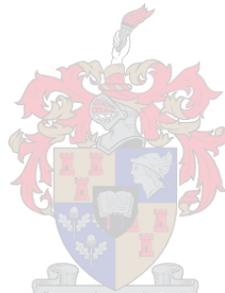


**Riparian plant community change and alien plant invasions
following geomorphological change in the Sabie River,
Kruger National Park, South Africa**

by

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Thesis presented in partial fulfilment of the requirements for the degree of
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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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Summary

Invasive species are among the biggest drivers of environmental change globally. Because of their ability to alter ecological and evolutionary processes they rank high among the most pressing environmental pressures facing protected areas. However, a major challenge in invasion ecology is identifying priority areas and species, and thus managers are unsure of which to prioritise. Two broad aims were examined in the thesis: 1) to assess if the distribution of alien plants is associated with the habitat template of the Sabie River and 2) to investigate the response of the native plant community to changes in alien plant density and diversity. Vegetation data were recorded in 2004 at 12 sites along the riparian zone of the Sabie River in Kruger National Park. Of these, 11 sites were resampled in February 2015, collated with the 2004 data and assigned trait information. Twenty-one modified Whitaker plots, placed parallel to the river channel and stratified by channel type, were sampled. Native and alien (tree, shrub and herbaceous) species abundance and species richness were recorded in each plot. Plant density, species richness, evenness and composition were examined to assess plant community changes. Alien plant density and species composition differed significantly between channel types, indicating that alien plants are not independent of the channel geomorphology. The dynamic braided channel type had the highest density of alien plants compared to the other channel types. This was not surprising given that most of the alien species in this study were herbaceous and annual species that tend to be ruderal in nature. Furthermore, there were two distinct types of alien plant communities. The first, a disturbance driven community that thrives in alluvial influenced channel types is dominated by ruderal species. The second is a combination of woody and short-lived species that is rooted in the water table within the bedrock influenced channel types. While the herbaceous species thrive in the disturbance driven community, they were not confined to alluvial influenced channel types. As expected, alien plants density was significantly higher than native species, while native species were more species rich. The high density of alien plants correlated with a decrease in native species evenness and species composition. Native and alien species were significantly dissimilar in plant strategies, suggesting that most alien species access or utilise differently to native species. I conclude that the decline in native species with the increase in alien species was an indirect consequence of the competitive dominance of alien species. The decline in native plant density when native and alien species shared a closer combination of plant trait strategies indicates that species with the highest potential to drive change are those that are similar in trait combinations to natives. This result supports the notion that alien species with the greatest potential to compete with natives are those that share a similar combination of traits to natives. By examining the patterns and effects of alien plants along the Sabie River, the study revealed some important considerations for land managers. Land manager could prioritise the bedrock-influenced channel types for alien plant, as they are most likely to be altered by the effects of alien

plants. Managers should priorities those alien species that have a similar combination of plant trait strategies to native species, as they have the highest potential to drive competitive exclusion of the less common species.

Opsomming

Indringerspesies is wêreldwyd een van die grootste oorsake van omgewingsverandering. Weens hulle vermoë om ekologiese en evolusionêre prosesse te beïnvloed, word indringerspesies gereken onder die dringendste omgewingsdrukfaktore wat beskermde gebiede bedreig. Een van die grootste uitdagings in indringerekologie is egter om gebiede en spesies te prioritiseer; grondbestuurders is onseker waaraan hulle moet voorkeur gee. Hierdie tesis het twee algemene oogmerke: 1) om te assesser of die verspreiding van uitheemse plante met die habitattemplaar van die Sabierivier ooreenkom; en 2) om te ondersoek hoe die inheemseplantgemeenskap reageer wanneer die digtheid en diversiteit van uitheemse plante verander. Plantegroei-data is in 2004 by 12 persele in die oewersone van die Sabierivier in die Kruger Nasionale Park aangeteken. In Februarie 2015 is monsters weer by 11 van die 12 persele geneem, met die 2004-data saamgestel en eienskap-inligting toegeken. Monsters is ingesamel by 21 aangepaste Whittaker-persele wat parallel met die rivier lê en volgens kanaaltipe gestratifiseer is. Die weligheid van elke inheemse en uitheemse spesie (bome, struik en kruidagtige) sowel as die rykdom aan spesies in elke perseel is aangeteken. Plantdigtheid sowel as die verskeidenheid, eweredige verspreiding en samestelling van spesies is ondersoek om veranderinge in die plantgemeenskap te assesser. Die digtheid en spesiesamestelling van uitheemse plante het aansienlik gewissel volgens kanaaltipe, wat aantoon dat uitheemse plante nie onafhanklik van kanaalgeomorfologie is nie. Dinamies gevlegte kanale het die hoogste digtheid van uitheemse plante vergeleke met die ander kanaaltipes gehad. Dit was te verwagte, aangesien die meeste uitheemse spesies in hierdie ondersoek kruidagtige en eenjarige spesies was, wat van nature neig om ruderaal te wees. Verder was daar twee duidelik onderskeibare tipes uitheemse plantgemeenskappe: (1) 'n versteuringsgedrewe gemeenskap wat in alluviaal-beïnvloede kanaaltipes floreer en waar ruderalespesies domineer; en (2) 'n samestelling van houtagtige en verganklike spesies met wortels in die watertafel binne die bodemrots-beïnvloede kanaaltipes. Hoewel die kruidagtige spesies in die versteuringsgedrewe gemeenskap floreer, is hulle nie tot alluviaal-beïnvloede kanaaltipes beperk nie. Soos te verwagte, was uitheemse plantdigtheid aansienlik hoër as dié van inheemse spesies, terwyl die inheemse spesies groter verskeidenheid getoon het. Die hoë digtheid van uitheemse plante korreleer met verlaagde eweredigheid en samestelling van inheemse spesies. Inheemse en uitheemse spesies verskil aansienlik wat plantstrategieë betref, wat daarop mag dui dat die meeste uitheemse spesies ander toegangs- of benuttingstrategieë as inheemse spesies volg. Die tesis kom tot die gevolgtrekking dat inheemse plantdigtheid afneem wanneer uitheemse spesies toeneem, as 'n onregstreekse gevolg van uitheemse spesies se mededingende dominansie. Die afname in inheemse plantdigtheid wanneer inheemse en uitheemse spesies 'n meer soortgelyke stel planteienskapstrategieë vertoon, dui daarop dat spesies met die sterkste potensiaal om verandering te veroorsaak dié is wat oor soortgelyke

eienskapstelle as inheemse spesies beskik. Hierdie bevinding ondersteun die gedagte dat die uitheemse spesies met die sterkste potensiaal om met inheemse plante mee te ding dié is wat 'n soortgelyke stel eienskappe met inheemse plante gemeen het. Deur die patrone en uitwerking van uitheemse plante langs die Sabierivier te ondersoek, het hierdie navorsing 'n paar belangrike oorwegings vir grondbestuurders aan die lig gebring: (1) Grondbestuurders kan aan die bodemrots-beïnvloede kanaaltipes voorkeur gee wat uitheemse plantegroei betref, aangesien sulke kanale die grootste gevaar loop om deur die uitwerking van uitheemse plante verandering te ondergaan. (2) Bestuurders moet die uitheemse spesies prioritiseer wat 'n soortgelyke stel planteienskapstrategieë met inheemse spesies gemeen het, aangesien daardie uitheemse spesies die sterkte potensiaal het om die minder algemene spesies deur mededinging te verdryf.

