; Figure 5.1). In the partially fenced enclosure, the ratio between encroachers and non-encroachers decreased between 2002 and 2015 (Table 5.2). Elephants commonly suppress tree dominance, which could not be confirmed in the trait results. Dominance by single-stemmed trees was replaced by multi-stemmed shrubs after 13 years of elephant exclusion (Table 5.2), although the ratio of palatable species to unpalatable species slightly increased in the absence of mega-herbivores.

In the absence of all herbivores, the ratio between encroachers and non-encroachers as well as between palatable and unpalatable woodies increased. A small decrease in shrub dominance was observed between 2002 and 2015, while dominance by deciduous species increased.

5.3.2.1.3 Sodic zone; Seedling functional type changes

The sodic zone in the control site did not have major changes in traits over time (Table 5.1). The partial enclosure was dominated by encroachers over non-encroachers over time – the ratio increased from 1:0.1 to 1:0.02 (Table 5.1). Single-stemmed trees remained dominant over multi-stemmed shrubs between 2002 and 2015 (Table 5.1). Dominance by palatable species increased over time. In the absence of all herbivores, encroaching species remained dominant over time (Table 5.1). A higher tree to shrub ratio was observed in 2015 and multi-stemmed species dominated over single-stemmed species (Table 5.1). Deciduous and palatable species were suppressed by the absence of herbivores (Table 5.1).

5.3.2.1.4 Sodic zone; Established community functional type changes

In the established community of the partially fenced enclosure, encroachers dominated over non-encroacher species in the sodic zone (Table 5.2). An increase was observed in the ratio between trees and shrubs (Table 5.2). A decrease in dominance by multi-stemmed species

occurred over time, which led to co-dominance by single- and multi-stemmed species in 2015 (Table 5.2). Evergreen woodies dominated in 2002, but were replaced by the dominance of deciduous woodies. Decreased palatability ratio was observed in the 2015 community as to the 2002 community. In the absence of all herbivores, the ratio between encroachers and non-encroachers increased more than three-fold (Table 5.2). The dominant growth form changed from single-stemmed trees to multi-stemmed shrubs (Table 5.2). The absence of herbivores promoted deciduous species to dominate over evergreen species (Table 5.2). The ratio between palatable and unpalatable woodies increased which again indicated protection for palatable woodies where all herbivores were excluded (Table 5.2).

5.3.2.1.5 Crest zone; Seedling functional type changes

The ratio of non-encroacher to encroacher species increased between 2002 and 2015 in the fully fenced area (Table 5.1). Shrubs remained dominant over trees and lianas in all herbivore treatments (Table 5.1). Multi-stemmed individuals increased in abundance over time in the presence of elephant and decreased in their absence where the ratio of single-stemmed to multi-stemmed individuals remained higher (Table 5.1). There was a decrease in deciduousness of species in the control site (Table 5.1). In all treatments palatable woody species dominated over unpalatable species (Table 5.1).

5.3.2.1.6 Crest zone; Established community functional type changes

In the established community of the partially fenced exclosure, non-encroachers dominated in abundance in 2002 and in 2015 abundance of encroachers (Table 5.2). In the fully fenced exclosure, the ratio of encroachers to non-encroachers was much higher than in 2002 (Table 5.2). An increase in shrub dominance occurred over time (Table 5.2). There was an increased dominance of deciduous woody abundances over abundances of evergreen species in the absence of mega-herbivores (Table 5.2). Abundance of palatable species to unpalatable species increased from 2002 to 2015 in the treatments where herbivores were excluded, irrespective whether all herbivores, or only elephants and giraffes have been excluded (Table 5.2).

Table 5.1: Plant functional type ratios for dominant seedling species over time across herbivore treatments and vegetation zones.

Vegetation zone	Herbivore treatment	Year	Plant Functional Types					Dominant traits*
			Encroachers: Non-encroachers	Tree:Shrub:Liana	Single-stemmed: Multi-stemmed	Evergreen:Deciduous	Unpalatable:Palatable	
Riparian	Control	2002	1 : 0.5	1 : 2 : 0	1 : 1.8	1 : 2	1 : 5	En/S/Mu/D/P
		2015	1 : 0.6	1 : 2 : 0	1 : 1.4	1 : 3	1 : 3	En/S/Mu/D/P
	Partial	2002	1 : 0.08	1 : 0.7 : 0	1 : 0.7	1 : 5	1 : 9	En/T/Si/D/P
		2015	1 : 0.06	1 : 3 : 0	1 : 3	1 : 4	1 : 4	En/S/Mu/D/P
	Full	2002	1 : 0.3	1 : 4 : 0	1 : 3	1 : 3	1 : 76	En/S/Mu/D/P
		2015	1 : 1.8	1 : 14 : 10	1 : 0.6	1 : 0.04	1 : 1.3	N/S/Si/E/P
Sodic	Control	2002	1 : 0.2	1 : 0.2 : 0	1 : 0.5	1 : 3	1 : 8	En/T/Si/D/P
		2015	1 : 0.2	1 : 0.3 : 0	1 : 0.8	1 : 2	1 : 6	En/T/Si/D/P
	Partial	2002	1 : 0.1	1 : 0.6 : 0	1 : 0.6	1 : 11	0 : 148	En/T/Si/D/P
		2015	1 : 0.02	1 : 0.8 : 0	1 : 0.7	1 : 7	0 : 322	En/T/Si/D/P
	Full	2002	1 : 0.01	1 : 1 : 0	1 : 1.4	1 : 27	0 : 340	En/TS/Mu/D/P
		2015	1 : 0.2	1 : 0.02 : 0	1 : 3	1 : 5	0 : 183	En/T/Mu/D/P
Crest	Control	2002	1 : 0.6	1 : 0.5 : 0	1 : 0.2	1 : 239	0 : 240	En/T/Si/D/P
		2015	1 : 0.9	1 : 0.7 : 0	1 : 0.3	1 : 41	0 : 251	En/T/Si/D/P
	Partial	2002	1 : 0.7	1 : 1.8 : 0	1 : 0.3	1 : 15	1 : 7	En/S/Si/D/P
		2015	1 : 0.6	1 : 2 : 1	1 : 0.2	1 : 10	1 : 9	En/S/Si/D/P
	Full	2002	1 : 0.07	1 : 1.2 : 0	1 : 0.8	1 : 107	0 : 325	En/S/Si/D/P
		2015	1 : 0.2	1 : 2 : 0	1 : 0.6	1 : 167	0 : 336	En/S/Si/D/P

*En=encroachers; N=non-encroachers; T=trees; S=shrubs; Si=single-stemmed; Mu=multi-stemmed; D=deciduous; E=evergreen; P=palatable; U=unpalatable;
Bold=dominant trait

Table 5.2: Plant functional type ratios for dominant established tree species over time across herbivore treatments and vegetation zones.

Vegetation zone	Herbivory treatment	Year	Plant Functional Types					Dominant traits*
			Encroachers: Non-encroachers	Tree:Shrub:Liana	Single-stemmed: Multi-stemmed	Evergreen:Deciduous	Unpalatable:Palatable	
Riparian	Control	2002	1 : 0.2	1 : 5 : 0	1 : 4	1 : 1.6	1 : 1.7	En/S/Mu/D/P
		2015	1 : 0.3	1 : 4 : 0	1 : 2	1 : 4	1 : 4	En/S/Mu/D/P
	Partial	2002	1 : 0.1	1 : 1 : 0	1 : 0.8	1 : 3	1 : 3	En/TS/Si/D/P
		2015	1 : 0.2	1 : 1 : 0	1 : 1	1 : 4	1 : 5	En/TS/SiMu/D/P
	Full	2002	1 : 0.8	1 : 4 : 0	1 : 1.2	1 : 1	1 : 1.2	En/S/Mu/ED/P
		2015	1 : 0.5	1 : 3 : 0	1 : 1.2	1 : 2	1 : 3	En/S/Mu/D/P
Sodic	Control	2002	1 : 0.2	1 : 0.6 : 0	1 : 1.3	1 : 0.8	1 : 1.5	En/T/Mu/E/P
		2015	1 : 0.1	1 : 0.9 : 0	1 : 0.8	1 : 2	1 : 4	En/T/Si/D/P
	Partial	2002	1 : 0.1	1 : 1.7 : 1	1 : 1.4	1 : 0.8	1 : 0.6	En/S/Mu/E/U
		2015	1 : 0.1	1 : 1.1 : 1	1 : 1	1 : 1.2	1 : 0.9	En/S/SiMu/D/U
	Full	2002	1 : 0.01	1 : 0.3 : 0	1 : 0.3	1 : 5	1 : 5	En/T/Si/D/P
		2015	1 : 0.003	1 : 1.2 : 0	1 : 1.2	0 : 566	0 : 566	En/S/Mu/D/P
Crest	Control	2002	1 : 0.8	1 : 0.4 : 0	1 : 0.3	1 : 71	0 : 432	En/T/Si/D/P
		2015	1 : 0.4	1 : 0.5 : 0	1 : 0.5	1 : 138	0 : 418	En/T/Si/D/P
	Partial	2002	1 : 1.1	1 : 0.8 : 0.1	1 : 0.6	1 : 8	1 : 9	N/T/Si/D/P
		2015	1 : 0.6	1 : 1 : 0	1 : 0.9	1 : 52	0 : 424	En/TS/Si/D/P
	Full	2002	1 : 0.3	1 : 1.2 : 0	1 : 1.2	0 : 245	0 : 245	En/S/Mu/D/P
		2015	1 : 0.1	1 : 1.8 : 1	1 : 1.2	1 : 341	0 : 683	En/S/Mu/D/P

*En=encroachers; N=non-encroachers; T=trees; S=shrubs; Si=single-stemmed; Mu=multi-stemmed; D=deciduous; E=evergreen; P=palatable; U=unpalatable; Bold=dominant trait.

5.3.2.2 Responses to fire treatments

Consistent abundant functional types for both seedlings and established communities in fire exposed areas were deciduous, palatable encroachers (Table 5.3; Table 5.4). Fire suppressed the abundance of shrubs (Table 5.3; Table 5.4). In the seedling community, multi-stemmed species were favoured by the presence of fire, while in the established community fire suppressed this trait (Table 5.3; Table 5.4).

5.3.2.2.1 Riparian zone; Seedling functional type changes

In the control site, main ratio changes occurred between fire treatments in the tree:shrub:liana ratio, with an increase in especially shrubs and lianas in the absence of fire (Table 5.3). Deciduous species dominated in the presence of fire, while the absence of fire led to dominance by evergreen species (Table 5.3). In the absence of elephant, a stronger encroacher to non-encroacher ratio as well as an increase in multi-stemmed shrubs was observed in the fire-excluded areas (Table 5.3). Palatability seem to be favoured by fire, but not in the absence of elephant where browsing by mesoherbivores negatively affect palatable seedlings (Table 5.3). In the fully fenced enclosure, fire favoured encroacher dominance over non-encroachers, whereas the opposite was observed in the absence of fire (Table 5.3). The no-fire area had a higher shrub:tree ratio compared to the area exposed to fire as well as more abundant evergreen individuals than deciduous individuals (Table 5.3).

5.3.2.2.2 Riparian zone; Established community functional type changes

In the control site, the ratio of encroachers to non-encroachers was higher in the fire-excluded area than where fire was present (Table 5.4). Single-stemmed shrubs dominated in abundance in the area where fire was present, while multi-stemmed trees dominated the area where fire was excluded (Table 5.4). The abundance ratio of deciduous to evergreen individuals increased in the presence of fire (Table 5.4). More palatable species were located in the fire exposed area (Table 5.4). In the partially fenced enclosure, a higher encroacher to non-encroacher ratio was observed in the presence of fire compared to absence of fire (Table 5.4). Single-stemmed trees dominated in abundance in the fire-exposed areas, while abundance of multi-stemmed shrubs dominated in the absence of fire (Table 5.4). Abundance of deciduous and palatable individuals dominated over evergreen and unpalatable individuals in the absence of fire (Table 5.4). In the fully fenced enclosure, the ratio between encroacher and non-encroacher abundances was less in the presence of fire than in the absence of fire (Table 5.4). In the absence of fire multi-stemmed shrubs

dominated in abundance (Table 5.4). Abundances of deciduous and palatable individuals was higher in the presence of fire compared to the no-fire treatment (Table 5.4).

5.3.2.2.3 Sodic zone; Seedling functional type changes

In the partially fenced enclosure, a higher ratio of encroacher to non-encroacher abundances was observed in the fire exposed areas compared to the areas excluded from fire (Table 5.3). The most abundant individuals in the area where fire was applied, were palatable (Table 5.3). The abundance ratio of deciduous to evergreen individuals was higher in areas protected from fire than the areas exposed to fire (Table 5.3). In the fully fenced enclosure, the encroacher to non-encroacher as well as the deciduous to evergreen ratio increased in the presence of fire (Table 5.3). Abundance of multi-stemmed shrubs dominated in both the fire and no-fire treatments, but dominance was stronger in the fire exclusion areas of the fully fenced enclosure (Table 5.3).

5.3.2.2.4 Sodic zone; Established community functional type changes

In the partially fenced enclosure, higher abundance of encroachers was observed in the presence of fire, with the main growth form being trees (Table 5.4). The abundance of the single-stemmed functional type dominated in the presence of fire, while abundance of multi-stemmed individuals dominated in the absence of fire (Table 5.4). Deciduous and palatable species were most abundant in fire exposed areas, while evergreen and unpalatable species were most abundant in the no-fire areas (Table 5.4). In the fully fenced enclosure, high encroacher to non-encroacher abundance ratio was observed in the presence and absence of fire (Table 5.4). Palatable, deciduous multi-stemmed, encroacher, shrub species dominated in abundance where herbivores and fire were excluded from this nutrient hot-spot (Table 5.4).

5.3.2.2.5 Crest zone; Seedling functional type changes

In the control site, non-encroacher abundance dominated over abundance of encroachers in fire-exposed areas. In the absence of fire, encroacher abundances dominated. Single-stemmed trees were most abundant in the presence of fire (Table 5.3). The areas protected from fire were dominated by higher abundances of deciduous and palatable individuals (Table 5.3). In the partially fenced enclosure, a slightly higher abundance ratio in encroacher to non-encroacher was observed in the absence of fire (Table 5.3). In the absence of fire, single-stemmed shrub abundances was higher than in areas where fire was excluded (Table 5.3). The presence of fire favoured deciduous and palatable species in the presence of mesoherbivores (control site and partial enclosure) (Table 5.3). In the fully fenced enclosure,

the absence of fire promoted encroacher to non-encroacher abundance ratio (Table 5.3). Dominance by shrubs were much stronger in the no-fire areas, while fire-exposed areas were dominated by trees (Table 5.3). More abundant deciduous individuals than evergreen individuals as well as more abundant palatable individuals than unpalatable individuals was observed in the absence of fire (Table 5.3).

5.3.2.2.6 Crest zone; Established community functional type changes

In the control site, the absence of fire favoured dominance of encroachers above non-encroachers (Table 5.4). Dominance in abundance of single-stemmed trees was higher in the presence of fire than in the areas where fire was excluded (Table 5.4). The ratio of deciduous to evergreen species increased in the absence of fire. Palatable species dominated both fire and no-fire areas (Table 5.4). In the partially fenced exclosure, encroachers dominated both fire and no-fire treatments (Table 5.4). The tree to shrub as well as single-stemmed to multi-stemmed ratio was more or less similar in both fire treatments (Table 5.4). Higher abundances of deciduous (than evergreen) and palatable (than unpalatable) individuals was observed in the presence of fire (Table 5.4). In the fully fenced exclosure, dominance of encroachers above non-encroachers increased in the presence of fire (Table 5.4). Shrub dominance was also favoured by the presence of fire (Table 5.4). The multi-stemmed functional type dominated in abundance in both the fire and no-fire treatments, while deciduous and palatable individuals had higher abundance dominance in the absence of fire (Table 5.4).

Table 5.3: Plant functional type ratios for dominant seedling species in 2015 across fire treatments and vegetation zones.

Vegetation zone	Fire treatment	Plant Functional Types					Dominant traits*
		Encroachers: Non-encroachers	Tree:Shrub:Liana	Single-stemmed: Multi-stemmed	Evergreen: Deciduous	Unpalatable:Palatable	
Riparian	Control; Fire	1 : 1	1 : 1.1 : 0	1 : 0.8	1 : 6	1 : 7	EnN/S/Si/D/P
	Control; No Fire	1 : 1.1	1 : 14 : 11	1 : 0.8	1 : 0.7	1 : 8	N/S/Si/E/P
	Partial; Fire	1 : 0.2	1 : 2 : 0	1 : 1.6	1 : 7	1 : 8	En/S/Mu/D/P
	Partial; No Fire	1 : 0.09	1 : 5 : 0.5	1 : 3	1 : 3	1 : 3	En/S/Mu/D/P
	Full; Fire	1 : 0.2	1 : 1.3 : 0	1 : 0.8	1 : 2	1 : 2	En/S/Si/D/P
	Full; No Fire	1 : 2	1 : 12 : 10	1 : 0.4	1 : 0.1	1 : 1.4	N/S/Si/E/P
Sodic	Partial; Fire	1 : 0.03	1 : 0.8 : 0.02	1 : 0.8	1 : 4	0 : 191	En/T/Si/D/P
	Partial; No Fire	1 : 0.2	1 : 0.9 : 0.03	1 : 0.5	1 : 8	1 : 7	En/T/Si/D/P
	Full; Fire	1 : 0.1	1 : 5 : 0.7	1 : 3	1 : 29	0 : 91	En/S/Mu/D/P
	Full; No Fire	1 : 0.3	1 : 1.1 : 0	1 : 3	1 : 4	0 : 117	En/S/Mu/D/P
Crest	Control; Fire	1 : 1.1	1 : 0.5 : 0	1 : 0.2	1 : 23	0 : 141	N/T/Si/D/P
	Control; No Fire	1 : 0.6	1 : 1 : 0	1 : 0.7	0 : 110	0 : 110	En/TS/Si/D/P
	Partial; Fire	1 : 0.8	1 : 1.2 : 0	1 : 0.5	0 : 213	0 : 213	En/S/Si/D/P
	Partial; No Fire	1 : 0.4	1 : 3 : 0.3	1 : 0.1	1 : 13	1 : 6	En/S/Si/D/P
	Full; Fire	1 : 0.4	1 : 0.7 : 0	1 : 0.7	1 : 5	1 : 5	En/T/Si/D/P
	Full; No Fire	1 : 0.1	1 : 11 : 0	1 : 0.7	1 : 220	0 : 221	En/S/Si/D/P

*En=encroachers; N=non-encroachers; T=trees; S=shrubs; Si=single-stemmed; Mu=multi-stemmed; D=deciduous; E=evergreen; P=palatable; U=unpalatable; Bold=dominant trait.

Table 5.4: Plant functional type ratios for dominant established tree species in 2015 across fire treatments and vegetation zones.

Vegetation zone	Fire treatment	Plant Functional Types					Dominant traits*
		Encroachers: Non-encroachers	Tree:Shrub:Liana	Single-stemmed: Multi-stemmed	Evergreen: Deciduous	Unpalatable: Palatable	
Riparian	Control; Fire	1 : 0.5	1 : 2 : 0	1 : 0.9	1 : 67	0 : 135	En/S/Si/D/P
	Control; No Fire	1 : 0.2	1 : 0.1 : 0	1 : 5	1 : 1.1	1 : 3	En/T/Mu/D/P
	Partial; Fire	1 : 0.1	1 : 0.7 : 0	1 : 0.7	1 : 3	1 : 4	En/T/Si/D/P
	Partial; No Fire	1 : 0.3	1 : 1.6 : 0	1 : 1.7	1 : 5	1 : 6	En/S/Mu/D/P
	Full; Fire	1 : 0.3	1 : 1.6 : 0	1 : 1.2	1 : 4	1 : 5	En/S/Mu/D/P
	Full; No Fire	1 : 0.4	1 : 6 : 0	1 : 2	1 : 1.6	1 : 1.7	En/S/Mu/D/P
Sodic	Partial; Fire	1 : 0.1	1 : 0.8 : 0.1	1 : 0.6	1 : 1.6	1 : 1.1	En/T/Si/D/P
	Partial; No Fire	1 : 0.1	1 : 1.9 : 0.2	1 : 1.6	1 : 1	1 : 0.7	En/S/Mu/ED/U
	Full; Fire	1 : 0.001	1 : 1 : 0	1 : 1	1 : 10	1 : 10	En/S/SiMu/D/P
	Full; No Fire	1 : 0.0003	1 : 1.8 : 0	1 : 1.8	0 : 379	0 : 379	En/S/Mu/D/P
Crest	Control; Fire	1 : 0.5	1 : 0.3 : 0	1 : 0.3	1 : 103	0 : 208	En/T/Si/D/P
	Control; No Fire	1 : 0.3	1 : 0.7 : 0	1 : 0.7	1 : 209	0 : 210	En/T/Si/D/P
	Partial; Fire	1 : 1	1 : 0.9 : 0	1 : 0.8	1 : 28	0 : 145	EnN/T/Si/D/P
	Partial; No Fire	1 : 0.6	1 : 1 : 0.2	1 : 0.8	1 : 12	1 : 7	En/T/Si/D/P
	Full; Fire	1 : 0.04	1 : 1.2 : 0.05	1 : 1.1	1 : 22	1 : 16	En/S/Mu/D/P
	Full; No Fire	1 : 0.2	1 : 3 : 0	1 : 3	1 : 258	0 : 259	En/S/Mu/D/P

*En=encroachers; N=non-encroachers; T=trees; S=shrubs; Si=single-stemmed; Mu=multi-stemmed; D=deciduous; E=evergreen; P=palatable; U=unpalatable; Bold=dominant trait.

5.3.3 Species composition changes

5.3.3.1 Response to herbivore exclusion

In both the fully and partially fenced enclosure, no significant changes in species assemblages of either life stage communities (i.e. seedling- and established woody community) were revealed when comparing the 2002 and 2015 communities of each life stage (Anosim, $R < 0.3$) (Figure 5.12; Figure 5.13). In 2002, when all herbivores had access to both the fully and partially fenced enclosure sites, seedling and established species composition were dissimilar in the riparian vegetation zone (Full: $R = 0.57$, Figure 5.14a; Partial: $R = 0.72$, Figure 5.15a) and the sodic zone (Full: $R = 0.39$, Figure 5.14a; Partial: $R = 0.31$, Figure 5.15a). Where all herbivores were excluded species composition was similar between seedlings and established community in all three vegetation zones ($R < 0.3$ for all three vegetation zones) (Figure 5.14b), whereas exclusion of only elephants led to dissimilar species composition between seedlings and established community in the riparian vegetation zone ($R = 0.32$) (Figure 5.15b). Meso-herbivores therefore affected species composition in especially the riparian vegetation zone.