Dedications

This thesis is dedicated to my family and friends, for their support through it all. The journey has not been easy but definitely rewarding.

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Preface

This thesis is presented as a compilation of four chapters. Chapters two and three have been written in the format of a journal article.

- | | |
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| Chapter 2 | Alien plant distribution and habitat association within the channel types of the Sabie River, Kruger National Park. |
| Chapter 3 | Plant community change in relation to alien plant invasions in the riparian zones of the Sabie River, Kruger National Park. |
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List of abbreviations

BA	Bedrock anastomosing (geomorphological channel type)
BR	Braided (geomorphological channel type)
GPS	Global positioning system
KNP	Kruger National Park
MA	Mixed anastomosing (geomorphological channel type)
m a.s.l	Metres above sea level
PA	Protected areas
PERMANOVA	Permutational Multivariate Analysis of Variance
PR	Pool rapid (geomorphological channel type)
SIMPER	Similarity percentage

Chapter 1: Introduction and literature review

1.1 Introduction

Biological invasions are increasing at an unprecedented rate, to the extent that their potential to disrupt ecosystem interactions, and the magnitude of those consequences, qualifies invasive alien species as a major driver of global environmental change (Ricciardi, 2007). Invasive alien species (IAS) challenge the resilience of ecosystems in many geographical realms. Evidence on impacts of invasive alien species has been quantified on species, community dynamics and overall structure and function of ecosystems (Catford et al., 2009; Foxcroft et al., 2013; Hulme et al., 2013).

The quest to determine which habitats are most vulnerable to plant invasions has been at the forefront since the start of invasion biology as a focussed field of science (Hejda et al., 2009; Pyšek and Chytrý, 2014). There is a wealth of literature on patterns of alien plants for different habitat types and includes a range of spatial scales, from specific landscape types (Carranza et al., 2011; Foxcroft et al., 2008, Moravcová et al., 2015), broad regional scales (Giorgis et al., 2016; Mandal and Joshi, 2015; Maskell et al., 2006; Thomas and Moloney, 2013) and at continental scales (Chytrý et al., 2008; Hejda et al., 2009). Although the complex interaction between environmental factors and their effects on species differs across scales, habitats and regions (González-Moreno et al., 2014), these studies have been important in developing generalizations on drivers of geographic patterns of alien species (Pyšek and Chytrý, 2014). This work has however been biased towards Europe, the United States and New Zealand (e.g. Hulme et al., 2013; Maskell et al., 2006; Pyšek and Chytrý, 2014). Pyšek and Chytrý (2014) accredit this bias to the variety of detailed assessments that have occurred on these continents across various habitat types in large regions. Despite the geographical differences, climate is generally an important driver of invasive species abundance at the continental scale (Chytrý et al., 2008). At regional scales topography, land use and land cover are most important, and at smaller scales disturbance, local soil conditions and biotic interactions become more important (Thomas and Moloney, 2013).

Riparian zone species composition and structure is an example of the outcomes of complex fine- and landscape-scale interactions, as they are a mosaic of plant communities formed in response to varying environmental, hydrological and habitat characteristics of the river (Hood and Naiman, 2000). While the frequency and intensity of inundation and susceptibility of riparian plants to damage by flooding has an overriding influence on the distribution of riparian vegetation (Hupp and Bornette, 2003; van Coller et al., 1997; van Coller et al., 2000). The interaction between landform characteristic and flow determine the disturbance regime, water and moisture availability (Moon et al., 1997; Parsons et al., 2005; Tickner et al., 2001; van Coller et al., 1997). For example, the height and surface substrate of the landforms affects water or moisture availability within that landform. Therefore, the likelihood of a riparian species being associated with a particular landform is determined by the landform being suitable for germination and establishment, as well as the environmental conditions permitting persistence until reproductive age (Hupp and Bornette, 2003).

It has been argued that to properly understand the dynamics of riparian invasions and their impacts, it is necessary to understand the factors that affect their distribution (e.g. Garófano-Gómez et al., 2011; Richardson et al., 2007; Tickner et al., 2001). Extreme climatic events, such as large infrequent floods, droughts, or heat waves can facilitate invasion further because they can disrupt ecological and evolutionary processes. Extreme climatic events facilitate invasions through two pathways, abrupt mortality of residence species or reducing capacity to access resources, ultimately reducing invasion resistance. While good progress has been made on the bio-geomorphic impacts of invasive species, surprisingly, little attention has been given to the distribution patterns of alien plants in relation to riparian landforms (see review by Fei et al., 2014).

The Sabie River in the Kruger National Park (KNP), like several of the major rivers in KNP, is a conduit for plant invasions into the park (Foxcroft et al., 2007). The Sabie River originates from outside the park, flowing through a complex array of land use types that do not always compliment biodiversity conservation (Foxcroft et al., 2007). For example, agriculture and rural settlements in the upper reaches of the catchment are sources of alien propagules and compete with the park for water. The river transports propagules from multiple land-use types from across the catchment into the KNP (Foxcroft et al., 2007). Thus, given the nature of the river and the configuration of the park to external sources of propagules, riparian zones in KNP are likely to be highly vulnerable to invasions and to changes in native plant diversity. Therefore as management requires prioritization of taxa most likely to cause significant harm, and the areas that are most vulnerable to ecosystem change (Foxcroft et al., 2018), improved understanding of riparian areas is required.

In KNP, control efforts are largely limited to a few species that tend to be widespread and have a large global distribution, for example, *Lantana camara* (lantana) and *Chromolaena odorata* (triffid weed) (Foxcroft et al., 2017a). In addition, these large, well-known and visible species are easier to control and maintain within an acceptable threshold. Many widespread herbaceous plants that dominate the riparian zones are currently considered low concern, because they are perceived to have no effect, and die at the end of the growing season, therefore making control redundant (Morris et al., 2008). However, some studies have shown that it is the most dominant species that have the highest potential to influence change in plant communities and of ecosystem function (Cleland, 2011; Richardson et al., 2007). While one herbaceous species alone may not have an effect and not be particularly dense, a community of many alien herbaceous species, with different growth forms, can together dominate and influence the availability of suitable habitats for native species.

Therefore, the overall objective of this thesis was to examine the distribution and habitat association of riparian alien plants along the Sabie River. Specifically, this study investigated whether alien and native plant density, species richness and alpha diversity differed significantly between geomorphological channel types. Thereafter I examined the response of native plant communities to temporal changes in alien plant density, diversity and community composition.

1.1.1 Overview: thesis structure

The thesis is divided into four chapters. Chapter 1 is the introduction and literature review. Chapter's 2 and 3 are presented in a journal article format (South African Journal of Botany). Chapter 2, titled "Alien plant distribution and habitat association within the channel types of the Sabie River, Kruger National Park", aims to determine whether the distribution of alien plants is independent of the Sabie River geomorphology or channel landtypes. To anticipate the effects of plant invasions and to improve the efficacy of alien plant control measures, a thorough understanding of the factors that play a role in the invasion of riparian habitats is required. Riparian zones are a mosaic of vegetation types and landforms due to flood disturbances of different frequency and magnitude. Riparian habitats thus differ in their biophysical conditions, which in turn affects the potential invasibility and presence of plant species. Therefore, this chapter examines the distribution and dominance of riparian plants by comparing native and alien species. Chapter 3, titled "Plant community change in relation to alien plant invasions in the riparian zones of the Sabie River, Kruger National Park", examines the effects of alien plants on

the native plant community. I do so by investigating whether the native plant community association is impacted negatively by changes in the abundance and diversity of alien plants over time. Further, I assess whether the role of life history influences the type of interactions between the alien and native plant communities. Chapter 4 presents the general discussion and conclusion. This final chapter gives a brief review of the major findings and a synthesis of the spatial and temporal patterns of alien plants and their interaction with the native plant community in the riparian habitat of the Sabie River.

1.1.2 Study site

As the core chapters are in the format of scientific journal article, there is unavoidably some level of overlap in the study site description. The following provides a broad overview of the study area to set the overall context of the study. The Kruger National Park (KNP, ~ 2 million ha) is situated in the north-eastern region of South Africa (Figure 1.1 A), bordering Mozambique (Figure 1.1B) in the east and Zimbabwe in the north (Venter et al., 2003). It is in a semi-arid savanna system, experiencing dry winters and wet summers, and with 84% of the total annual rainfall concentrated in the summer months of November to April (MacFadyen et al., 2018). The rainfall varies from 2000 mm/year in the high lying escarpment area in the catchment and 400 mm/year closer to the Mozambique border (Moon et al., 1997). The KNP falls within two climatic zones, 1) the Lowveld bushveld, covering the south and central regions of KNP, in which the Sabie River occurs (Figure 1.1B), receives about 500-700 mm annual rainfall, and 2) the Northern Arid bushveld covering the northern region of the KNP, which receives 300-500 mm of annual rainfall (MacFadyen et al., 2018). Both climatic regions experience hot summers and mild frost-free winters (Venter et al., 2003). The Sabie River originates from the Klein Drakensberg escarpment flowing through the towns of Sabie, Graskop and Hazyview, before flowing through the Lowveld to intersect KNP on its western boundary. The Sabie River drains into Mozambique at the eastern border of KNP (Figure 1.1B,C) (Moon et al., 1997). The Sabie River catchment is important economically and ecologically, supporting many different land users west of the park (Mallory et al., 2013). The predominant land use forms in the catchment rely on water abstraction from the Sabie River for irrigation (e.g. banana farms) and plantation forestry, followed by water supply to nature reserves and domestic water supply for a growing human settlement (Mallory et al., 2013). Therefore, the river connects the Kruger Park with numerous land use types within the catchment, many of which are not highly compatible with biodiversity conservation.

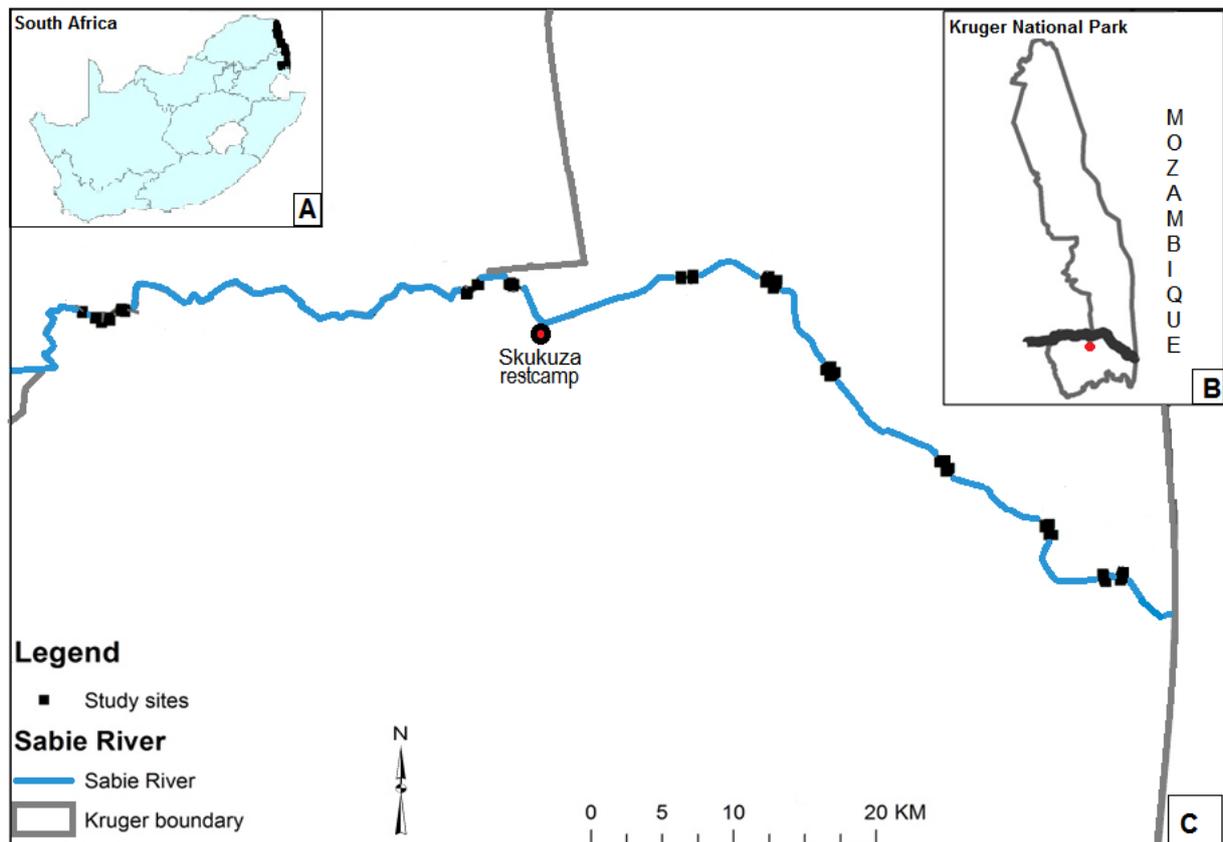


Figure 1.1 The study area occurs in north-eastern region of South Africa. Panel A shows Kruger National Park in relation to South Africa, Panel B depicts the Sabie River within the Kruger National Park, Panel C shows the eleven study sites along the Sabie River.