Scogings *et al.* (2012) evaluated woody species composition change over a short term period at the Nkuhlu exclosures in the absence of large mammalian herbivores. The study revealed no significant change in woody species composition over 5 years (Scogings *et al.*, 2012). After 13 years of large mammalian herbivore exclusion, woody species composition still remained unchanged, when comparing seedlings and established life stages separately between 2002 and 2015. Long-term absence of herbivores, however, reduces the dissimilarity in species assemblages between the seedling and established woody communities. Dissimilar species composition between the seedling- and established woody community could be ascribed to browsing effects (Bond *et al.*, 2001; Guldemon & Van Aarde, 2009; Staver *et al.*, 2009; Sankaran *et al.*, 2013). Direct utilisation by browsing herbivores inhibits woody recruitment, either by removing palatable woody seedlings from the ecosystem, or by suppressing their growth (Sankaran *et al.*, 2013). Palatable species are most likely to get trapped inside a bottleneck while unpalatable species can get established (Fornara & Du Toit, 2008). Results from this study revealed that the release from herbivore pressure led to woody establishment and hence to similar seedling and established woody communities. Results suggest that mega-herbivores especially impacted species composition in the uplands while meso-herbivores drive changes in the bottomlands.

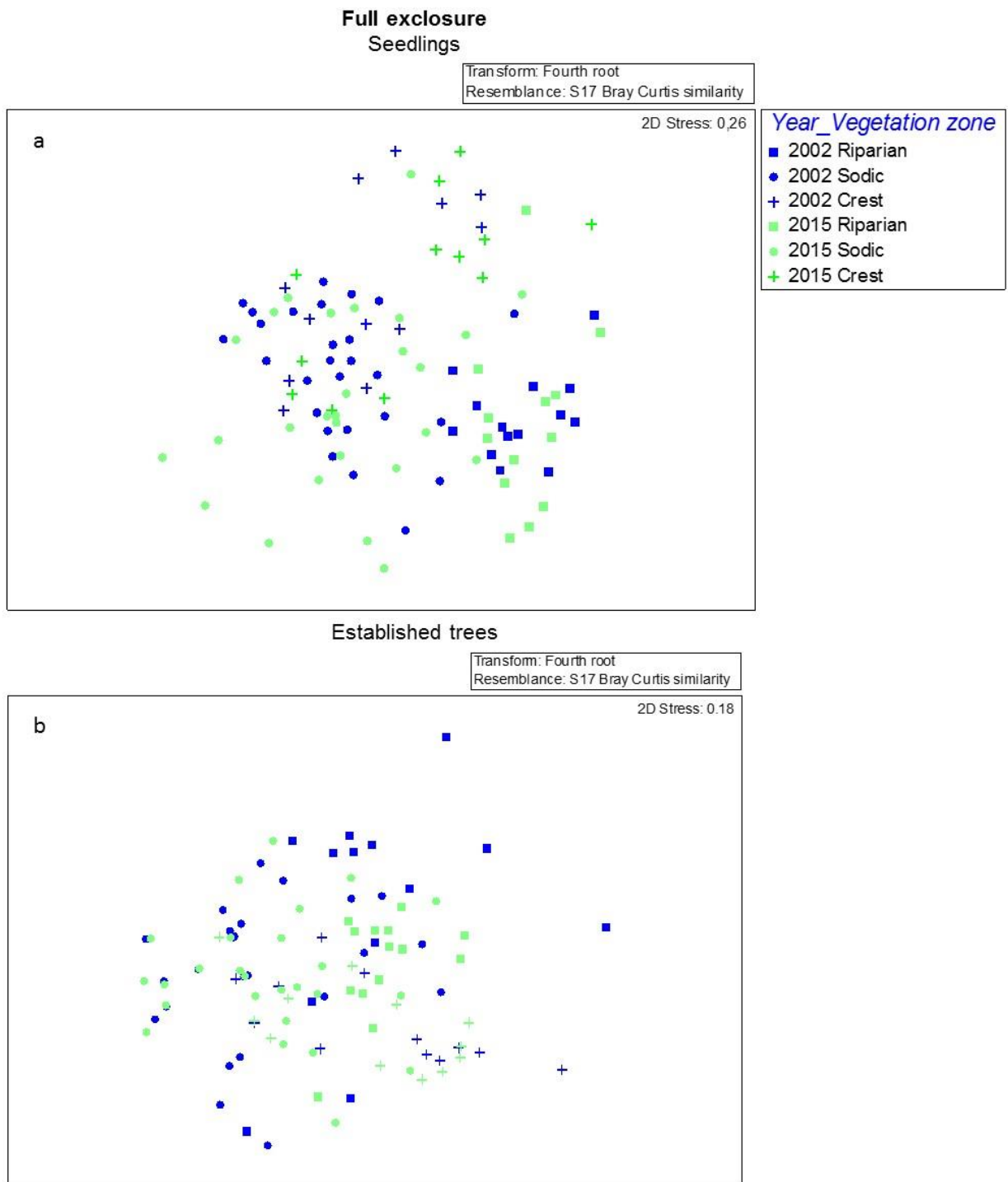


Figure 5.12: NMDS ordination scatter plot to visually display the distribution of seedling (a) and established (b) woody species composition in 2002 (blue) and 2015 (green) in the fully fenced enclosure. Different symbols represent different positions along a granitic toposequence (i.e. different vegetation zones).

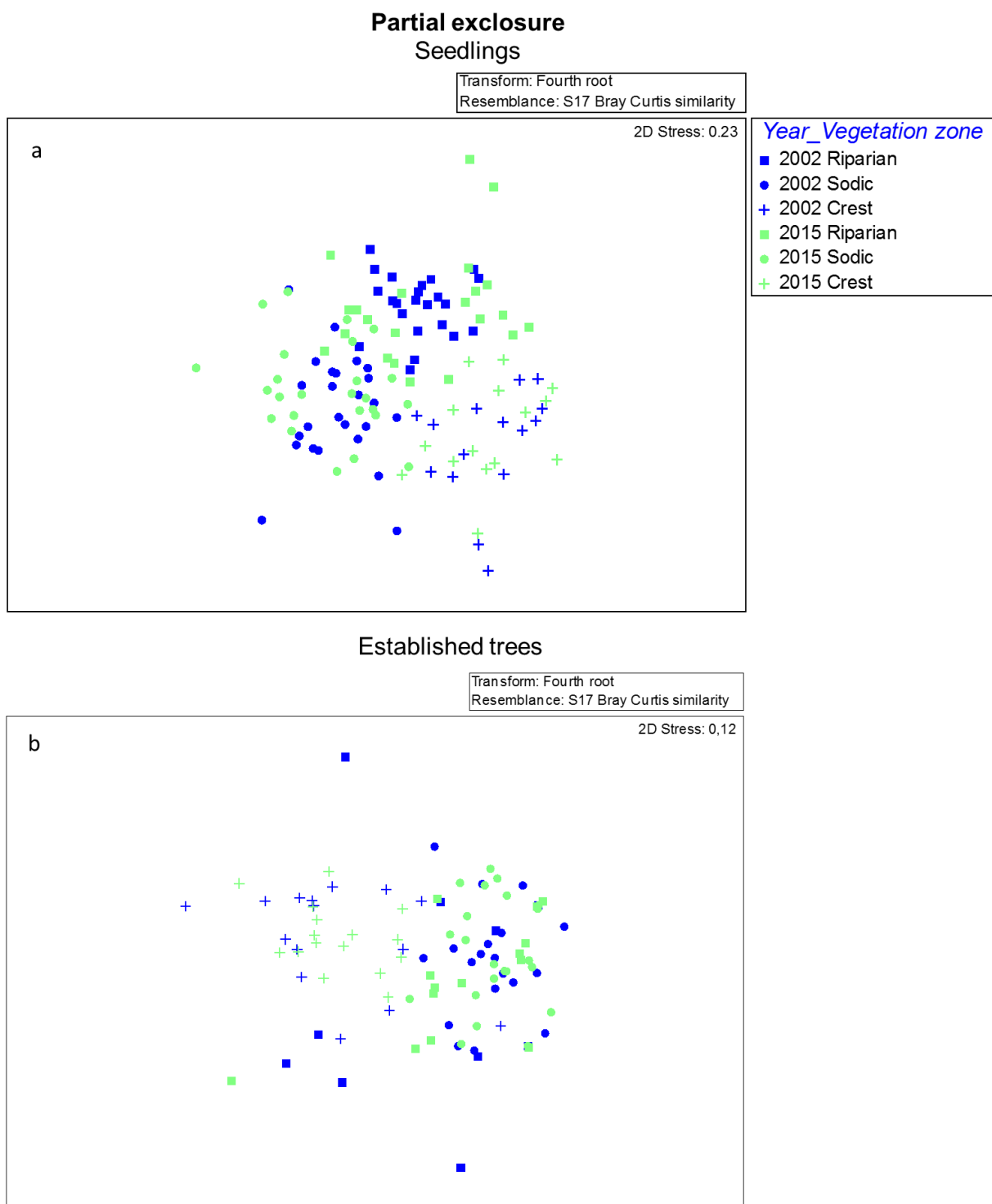


Figure 5.13: NMDS ordination scatter plot to visually display the distribution of seedling (a) and established (b) woody species composition in 2002 (blue) and 2015 (green) in the partially fenced enclosure. Different symbols represent different positions along a granitic toposequence (i.e. different vegetation zones).

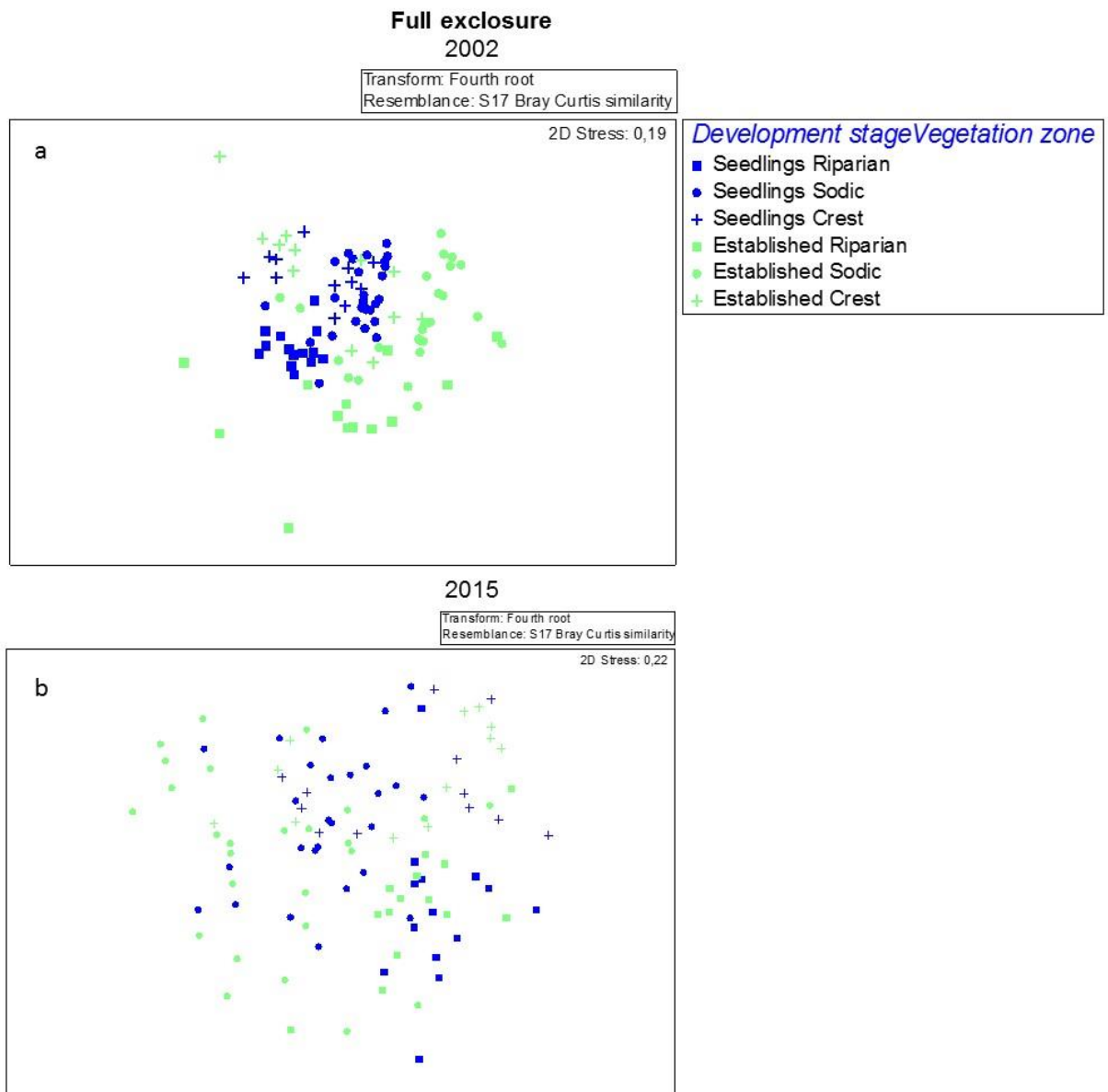


Figure 5.14: NMDS ordination scatter plot to visually display the distribution of 2002 (a) and 2015 (b) woody species composition for the seedling (blue) and established (green) communities in the fully fenced enclosure. Different symbols represent different positions along a granitic toposequence (i.e. different vegetation zones).

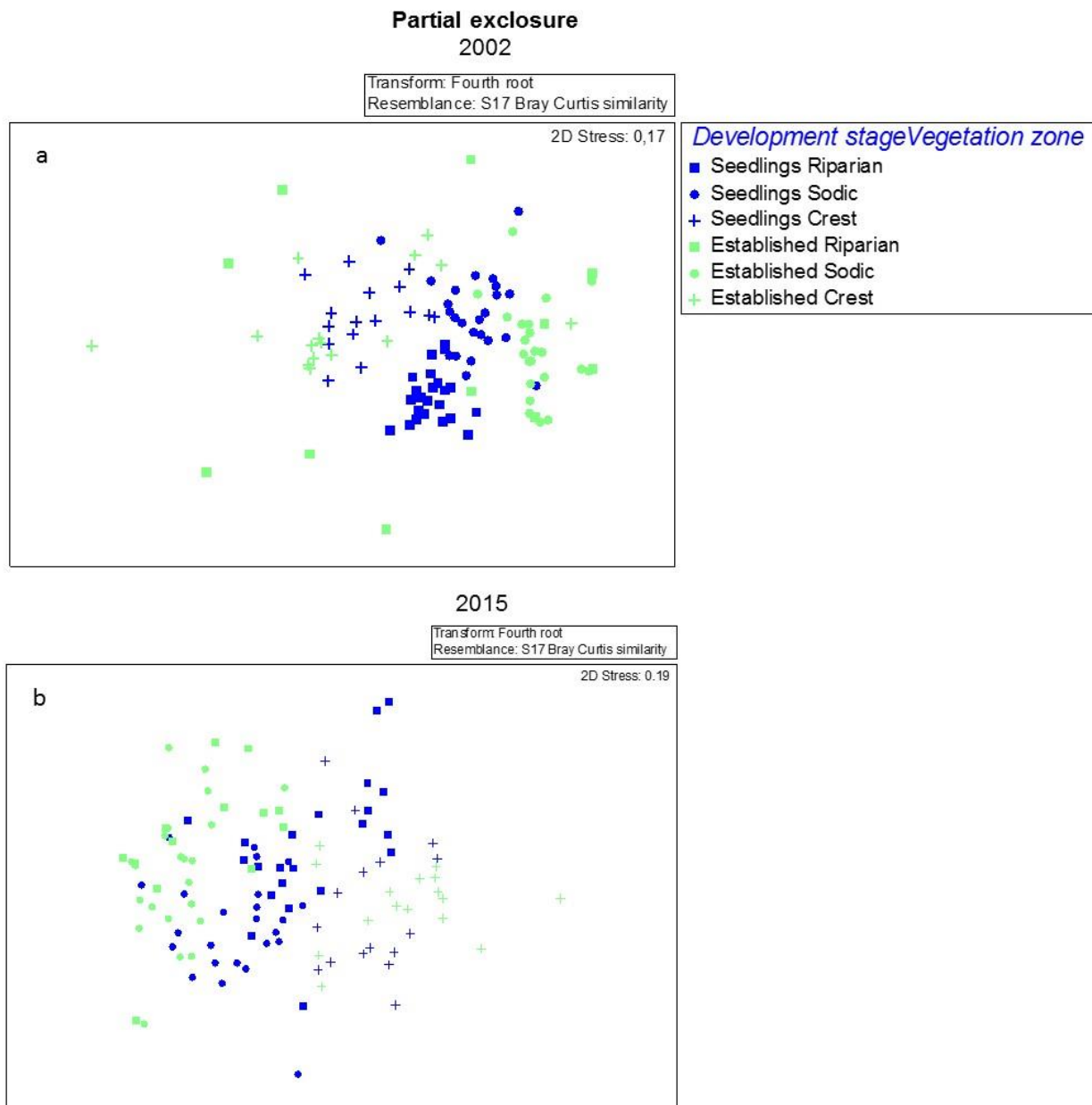


Figure 5.15: NMDS ordination scatter plot to visually display the distribution of 2002 (a) and 2015 (b) woody species composition for the seedling (blue) and established (green) communities in the partially fenced enclosure. Different symbols represent different positions along a granitic toposequence (i.e. different vegetation zones).

5.4 Conclusion

It was expected that the floristic composition of the woody layer at the study site would change in response to exclusion of herbivory and fire. Changes in most abundant woody families in response to herbivore exclusion were especially observed in the eutrophic bottomlands, which are usually favoured by herbivores. PFT's also indicated changes in response to herbivore exclusion, which further contribute to support the hypothesis. Woody floristic responses to fire were especially recognised in areas where herbivores were excluded. This means that herbivory, in this study site, override effects of fire. Most changes occurred in the upland areas which are characterised as a dystrophic savanna. This corresponds to studies which suggested that especially dystrophic savannas mostly indicate fire responses in its floristic composition (Scholes, 1990; Lehmann *et al.*, 2011; Hempson *et al.*, 2015). Results from this chapter therefore suggest that 13 years of excluding fundamental drivers of savanna systems (herbivory and fire), is long enough to initiate changes in dominant families and basic PFT's. The nature of these changes can however not yet be classified as permanent as it could be in a transitional state.

Herbivore activity suppresses seedling growth and inhibiting woody healthy recruitment. It is therefore expected that only those species adapted to herbivore utilisation can get established. Therefore, dissimilar seedling and established species composition was found in the presence of herbivores (except for the sodic vegetation zone), while similar species compositions were found in the absence of herbivores, with the exception of the riparian in the partial enclosure. The release of all large mammalian herbivore activity from this system could therefore result in a more homogeneous woody community by creating similar species composition groups for seedlings and established trees. Herbivory can therefore be identified as a driver of heterogeneity in this semi-arid savanna ecosystem.

CHAPTER 6

Woody abundance changes across herbivore and fire treatments

6.1 Introduction

Seedlings are considered the fundamental stage in regeneration. Seedling survival and/or mortality define future woody community composition and structure (Barton & Hanley, 2013). The seedling stage is the most vulnerable due to their small size, limited structural support as well as inter- and intraspecific competition (Miranda *et al.*, 1993). Both bottom-up and top-down controls may affect successful seedling establishment.

High herbaceous biomass, leading to competition between the herbaceous and woody layer, can be considered a constraint for seedling recruitment and establishment (Kambatuku *et al.*, 2011). Extensive below-ground grass root biomass may compete with woody seedlings for resources, inhibiting successful establishment of woody individuals (Eckhardt *et al.*, 2000; Riginos, 2009; Kambatuku *et al.*, 2011; Vadigi & Ward, 2014).

While the herbaceous layer performs bottom-up competition with seedling establishment, certain top-down controls (i.e. herbivory and fire) may also contribute to changes in woody community structure, including woody regeneration success. Both herbivory and fire may inhibit sapling growth into established adult tree size-classes through direct consumption, imposing a recruitment bottleneck in the form of 'browse or fire traps' (Bond & Keeley, 2005). Recent studies indicated that herbivory, or rather herbivore exclusion, will cause change in woody species composition (see results from previous chapter; Levick & Rogers, 2008; Barton & Hanley, 2013). Such changes may be attributed to the suppression effect of browsers on woody seedlings and saplings, keeping them in the browse trap (Bond *et al.*, 2001; Guldmond & Van Aarde, 2009; Staver *et al.*, 2009; Sankaran *et al.*, 2013). Palatable woody species are more likely to get trapped, while unpalatable species have the ability to grow into higher size-classes (Fornara & Du Toit, 2008). When woody species are being released from this trap through the exclusion of herbivore activity (Staver *et al.*, 2009), the once suppressed seedlings and saplings, often referred to as gullivers (Bond & van Wilgen, 1996) may grow into established size-classes (Asner *et al.*, 2009). This will contribute to increases in the abundance of established woody individuals. Impacts of fire on woody species are expected to be similar to that of herbivory since fire also consumes woody biomass, killing trees/shrubs or limits their growth (Bond & Keeley, 2005; Staver *et al.*, 2009). Woody seedlings and saplings are limited in growth through fire keeping them within the fire-trap (0-3 m in height). Only fire-prone or fire-adapted species will survive and grow beyond the fire-trap to reach heights unaffected by fire (Bond & Keeley, 2005). This may contribute to changes in woody structure over the longer term.

Therefore, both bottom-up and top-down controls may create two major demographic bottlenecks in savanna tree populations (Higgings *et al.*, 2000; Sankaran *et al.*, 2004): (i) recruitment bottleneck, where seedlings are trapped within the grass sward, and (ii) sapling release bottleneck, where herbivory and fire inhibit growth past sapling stage to form large adult trees (also known as the 'browse or fire traps'). These bottom-up and top-down controls may in the long-term contribute to changes in woody abundances (Fornara & Du Toit, 2008; Barton & Hanley, 2013).

Woody encroachment is a growing concern for rangeland scientists and conservationists of savanna ecosystems (Archer *et al.*, 1995; Scholes and Archer, 1997; Roques *et al.*, 2001; Wiegand *et al.*, 2006; Wigley *et al.*, 2010). Global and regional drivers have been identified to explain this phenomenon (Stevens *et al.*, 2016). At a global scale, (Asner *et al.*, 2003; Cabral *et al.*, 2003; Laiolo *et al.*, 2004; Wiegand *et al.*, 2006), increasing atmospheric CO₂ levels have been identified as one of the major contributors to increasing woody encroachment (Stevens *et al.*, 2016). At a regional scale, increasing atmospheric CO₂ levels combined with disturbances such as herbivory and fire, and to some extent the release thereof from a system, are considered attributes to encroachment (Bond & Midgley, 2000; Stevens *et al.*, 2016). Herbivory and fire can also, if managed well, control or even suppress woody encroachment in savanna systems. Responses of the woody layer to herbivory and fire are often species-specific (Levick & Rogers, 2008; Migley *et al.*, 2014), which ultimately lead to a species being categorized as either an encroaching or a non-encroaching woody species.