1. 2 Literature review

The literature review provides background to riparian landscapes, highlighting the general principles governing riparian landscapes that are important to this study. The review briefly introduces the concept of environmental gradients (distance from the river), geomorphic processes, and geomorphic features that determine patterns of riparian vegetation. I do this to illustrate complexities driving vegetation patterns on the riverine landscape. The review then focuses on the link between riparian vegetation and riparian habitats/landforms. I discuss these briefly to unpack how these processes shape the river landscape and their biotic attributes. In the second section, the literature review highlights the threat of alien plant invasions, followed by their impacts and frameworks for interpreting impacts.

River ecologists have long recognised rivers as landscapes in their own right, influenced by their surrounding environment through which they flow (Allan, 2004). The term riverscape was born of the merger between landscape and fluvial ecology (Ward 1998). The term represents a holistic way of studying patterns and processes of fluvial environments (streams and rivers) (Allan, 2004). It recognises that rivers are heterogeneous landscapes, which are spatially complex due to the network of interconnected habitats and environmental gradients at different scales (Allan, 2004; Price et al., 2011).

Two concepts are important for understanding and interpreting vegetation patterns on the riverine landscape (channel and riparian zone), namely, environmental gradients and patch dynamics (van Coller et al., 2000; Winemiller et al., 2010). The former emphasises connectivity (vertical, lateral and longitudinal connectivity) and the perpetual state of disequilibrium (disturbance) of the river landscape (van Coller et al., 2000). The latter views rivers as a dynamic mosaic of patches interconnected hierarchically (Winemiller et al., 2010). The environmental gradients and patch dynamics, forming the hydro-geomorphic processes (flooding, erosion and deposition) of the river, determine the structural diversity (habitat diversity) and habitat conditions, from which riparian and aquatic species assemblages evolve. The channel type scale, the highest hierarchical level feature found in the Sabie River (Parsons et al., 2005b) allows for examining plant community patterns across the river landscape (see chapter 2). However, while rivers are dynamic systems, the process of invasion by alien species adds a further layer of complexity. The literature abounds with mechanisms of invasions and generalisations, but these are frequently site and species specific (see review by Hulme and Bernard-Verdier (2017); Ricciardi et al., (2013)).

1.2.1 Riparian vegetation

Riparian zones can be harsh environments for the establishment of plants; the species that occur there are specialists in utilising this habitat. Species must survive prolonged saturation of roots, erosion of substrate that they are rooted into, scouring and drought (Naiman and Decamps, 1997). Riparian species employ unique morphological, physiological and reproductive adaptations to survive the dynamic riparian environment (Naiman et al., 2010). These include, for example, trees being able to grow on wood debris (Pettit and Naiman, 2005) or hydrophytes growing on saturated soil (Chen et al., 2002) and adapting to deposition, erosion or stem breakage (Naiman et al., 2010). Alternatively, riparian plants establish in “safe sites” to be able to survive (Naiman et al., 2010). Riparian plants may colonize a variety of sites, however plants only successfully establish

in sites where they are able to germinate, survive flooding, and have conditions that are compatible with their life history (Naiman et al., 2010). Reed and shrub assemblages, for example, are correlated with wet and periodically flooded environments, while riparian forests (trees) are associated with dryer seasonally flooded geomorphic features (Moon et al., 1997). Therefore, riparian plant communities are comprised of specialised disturbance-adapted species in a mosaic of less-specialised species (Naiman and Decamps, 1997).

Six principal plant communities are associated with the geomorphological structure of the Sabie River (van Coller et al., 1997). Four of those plant communities are comprised of species that are restricted to the dynamic channel floor. The last two communities are found on the macro-channel bank and comprise of species that occur in the surrounding savanna but occur in high numbers along riparian zones. Van Coller et al. (1997) attributed this to the contrasting morphologies of the channel bank and floor, and the vertical and lateral position relative to the active channel. Van Coller et al. (1997) also observed that vegetation shifts from *Syzygium guineense*, *Breonadia salicina*, *Nuxia oppositifolia*, *Kraussia floribunda* dominated in bedrock states to *Pavetta lanceolata*, *Ficus sycomorus*, *Combretum erythrophyllum*, *Lantana camara* (alien) dominated in alluvial states (van Coller et al., 1997). They conclude that the degree of bedrock influence is an important determinant in the distribution of species along the different channel states. Therefore, species along riparian zones survive this harsh environment because they are adapted to floods or establish in sites higher up the river, depending on the water table for water supply.

1.2.2 Biogeography of riparian vegetation

Riparian zones encompass sharp gradients of environmental factors, ecological processes and plant communities (Gregory et al., 1991). Most of our understanding of the vegetation-environment relationship along the riparian zones of the Sabie River has emerged from relationships established through the study of lateral and vertical gradients (Hood and Naiman, 2000; Reinecke et al., 2008; van Coller et al., 2000; Ward and Tockner, 2001). These studies show that the distribution of plant communities strongly reflect flood frequency and water availability. This is reflected in the variation in species distribution along the elevation gradient of the channel (Rogers and O’Keeffe, 2003). For example, species turnover along the elevation gradient of the Sabie River is characterised by peaks in individual species abundance starting with *Breonadia salicina* at the lowest elevation and *Spirostachys africana* at the highest elevation (Rogers and O’Keeffe, 2003). This emphasises the linear connectivity of the riverscape (from

headwater to mouth and from channel floor to bank), and that vegetation distribution is predictable along vertical and lateral gradients.

From a landscape perspective, riparian vegetation comprises different species distributed across the geomorphological template (Rogers and O'Keeffe, 2003). Geomorphic landforms play a crucial role in the ecosystem dynamics of the Sabie River (Heritage and Moon, 2000). The geomorphology forms the template (i.e. sediment load, stability) on which fluvial processes such as the flow of water, nutrients and sediments act to determine available physical habitats (Rowntree et al., 2000). Large infrequent floods create geographic structures that may persist for decades, therefore setting the geometry of the landforms (Naiman and Decamps, 1997). Intermediate intensity floods shape the riparian landscape further by delineating plant community zonation (Naiman and Decamps, 1997). Lastly, low intensity annual floods further shape the riparian zone by reshuffling sediment to create a patchwork of sites that are aggregating, eroding or maintaining their state, which can be exploited by different plant species (Naiman and Decamps, 1997). Landforms therefore differ in productivity, organic matter dynamics, nutrients and plant community composition (Gregory et al., 1991; Thorp et al., 2006). In the Sabie River for example, van Coller et al. (1997) found that vegetation distribution was correlated with the elevation gradient and geomorphology of the channel. This link with elevation was due to differences in flooding intensity and water availability, which was apparent in the vegetation distribution patterns. Meanwhile, the link with geomorphology was due to bedrock or alluvial influence in geomorphic features. The interplay between flow and riparian landforms creates a mosaic of inundation patterns, and nutrient and water availability patterns to which riparian vegetation responds accordingly to conditions (Reinecke et al., 2015).

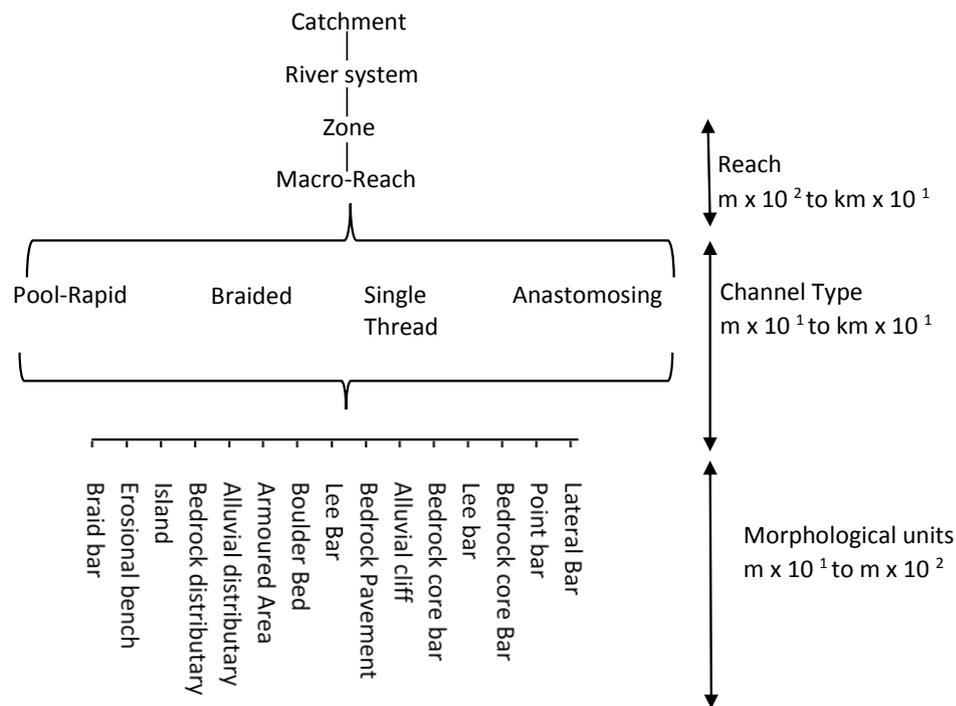


Figure 1.2 A hierarchical classification for the Sabie River, indicating the different geomorphic features and scale (Redrawn from: van Niekerk, Heritage and Moon (1995)). Channel types differ in the combination of morphological units and some morphological units are unique to a channel type. Scale is the approximate size of the landform.

The Sabie River is characterised by four channel types or states: Bedrock Anastomosing (multiple channels flowing through bedrock crevices), Braided (alluvial braiding within the confines of the macro-channel), Mixed Anastomosing (multiple channels flowing through alluvium on a bedrock base), and Pool-rapid (pools separated by bedrock rapids) (Foxcroft et al., 2008) (Figure 1.3). Each channel type has a different combination of morphological units (e.g. lateral bars, mid-channel bars, sandbars or benches), which affects the nature of the channel processes (i.e. the flow of water) (Heritage and Moon, 2000; Rountree et al., 2001). For example, the riffles causes the high energy in the pool rapid channel states. The morphological units have different substrate types (sand, bedrock) and vary in elevation, which determines their flooding intensity and water availability (Heritage and Moon, 2000; Rountree et al., 2001). Therefore, each individual channel state displays unique hydraulics, channel flow, and a variable mix of bedrock and alluvial influence and varies in characteristic vegetation assemblages (species composition).

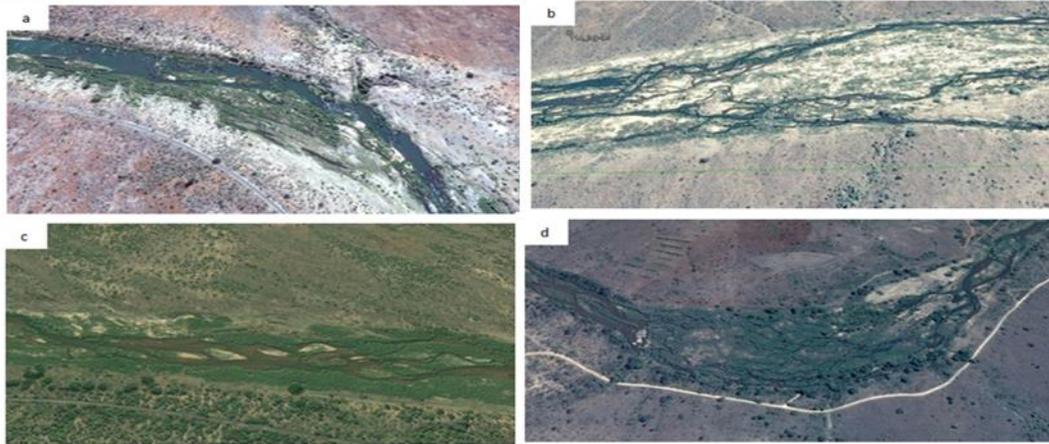


Figure 1.3 An Aerial view of the four most a - Pool-rapid (PR), b - Mixed Anastomosing (MA), c - Braided (Br), and d - Bedrock Anastomosing (BA).

Bedrock Anastomosing (BA)

The bedrock anastomosing type is a bedrock-controlled section within the channel that is generally associated with outcrops of resistant rock in the channel. This channel state is characterised by multiple distributary channels flowing over un-weathered bedrock (van Coller et al., 1997). These segments of the channel are steep and generally inhibit sedimentation; however, sediment may accumulate on topographic highs (Rountree et al., 2001). The bedrock anastomosing channels often feature pools, rapids, bedrock cores, and small waterfalls as morphological units (Ayres 2012). Trees rooted in bedrock sections rely on water table replenishment for survival and prolonged drought can result in vegetation mortality. Vegetation associated with BA are strictly riparian species and are not found outside of riparian zones, including *Breonadia salicina*, *Diospyros mespiliformis* and *Phragmites mauritianus* (Moon et al., 1997).

Braided (Br)

Braided channels are alluvial controlled segments in the channel, with widespread sediment bars across the channel floor. These channel types are characterised by low energy flows, which facilitates sediment deposition on the channel floor and the formation of sediment bars. This section of the channel has no bedrock due to the deep alluvial deposits (Rountree et al., 2001). Vegetation linked to this channel type is likely dependent on subsurface flows (Moon et al., 1997). The dominant species are *Ficus sycomorus*, *Combretum erythrophyllum* and *Gymnosporia senegalensis* (van Coller et al., 1997).