During their seedling stage, both encroachers and non-encroachers are affected by herbivory and fire, either directly through consumption or indirectly through grazing herbivores or fire events that create gaps for seedling establishment. How herbivory and fire control encroachment of woody species without negatively affecting non-encroacher species in a natural, protected semi-arid savanna ecosystem still remains relatively unexplored.

The Nkuhlu exclosures provided the opportunity to test how the presence of, or release from herbivores and fire affected woody community changes by comparing abundances of woody encroacher and non-encroacher species between 2002 and 2015 for both seedlings and established woody individuals.

It is hypothesised that exposure to herbivory and fire will not significantly reduce encroacher seedling abundances due to their adaptive strategies, such as resprouting, in savanna ecosystems (Moe *et al.*, 2009). It is rather expected that encroacher seedling abundances will increase in sites that are open to herbivore disturbance. Herbivore activity prevents herbaceous biomass accumulation (Van Coller *et al.*, 2013), therefore inhibit warm fires and hence reduce the competitive exclusion effect on encroacher seedlings. Non-encroacher seedling

abundances are expected to be lower in the presence of herbivores and fire and more specifically in the nutrient-rich bottomlands (i.e. riparian and sodic vegetation zones), which are favoured by most browsers (Scholes, 1990). Elephant effects are expected to be strongest on the abundance of established trees rather than on seedlings.

6.2 Methods

A detailed account of data sampling methods is provided in the Methods chapter (Chapter 4). Only the methodology that is designed to meet the specific objectives stated in this chapter will be discussed here.

Woody seedlings are referred to those individuals with a height of less than 1 m and a basal diameter of less than 1 cm, while established individuals have a height of ≥ 1 m and a basal diameter of ≥ 1 cm.

Hierarchical Linear Modelling (Hancock & Mueller, 2010) was used to determine whether herbivore/fire treatments affected mean woody abundance per plot across different vegetation zones between 2002 and 2015. The interaction between fixed effects, which included herbivore treatments, fire treatments, vegetation zones, and years, was tested for (i) all woody seedlings and established individuals and (ii) encroacher and non-encroacher seedlings and established individuals respectively. Significant interaction effects were identified at $p < 0.05$. To test for significance within effects, particularly temporal changes in abundance, the data were further analysed through the calculation of effect sizes. Effect size is normally used to determine practical significance, i.e. difference between two means divided by the estimate of standard deviation, by making the difference independent of units and sample size, and relate it to the spread of the data (Ellis & Steyn, 2003). Small effect sizes (eg. $d < 0.5$) indicated non-significant changes, while medium effect sizes ($d = 0.5 - 0.6$) and large effect sizes ($d > 0.6 - 1$) indicated significant changes. Highly significant changes in abundances were reported by an effect size of > 1 .

6.3 Results

Across both life stages (seedlings and established woodies) as well as woody communities (complete, encroachers and non-encroachers), various combination of interaction effects were revealed (Table 6.1). The only two treatments that consistently interacted significantly were herbivory and fire - in some cases with herbivory and in other cases with vegetation zone (Table

6.1). Fire treatment revealed no significant interaction effects with any other treatments in the established woody community. Seedling abundances, however, were stronger affected by fire. Both encroacher and non-encroacher seedlings were affected by fire, which suggests their sensitivity to fire (Table 6.1). The only four-way interaction effect was revealed for the encroacher seedling community (Table 6.1). Linear modelling results suggest that 13 years of herbivory and fire manipulations were adequate to observe changes due to the significant year effects in both life stages and all communities (Table 6.1). Herbivore treatment can be considered as the main driver of system dynamics at the study site since it interacted significantly with all other effects (Table 6.1). Vegetation zone also played an important role in the system, but is considered secondary to the interactions between herbivory and year.

Table 6.1: Summary of significant interaction effects between treatments (vegetation zones, herbivore treatments, fire treatments and year (2002–2015)) for seedlings and established individuals separately. The complete woody community assessment included all woody individuals, which was then separated into encroacher and non-encroacher species for separate analyses on these functional groups.

Life stage	Woody community	Fixed effects	F	p
Seedlings	Complete woody community	Vegetation zone*Herbivory treatment*Year	7.72	< 0.01
		Herbivory treatment*Fire treatment*Year	4.8	0.011
	Encroachers	Vegetation zone*Herbivory treatment*Fire treatment*Year	5.63	0.001
	Non-encroachers	Vegetation zone*Herbivory treatment*Year	6.14	0.000
		Vegetation zone*Fire treatment*Year	4.61	0.012
		Herbivory treatment*Fire treatment*Year	8.43	0.000
Established	Complete woody community	Vegetation zone*Herbivory treatment*Year	4.44	0.003
	Encroachers	Vegetation zone*Herbivory treatment*Year	2.92	0.026
	Non-encroachers	Vegetation zone*Herbivory treatment*Year	4.15	0.004

Vegetation zone: Riparian, Sodic, Crest; *Herbivore treatment:* Control site, Partial enclosure, Full enclosure; *Fire treatment:* exposure to fire, fire exclusion; *Year:* between 2002 and 2015. *F:* variance in group means, *p:* significant when $p < 0.05$.

6.3.1 Complete woody community

Seedlings

There was a significant interaction effect between year, vegetation zone and herbivore treatment for woody seedling abundances at the study site (Table 6.1). These results suggest that seedling abundance changes between 2002 and 2015 varied across the different vegetation zones and herbivore treatments, regardless whether fire was applied or not. Contrasting patterns were revealed between herbivore treatments in the riparian zone since seedling abundance between 2002 and 2015 increased significantly in both the fully fenced enclosure and the control site (Table 6.2). Seedlings in the sodic zone were favoured by the presence of meso-herbivores (control and partial enclosure sites), regardless of the presence or

absence of elephants (Table 6.2). The exclusion of elephants on the crest zone led to a highly significant increase in seedling abundance over time (Table 6.2). Therefore, the largest increases in seedling abundance were in the absence of elephant, but only on the midslopes and upland areas (sodic and crest zones).

Table 6.2: Woody seedling abundances per year across vegetation zones and herbivore treatments.

Vegetation zone	Herbivore treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Riparian	Control	2002	33.58	6.98	1.20 ***
		2015	57.25	6.98	
	Partial	2002	33.75	5.70	0.27
		2015	28.33	5.70	
	Full	2002	31.60	5.69	0.98 **
		2015	50.86	5.69	
Sodic	Control	2002	19.41	8.04	0.81 **
		2015	35.30	8.04	
	Partial	2002	21.83	5.70	1.27 ***
		2015	46.83	5.70	
	Full	2002	35.68	5.68	0.43
		2015	27.25	5.68	
Crest	Control	2002	21.56	5.69	0.29
		2015	27.36	5.69	
	Partial	2002	35.83	5.70	1.95 ***
		2015	74.25	5.70	
	Full	2002	35.86	5.68	0.47
		2015	45.20	5.68	

d: *d*<0.5=non-significant; *d*=0.5–0.6=medium effect*; *d*>0.6–1 =large effect**;
d>1=significant large effect***.

Fire interacted significantly with herbivory and year, irrespective of vegetation zones (Table 6.1). The fire exposed plots in the control site and partially fenced exclosure increased significantly in seedling abundance between 2002 and 2015 (Table 6.3). In the plots where fire was excluded from 2002 onwards, all herbivore treatments (control site, partially and fully fenced exclosures) revealed significant increases in seedling abundance 13 years later (Table 6.3). The highest increase was observed in the absence of elephant (Table 6.3).

Table 6.3: Woody seedling abundances per year across fire and herbivore treatments.

Fire treatment	Herbivore treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Fire	Control	2002	25.42	6.98	1.08 ***
		2015	47.67	6.98	
	Partial	2002	32.28	4.65	0.57 *
		2015	43.56	4.65	
	Full	2002	36.32	4.64	0.06
		2015	35.05	4.64	
No Fire	Control	2002	26.29	4.64	0.55 *
		2015	37.07	4.64	
	Partial	2002	28.67	4.65	1.39 ***
		2015	56.06	4.65	
	Full	2002	32.44	4.64	0.75 **
		2015	47.15	4.64	

d: $d < 0.5$ = non-significant; d between 0.5 and 0.6 = medium effect*; $d > 0.6-1$ = large effect**; $d > 1$ = significant large effect***.

Established individuals

For the established woody community a significant three-way interaction effect was revealed between vegetation zone, herbivore treatment and year (Table 6.1). A strong elephant exclusion effect was observed in the riparian zone where significant increases in established individuals between 2002 and 2015 were observed, despite the presence (partial exclosure) or absence (full exclosure) of other large herbivores (Table 6.4).

No herbivory effects were observed in the sodic zone, whereas a strong elephant effect was noticed on the crest (Table 6.4). This was detected in the decrease of established tree abundances in the control site, while an increase in abundance was observed in the absence of elephant, regardless of the presence of other herbivores (Table 6.4).

Table 6.4: Woody abundances of established individuals per year across vegetation zones and herbivore treatments.

Vegetation zone	Herbivore treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Riparian	Control	2002	6,29	2,44	0,17
		2015	7,49	2,50	
	Partial	2002	1,42	2,05	0,73 **
		2015	6,58	2,05	
	Full	2002	5,70	2,05	2,30 ***
		2015	22,02	2,04	
Sodic	Control	2002	4.27	2.87	0.45
		2015	7.49	2.87	
	Partial	2002	6.17	2.05	0.12
		2015	5.33	2.05	
	Full	2002	8.33	2.05	0.01
		2015	8.25	2.05	
Crest	Control	2002	12.42	2.05	0.51 *
		2015	8.83	2.05	
	Partial	2002	8.50	2.05	0.92 **
		2015	15.00	2.05	
	Full	2002	9.67	2.05	0.78 **
		2015	15.17	2.05	

d: *d*<0.5=non-significant; *d* between 0.5 and 0.6=medium effect*; *d*>0.6–1=large effect**; *d*>1=significant large effect***.

6.3.2 Woody abundances of encroacher species

Seedlings

There was a significant four-way interaction effect of vegetation zone, herbivore treatment, fire treatment and year on encroacher seedling abundances (Table 6.1). Significant increases in the abundance of encroacher seedlings were present in four of the six treatments in the riparian zone, two with fire and two without fire (Table 6.5). Exclusion of elephants had the largest effect on encroacher seedling increases, since significant increases were revealed irrespective of fire treatment (Table 6.5). Therefore, for encroacher species seedling abundances, the exclusion of elephants predominate fire effects. Accumulation of herbaceous biomass in the fully fenced exclosure in combination with fire seem to have favoured encroacher seedlings (Table 6.5), which suggests their resistance to fire, even to assumingly high intensity fires produced by high fuel loads.

In the sodics vegetation zone, fire did not play an important role in the control of encroacher seedlings, except where all herbivores were excluded. Encroacher seedlings in the sodic zone were favoured by the presence of meso-herbivores, regardless of the presence or absence of elephant (Table 6.5).

The prolonged activity of all herbivores on the crest zone (i.e. control site) seem to have controlled encroacher seedling abundances, irrespective of fire treatment (Table 6.5). Where elephants were excluded (partial exclosure), significant increases in encroacher seedling abundances were observed, irrespective of fire treatment (Table 6.5). These observations therefore suggest elephant control over increase in encroacher seedling abundances, but mostly on the upland crest.

Table 6.5: Woody abundances of encroacher seedlings per year across vegetation zones, herbivore treatments and fire treatments.

Vegetation zone	Herbivore treatment	Fire treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Riparian	Control	Fire	2002	19.00	7.19	0.43
			2015	24.33	7.19	
		No Fire	2002	20.50	5.08	0.58 *
			2015	27.67	5.08	
	Partial	Fire	2002	40.17	5.08	1.85 **
			2015	17.17	5.08	
		No Fire	2002	11.50	5.08	0.95 **
			2015	23.33	5.08	
	Full	Fire	2002	17.67	5.08	0.64 **
			2015	25.67	5.08	
		No Fire	2002	23.26	5.08	0.48
			2015	17.34	5.08	
Sodic	Control	No Fire	2002	13.55	5.08	1.13 ***
			2015	27.64	5.08	
	Partial	Fire	2002	16.67	5.08	2.13 ***
			2015	43.17	5.08	
		No Fire	2002	12.83	5.08	1.63 ***
			2015	33.17	5.08	
	Full	Fire	2002	24.53	5.08	0.49
			2015	18.48	5.08	
		No Fire	2002	37.24	5.08	1.33 ***
			2015	20.72	5.08	
Crest	Control	Fire	2002	8.00	5.08	0.12
			2015	9.50	5.08	
		No Fire	2002	8.37	5.08	0.17
			2015	10.49	5.08	
	Partial	Fire	2002	8.33	5.08	1.22 ***
			2015	23.50	5.08	
		No Fire	2002	14.67	5.08	0.74 **
			2015	23.83	5.08	
	Full	Fire	2002	43.45	5.08	1.39 ***
			2015	26.16	5.08	
		No Fire	2002	10.38	5.08	0.75 **
			2015	19.71	5.08	

d: *d*<0.5=non-significant; *d* between 0.5 and 0.6=medium effect*; *d*>0.6–1=large effect**; *d*>1=significant large effect***.

Established individuals

A significant three-way interaction effect was revealed between established encroacher species abundances and vegetation zone, herbivore treatment and year (Table 6.1). The strongest elephant effect on encroacher abundances was observed in the riparian and crest zones. In the presence of elephant (control site), increases in established encroacher individuals occurred, although these increases were negligible compared to treatments where elephants have been excluded for 13 years. Significant increases in established encroacher species abundances were noticed in the absence of elephant, regardless the presence of other herbivores (partial exclosures) or without them (full exclosure) (Table 6.6). In the nutrient-rich sodics zone, encroacher species abundances did not increase significantly over time in any of the treatments (Table 6.6).

Table 6.6: Woody abundances of established encroacher individuals per year across vegetation zones and herbivore treatments.

Vegetation zone	Herbivore treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Riparian	Control	2002	3.750	1.827	0.35
		2015	5.583	1.827	
	Partial	2002	1.083	1.492	0.79 **
		2015	5.167	1.492	
	Full	2002	2.417	1.492	1.97 ***
		2015	12.583	1.492	
Sodic	Control	2002	4.167	2.110	0.35
		2015	6	2.110	
	Partial	2002	4.500	1.492	0.06
		2015	4.167	1.492	
	Full	2002	7.500	1.492	0.06
		2015	7.167	1.492	
Crest	Control	2002	4.500	1.492	0.39
		2015	6.500	1.492	
	Partial	2002	2.500	1.492	0.98 **
		2015	7.583	1.492	
	Full	2002	7.667	1.492	0.92 **
		2015	12.417	1.492	

d: *d*<0.5=non-significant; *d* between 0.5 and 0.6=medium effect*; *d*>0.6–1=large effect**; *d*>1=significant large effect***.

6.3.3 Woody abundances of non-encroacher species

Seedlings

Abundances of non-encroacher seedling interacted significantly with vegetation zone, herbivore treatment and year (Table 6.1), which suggests a limited fire effect. Increases in non-encroacher seedlings in the riparian zone cannot be attributed to herbivore effects since seedling abundances increased significantly in both the presence (control site) and absence (full enclosure) of all herbivores (Table 6.7). On the uplands (crest zone), non-encroacher seedling abundances increased significantly where elephants have been excluded for 13 years (partial enclosure), and also where all herbivores have been excluded (Table 6.7). Similar to encroacher seedlings, non-encroacher seedlings of the dystrophic upland crests also seem to be controlled by elephant.

Table 6.7: Woody abundances of non-encroacher seedlings per year across vegetation zones and herbivore treatments.

Vegetation zone	Herbivore treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Riparian	Control	2002	13.83	4.78	1.29 ***
		2015	31.25	4.78	
	Partial	2002	7.92	3.90	0.01
		2015	8.00	3.90	
	Full	2002	10.99	3.89	1.36 ***
		2015	29.43	3.89	
Sodic	Control	2002	5.68	5.47	0.14
		2015	7.61	5.47	
	Partial	2002	7.08	3.90	0.12
		2015	8.67	3.90	
	Full	2002	5.06	3.86	0.20
		2015	7.78	3.86	
Crest	Control	2002	13.31	3.89	0.32
		2015	17.70	3.89	
	Partial	2002	24.33	3.90	1.89 ***
		2015	49.83	3.90	
	Full	2002	8.51	3.86	1.01 ***
		2015	22.14	3.86	

d: *d*<0.5=non-significant; *d* between 0.5 and 0.6=medium effect*; *d*>0.6–1=large effect**; *d*>1=significant large effect***.

A second significant interaction effect was observed between vegetation zone, fire treatment and year (Table 6.1). Non-encroacher seedlings had better recruitment in the no-fire treatments, specifically in the riparian zone, while species of the crest zone did not indicate sensitivity to fire in their seedling stage. (Table 6.8).

Table 6.8: Mean woody abundance of non-encroacher seedlings between 2002 and 2015 in different fire treatments per vegetation zone.

Vegetation zone	Fire treatment	Year	Mean abundance per plot	Std.Error	Effect size <i>d</i> (2002 vs 2015)
Riparian	Fire	2002	12.444	3.681	0.42
		2015	18.167	3.681	
	No Fire	2002	9.383	3.178	1.35 ***
		2015	27.620	3.178	
Sodic	Fire	2002	4.917	3.875	0.25
		2015	8.301	3.875	
	No Fire	2002	6.706	3.168	0.09
		2015	7.967	3.168	
Crest	Fire	2002	10.518	3.172	0.91 **
		2015	22.809	3.172	
	No Fire	2002	20.247	3.168	1.24 ***
		2015	36.974	3.168	

d: *d*<0.5=non-significant; *d* between 0.5 and 0.6=medium effect*; *d*>0.6–1=large effect**; *d*>1=significant large effect***.

In the significant three-way interaction between herbivore treatment, fire treatment and year (Table 6.1), non-encroacher seedling abundances did not increase in all the fire exclusion treatments. Significant increases in non-encroacher abundances was observed in the full and partial exclosures, where herbaceous biomass have accumulated more significantly over time. The fire exposed treatments in the full and partial herbivore exclosures would have produced warmer fires, which can suppress seedling recruitment (Table 6.9). Significant increases in seedling abundances in the fire-exposed area of the control site can possibly be ascribed to very low fire intensity (low fuel load) due to prolonged grazing in the control site.

Table 6.9: Woody abundances of non-encroacher seedlings per year herbivory treatments and fire treatments.

Herbivore treatment	Fire treatment	Year	Mean abundance per plot	Std.Error	Effect size over years (Es)
Control	Fire	2002	11.92	4.78	1.32 ***
		2015	29.75	4.78	
	No Fire	2002	12.04	3.17	0.24
		2015	15.34	3.17	
Partial	Fire	2002	10.61	3.19	0.33
		2015	15.06	3.19	
	No Fire	2002	15.61	3.19	1.01 ***
		2015	29.28	3.19	
Full	Fire	2002	7.69	3.16	0.29
		2015	11.62	3.16	
	No Fire	2002	8.68	3.16	1.42 ***
		2015	27.95	3.16	

d: *d*<0.5=non-significant; *d* between 0.5 and 0.6=medium effect*; *d*>0.6–1=large effect**; *d*>1=significant large effect***.

Established individuals

A significant three-way interaction effect was observed for vegetation zone, herbivore treatment and year in the established non-encroacher community (Table 6.1). The abundances of established non-encroacher individuals did not increase where elephants have been excluded for 13 years, but only in the riparian and upland crest zones (Table 6.10). The only significant increase was revealed in the riparian bottomlands in the absence of all herbivores. Declining abundances of non-encroacher species were observed in the area exposed to all herbivores (control site) with significant decreases on the upland crests (Table 6.10). Since individuals increased in areas where only elephants have been excluded (partially fenced site), elephants are suggested as the main driver of declining abundances of established non-encroacher species. The impacts of giraffes are not being neglected, although their feeding behaviour give evidence to minor destructive effects, but rather of selective defoliation of the leaf canopy (Furstenburg & Van Hoven, 1994).

Table 6.10: Woody abundances of established non-encroacher individuals per year across vegetation zones and herbivore treatments.

Vegetation zone	Herbivore treatment	Year	Mean abundance per plot	Std.Error	Effect size over years (Es)
Riparian	Control	2002	2.60	1.22	0.18
		2015	1.99	1.22	
	Partial	2002	0.33	1.00	0.31
		2015	1.42	1.00	
	Full	2002	2.90	1.00	1.87 ***
		2015	9.36	1.00	
Sodic	Control	2002	0.29	1.40	0.39
		2015	1.63	1.40	
	Partial	2002	1.63	1.00	0.15
		2015	1.12	1.00	
	Full	2002	0.83	1.00	0.07
		2015	1.08	1.00	
Crest	Control	2002	7.92	1.00	1.61 ***
		2015	2.33	1.00	
	Partial	2002	6.00	1.00	0.39
		2015	7.33	1.00	
	Full	2002	2.00	1.00	0.22
		2015	2.75	1.00	

d: $d < 0.5$ = non-significant; d between 0.5 and 0.6 = medium effect*; $d > 0.6 - 1$ = large effect**; $d > 1$ = significant large effect***.

6.4 Discussion

Established trees are commonly debarked, pushed over, and broken by elephants leading to a decline in tree densities in semi-arid savannas (Cumming *et al.*, 1997; Shannon *et al.*, 2008; Woolley *et al.*, 2011). In both the riparian and crest vegetation zones, exclusion of elephants led to increases in established tree abundances. Stronger elephant effects on the upland crests correspond with findings by Lagendijk *et al.* (2015), who also reported elephant impacts to be more pronounced on upland areas. Stronger elephant effects on the crests compared to the riparian bottomlands may also be explained by findings by Smit *et al.* (2007) who reported that the riparian zone is able to maintain higher elephant densities due to higher forage availability. Results did not reveal significant elephant effects in the sodics vegetation zone. It is therefore suggested that elephants do not actively browse in the sodic zone, but rather pass through this area on their way to water. Although the sodics zone is considered a nutrient hotspot that produces vegetation that is more palatable than surrounding vegetation types (Grant & Scholes, 2006), studies confirmed higher palatability only for the herbaceous layer (Siebert & Scogings, 2015) with limited evidence of increased palatability in the woody layer. Results obtained through this study, which suggest that herbivore impact on the woody layer is lowest in the sodic zone, call for further investigation into the nutritious value of woody plants in this nutrient hotspot.