Mixed Anastomosing (MA)

These sections are former bedrock anastomosing channel types that develop where there is extensive lateral sediment accumulation over extended periods (van Coller et al., 1997). This channel type has bedrock and alluvial influence, and features bedrock core bars, backwater and armoured areas (very coarse surface) as morphological units. The channel is characterised by multiple alluvial and occasional bedrock distributary channels that divide and re-join over a distance much greater than the width of the channel (van Coller et al., 1997). Mixed anastomosing channels are stable sections (like the BA) because they disperse the energy from flow to minimize the force of the running water. Secondly, sediment accumulation in these channel types is by vertical accretion, which is aided by the reed growth (Rountree et al., 2001). The reed species *Phragmites mauritianus* and shrub species *Phyllanthus reticulatus*, *Flueggea virosa* and *Gymnosporia senegalensis* are closely associated with, and occur more frequently, in this channel state (van Coller et al., 1997). This vegetation type is also common in low-lying sites of loose, coarse alluvium and bedrock close to the active channel.

Pool-rapid (PR)

The pool-rapid channel type is usually a wide and single strand channel type (Ayres 2012). This segment of the river usually occurs where there are dykes or sills, which are areas of more resistant rock (e.g. Timbavati Gabbro) within the host rock (e.g. shale diamictite and quartzite) (van Coller et al. 1997). This results in a sequence of high-energy rapids in the un-weathered section followed by low-energy pools in the weathered sections of the channel. Rapids are bedrock-influenced while pools vary between bedrock and alluvial influence (van Coller et al. 1997). Sedimentation usually occurs in downstream of the bedrock outcrop, which results in the formation of the braid bar and lee bar geomorphic units. This channel type is usually associated with *Phragmites mauritianus*, *Ziziphus mucronata* and *Dichrostachys cinerea* (van Coller et al., 1997). Most species find it difficult to establish in this channel because of the high energy of the channel (van Coller et al., 1997).

Although a large body of literature recognises geomorphology as an important determinant of vegetation distribution patterns along riparian zones (e.g Hupp and Bornette, 2003; Montgomery and Wohl, 2003; Poole, 2002), little consideration has been given to establishing the role of riparian landforms on invasive species distribution (see reviews by Fei et al., 2014; Tickner et al., 2001; Stallins, 2006). Of the few studies that have examined the distribution of alien plants in relation to the available riparian landforms (e.g. Thomas and Moloney, 2013; Foxcroft et al., 2008; Maskell et al., 2006; Mandal and Joshi, 2015), most of the studies focused on broad- regional scale patterns (e.g. comparisons between entire rivers) (Pyšek and Chytrý, 2014). Although

important for understanding regional process such as dispersal, van Coller et al., (1997) found that the link between riparian species and geomorphology was particularly evident at the channel type scale. For example, van Coller et al., (1997) observed that a change in channel type mirrored a change in species composition. Therefore, smaller riverscape elements may be more important for understanding the establishment of alien species and their management. For example, Foxcroft et al. (2008) examined the distribution of alien plants in relation to patchiness (zones, channel types, elevations, morphological units, substrates and flood imprint types) along the Sabie River after a flood. They observed that some patches had higher densities and species richness of alien plants after the flood, and therefore concluded that not all riparian patches are suitable habitats for the establishment of alien species.

1.2.3 Plant invasions along riparian zones

Alien plants contribute the most species to the global invasion problem because of their longest exploration history (Van Kleunen et al., 2015), and within this context, plant invasions rank high on the list of pressing environmental concerns in the KNP (Foxcroft et al., 2017b; van Wilgen et al., 2017). So great is the threat that a large programme requiring a considerable amount of resources (over ZAR 350 million from 1997-2016), has focused on the control of alien plants (van Wilgen et al., 2017). Riparian zones in the KNP are the most vulnerable to invasion, because rivers link the park to the many land-use types within the catchment with different land-use objectives to biodiversity conservation (Foxcroft et al., 2007; Hood and Naiman, 2000). Therefore, river are a significant pathway for the introduction and spread of invasive species. In an assessment of invasion pathways and impacts in 19 national parks, Foxcroft et al. (2019) found that rivers were second most important pathway for invasions. In addition, Foxcroft et al. (2019) found that the most frequent impacts of these invasive species they examined were aspects associated to the riparian zone, i.e. physical structure and hydrology, making river the most vulnerable landscapes in protected areas.

Impacts from plant invasions can be dramatic, including the disruption of the entire ecosystem due to the ability of invasive species to alter: community composition, nutrient cycling rates, disturbance regimes and the geomorphology of the invaded system (Chamier et al., 2012; Downey and Richardson, 2016; Fei et al., 2014). Evidence for this is best documented for woody plants; plants termed transformers (Iponga et al., 2008; Tanner et al., 2013). Transformers are those species that have the ability to alter the ecosystem function by changing plant community composition, nutrient cycling rates, or disturbance regimes (Aguiar and Ferreira, 2013). For

example, invasion by *Acacia mearnsii* or *Eucalyptus* species in riparian zones increased water abstraction by the vegetation (Le Maitre et al., 2002; Dye and Jarman, 2004), which in turn alters hydrology and ultimately reduces water flow. Another example is the invasion by *Chromolaena odorata*, which changes the flammability of South African riparian vegetation resulting in frequent fires (Macdonald and Frame, 1988), and in turn increasing the mortality of native vegetation. Te Beest et al. (2012) in an experimental study observed that cleared *C. odorata* biomass interacted with fire and caused a shift in vegetation from woodland to grassland. In riparian zones, impacts have been associated with 1) reductions in stream flow and groundwater storage due to increased water abstraction, 2) increase alien plant biomass and altered nutrient cycling, 3) alteration in fire regimes (fuel load and fire behaviour) leading to soil erosion and reduced water quality, and 4) aquatic alien plants and reduced water quality (Chamier et al., 2012). There are also studies that document how invasive species can alter a community (Cushman and Gaffney, 2010; Tanner et al., 2013) and ecosystem processes (te Beest et al., 2015; Yelenik et al., 2007). However, in many cases the evidence of invasive alien species impacts is from a narrow spectrum of alien species that have a well-documented invasion history. Therefore, it remains unclear whether the majority of alien plant introductions are a threat. For example, in South Africa evidence on impacts of invasive species on fire regimes is based on a few *Acacia* and *Pinus* species (e.g. *A. cyclops*, *A. saligna*, and *P. pinaster*), *Hakea sericea* and *Chromolaena odorata* (see review by Chamier et al. 2012). Meanwhile, a substantial proportion of alien species lack sufficient quantitative data to make spatial or temporal comparisons on their invasions and assign their risk (Kumschick et al., 2015). Likewise, the KNP lacks consistent records or monitoring on many of the alien species inside the park (van Wilgen et al., 2017), which has led to difficulties when deciding which plant invasions to prioritize. Van Wilgen et al. (2017) observed that prioritization exercises in the park are primarily influenced by perceptions, as many of the alien species inside KNP have not been demonstrated to have a negative impact in the park or elsewhere. Therefore, the next logical step would be to determine the nature of the invasion problem, determine which alien species are a significant threat to native plants and where along the riparian zones of the park.

1.2.4 The context dependency of impacts

Although the study of impacts has been the focus of intensive research in the past decade, our understanding of impacts however, is still fragmented (Kumschick et al., 2015; Pyšek et al., 2012; Ricciardi et al., 2013). Invasion biologists still lack consensus on which introductions to prioritise and the extent to which management intervention is warranted (Kumschick et al., 2015). One reason is that impact studies have been biased towards temperate regions, which has limited our predictive understanding of impacts in tropical and sub-tropical regions (te Beest et al., 2015).

Kumschick et al. (2015) further argued this is partly due to the lack of consolidated terminology for impacts to facilitate communication.

There are two definitions of impacts within the field of biological invasions, the first is from a societal perspective, and the other is from an ecological perspective. The former focuses on the economic cost and benefit to society, and is dependent on stakeholder perceptions, which may fail to capture the broad range of impacts of alien species (Catford et al., 2009; Ricciardi et al., 2013). Foxcroft et al. (2017) in a review on plant invasion studies in protected areas, observed that impact studies often focused on factors that threaten elements of biodiversity with extinction, although few plant invasions appear to cause extinction (Ricciardi et al., 2013). Ricciardi et al. (2013) define ecological impact by invasive species as “a measurable change to the properties of an ecosystem by an alien plant”. This definition therefore, implies that alien species have an impact by becoming integrated into the system (Ricciardi et al., 2013). Furthermore, invasive species ecosystems impacts can be either positive or negative, and the magnitude of their impact can vary across a heterogeneous landscape (Ricciardi et al., 2013). Biotic and abiotic variables can further affect the performance of alien species, and the magnitude and direction of impacts of the same species can differ across heterogeneous sites (Foxcroft et al., 2017a; Kumschick et al., 2015; Ricciardi et al., 2013). Environmental stressors associated with the site, such as disturbance can also modify the magnitude of impact of alien species (Price et al., 2011). Given the complexities that affect the impacts of alien species, it remains unclear whether negative impacts are a common occurrence with introductions (Bernard-Verdier and Hulme, 2015). These definitions and concepts highlight the context dependency of impacts. Consequently, there is uncertainty for land managers on how best to respond to introductions.

Given that the consequences of alien plant invasions provide motivation for resources to be allocated towards the control of alien species, a predictive understanding of the impacts should be a central goal (Ricciardi et al., 2013). There are now established methods for elucidating between introductions that are safe and those that prioritised for control, for example, Australian Weed risk assessment, Risk analysis of alien taxa (Kumschick et al., 2018), another key approach being used is the impact-scoring system (Kumschick et al., 2015; Ricciardi et al., 2013). Many of the current hypotheses regarding impacts originated from studies on the invasiveness of a species, including establishment and spread. They evolved to assessing impacts because they could account for variation in abundance and range size, as in the well-known equation by Parker et al. (1999) ($I = RxAxE$; (I) the overall ecological impact is a function of, (A) in numbers or biomass per square meter, (R) the invaded range, and (E) its per capita effect; see Ricciardi et al. (2013)). Many hypotheses either mirror, overlap or share similarities to other invasion hypotheses, a

phenomenon that is common with ecological theory (Catford et al., 2009). For example the empty niche hypothesis, which states that invaders are successful because they use unused resources, reflects the limiting similarity hypothesis (Catford et al., 2009; MacDougall et al., 2009; Ricciardi et al., 2013). The limiting similarity/niche replacement predicts that successful invaders should be functionally different from the present species pool of natives, which is mirrored by the biotic resistance hypothesis (Catford et al., 2009; Pacala and Tilman, 1994; Strauss et al., 2006; Thompson et al., 2010). Although the approaches have contrasting implications for the direction and the magnitude of impacts, both approaches can lead to significant community-level impacts (Ricciardi et al., 2013). A key unifying theme among these approaches is that they compare differences between the resident native species and the invading alien species. It is also evident that the functional ecology of alien species is a major factor underpinning many impact approaches (Pyšek et al., 2012; Ricciardi et al., 2013).

The differences between an invading species and the recipient community are considered a major determinant of invasion success and impact (Loiola et al., 2018; MacDougall et al., 2009; Maron and Marler, 2008; Scharfy et al., 2011). It is argued that unique traits allow an invading species to exploit resources better than the resident species, by accessing unexploited resources or being a better competitor than native species (Ricciardi et al., 2013). For example, the novel weapons or novel resource use hypothesis predicts that substantive impacts occur when an alien species transforms key resources or uses them differently from native species (Ricciardi et al., 2013). For example, when nitrogen-fixing alien species alter nutrient availability and dynamics in a non-nitrogen producing community (Chamier et al., 2012). Hence, being different is often associated with being successful (MacDougall et al., 2009).

Community-level impacts are implicated to arise from two pathways, via niche differences and fitness differences (MacDougall et al., 2009; Ordonez et al., 2010; Ricciardi et al., 2013). Niche differences are those that cause population growth rates to increase as an alien species becomes rare. The implication for this pathway is that impacts of that alien species are unlikely to arise from direct influence but rather indirect effects (e.g. through the alteration of ecosystem properties) (MacDougall et al., 2009; Ricciardi et al., 2013). Fitness differences, by contrast, are those differences that drive competitive exclusion and the implication for this approach is that alien species access limited resources at the expense of native species (MacDougall et al., 2009; Ricciardi et al., 2013). Similar to the empty niche and limiting similarity hypotheses mentioned above, impacts can arise from either pathway but they have different consequences for impact. It is within this context that this thesis examined impacts. Therefore, by providing a link between

plant community change and invasive species, trait based studies provide justification for labelling alien species as causing an impact.

Despite alien species having a long history in the Kruger National Park (KNP), the first attempt to control aliens was in 1958, and not much is known about their impacts on plant community. This phenomenon is not exclusive to KNP but common for many protected areas. For example, Hulme et al. (2013) in a global assessment of 258 quantitative studies on impacts, found that only 37 % of those studies were conducted in protected areas. A key challenge in assessing the impacts of alien plants in KNP is the lack of consistent records or monitoring data on most alien species (van Wilgen et al., 2017). Therefore, a key priority in KNP is to determine the impacts of alien species. The scope of the second paper (chapter 3) in the thesis was to examine plant community change in relation to plant traits to determine the impacts of alien species and the mechanism behind the change.

1.2.5 Conclusion

Mitigating against the threat of plant invasions is a key part of conserving biodiversity in many protected areas. Because conservation resources are scarce, land managers have to ensure that limited resources are utilised wisely by prioritising priority areas and unsafe alien species. Therefore, the distribution and impacts of alien plants has important implications for their management. This review highlighted important considerations for interpreting the patterns and impacts of alien plants in a riparian setting. It has highlighted that the riparian template is important in determining the distribution of the vegetation that occur there and may be useful for when planning control. It has also highlighted the importance of traits when examining the impacts of alien species, which the thesis uses to examine impacts in the second paper.