The suggested high impact of elephants on the crest was not restricted to larger woody individuals. Seedling abundances increased where only elephants were excluded. Similarly, non-encroacher seedlings, which are all palatable species favoured by herbivores, increased in the absence of elephant, regardless of the presence or absence of other herbivores. This corresponds to the findings by Lagendijk *et al.* (2015) which stated that meso-herbivore effects were less severe in upland areas where elephant impact was high. Elephants are known to displace meso-herbivore activity (Fritz *et al.*, 2002; Valeix *et al.*, 2008; Hilbers *et al.*, 2015; Lagendijk *et al.*, 2015). Results from this study therefore support this hypothesis.

Guldemon & Van Aarde (2008) stated that presence of elephants, especially in African savanna conservation areas, could cause a decline in woody cover. It was predicted by Stevens *et al.* (2016) that the combined effect of mega-herbivores and fire could slow down woody encroachment. This was partially supported in the results, but mainly on the crest zone where encroacher species abundances (seedlings and established individuals) significantly increased in the absence of elephant. Fire, however did not play a significant role in the suppression of encroacher species abundances. Encroaching woody seedlings in the lowland areas indicated to be best controlled by the combined presence of meso-herbivores and fire. The exclusion of elephants led to higher meso-herbivore activity (Fritz *et al.*, 2002; Valeix *et al.*, 2008; Hilbers *et al.*, 2015; Lagendijk *et al.*, 2015) in the riparian zone which, in combination with fire exposure

significantly decreased encroacher species abundances. The high abundance of encroacher species seedlings in the sodic vegetation zone asks for ecological monitoring of this valuable nutrient hotspot.

Other than expected, the non-encroaching seedling abundances were not significantly reduced by meso-herbivore activity and fire, which suggests resistance towards bush encroachment controls (eg. fire and herbivory). However, non-encroacher species abundance increased significantly in the absence of fire, which suggests some sensitivity to fire, especially in the seedlings stage. Results further suggest that non-encroacher seedling species of the crest zone are less sensitive to fire.

To conclude, elephants remain one of the strongest drivers of woody species abundances (for both encroachers and non-encroachers) (Asner *et al.*, 2016) in both life stages. Encroacher species will be best controlled during seedling stage (Hoffmann *et al.*, 2009), but particularly by the presence of elephant on the crest, and the presence of meso-herbivores in lowland areas. Non-encroachers can, to some extent, resist impacts from bush encroachment controls (herbivory and fire).

6.5 Conclusion

Considering woody abundances, the entire woody community, which includes established trees, seedlings, encroacher and non-encroacher species was negatively impacted by elephants, especially on the upland (crest) areas. In the presence of elephants, meso-herbivore effects were less severe because elephants are known to displace meso-herbivores across the landscape. Elephant browsing is suggested to act as a bush encroachment control measure in the upland areas, regardless of the presence or absence of fire, while the combination of intense meso-herbivore activity (where elephants are excluded) together with fire exposure could decrease encroaching woody seedling abundances without negatively suppressing non-encroaching species in lowland areas. It is further suggested that elephants only pass through the sodic vegetation zone towards water, without significantly affecting the woody vegetation.

CHAPTER 7

Demography of the woody community after 13 years of herbivore and fire manipulations

7.1 Introduction

Size-class distributions (population demography) are commonly used to assess woody population structures and the stability thereof (Shackleton, 1993; Mwavu & Witkowski, 2009; Venter & Witkowski, 2010; Byakagaba *et al.*, 2011; Shackleton *et al.*, 2015). In areas exposed to environmental disturbances, woody plant population demography may provide information on the most affected size classes for a particular species (Staver & Bond, 2014).

Herbivory and fire are important factors in the maintenance of the tree-grass balance in semi-arid savanna ecosystems. These top-down controls are known to suppress bush encroachment (Roques *et al.*, 2001; Joubert *et al.*, 2012; Lohmann *et al.*, 2014), maintain heterogeneity in vegetation structure (Holdo *et al.*, 2009; Levick *et al.*, 2009; O’Kane *et al.*, 2012) and recycle soil nutrients (Fornara & Du Toit, 2008). In savannas where tree-grass co-existence is a characteristic feature (Frost *et al.*, 1986; Skarpe, 1992), herbivory and fire play an important role in controlling the tree-grass balance directly or indirectly, which eventually determines vegetation structure and composition (Skarpe, 1991).

Demography of woody species in a savanna may be affected by several factors, such as (i) the grass layer (Sankaran *et al.*, 2008), which is considered as a fundamental filter for woody seedling recruitment; (ii) herbivory (Goheen *et al.*, 2010) through grazing, browsing and trampling, and (iii) fire (Prior *et al.*, 2010). All these factors may alter size-class distributions, causing changes from the commonly accepted normal inverse J-curve shape (Silvertown, 1992; Oliver & Larson, 1990; Condit *et al.*, 1998; Wilson & Witkowski, 2003; Mwavu & Witkowski, 2009; Holdo *et al.*, 2014).

In this chapter, woody community and population demography patterns will be assessed to address the effect of herbivory and fire, including their exclusion, on size-class distributions. This assessment will be undertaken at the community level, as well at species level where pre-selected dominant encroacher and non-encroacher populations will be assessed. The aim of this study was to test the effects of herbivore and fire treatments at the Nkuhlu exclosures site on woody regeneration success, therefore evaluating whether or not on-going regeneration occurred and whether the woody community or population can be considered stable or not.

The presence of herbivores and fire may affect size-class distribution of woody species by creating demographic bottlenecks through browse and fire traps (Higgins *et al.*, 2000; Bond *et al.*, 2001; Guldmond & Van Aarde, 2009; Staver *et al.*, 2009; Sankaran *et al.*, 2013; Staver & Bond, 2014; Levick *et al.*, 2015). This may cause community and population instability. It is therefore expected that the exclusion of large mammalian herbivores and fire from the system will release trapped woody individuals (mostly seedlings or saplings), which will lead to changes in size-class distributions and ultimately reveal an inverse J-shaped demography and stable communities and populations. Encroacher woody species that have been shown to be suppressed by herbivores and fire in this savanna ecosystem (Chapter 6) are expected to revert to stable regeneration after the exclusion of these bush encroachment controls. Non-encroacher regeneration is expected to be favoured by the exclusion of all herbivores.

7.2 Methods

A detailed account of the data sampling approach is presented in chapter 4 (Material and methods). Analyses relevant to woody community regeneration patterns are discussed below.

To meet the objectives of this particular chapter, only the 2015 data sets were analysed to assess woody community demography after 13 years of herbivore and fire manipulations. All woody individuals were grouped into six size-classes according to their maximum canopy height (Table 7.1). Basal stem diameter of size-class 1 was <1 cm and ≥ 1 cm for size-classes 2-6.

Table 7.1: Size-classes for woody individuals based on their height (m).

Size-class	Height division
1	<1m
2	1-2m
3	>2-3m
4	>3-4m
5	>4-5m
6	>5m

Size-class distributions (SCD) were constructed for: (i) the complete woody community, which included all woody species, (ii) pre-selected encroacher species and (iii) pre-selected non-encroacher species. SCD were graphically displayed for visual comparisons. Ordinary least-squares regressions (OLS) (Hutcheson, 2011) were performed on the SCD data set of 2015 to test SCD of woody species. Mean individuals per plot for each size class was used for the complete woody community, whereas the total number of individuals was plotted for the pre-

selected encroacher and non-encroacher species (also referred to as the 'key species'). These were set as the dependent variables (N_i), whereas the midpoint of each size-class was used as the independent variable (m_i). Variables were transformed using $\ln(N_i+1)$ and $\ln(m_i)$ prior to analyses (Lagendijk *et al.*, 2011). SCD slopes were used as indicators of community and population structure (Obiri *et al.*, 2002; Mwavu & Witkowski, 2009; Venter & Witkowski, 2010; Lagendijk *et al.*, 2011). Interpretation of SCD slopes was based on Obiri *et al.* (2002) who reported negative slopes as indicative of good recruitment with more individuals recorded in the lower size-classes than in the larger size-classes and positive slopes related to poor recruitment with more individuals in the larger size-classes than in the lower size-classes. Steepness of the slopes was used to describe recruitment trends. A steep negative slope is commonly used to indicate healthier recruitment than shallow slopes (Lykke, 1998; Obiri, 2002; Mwavu & Witkowski, 2009; Venter & Witkowski, 2010). The R^2 coefficient determines the variability of the dependent variable. R^2 -values closer to 1 indicate that the variability of the dependent variable can be explained by the independent variable (Hutcheson, 2011). If the information provided by the explanatory variables (SCD slope) was significant, it was indicated by $p < 0.05$.

Population stability was evaluated by determining quotients between successive size-classes and by displaying the results graphically. The interpretation of the quotients follows Shackleton (1993), Botha *et al.* (2004), and Venter & Witkowski (2010), who stated that constant quotients between successive size-classes indicate a stable population, while fluctuations in quotients display unstable populations.

The Permutation Index (Equation 1) evaluates the deviation of a population from a monotonic decline, which can be expected to be present in a stable population. It is the sum of the absolute distances between the expected and real location (rank) of all size classes (Wiegand *et al.*, 2000). The permutation index is higher in a discontinuous size-class distribution than in a continuous, monotonically declining population, which indicates stability.

$$P = \sum_{i=1}^K |J_i - i|; \quad J_i = 1, \dots, K$$

Equation 1

where J_i is the rank of size class i ($i = 1$ for the smallest trees), with the highest rank ($J_i = 1$) given for the most frequent size class, and K is the total number of size classes.

Simpson's Index of Dominance (Equation 2) measures the evenness of occupation of the size class, ignoring the order in which size classes are arranged (Wiegand *et al.*, 2000). Values

above 0.1 reveal steeper size frequency than would be expected from an exponentially declining population, suggesting that the size classes are arranged in descending order, and values below 0.1 shows that size classes are more evenly distributed.

$$C = \frac{1}{N(N-1)} \sum_{i=1}^K Ni(Ni-1)$$

Equation 2

where N is the total number of trees, Ni the number of trees in class i , and K is the total number of size classes.

Analyses of variance (ANOVA) were used in Statistica 13 to determine whether woody individuals in the respective size classes differed among the herbivory and fire treatments for the complete woody community at the Nkuhlu exclosures. The data set was firstly tested for normality by using Kolmogorov-Smirnov & Lilliefors tests. For data sets that met normality, a One-way ANOVA was applied, whereas $\text{Log}_{10}(x+1)$ transformation was applied to data that did not meet normality. In cases where normality could still not be revealed after transformation, a non-parametric Kruskal Wallis ANOVA was applied. To test for significant woody abundance differences ($p < 0.05$) between treatments for each size-class, unequal N Tukey's t-tests were applied.

The species considered for demographic analyses were selected according to their dominance and ecological importance in this savanna ecosystem. Species dominance in each vegetation zone across the riparian topographic sequence were taken into consideration during species selections (Figure 3.2) (Siebert & Eckhardt, 2008). They include *Diospyros mespiliformis*, *Ziziphus mucronata*, *Pappea capensis*, *Senegalia nigrescens*, *Vachellia exuvialis*, *Gymnosporia senegalensis*, *Spirostachys africana*, *Flueggea virosa*, *Vachellia grandicornuta*, *Rhigozum zambesiacum*, *Dichrostachys cinerea*, and *Combretum apiculatum* (Table 5.2). The abundance of a species was also considered in the selection since some ecologically important species are sparsely represented in the study area. The species were also classified as either an encroacher or non-encroacher species based upon their specific ecology (i.e. ability to respond to disturbance or to occupy open spaces) and their palatability (Skarpe, 1990; Hudak & Wessman, 1998; Eggemeyer & Schwinning, 2009; Van Auken, 2009; Eldridge et al., 2011; Twidwell et al., 2013) (Table 7.2).

Regeneration of the communities and populations was considered good when the following was observed: SCD indicated a negative slope together with the R^2 -value closer to 1; PI of 0 (monotonic decline in SCD); and SDI > 0.1 – 0.4 , which suggests slightly uneven size-classes

frequency distribution without the complete dominance of a few size classes. These parameters graphically display a typical inverse J-shaped SCD curve, which is considered good regeneration, with highest mean or most abundant individuals in size-class 1 and successive size-classes declining in abundance.

Table 7.2: Pre-selected diagnostic encroacher and non-encroacher woody species per vegetation zone.

Vegetation zone	Encroachers	Non-encroachers
Riparian	<i>Gymnosporia senegalensis</i> <i>Spirostachys africana</i> <i>Flueggea virosa</i>	<i>Diospyros mespiliformis</i> <i>Ziziphus mucronata</i>
Sodic	<i>Vachellia grandicornuta</i> <i>Rhigozum zambesiaceum</i>	<i>Pappea capensis</i>
Crest	<i>Dichrostachys cinerea</i> <i>Combretum apiculatum</i>	<i>Senegalia nigrescens</i> <i>Vachellia exuvialis</i>

7.3 Results

7.3.1. Population structure of the complete woody community

The demography of the 2015 Nkuhlu woody community revealed good regeneration through a typical inverse J-shaped pattern in its size-class distribution (Figure 7.1a). The highest mean number of individuals per plot was found in the seedling height class (<1 m) and declined in abundance within successive height classes (Figure 7.1a). This is also confirmed by the steep negative slope of -1.204 (Table 7.3). The Simpson's dominance index for the overall woody community indicated slightly uneven distribution of size-class occupation ($SDI > 0.1$) whereas the permutation index of 0 indicated that the occupation of size-classes was declining monotonically (Table 7.3). Quotient analyses revealed stability in the lower size classes, whereas the higher size-classes (between 4 & 5 and 5 & 6) were unstable (Figure 7.1b).

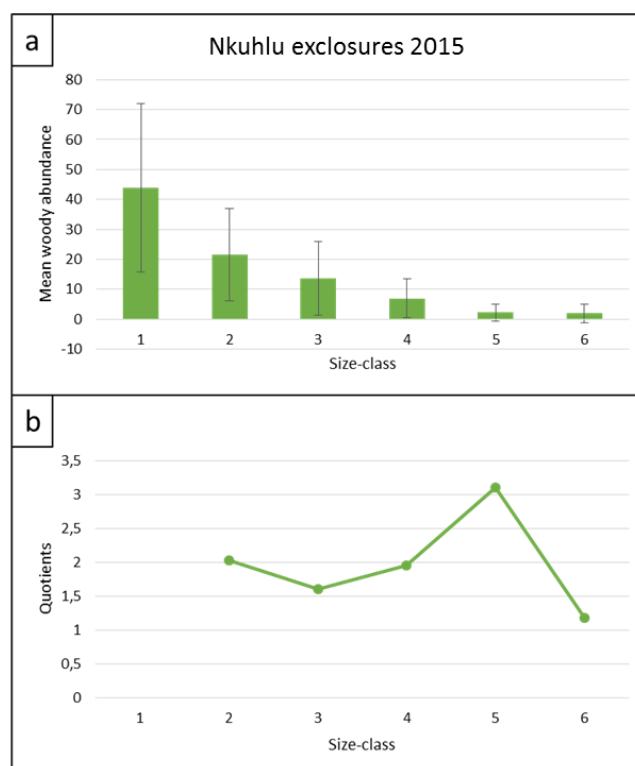


Figure 7.1: Size-class distributions (plant canopy height in 1 m intervals) for mean number of woody individuals per plot ($\pm$ SE) in successive size-classes (a) and quotients between successive size classes (b) for the complete woody community of 2015.

Table 7.3: Summary of size-class distribution measures of the complete woody community in 2015 for each herbivore and fire treatment. Ordinary least square regression analyses (Slope, SE Slope, R^2 , p), Permutation Index (PI) and Simpson's Dominance Index (SDI).

Treatment	Size class distribution					
	Slope	SE Slope	R^2	p	PI	SDI
Complete community	-1.204	0.210	0.892	0.005*	0	0.32
Control	-1.286	0.230	0.886	0.005*	0	0.33
Partial	-1.315	0.141	0.956	0.001*	0	0.41
Full	-1.032	0.261	0.796	0.017*	0	0.27
Control, Fire	-1.232	0.252	0.857	0.008*	0	0.32
Control, No Fire	-1.285	0.230	0.886	0.005*	0	0.34
Partial, Fire	-1.347	0.101	0.978	0.000*	0	0.45
Partial, No Fire	-1.296	0.170	0.936	0.002*	0	0.38
Full, Fire	-0.950	0.264	0.763	0.023*	0	0.26
Full, No Fire	-1.113	0.273	0.806	0.015*	0	0.28

Size-class distribution Slope: negative slope=healthy regeneration, SE Slope: standard error of slope, R^2 : closer to 1=size-class explain variability of mean woody abundance, Significant SCD slope when $p < 0.05$ indicated by *. PI: Permutation Index of 0=monotonic decline in SCD. SDI: Simpson's Dominance Index > 0.1 =uneven size-class occupation. Treatments: Control=all herbivores were present, Partial=elephant and giraffe excluded, Full=all herbivores excluded.

The effect of herbivory (control site) and release from herbivory (in the partially and fully fenced enclosure) on the demography of the woody community revealed an inverse J-shaped distribution of the size-classes for all treatments (Figure 7.2a). The Simpson's dominance index value indicated that the size classes of the woody community was unevenly distributed, although values are less than or close to 0.4, which is still within the 'stable' zone (Table 7.3). The permutation index values of 0 for all treatments indicated a monotonic decline in number of individuals present in each successive size-class (Table 7.3). Therefore, all three treatments hosted good regeneration, although the exclusion of elephant revealed the best regeneration. This was indicated by the significant negative slope and highest R^2 value for the partially fenced enclosure compared to the values of the other treatments (Table 7.3).

Quotient analyses of the complete woody community across herbivory treatments revealed uneven distributions for all communities, although highest stability was revealed for the woody community in absence of all herbivores (full enclosure) (Figure 7.2b). The SDI for this community was between 0.1 and 0.3, which further support community stability.

Significant variance in mean woody abundances per plot was revealed for size classes 2, 3, 5 and 6 across herbivore treatments. Post hoc tests revealed significantly more ($p < 0.05$) individuals in these size classes in the full enclosure compared to the control site and partially fenced enclosure (Figure 7.2a). This explains the higher stability of woody regeneration in the absence of all herbivore activity (Figure 7.2b).

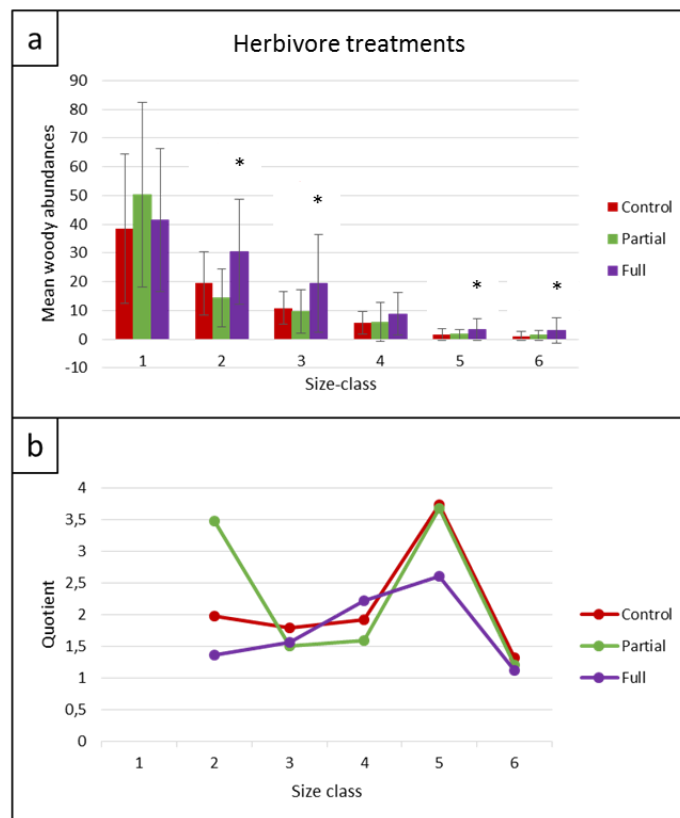


Figure 7.2: Size-class distributions (plant height in 1 m intervals) for mean number of woody individuals per plot ($\pm$ SE) in successive size-classes (a) and quotients between size-classes (b) across herbivory treatments in 2015. Control: all herbivores were present; Partial: elephant & giraffe were excluded; Full: all herbivores were excluded. Significant differences from ANOVA statistics are indicated with *.

Good regeneration was revealed for both the fire and no-fire treatments (Table 7.3a). Quotient analyses, however, revealed unstable woody communities in all three herbivore treatments, irrespective of fire treatment (Figure 7.3b). No significant effect of fire on woody abundances could be detected for any of the size-classes within the different herbivore treatments, with the exception of woody individuals between 4 m and 5 m (size class 5). Post hoc tests revealed significantly higher abundance ($p=0.045$) of woody individuals in the partially fenced enclosure where fire was absent (Figure 7.3).

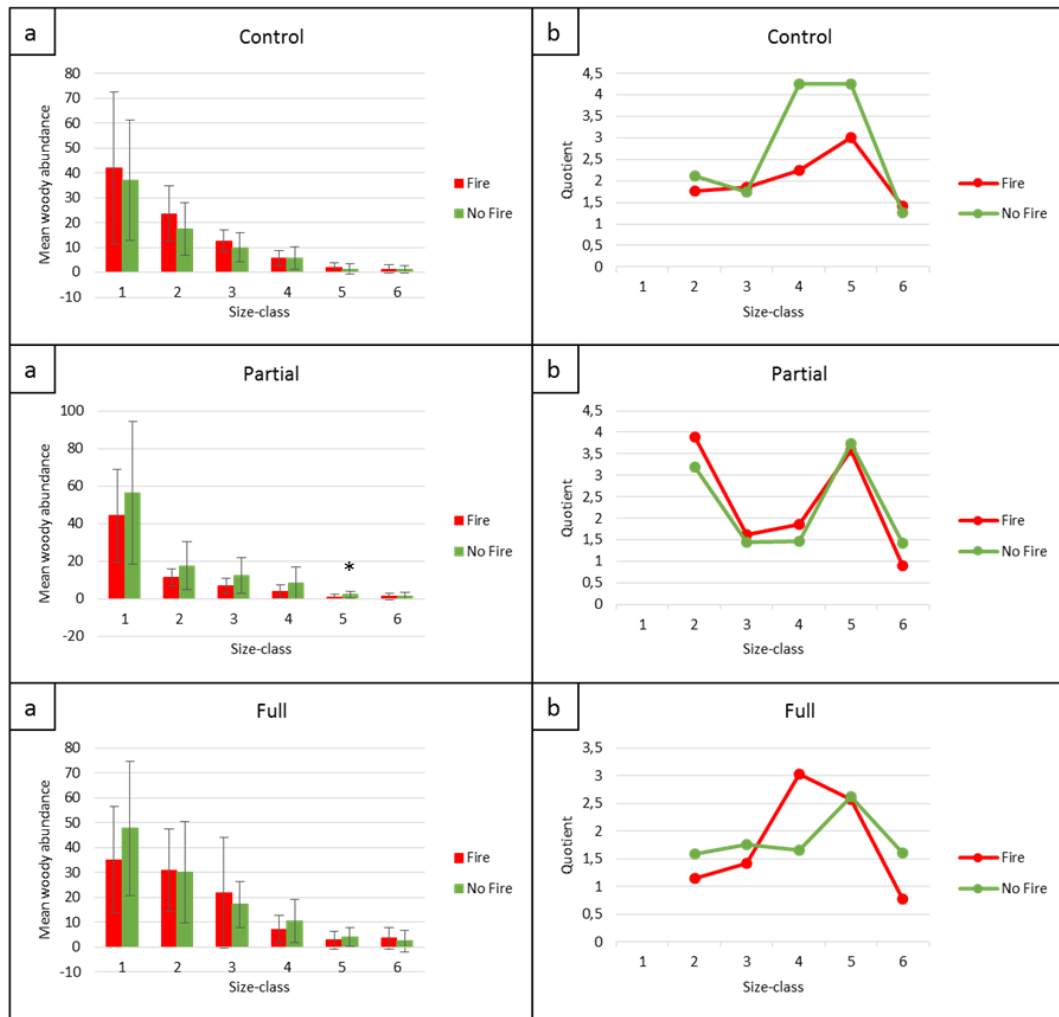


Figure 7.3: Size-class distributions (plant height in 1 m intervals) for mean number of woody individuals per plot ($\pm$ SE) in successive size-classes (a) and quotients between size-classes (b) across fire treatments in 2015. Control: all herbivores were present; Partial: elephant & giraffe were excluded; Full: all herbivores were excluded. Significant differences from ANOVA statistics are indicated with *.

7.3.2. Population structure of preselected key species

To investigate the population demography of key species, differentiation between fire treatments were not considered, due to limited evidence of a significant fire effect (see 7.3.1) and low numbers of individuals per species for each fire treatment respectively. Patterns observed through analyses therefore only represent herbivore treatment and catenal position effects.

Riparian vegetation zone:

When all measures of size-class distribution were considered (ordinary least square (OLS) regression, PI and SDI), regeneration of encroacher species *Gymnosporia senegalensis* and *Spirostachys africana* was favoured by the exclusion of all herbivores (Table 7.4). Size-class

distribution for individuals of these two species revealed R^2 values above 0.9 in the fully fenced enclosure, which indicated that size-class explained more than 90% of the variability in number of individuals (Table 7.4). An inverse J-shaped SCD was displayed for *G. senegalensis* (Figure 7.4a) with more individuals in the lower size classes, which was confirmed by a PI value of 0 (Table 7.4). This was also evident from the quotient analyses. SCD of *S. africana* population in the fully fenced enclosure was altered from the J-shaped curve, which was supported by a PI value of 2 (monotonic decline was interrupted) (Table 7.4). Recruitment bottlenecks occurred in size-classes 2, 3, and 4. The *S. africana* population was less stable than *G. senegalensis* (lower R^2 values, but higher p and PI values, Figure 7.4), although highest population stability was in the fully fenced enclosure (negative slope, $R^2 = 0.9$, $p < 0.005$, SDI = 0.21).

Results from the ordinary least square (OLS) regression results indicated that regeneration of the encroacher *Flueggea virosa* was healthy in the partially fenced enclosure where only mega-herbivores (in this experiment, elephant and giraffe) were excluded (Table 7.4). The negative slope of SCD together with a PI of 0 and SDI of 0.31 indicated an inverse J-shaped SCD slope (Table 7.4). Alteration in an inverse J-shaped SCD curve occurred in the presence (PI=2) and absence (PI=2) of all herbivores due to recruitment bottlenecks (Figure 7.4). Population stability decreased for individuals between 4 m and 5 m in the partially fenced enclosure.

The non-encroacher species of the riparian vegetation zone were considerably less abundant than the encroacher species (Figure 7.4 and 7.5). SCD of *Diospyros mespiliformis* did not conform to the typical J-shaped curve across any of the three herbivore treatments (Figure 7.5). The PI values of all herbivore treatments were above 0 which indicated that SCD's did not decline monotonically (Table 7.6). Despite a recruitment bottleneck imposed by low numbers of individuals in size-class 4 (PI=2) (Figure 7.5), the fully fenced enclosure hosted the most stable population for *D. mespiliformis*. Variability explained by size-classes for the full enclosure was 94.2% (R^2 -value) with a significant SCD slope ($p=0.001$) (Table 7.4). Quotient analysis further revealed that the most stable population occurred in the fully fenced enclosure (Figure 7.5).

Ziziphus mucronata had bad regeneration in all herbivore treatments with high PI values, low R^2 and p -values > 0.05 (Table 7.4), skewed size-class frequencies and fluctuating quotients (Figure 7.5). Instability was revealed for the population inside the full enclosure where no individuals in four of the six size-classes were recorded (positive SCD slope; PI=10, SDI=0.5 (Table 7.4)).

Table 7.4: Summary of size-class distribution measures for the key woody encroacher and non-encroacher species of the riparian vegetation zone in different herbivory treatments in 2015; Ordinary least square regression analyses (Slope, SE Slope, R^2 , p), Permutation Index (PI) and Simpson's Dominance Index (SDI).

Vegetation zone	Ecological status	Species	Treatment	Size class distribution					
				Slope	SE Slope	R^2	p	PI	SDI
Riparian	Encroachers	<i>Gymnosporia senegalensis</i>	Overall	-2.080	0.499	0.813	0.014*	0	0.42
			Control	-1.627	0.321	0.865	0.007*	0	0.41
			Partial	-1.339	0.342	0.793	0.017*	0	0.32
			Full	-1.829	0.297	0.905	0.004*	0	0.49
		<i>Spirostachys africana</i>	Overall	-0.597	0.069	0.949	0.001*	2	0.22
			Control	-0.638	0.166	0.787	0.018*	2	0.21
			Partial	-0.769	0.253	0.698	0.038*	2	0.26
			Full	-0.518	0.077	0.919	0.003*	2	0.21
		<i>Flueggea virosa</i>	Overall	-1.942	0.670	0.678	0.044*	2	0.33
			Control	-1.756	0.609	0.675	0.045*	2	0.34
			Partial	-1.479	0.462	0.719	0.033*	0	0.31
			Full	-1.511	0.442	0.745	0.027*	2	0.34
	Non-encroachers	<i>Diospyros mespiliformis</i>	Overall	-0.571	0.148	0.789	0.018*	4	0.21
			Control	-0.710	0.240	0.687	0.041*	4	0.23
			Partial	0.115	0.156	0.119	0.503	12	0.11
			Full	-0.580	0.072	0.942	0.001*	2	0.22
		<i>Ziziphus mucronata</i>	Overall	-0.445	0.415	0.224	0.343	4	0.28
			Control	-0.307	0.235	0.299	0.262	4	0.13
			Partial	-0.458	0.352	0.297	0.264	4	0.39
			Full	0.141	0.321	0.046	0.684	10	0.5

Size-class distribution Slope: negative slope=healthy regeneration, SE Slope: standard error of slope, R^2 : closer to 1=size-class explain variability in number of individuals, Significant SCD slope when $p < 0.05$ indicated by *. PI: Permutation Index of 0=monotonic decline in SCD. SDI: Simpson's Dominance Index > 0.1 =uneven size-class occupation. Treatments: Control=all herbivores present, Partial=elephant and giraffe excluded, Full=all herbivores excluded; Overall=across all three herbivore treatments.

Encroachers

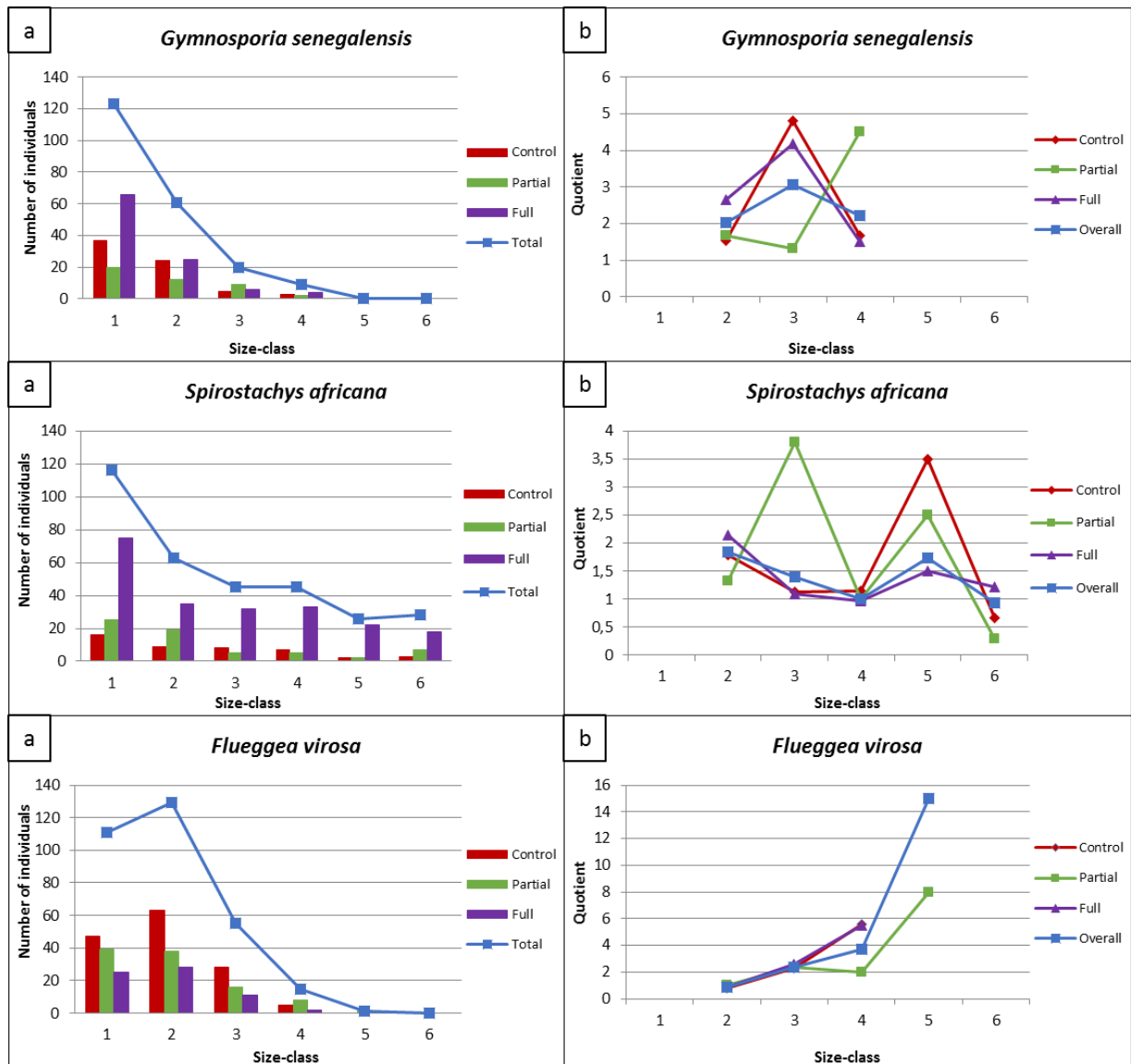


Figure 7.4: Size-class distributions (plant height in 1 m intervals) for the abundance of *Gymnosporia senegalensis*, *Spirostachys africana*, and *Flueggea virosa* in successive size-classes (a) and quotients for these individuals between size-classes (b) across herbivory treatments. Control: all herbivores present; Partial: elephant and giraffe excluded; Full: all herbivores excluded. Total/Overall: indicate SCD/Quotients of population, without distinguishing between herbivore treatments.

Non-encroachers

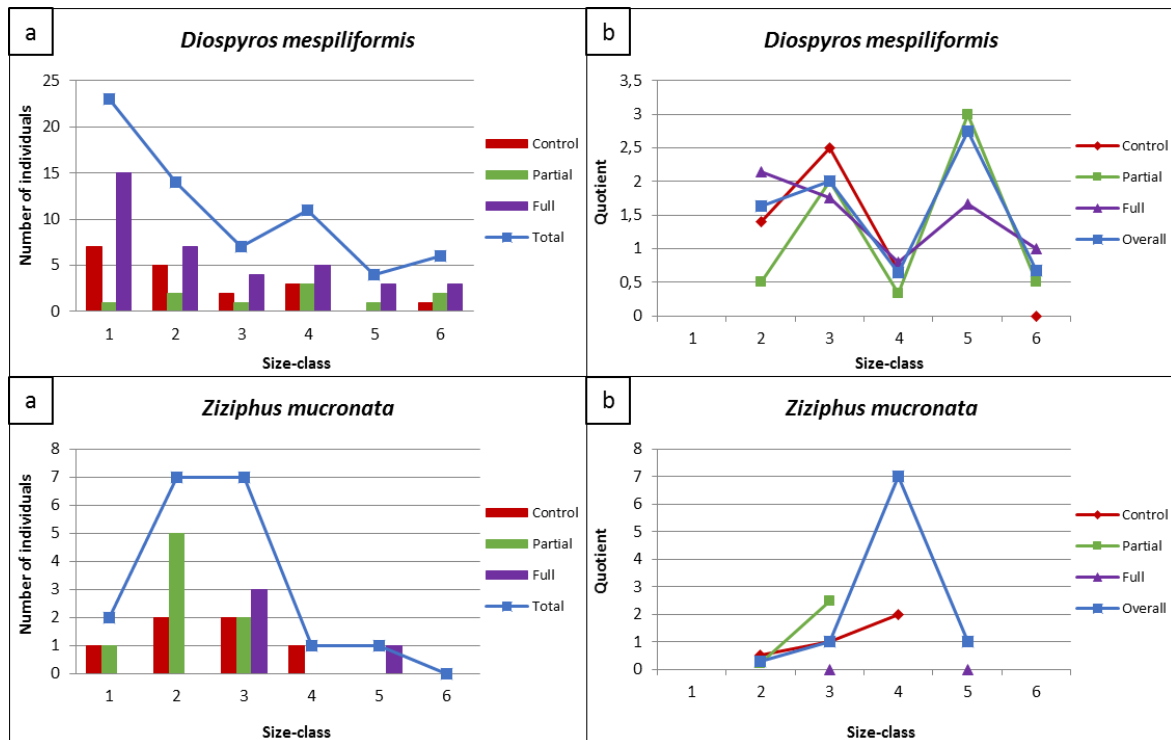


Figure 7.5: Size-class distributions (plant height in 1 m intervals) for the abundance of *Diospyros mespiliformis* and *Ziziphus mucronata* in successive size-classes (a) and quotients for these individuals between size-classes (b) across herbivory treatments in 2015. Control: all herbivores present; Partial: elephant and giraffe excluded; Full: all herbivores excluded. Total/Overall: indicate SCD/Quotients of population, without distinguishing between herbivore treatments.

Sodic vegetation zone:

Vachellia grandicornuta, an encroaching species dominating the sodic vegetation zone, showed the best regeneration in the absence of mega-herbivores (Table 7.5). A monotonic decline in SCD were present for size-classes 1 to 5 followed by a slight increase in abundance in size-class 6 (therefore $PI=2$) (Figure 7.6). It was also evident from the quotient analyses that the population in the partially fenced enclosure was more stable than populations in the control site and fully fenced enclosure (Figure 7.6). Recruitment bottlenecks were present in the fully fenced enclosure, indicated by the high PI value ($PI=8$, Table 7.5; Figure 7.6).

Regression and SCD analyses of the encroacher species *Rhigozum zambesiaceum* revealed revealed bad regeneration in all herbivore treatments ($PI > 2$, $SDI > 0.4$, fluctuating quotients and low R^2 values). The total number of individuals in size-class 2 (saplings) were more than double than that in size-class 1 (seedlings) (Figure 7.6), which furthermore support that the *R. zambesiaceum* population is unstable at this study site (Figure 7.6).

Only one non-encroacher species, *Pappea capensis*, had enough individuals to compare across herbivore treatments. As expected, the exclusion of all herbivores led to good regeneration (Slope=-1.554; $R^2=0.91$; $p=0.003$) (Table 7.5) and a stable population structure (inverse J-shaped curve, PI =0), although uneven SCD's were revealed (SDI>0.4, Table 7.5, Figure 7.7). Little fluctuation occurred in quotients for this species in the full enclosure, suggesting population stability in the absence of herbivores (Figure 7.7). Herbivores inevitably led to unstable population structure of *P. capensis*, with or without elephant (Table 7.5, Figure 7.7). Seedling recruitment was high in all herbivore treatments, although seedling establishment, measured as abundances in size class 2 (i.e. from seedlings to saplings) was lower in the presence of herbivores, including elephant.

Table 7.5: Summary of size-class distribution measures for the key woody encroacher and non-encroacher species of the sodic vegetation zone in different herbivory treatments in 2015; Ordinary least square regression analyses (Slope, SE Slope, R^2 , p), Permutation Index (PI) and Simpson's Dominance Index (SDI).

Vegetation zone	Ecological status	Species	Treatment	Size class distribution					
				Slope	SE Slope	R^2	p	PI	SDI
Sodic	Encroachers	<i>Vachellia grandicornuta</i>	Overall	-0.960	0.216	0.832	0.011*	4	0.28
			Control	-1.008	0.131	0.936	0.002*	2	0.42
			Partial	-1.202	0.104	0.971	0.000*	2	0.4
			Full	-0.615	0.391	0.382	0.191	8	0.26
		<i>Rhigozum zambesiacum</i>	Overall	-1.618	0.504	0.720	0.033*	2	0.42
			Control	-0.652	0.304	0.534	0.099	6	0.71
			Partial	-1.211	0.313	0.789	0.018*	4	0.52
			Full	-1.495	0.546	0.652	0.052	2	0.48
	Non-encroachers	<i>Pappea capensis</i>	Overall	-1.463	0.158	0.955	0.001*	0	0.48
			Control	-1.339	0.249	0.878	0.006*	2	0.7
			Partial	-1.008	0.183	0.884	0.005*	2	0.37
			Full	-1.554	0.244	0.910	0.003*	0	0.45

Size-class distribution Slope: negative slope=healthy regeneration, SE Slope: standard error of slope, R^2 : closer to 1=size-class explain variability in number of individuals, Significant SCD slope when $p<0.05$ indicated by *. PI: Permutation Index of 0=monotonic decline in SCD. SDI: Simpson's Dominance Index >0.1=uneven size-class occupation. Treatments: Control=all herbivores present, Partial=elephant and giraffe excluded, Full=all herbivores excluded; Overall=Population across all three herbivore treatments.

Encroachers

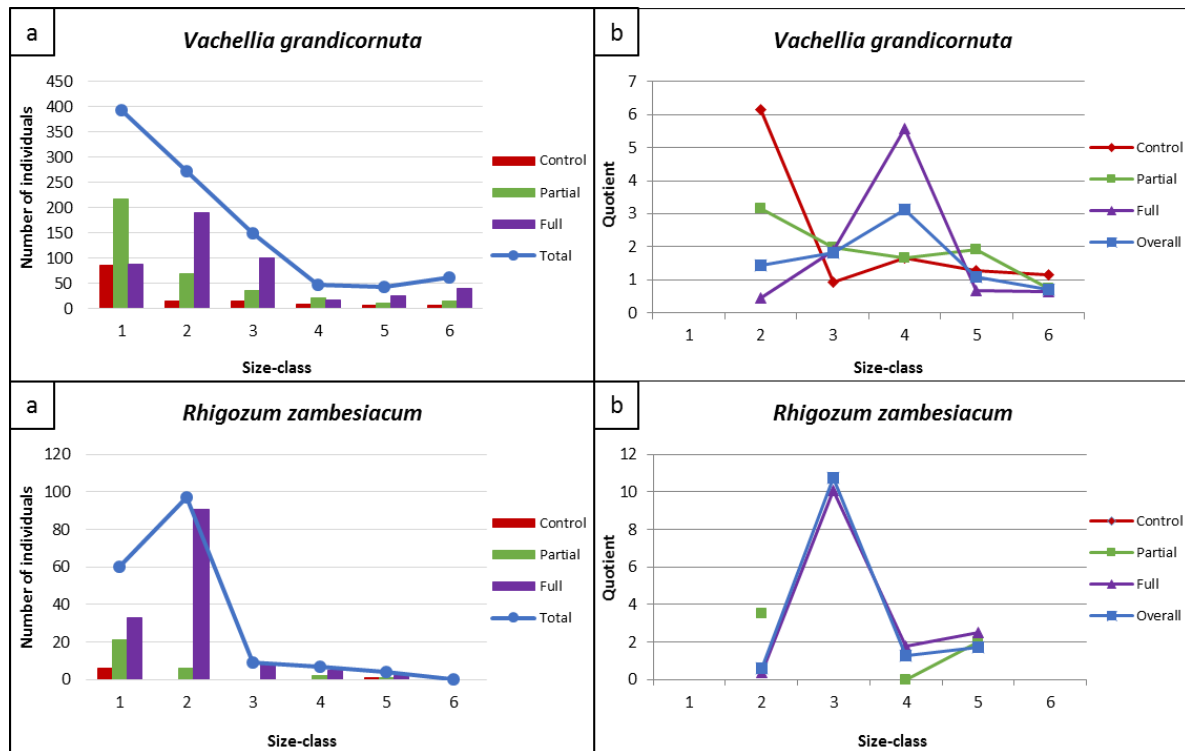


Figure 7.6: Size-class distributions (plant height in 1 m intervals) for the abundance of *Vachellia grandicornuta* and *Rhigozum zambesiacum* in successive size-classes (a) and quotients for these individuals between size-classes (b) across herbivory treatments in 2015. Control: all herbivores present; Partial: elephant and giraffe excluded; Full: all herbivores excluded. Total/Overall: indicate SCD/Quotients of population, without distinguishing between herbivore treatments.

Non-encroacher

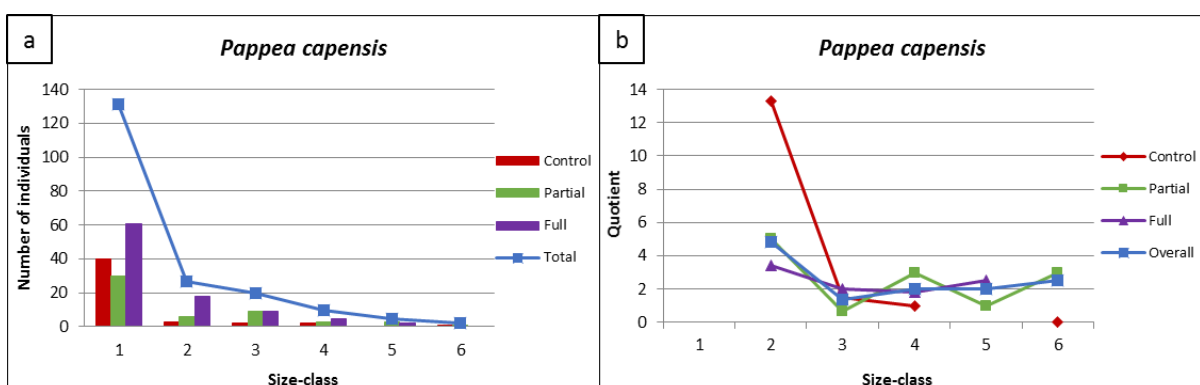


Figure 7.7: Size-class distributions (plant height in 1 m intervals) for the abundance of *Pappea capensis* in successive size-classes (a) and quotients for these individuals between size-classes (b) across herbivory treatments in 2015. Control: all herbivores present; Partial: elephant and giraffe excluded; Full: all herbivores were excluded. Total/Overall: indicate SCD/Quotients of population, without distinguishing between herbivore treatments.

Crest vegetation zone:

Regeneration of *Dichrostachys cinerea* was most stable in the control site (Table 7.6; Figure 7.8). This was indicated by a significant negative SCD slope ($p=0.039$; Slope=-1.59) together with a high R^2 value, a low PI value (2) and SDI values between 0.1 and 0.2 (Table 7.6). Although *D. cinerea* was most abundant in the fully fenced enclosure (Figure 7.8), its negative SCD slope was insignificant ($p=0.119$) and had a PI of 4 (Table 7.6), which indicated recruitment bottlenecks.

Regeneration of *Combretum apiculatum* did not indicate good regeneration in any herbivore treatments as revealed by OLS regression analyses (Table 7.6). This was also confirmed by the high PI for populations in all three treatments (Table 7.6). The partially fenced enclosure hosted the most stable population with a steep negative SCD slope (-0.744, although insignificant with $p=0.065$) and highest R^2 value (0.613) (Table 7.6; Figure 7.8).

Demography of the non-encroacher *Senegalia nigrescens* revealed abundant seedlings (size-class 1) followed by over 70% decline in sapling individuals (size-class 2) across all three herbivore treatments (Figure 7.9). Good regeneration was not revealed for any of the three herbivore treatments (PI>0 and unstable quotients) (Table 7.6; Figure 7.9). The control site hosted the most stable population (slope=-1.518; $R^2=0.876$; $p=0.006$; PI=2; SDI=0.25) (Table 7.6).

Regeneration of *Vachellia exuvialis* was good in the control site (PI=0, uneven SCD's (SDI=0.48)), conforming to an inverse J-shaped curve (slope=-1.784; $R^2=0.852$; $p=0.009$) (Table 7.6; Figure 7.9). Fluctuation of quotients was however present in all three herbivore treatments (Figure 7.9).

Table 7.6: Summary of size-class distribution measures for the key woody encroacher and non-encroacher species of the crest vegetation zone in different herbivory treatments in 2015; Ordinary least square regression analyses (Slope, SE Slope, R^2 , p), Permutation Index (PI) and Simpson's Dominance Index (SDI).

Vegetation zone	Ecological status	Species	Treatment	Size class distribution					
				Slope	SE Slope	R^2	p	PI	SDI
Crest	Encroachers	<i>Dichrostachys cinerea</i>	Overall	-1.799	0.779	0.571	0.082	0	0.27
			Control	-1.590	0.526	0.696	0.039*	2	0.31
			Partial	-1.794	0.666	0.645	0.054	4	0.35
			Full	-1.621	0.818	0.495	0.119	4	0.29
		<i>Combretum apiculatum</i>	Overall	-0.573	0.300	0.477	0.129	4	0.22
			Control	-0.471	0.351	0.310	0.251	6	0.22
			Partial	-0.744	0.295	0.613	0.065	2	0.25
			Full	-0.507	0.239	0.530	0.101	6	0.2
	Non-encroachers	<i>Senegalia nigrescens</i>	Overall	-1.327	0.246	0.879	0.006*	4	0.65
			Control	-1.518	0.285	0.876	0.006*	2	0.82
			Partial	-1.161	0.268	0.824	0.012*	4	0.63
			Full	-1.111	0.203	0.882	0.005*	4	0.55
		<i>Vachellia exuvialis</i>	Overall	-1.392	0.363	0.786	0.019*	2	0.37
			Control	-1.784	0.372	0.852	0.009*	0	0.48
			Partial	-1.115	0.347	0.721	0.032*	4	0.32
			Full	-0.816	0.310	0.635	0.058	6	0.24

Size-class distribution Slope: negative slope=healthy regeneration, SE Slope: standard error of slope, R^2 : closer to 1=size-class explain variability in number of individuals, Significant SCD slope when $p < 0.05$ indicated by *. PI: Permutation Index of 0=monotonic decline in SCD. SDI: Simpson's Dominance Index > 0.1 =uneven size-class occupation. Treatments: Control=all herbivores present, Partial=elephant and giraffe excluded, Full=all herbivores excluded; Overall=Population across all three herbivore treatments.

Encroachers

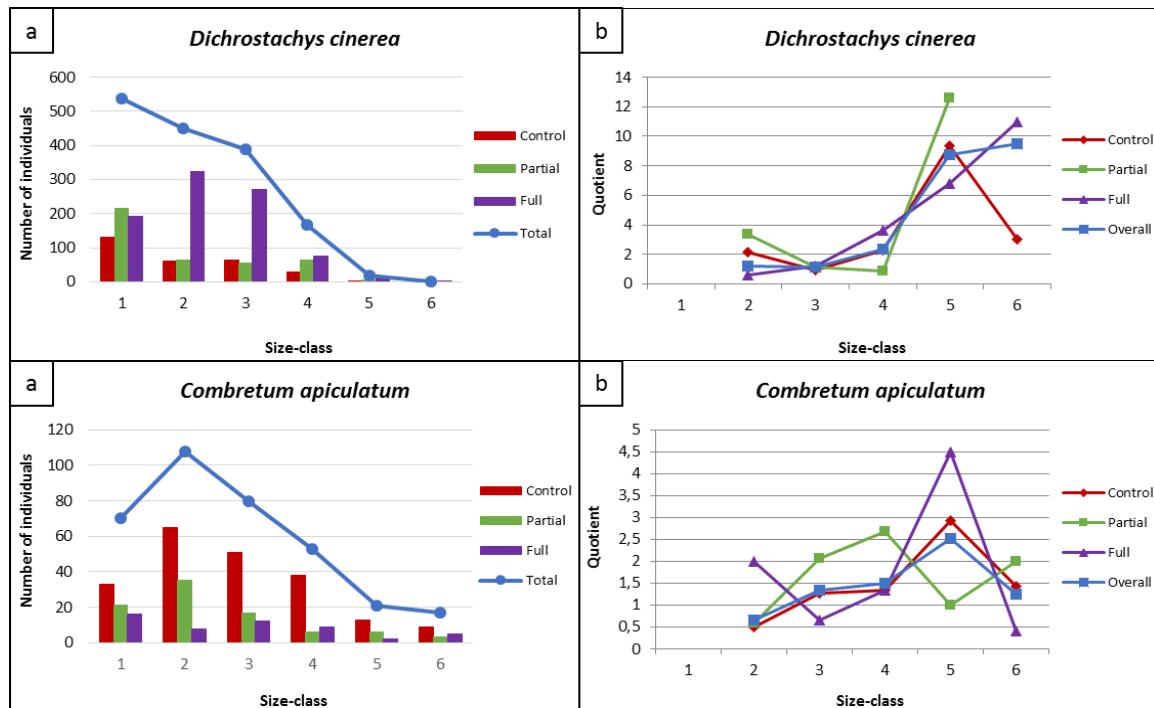


Figure 7.8: Size-class distributions (plant height in 1 m intervals) for the abundance of *Dichrostachys cinerea* and *Combretum apiculatum* in successive size-classes (a) and quotients for these individuals between size-classes (b) across herbivory treatments in 2015. Control: all herbivores were present; Partial: elephant and giraffe excluded; Full: all herbivores were excluded. Total/Overall: indicate SCD/Quotients of population, without distinguishing between herbivore treatments.

Non-encroachers

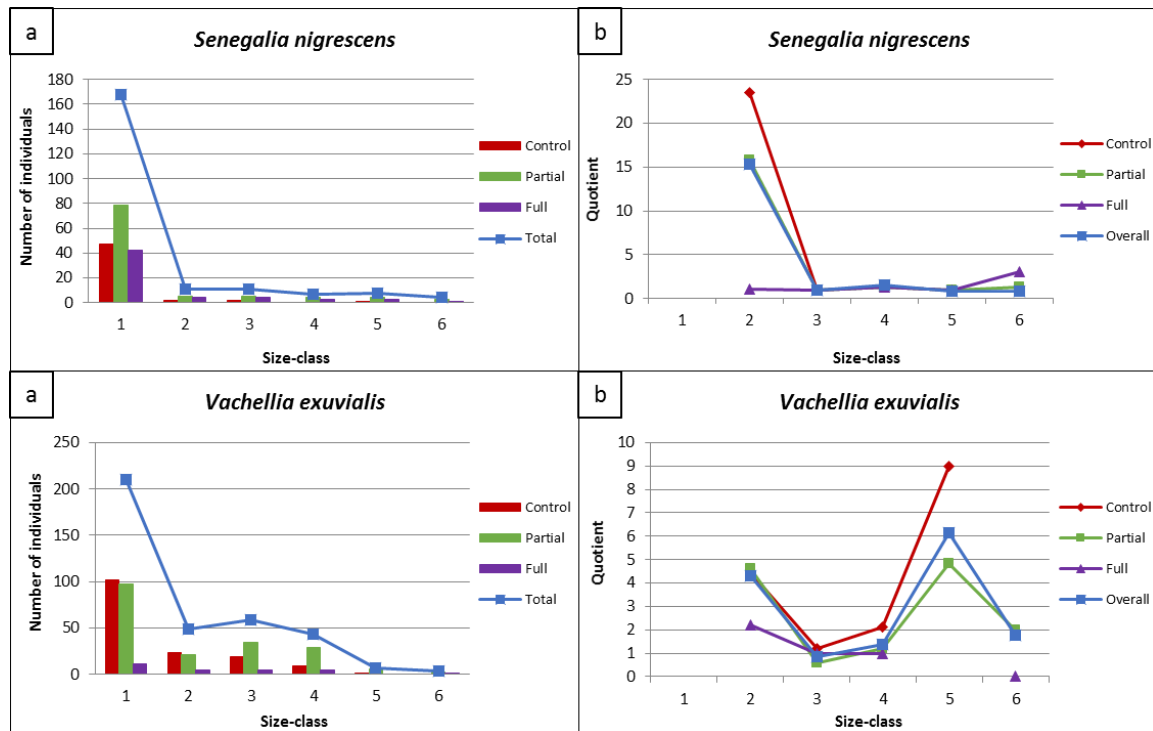


Figure 7.9: Size-class distributions (plant height in 1 m intervals) for the abundance of *Senegalia nigrescens* and *Vachellia exuvialis* in successive size-classes (a) and quotients for these individuals between size-classes (b) across herbivory treatments in 2015. Control: all herbivores present; Partial: elephant and giraffe excluded; Full: all herbivores were excluded. Total/Overall: indicate SCD/Quotients of population, without distinguishing between herbivore treatments.

Regeneration of encroacher species was better in the absence of herbivores (either only elephant or all herbivores) (Table 7.7). Response of non-encroacher regeneration was species specific. Regeneration of broad-leaved palatable species was better where elephants or all herbivores were excluded, while microphyllous palatable species were adapted to herbivores (through spinescent traits) and had better regeneration in the presence of herbivores (Table 7.7).

Table 7.7: Summary of the herbivore effect on pre-selected woody species demography (i.e. regeneration) at the Nkuhlu enclosure in 2015.

Vegetation zone	Species	Ecological status	Treatment with healthy regeneration
Riparian	<i>Gymnosporia senegalensis</i>	Encroacher	Full enclosure
	<i>Spirostachys africana</i>	Encroacher	None; ^a Full enclosure
	<i>Flueggea virosa</i>	Encroacher	Partial enclosure
	<i>Diospyros mespiliformis</i>	Non-encroacher	None; ^a Full enclosure
	<i>Ziziphus mucronata</i>	Non-encroacher	None; ^a Partial enclosure
Sodic	<i>Vachellia grandicornuta</i>	Encroacher	Partial enclosure
	<i>Rhigozum zambesiaceum</i>	Encroacher	None; ^a Partial enclosure
	<i>Pappea capensis</i>	Non-encroacher	Full enclosure
Crest	<i>Dichrostachys cinerea</i>	Encroacher	None; ^a Control site
	<i>Combretum apiculatum</i>	Encroacher	None; ^a Partial enclosure
	<i>Senegalia nigrescens</i>	Non-encroacher	None; ^a Control site
	<i>Vachellia exuvialis</i>	Non-encroacher	Control site

Herbivore treatments: Control site=all herbivores present, Partial enclosure=elephant and giraffe excluded, Full enclosure=all herbivores excluded; ^a treatment with most stable population.

7.4 Discussion

This study revealed strong evidence of positive community responses to herbivore exclusion. All herbivore treatments hosted significant SCD slopes, but the absence of all herbivore activity for 13 years resulted in a more stable woody community, especially in higher size-classes. These increases in woody SCD stability was ascribed to a higher woody abundance in higher size-classes. Therefore, where trees were released from browsing suppression, i.e. browse-trap, more woody individuals could grow into higher size-classes (Staver & Bond, 2014). It is still unclear whether the patterns observed are a possible mega-herbivore (specifically elephant) effect, which have previously been considered a main attribute to woody structure change (Eckhardt *et al.*, 2000; Whyte *et al.*, 2003; Wiseman *et al.*, 2004; Asner *et al.*, 2009), or a meso-herbivore (i.e. impala, kudu, nyala etc.) effect. Recent studies found evidence that meso-herbivores have an equal or even a stronger effect than mega-herbivores on woody population structure in savanna ecosystems (Moe *et al.*, 2009; O’Kane *et al.*, 2012). This study revealed that meso-herbivores were responsible for instability in higher size-classes. In the presence or absence of elephants, populations were unstable due to instability in numbers in the size classes >4 m. Although meso-herbivores do not directly affect higher size-classes (>2 m) through browsing, they created a browse-trap in lower size-classes which over a long-term period inhibited woody growth (Prins & Van der Jeugd, 1993; Augustine & McNaughton, 2004; Moe *et al.*, 2009). This browse-trap is evident in the quotient results of the partially fenced enclosure. Exclusion of elephants assumingly led to increased meso-herbivore activity (Fritz *et*

al., 2002; Valeix *et al.*, 2008; Hilbers *et al.*, 2015; Lagendijk *et al.*, 2015), which prompted instability between size class 1 and 2. Seedlings (size-class 1) were much more abundant than saplings (size-class 2). This severe drop in abundance indicated a bottleneck in recruitment of seedlings (Lykke, 1998; Prior *et al.*, 2009). These size-classes were directly subjected to utilisation by browsers, which inhibited woody growth past seedling stage. Only those species able to tolerate browsing (either they were unpalatable or fast growing (Fornara & Du Toit, 2008)), have grown into higher size-classes. This could have resulted in the instability noted in higher size-classes in both the control site (presence of elephant) and partially fenced enclosure (absence of elephant).

The fire treatments applied at the Nkuhlu enclosure revealed no significant effect on the woody community demography. The fire-mediated recruitment bottleneck hypothesis states that fire disturbances restrict the number of juveniles growing past the seedling size class to become fire tolerant trees (Bond, 2008; Lehman *et al.*, 2009). This was not observed in the results from the fire treatments in this specific experimental setting (Nkuhlu enclosures), which revealed an inverse J-shaped curve, with the highest abundance of individuals in the seedling height class, in both the fire and no fire treatments. Herbivory is therefore suggested as the main driver of woody community structure in this particular savanna ecosystem. This corresponds with Sankaran *et al.* (2013) who reported strong herbivore control of woody vegetation, even in the absence of fire. This is especially true for arid and semi-arid savannas (such as this study site) and not mesic savannas, where fire has a substantial effect on woody recruitment (Sankaran *et al.*, 2013).

Species-specific demographic analyses revealed unique responses to herbivory and the exclusion thereof, irrespective of being an encroacher or non-encroacher species. The different vegetation zones along the catenal sequence are known to host unique assemblages of plant species and vegetation structure (Siebert & Eckhardt, 2008). The riparian zone on the banks of the Sabie River, which is also considered nutrient-rich, is particularly favoured by herbivores due to access to water and nutritious vegetation (Scholes, 1990). The presence of herbivores in this zone resulted in the suppression of key encroacher and non-encroacher regeneration. For the encroacher populations *Spirostachys africana* and *Flueggea virosa* were suppressed by presence of all mammalian herbivores (mega- and meso-herbivores), while *Gymnosporia senegalensis* was suppressed by especially meso-herbivores (absence of mega-herbivores). Therefore, encroachment by these species could be controlled by the presence of herbivores. However, results from this study indicated that herbivory is likely to cause negative regeneration responses of the desirable non-encroaching key species *Diospyros mespiliformis*. All four these key species are commonly browsed by herbivores (Sauer *et al.*, 1977; Bowland, 1990; Pooley,

1997; Watson & Owen-Smith, 2002; Makhabu *et al.*, 2006; Scogings *et al.*, 2012; Penderis & Kirkman, 2014; Wigley *et al.*, 2014).

The non-encroacher *Ziziphus mucronata* is a palatable woody species (Owen-Smith & Cooper, 1987) highly favoured by both meso- (Sauer *et al.*, 1977; Bowland, 1990; Pooley, 1997) and mega-herbivores (Owen-Smith & Cooper, 1987; Wiseman *et al.*, 2004). The population of this species was in general unstable, due to low numbers of individuals recorded across the treatments. In the presence of all herbivores and the absence of only mega-herbivores, regeneration of *Z. mucronata* was better compared to where all herbivores were excluded. This species is generally fast-growing and could therefore be expected to recruit into higher size-classes despite utilisation by herbivores (Rooke *et al.*, 2004). Poor recruitment was revealed for the population inside the fully fenced enclosure. Sufficient number of individuals between 5 m and 6 m present in 2015 could be ascribed to rapid recruitment (Rooke *et al.*, 2004) after fences of the enclosure have been raised. The lack of individuals in the lower size-classes could be the result of competition with increased herbaceous biomass (Sankaran *et al.*, 2008).

The sodic vegetation zone is known its nutrient rich vegetation associated with high herbivore activity (Grant & Scholes, 2006). These areas are commonly characterized by grazing lawns and open sites, and overutilization by herbivores can be expected in these nutrient 'hotspots' (Grant & Scholes, 2006; Khomo & Rogers, 2005). The non-encroacher *Pappea capensis*, which is a palatable woody species, mainly utilized by herbivores such as elephant, giraffe, kudu, nyala and bushbuck (Owen-Smith, 2010; Schmitt *et al.*, 2016), indicated good regeneration in the absence of all herbivores. Regeneration of the two encroacher species *Rhigozum zambesiaceum* and *Vachellia grandicornuta* were favoured by the presence of meso-herbivores and absence of mega-herbivores (partially fenced enclosure). Mega-herbivores, specifically elephant was therefore identified as the browsing guild to control regeneration of these two encroacher species, which correlated with the study done by Scogings *et al.* (2012) that recognised elephant effects on these two species through tree felling, debarking, branch breaking and complete uprooting.

On the dystrophic, drier uplands (the so-called crest zone), the well-known encroacher *Dichrostachys cinerea* revealed the most stable population in the presence of all herbivores, which corresponds with the study of Roques *et al.* (2001) where a positive relationship occurred between *D. cinerea* encroachment and grazing pressure. Where all herbivores were released, an increase in abundance (and therefore cover) was noticed for this shrub across the size-classes (Levick *et al.*, 2009) as well as a bottleneck in the lower size-classes. This could be explained by increased interspecific competition with the herbaceous layer (Sankaran *et al.*, 2008) as well as for intraspecific competition, or self-thinning. Encroachment by this species will therefore be difficult to control because of a more stable population in the presence of

herbivores but an increase in abundance (leading to densification) where herbivores have been excluded. Considering these two challenges, it is suggested that the presence of herbivores, and especially elephant would be the best option to control *D. cinerea* encroachment because it will suppress densification of the species across the size-classes.

Combretum apiculatum, also considered an encroacher species at this study site, did not exhibit significantly good regeneration in any herbivore treatment. The most stable population was located in the partially fenced enclosure, where mega-herbivores were excluded. In their study, Scogings *et al.* (2012) noted that *C. apiculatum* was one of their studied species that was most affected by elephants. This explains why elephant exclusion in this study favoured regeneration of *C. apiculatum*. It could furthermore be concluded that regeneration of *C. apiculatum* is stimulated by the presence of especially meso-herbivores because in the absence of all herbivores, recruitment of this species was suppressed. This can be due to competition with the herbaceous layer or with the intense increase in *D. cinerea* individuals, as hypothesized by Scogings *et al.* (2012).

Senegalia nigrescens is a well-known keystone forage species in the Kruger National Park. This non-encroacher species is well adapted to browsing by developing both tolerance (high regrowth rates, extensive branching) and resistance (close thorn spacing) traits (Fornara & Du Toit, 2007). The population demography for *S. nigrescens* revealed evidence for this adaptation through indicating highest stability in the presence of all herbivores. High numbers of seedlings (size-class 1) were present followed by a sharp decline in number of individuals in size-class 2. According to Lykke (1998), this decline can be indicative of a recruitment bottleneck. This pattern in SCD was present in all three herbivore treatments, and therefore the bottleneck in the control site and partially fenced treatment can be attributed to a meso-herbivore induced browse-trap, while in the fully fenced treatment it was the herbaceous layer that imposed a recruitment filter (Sankaran *et al.*, 2008) in which most individuals were trapped.

Vachellia exuvialis, also a non-encroacher species that is commonly browsed upon by herbivores, such as black rhino and elephants (Scogings *et al.*, 2012), revealed most stable regeneration in the presence of all herbivores, whereas the fully fenced treatment hosted very few individuals overall in each size-class. This suggests that *V. exuvialis* can be adapted to herbivore activity (especially meso-herbivores) and mega-herbivores do not explicitly affect their regeneration.

7.5 Conclusion

Healthy, on-going regeneration is evident for the complete woody community at the Nkuhlu exclosures site, regardless of the different herbivore and fire treatments. Results revealed that 13 years of all mammalian herbivore exclusion had significant effects on the abundances of woody individuals in the successive size-classes, hosting a woody community demographically more stable than communities in the control site and partially fenced exclosure. The instabilities revealed for woody community demography of the partial exclosure suggest a meso-herbivore effect, which imposed a recruitment bottleneck in the form of a browse trap. Fire did not have a profound effect in this specific experimental setup, which revealed that herbivory is the main contributor to woody population structure in this study site.

Herbivory is considered as an encroachment control in savanna ecosystems by suppressing woody growth as well as densification. Therefore, it was expected that the absence of herbivore activity, whether only elephant or all herbivores would contribute to stable regeneration of encroacher species. This was true for most of the encroacher species. Results suggest that regeneration of *G. senegalensis* and *S. africana* was suppressed by meso- and mega-herbivores, and therefore the absence of all herbivores contributed to more stable populations. Populations of *F. virosa*, *V. grandicornuta*, *R. zambesiaceum*, and *C. apiculatum* experienced regeneration suppression by mega-herbivores (elephants). This was observed in the more stable populations where only mega-herbivores were excluded. These species could therefore be a problem on game farms located in similar savanna ecosystems where no elephants are present to control their regeneration.

The only encroacher species that did not conform to the hypothesis, which states that herbivore exclusion will cause stable regeneration of encroacher species, was *D. cinerea*. Its population structure was less stable in the absence of herbivores, while the presence of all herbivores led to more stability in its regeneration. Although the population structures of this species indicated that release from all herbivores negatively affected its SCD, this same scenario also led to an increase in abundance of these individuals. This, in turn, could negatively affect regeneration of other woody species. It is therefore suggested that encroachment by *D. cinerea* cannot be controlled by herbivores only.

Regeneration of three desirable non-encroaching species (*Diospyros mespiliformis*, *Pappea capensis* and *Ziziphus mucronata*) was sensitive to herbivory, with or without elephants, while two species, *Senegalia nigrescens* and *Vachellia exuvialis*, were adapted to herbivory. The two species adapted to herbivory will most likely, in the long term, be more abundant than the other key non-encroaching species in this semi-arid savanna area because of their ability to regenerate despite presence of herbivores.

The selected species are only a few of the sensitive key non-encroaching species located in the southern parts of Kruger National Park. Other important key species include *Sclerocarya birrea*, *Lannea schweinfurthii* and *Comretum imberbe*. Unfortunately, due to limited number of individuals across the herbivore treatments in this particular study site, their regeneration status could not be assessed, but should be considered in population demography studies.

CHAPTER 8

Summary and general recommendations

8.1 Main findings

Floristic composition assessment revealed both herbivore and fire effects. Findings corresponded and contributed to the understanding that herbivores and fire are key determinants of savanna structure. After 13 years of herbivore and fire manipulations in this savanna system, changes occurred in the woody floristic composition, which supported the hypothesis that herbivore and fire exclusion will cause alteration in floristic composition. It was evident that the catena interplayed effects of herbivory and fire on the floristics. The eutrophic bottomlands were mostly affected by herbivores in terms of changes in dominant plant families and traits, while the dystrophic uplands were more susceptible to fire-induced changes.

Herbivore exclusion affected woody species composition when seedling and established communities were compared within the same year. The hypothesis tested stated that exclusion of herbivore activity will cause seedling and established communities to be more similar in species composition. This hypothesis was supported by the results from this study. It was derived from the results that the presence of herbivores contributed to dissimilar seedling and established woody community assemblages. The release of herbivores is therefore suggested to create a more similar woody community.

The demographic bottleneck model of savanna systems takes in consideration herbivory, fire and the herbaceous layer to create recruitment bottlenecks in woody regeneration. In this study, results managed to disentangle the effects of meso- and mega-herbivores in combination with fire on encroaching and non-encroaching species. Recruitment bottlenecks were used to interpret many of the patterns observed in the results.

Comparison of seedling and established individual abundances of both encroacher and non-encroacher species revealed that herbivores play an important role in structuring the woody layer. Herbivory negatively affected recruitment of both encroacher and non-encroacher species. Elephants primarily impacted woody abundance, especially in the riparian- and on the crest vegetation zones. It was expected that elephants would affect established individuals more than seedling abundances. Results, however, indicated that elephants affected both these development stages. Meso-herbivore effects were documented in the absence of elephant, especially in the riparian vegetation zone. These results confirmed the hypothesis that elephants indirectly facilitate healthy regeneration through displacement of meso-herbivores. These conclusions were made after results revealed bad woody regeneration trends in the

absence of elephants. The hypothesis that exposure to herbivory and fire will not negatively affect encroacher species abundances, but rather abundances of non-encroachers, was partially supported by the results obtained in this study. Abundance of encroaching seedling species increased in the presence of all herbivores and decreased in the absence of only elephants. Non-encroaching seedling abundances were not significantly reduced by meso-herbivore activity and fire.

Demography analyses in terms of size-class distributions revealed that herbivore exclusion positively affected regeneration of the woody community at the study site. Exclusion of only elephant led to good regeneration patterns, while exclusion of all herbivores resulted in the most stable woody community. Fire did not have a profound effect on size-class distributions in this experimental setup, and therefore herbivory was identified as the main contributor to woody population structure in this savanna type.

The hypothesis that herbivore exclusion will enhance regeneration and population stability of encroacher species was supported by the results, which revealed that herbivory by both meso- and mega-herbivores suppressed the regeneration of key encroacher species. Meso-herbivores were responsible for the suppression of *Gymnosporia senegalensis* and *Spirostachys africana*, while mega-herbivores suppressed *Flueggea virosa*, *Vachellia grandicornuta*, *Rhigozum zambesiaceum* and *Combretum apiculatum*. The hypothesis was, however, not supported for *Dichrostachys cinerea* populations. The presence of all herbivores enhanced population stability of *Dichrostachys cinerea*, while the absence of all herbivores led to higher abundances by this species. Encroachment by *Dichrostachys cinerea* can therefore not be controlled by herbivory alone. Future studies in similar semi-arid savanna ecosystems, where fire is present, should focus on *Dichrostachys cinerea* demography to determine whether the combination of herbivory and fire is suitable to control regeneration.

The demography of three palatable non-encroaching species, *Diospyros mespiliformis*, *Pappea capensis* and *Ziziphus mucronata*, revealed sensitivity to herbivore exposure, while *Senegalia nigrescens* and *Vachellia exuvialis* were adapted to herbivore activity. It can therefore be expected that the latter two species would be more successful in a savanna ecosystem exposed to herbivory than *D. mespiliformis*, *P. capensis* and *Z. mucronata*.

The results of this study support the disturbance-based explanation of savanna dynamics. In particular it support the disequilibrium dynamic argument which assume that competition between trees and grasses occur at all life-stages and disturbances prevent dominant life-form transitions (Van Langevelde *et al.*, 2011). Competition between trees and grasses was noticed in the fully fenced enclosure, where high biomass could explain suppressed recruitment of

woody seedlings. In the presence of herbivores, where herbaceous biomass is low, disturbances such as herbivory and fire prevented woody recruitment.

Facilitation of woody recruitment is a topic of interest for savanna ecology. Results from this study revealed evidence that the catena played an important role in structuring and facilitating regeneration of the woody layer. The effect of facilitation by nursing sites is however still unexplored in this study site.

8.2 Recommendations for future studies

Future studies on regeneration of woody species in semi-arid savanna ecosystems exposed to herbivory and fire could consider the following:

- Test the effects of herbivores on woody species in the sodic vegetation zone, as this zone is suggested to be a limited elephant-browsing zone; they seem to use this area as a corridor between the upland crest and riparian zones.
- Investigation of the nutritious value of woody plants in the sodic vegetation zone.
- It is expected that elephant effects on woody abundance (without fire) can possibly be analogous to that of the combined effects of meso-herbivores and fire. This can especially be true for effects on encroaching woody species.
- Regeneration of *D. cinerea* should be studied to determine whether the combination of herbivore presence (both meso- and mega-herbivores), as well as fire exposure could control encroachment by this species.
- Demography studies in southern parts of Kruger National Park should specifically address regeneration status of desirable non-encroaching species such as *Sclerocarya birrea*, *Lannea schweinfurthii*, *Combretum imberbe* and *Commiphora* species, since elephant selectively feed on these species.
- Test the hypothesis that abiotic amelioration is stronger than facilitation (protection against herbivory) where water and nutrients are limited, i.e. on the upland crests, but protection from herbivory in the form of nursing sites is expected to assist in good recruitment on nutrient-rich sites, such as the sodic zone.

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Appendix A: Nkuhlu enclosure woody species list

Table A-1: Complete species list of all recorded woody species in 2002 and 2015 at the Nkuhlu enclosures, Kruger National Park.

Family	Species
Achariaceae	<i>Kiggelaria africana</i> L. <i>Flacourtia indica</i> (Burm.f.) Merr.
Anacardiaceae	<i>Lannea schweinfurthii</i> (Engl.) Engl. <i>Sclerocarya birrea</i> (A.Rich.) Hochst. <i>Searsia gueinzii</i> (Sond.) F.A.Barkley <i>Searsia tenuinervis</i> (Engl.) Moffett
Aristolochiaceae	<i>Aristolochia elegans</i> Mast.
Apocynaceae	<i>Adenium multiflorum</i> Klotzsch
Asparagaceae	<i>Asparagus africanus</i> Lam. <i>Asparagus laricinus</i> Burch.
Bignoniaceae	<i>Rhigozum zambesiaceum</i> Baker
Boraginaceae	<i>Cordia ovalis</i> R.Br. ex A.DC. <i>Ehretia amoena</i> Klotzsch <i>Ehretia obtusifolia</i> Hochst. ex A.DC. <i>Ehretia rigida</i> (Thunb.) Druce
Burseraceae	<i>Commiphora africana</i> (A.Rich.) Engl. <i>Commiphora edulis</i> (Klotzsch) Engl. <i>Commiphora neglecta</i> I.Verd.
Cannabaceae	<i>Trema orientalis</i> (L.) Blume
Capparaceae	<i>Cadaba natalensis</i> Sond. <i>Cadaba termitaria</i> N.E.Br. <i>Capparis fascicularis</i> DC. <i>Maerua juncea</i> Pax <i>Maerua parvifolia</i> Pax <i>Maerua racemulosa</i> (A.DC.) Gilg & Gilg-Ben.
Celastraceae	<i>Elaeodendron transvaalense</i> (Burt Davy) R.H.Archer <i>Gymnosporia buxifolia</i> (L.) Szyszyl. <i>Gymnosporia senegalensis</i> (Lam.) Loes. <i>Gymnosporia tenuispina</i> (Sond.) Szyszyl. <i>Hippocratea longipetiolata</i> Oliv.

Combretaceae	<i>Combretum apiculatum</i> Sond.
	<i>Combretum collinum</i> Fresen.
	<i>Combretum hereroense</i> Wawra
	<i>Combretum imberbe</i> Wawra
	<i>Combretum microphyllum</i> Klotzsch
	<i>Combretum molle</i> R.Br. ex G.Don
	<i>Combretum mosambicense</i> (Klotzsch) Engl.
	<i>Combretum zeyheri</i> Sond.
	<i>Terminalia prunoides</i> M.A.Lawson
Ebenaceae	<i>Diospyros mespiliformis</i> Hochst. ex A.DC.
	<i>Euclea divinorum</i> Hiern
	<i>Euclea natalensis</i> A.DC.
Euphorbiaceae	<i>Bridelia cathartica</i> G.Bertol.
	<i>Flueggea virosa</i> (Roxb. ex Willd.) Voigt
	<i>Spirostachys africana</i> Sond.
Fabaceae	<i>Albizia anthelmintica</i> (A.Rich.) Brongn.
	<i>Albizia forbesii</i> Benth.
	<i>Albizia harveyi</i> E.Fourn.
	<i>Cassia abbreviate</i> Oliv.
	<i>Dalbergia melanoxydon</i> Guill. & Perr.
	<i>Dichrostachys cinerea</i> (L.) Wight & Arn.
	<i>Ormocarpum trichocarpum</i> (Taub.) Engl.
	<i>Peltiphorum africanum</i> Sond.
	<i>Philenoptera violaceae</i> (Klotzsch) Schrire
	<i>Schotia brachypetala</i> Sond.
	<i>Schotia capitata</i> Bolle
	<i>Senegalia burkei</i> (Benth.) Kyal. & Boatwr.
	<i>Senegalia nigrescens</i> (Oliv.) P.J.H.Hurter
	<i>Senegalia schweinfurthii</i> (Brenan & Exell) Seigler & Ebinger
	<i>Senegalia senegal</i> (L.) Britton
	<i>Vachellia exuvialis</i> (I.Verd.) Kyal. & Boatwr.
	<i>Vachellia grandicornuta</i> (Gerstner) Seigler & Ebinger
	<i>Vachellia robusta</i> (Burch.) Kyal. & Boatwr.
	<i>Vachellia xanthophloea</i> (Benth.) P.J.H.Hurter
Flacourtiaceae	<i>Scolopia zeyheri</i> (Nees) Harv.
Loganiaceae	<i>Strychnos madagascariensis</i> Poir.
	<i>Strychnos spinose</i> Lam.

Meliaceae	<i>Trichilia emetica</i> Vahl
Menispermaceae	<i>Cocculus hirsutus</i> (L.) Diels
Moraceae	<i>Ficus sycomorus</i> L.
Ochnaceae	<i>Ochna inermis</i> (Forssk.) Schweinf.
Olacaceae	<i>Ximenia caffra</i> Sond.
Oleaceae	<i>Jasminum fluminense</i> Vell.
Phyllanthaceae	<i>Phyllanthus reticulatus</i> Poir.
Rhamnaceae	<i>Berchemia discolor</i> (Klotzsch) Hemsl. <i>Ziziphus mucronata</i> Willd.
Rubiaceae	<i>Canthium ciliatum</i> (Klotzsch) Kuntze <i>Gardenia volkensii</i> K.Schum. <i>Pavetta catophylla</i> K.Schum. <i>Pavetta lanceolata</i> Eckl. <i>Plectroniella armata</i> (K.Schum.) Robyns <i>Pyrostria hystrix</i> (Bremek.) Bridson <i>Tricalysia junodi</i> (Schinz) Brenan <i>Vangueria infausta</i> Burch.
Rutaceae	<i>Teclea pilosa</i> (Engl.) I.Verd. <i>Zanthoxylum capense</i> (Thunb.) Harv.
Salvadoraceae	<i>Azima tetracantha</i> Lam.
Sapindaceae	<i>Pappea capensis</i> Eckl. & Zeyh.
Sapotaceae	<i>Manikara mochisia</i> (Baker) Dubard
Tiliaceae	<i>Grewia bicolor</i> Juss. <i>Grewia flava</i> DC. <i>Grewia flavescens</i> Juss. <i>Grewia hexamita</i> Burret <i>Grewia villosa</i> Willd.
Verbenaceae	<i>Clerodendrum glabrum</i> <i>Lippia javanica</i> (Burm.f.) Spreng.
Vitaceae	<i>Cissus cornifolia</i> (Baker) Planch. <i>Rhoicissus revoili</i> Planch. <i>Rhoicissus tridentata</i> (L.f.) Wild & R.B.Drumm.

Appendix B: Dominant family changes between 2002 and 2015 in response to fire

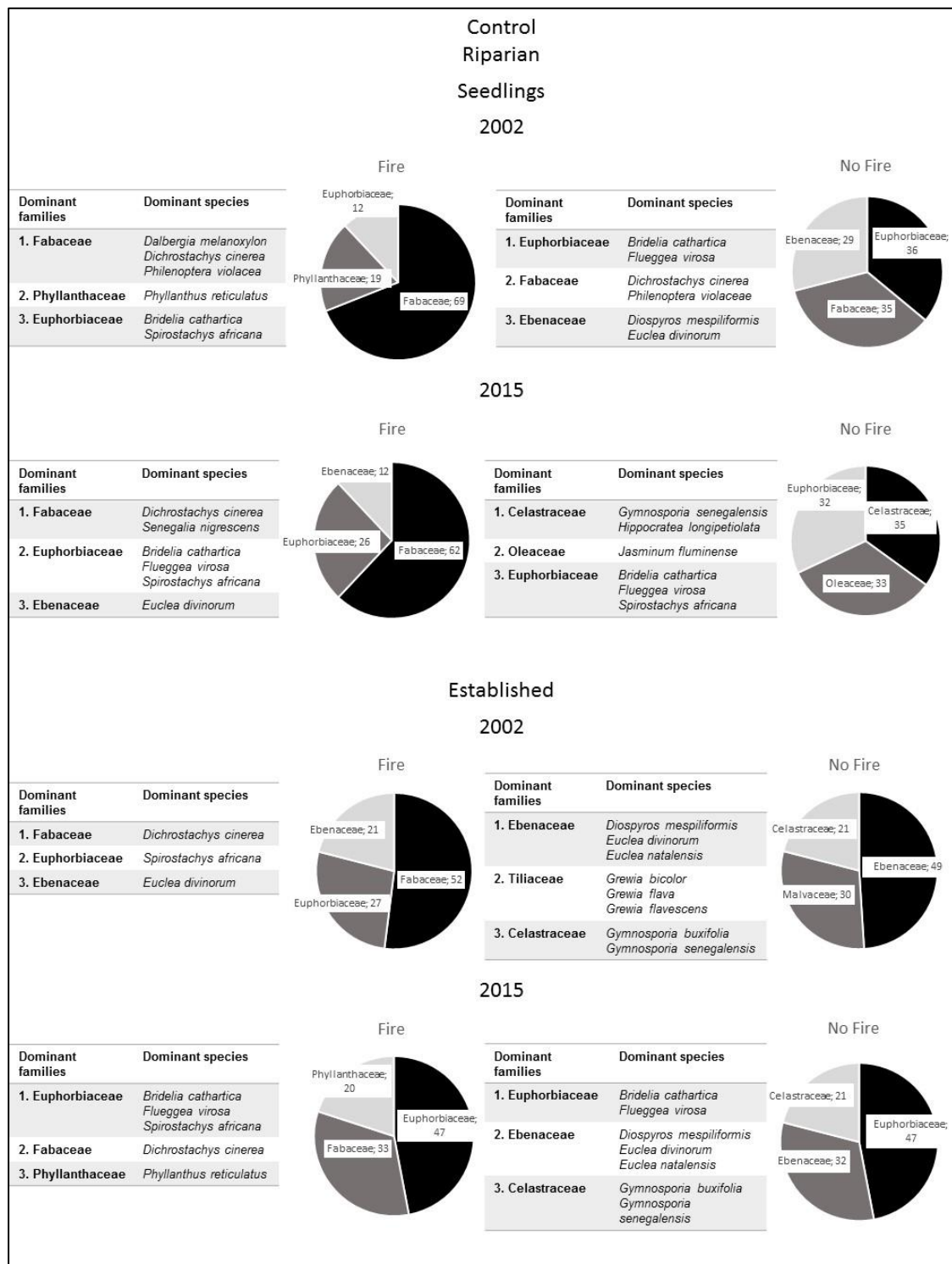


Figure B-1: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the riparian zone of the control treatment.

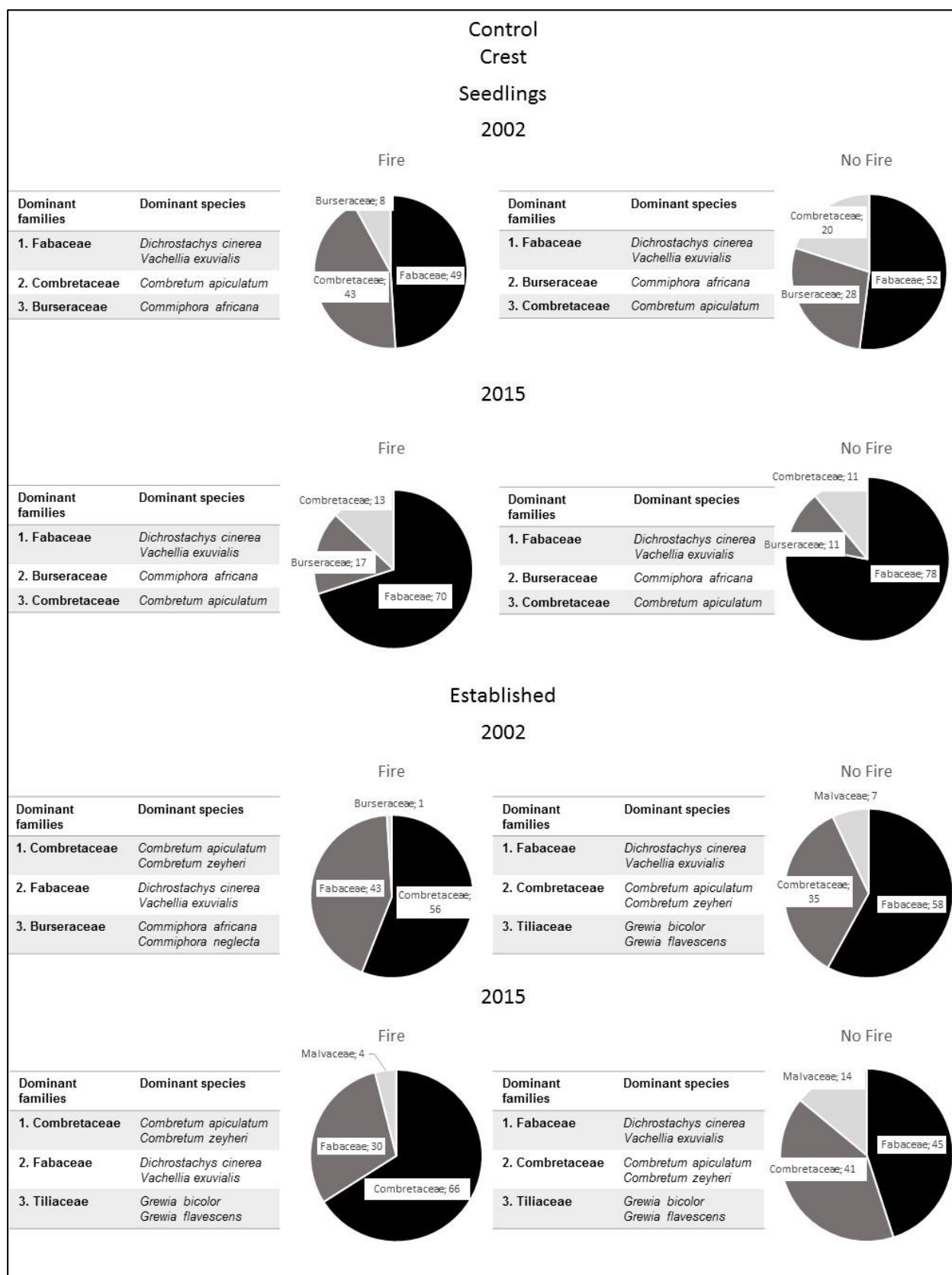


Figure B-2: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the crest zone of the control treatment.

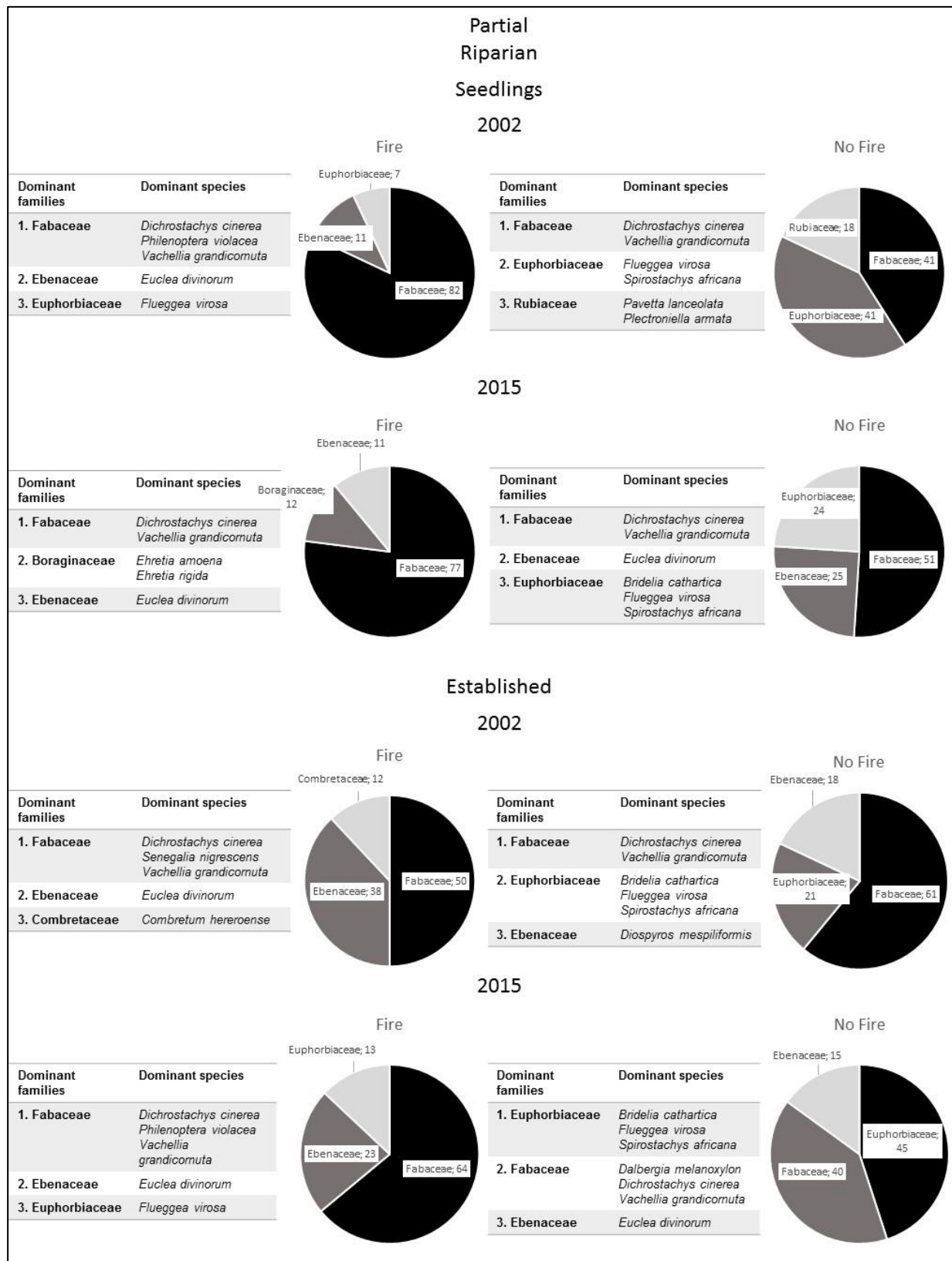


Figure B-3: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the riparian zone of the partially fenced treatment.

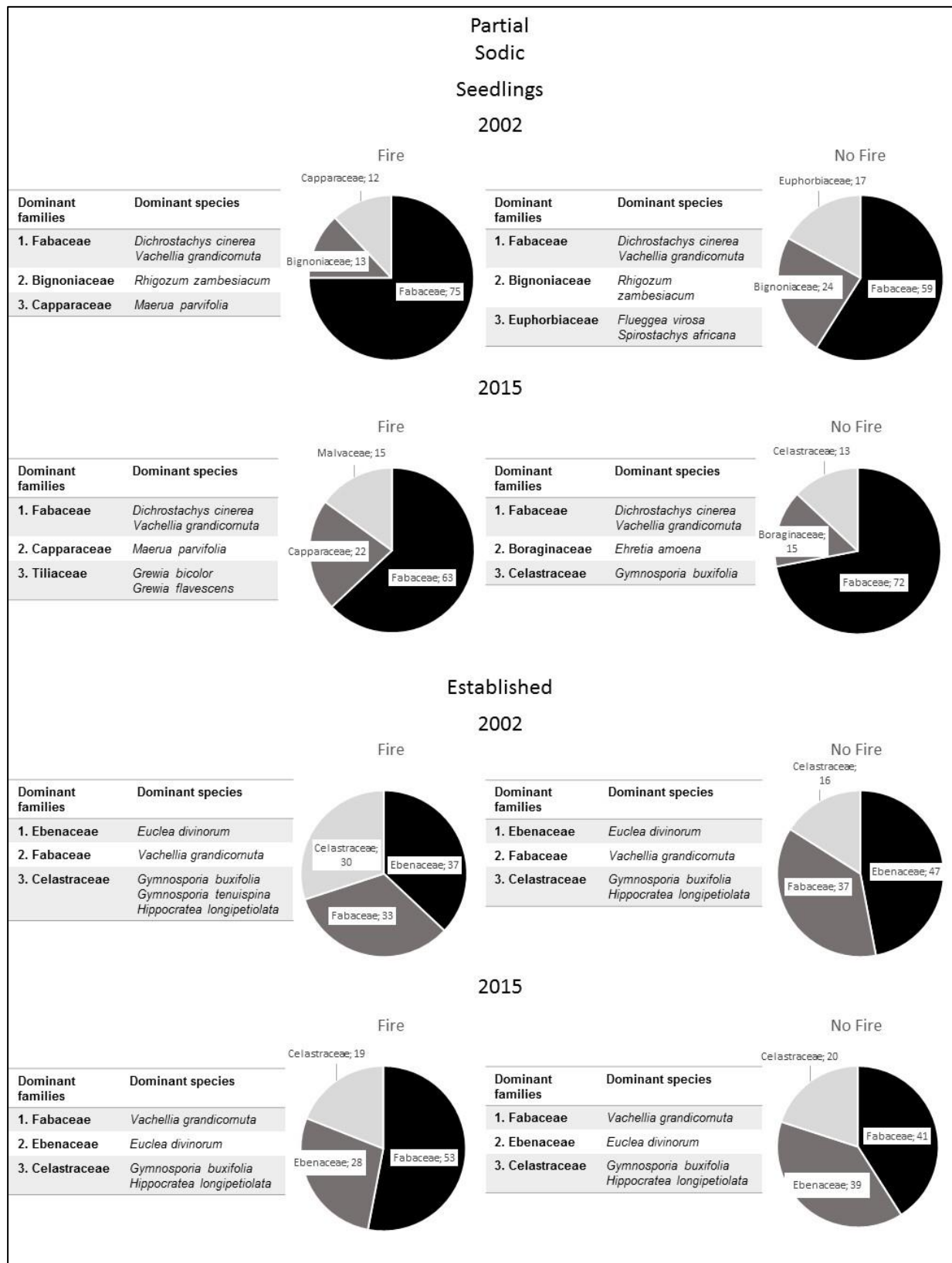


Figure B-4: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the sodic zone of the partially fenced treatment.

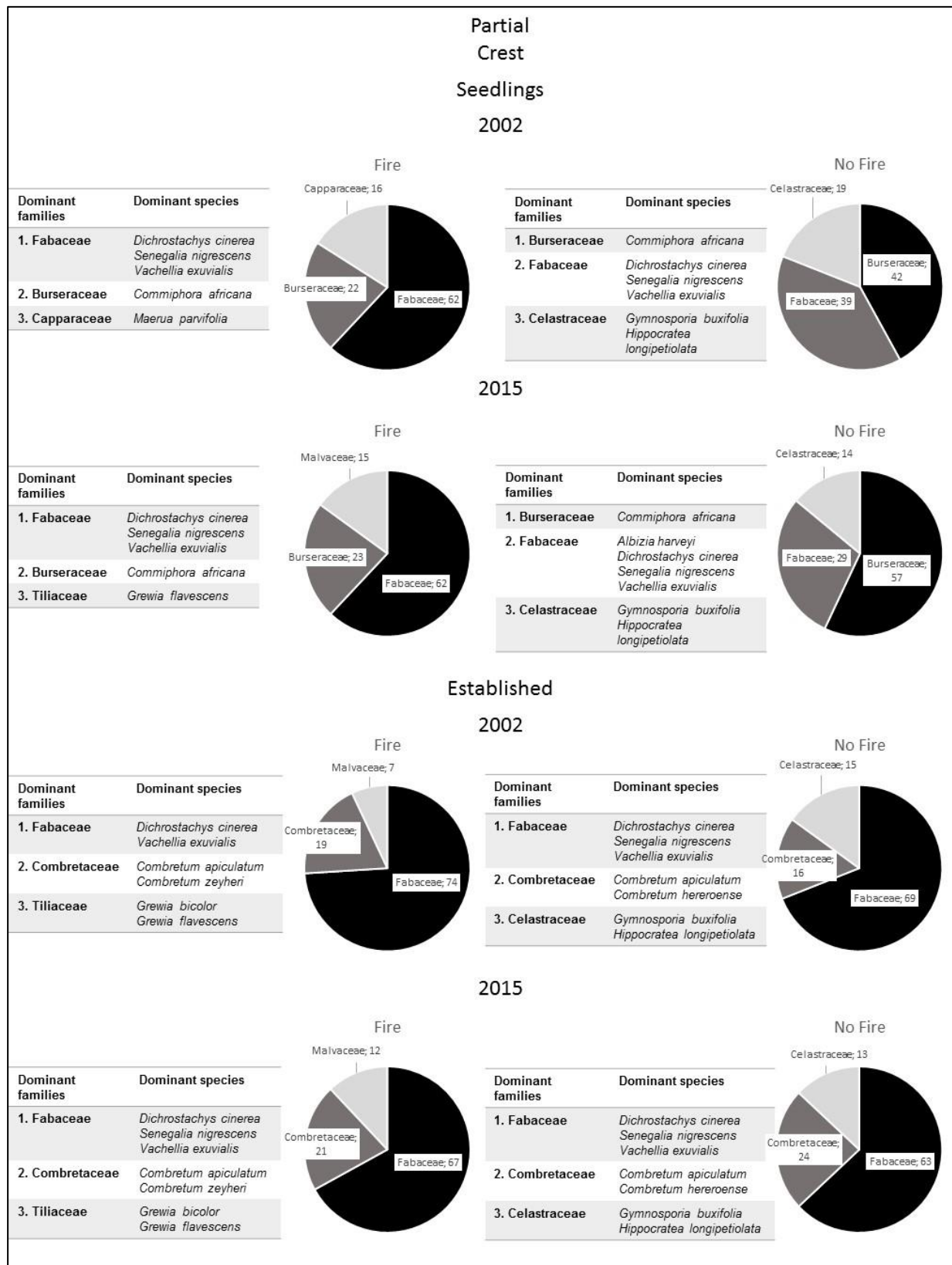


Figure B-5: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the crest zone of the partially fenced treatment.

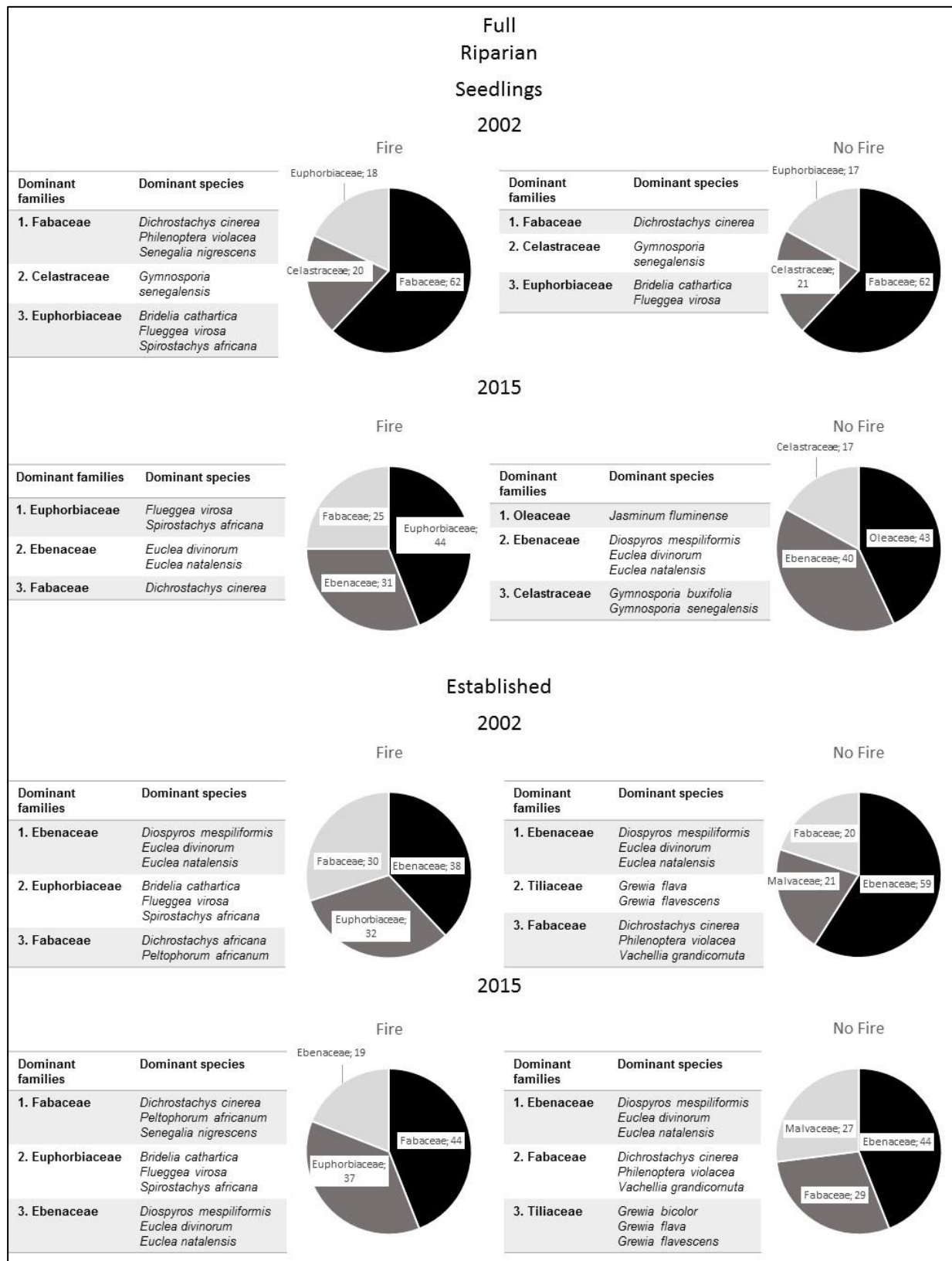


Figure B-6: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the riparian zone of the fully fenced treatment.

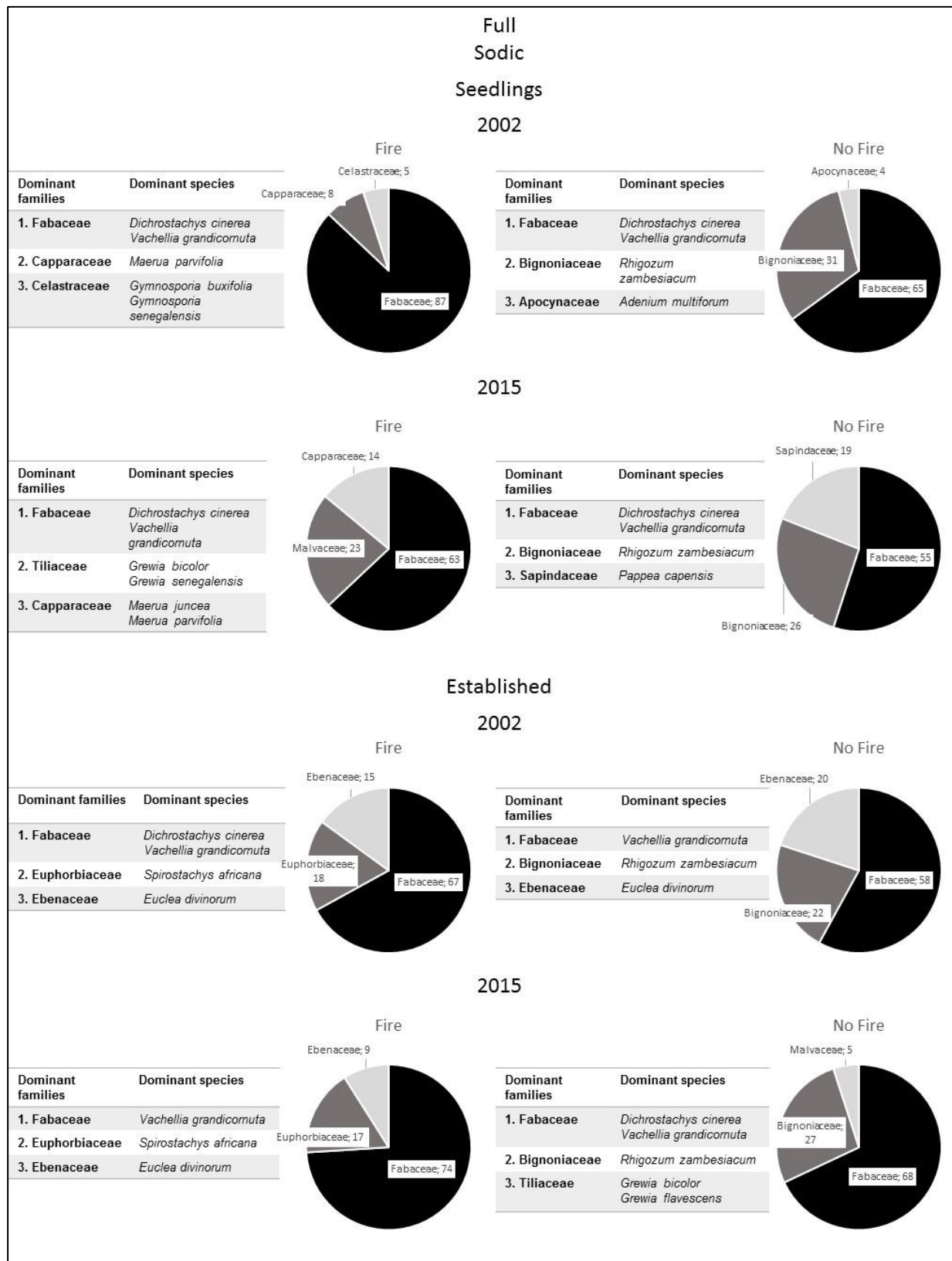


Figure B-7: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the sodic zone of the fully fenced treatment.

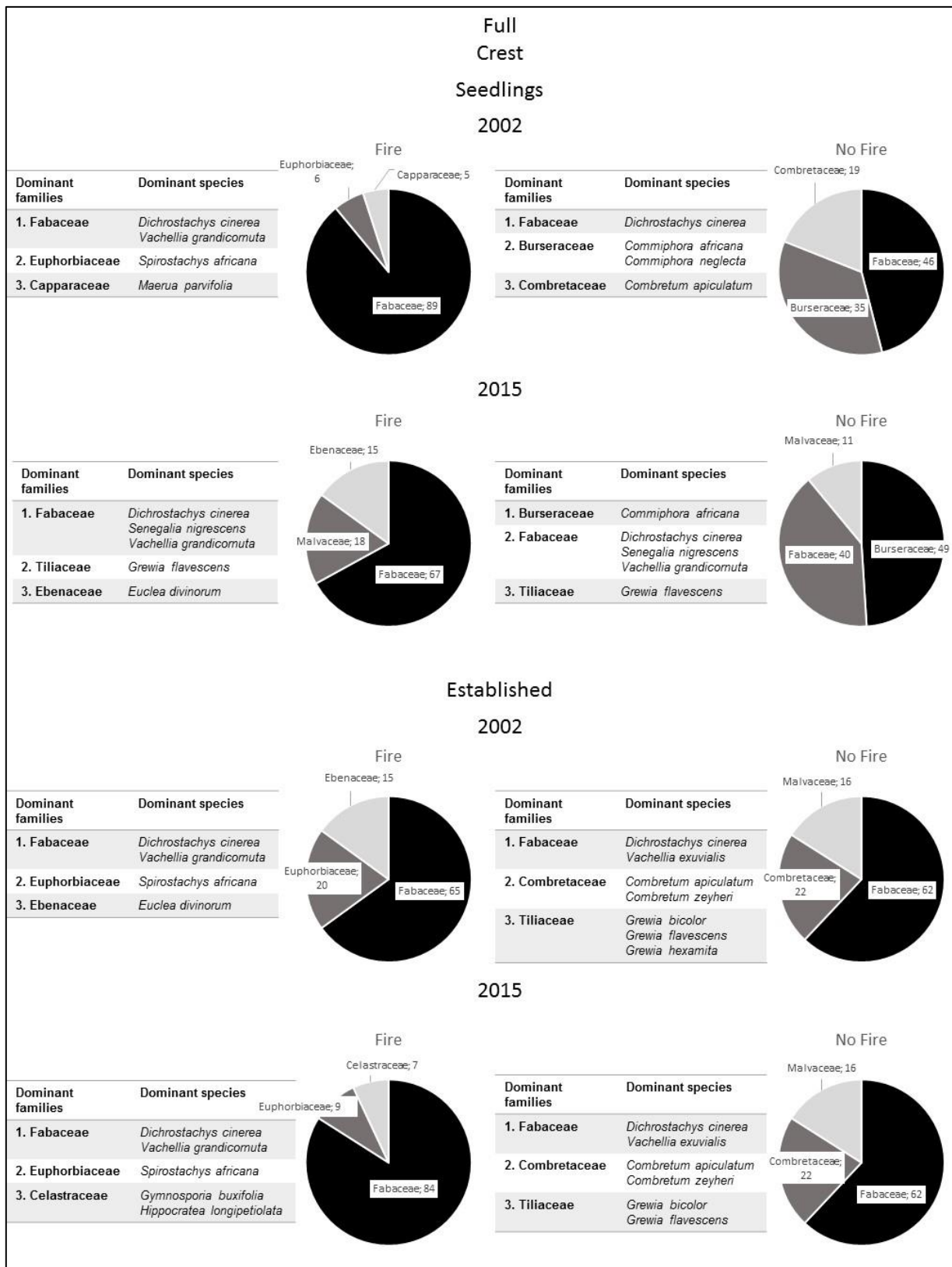


Figure B-8: Top three dominant woody families (expressed as frequency in %) and species per fire treatment per year (i.e. 2002 and 2015) for both seedling and established communities in the crest zone of the fully fenced treatment.