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Chapter 2: Alien plant distribution and habitat association within the channel types of the Sabie River, Kruger National Park

2.1 Abstract

Riparian habitats are highly vulnerable to invasion by alien plant species because they are areas of high energy, filter propagules in the catchment and they provide opportunities for the establishment of alien species in a resource-rich environment. However, riparian zones have distinct landforms with different biophysical conditions forming the habitat template against which riparian vegetation is structured. The aim of this study was to assess if the distribution of alien plants is associated with the habitat template of the Sabie River. During February 2015, I sampled twenty-one modified-Whitaker plots, placed parallel to the river channel and stratified by channel type. Native and alien plant abundances and species richness were recorded in each plot (tree, shrub and herbaceous). Species density per plot was calculated and a two-way ANOVA performed to test for significant differences between native and alien species by channel type. Across all channel types, the density of alien plants was significantly greater than native plants, but not alien species richness and diversity. Woody alien plant density was low (< 10% total woody), while herbaceous alien species were highly dense throughout all channel types (> 70% total herbaceous species). Herbaceous alien plants had the highest density in the alluvial-influenced channel type, indicating that disturbance by river flow was likely the driver of their presence. Woody alien plants were associated with the bedrock-influenced channel types, namely the bedrock anastomosing and pool-rapid channels. These sites also supported higher species richness and alpha diversity of alien plants, suggesting that these localities have the necessary resources to support the persistence of these species. The high abundance of alien species, especially in areas where habitat-specific native species recruit, such as *Breonadia salicina*, could result in long-term demographic changes.

Keywords: Channel dynamics, Geomorphology, Invader plants, Invasion success, Riparian habitats

2.2 Introduction

The riparian zone occurs at the interface between terrestrial and aquatic environments and plays a role in mediating the transportation of propagules across the landscape (Hood and Naiman, 2000). These zones are comprised of a mosaic of plant communities that are formed in response to varying environmental processes and habitat characteristics (Bagstad et al., 2006; Guillaume, 2002; van Coller et al., 1997). Disturbance, in the form of floods, may remove some established plants, but not all, to create vegetation stands of different successional stages in addition to reshuffling sediments. Severe large infrequent floods strip the river to bare bedrock (Bagstad et al., 2006; Parsons et al., 2005a), thereby resetting the habitat template. Due to the redistribution of sediments and water availability, the type of habitat that vegetation can colonise will vary (Bagstad et al., 2006; Hood and Naiman, 2000; Parsons et al., 2005b). Riparian habitats therefore, have a diversity of microhabitats that can be colonized by a new alien and invasive species.

Depending on where in the riparian zone alien plants are introduced and naturalized, these habitats may serve as foci for their subsequent introduction into adjacent landscapes (Pyšek and Prach, 1993). Rivers and riparian corridors act as conduits for the efficient dispersal of propagules (Alpert et al., 2000; Dyakov and Zhelev, 2013; Hood and Naiman, 2000; Richardson et al., 2007), transporting seeds by multiple modes of transport, for example, water flow, wind or animals. Therefore, propagules can be transported through otherwise unsuitable landscapes (Richardson et al., 2007) until a suitable habitat is reached. While regular flooding may generate gaps and disperse seeds into riparian habitats, it can also damage a plant or create waterlogged conditions that are not suitable for most plants. In addition the geomorphology of the channel influences the vertical and horizontal deposition of different sediment types (e.g. sand or silt) with varying organic content, which in turn determines the soil moisture dynamics of the riparian habitats (Tickner et al., 2001). The character of a substrate affects its ability to retain moisture and therefore the degree to which water is available to plants during different water table levels and floods (Tickner et al., 2001). Therefore, not all gaps in the riparian zone are created on suitable habitats for an alien plant to colonize.

Substantial advances have been made on understanding factors that are important in the invasion of riparian plant communities, for example, fluctuating resources, which incorporates aspects of resource availability, disturbance and species diversity to explain invasion of plant communities (e.g. Davis et al. 2000; Alpert et al. 2000). Studies assessing patterns of alien plants in relation to the availability of habitats in the landscape have received less attention. Despite an increase in

habitat studies over the last decade (e.g. Thomas and Moloney 2013; Foxcroft et al. 2008; Maskell et al. 2006; Mandal and Joshi 2015), most were focused on broad scale patterns (Pyšek and Chytrý, 2014). In this study, I focus on the smaller landscape elements (habitat types) to understand the importance of the riparian landscape on the distribution of alien plants along the Sabie River. Given the configuration of the park, the riparian habitats of Sabie River are highly susceptible to invasion. Furthermore, given the considerable effects that alien plants species can have on the ecosystem (Cushman and Gaffney, 2010; Gooden and French, 2014; Tanner et al., 2013), understanding the patterns of plant invasions in different habitat types is important for managing their spread and anticipating their impacts.

South Africa's Kruger National Park (KNP) includes about 363 alien plant species (Foxcroft et al., 2017b), with riparian zones being the most severely invaded (Foxcroft and Richardson 2003). These areas rely on substantial management intervention to control the dominance and spread of alien plants to previously unaffected areas in the park (Foxcroft and Richardson 2003). For example, many of KNP's widespread invaders (i.e. *Lantana camara*, *Chromolaena odorata*) are introduced via riparian corridors (Foxcroft and Richardson 2003). Most of the KNP's major rivers are severely affected by alien plants (Foxcroft and Richardson 2003). These rivers connect numerous landuse types in the catchment before entering KNP. A variety of alien plant species are associated with the different landuse types and therefore the catchment is the source of many of the alien plant introductions in the park (Foxcroft, Rouget, and Richardson 2007; Foxcroft and Richardson 2003). Although riparian habitats are highly vulnerable to invasion because of the efficient dispersal of propagules by rivers, the fine scale habitat preferences of alien plants in riparian zones are less well understood (Carranza et al., 2011; Tickner et al., 2001). Anticipating the effects of plant invasions and facilitating the efficacy of alien plant control efforts requires that we have a thorough understanding of the factors that determine the extent and distribution of successful plant invaders in riparian habitats.

The aim of this paper was to examine the distribution and habitat association of alien riparian plants along the Sabie River. Specifically, this study investigated whether alien and native plant density, species richness, and alpha diversity differed significantly between channel types.

2.3 Methods

2.3.1 Study site: Sabie River in KNP

The Kruger National Park (KNP) is situated in the north-eastern region of South Africa (Figure 2.1 A), bordering Mozambique in the east and Zimbabwe in the north (Venter et al., 2003). The Lowveld region is classified as a semi-arid Savana system with a subtropical climate characterised by dry winters and wet summers (du Toit et al., 2003). The Sabie River originates west of the KNP border in the Klein Drakensberg escarpment and flows through the park into Mozambique in the east. It is a perennial river with highly seasonal rainfall causing high flows and periodic flooding in summer (October-March) and low flows in winter months (April to September) (du Toit et al., 2003).

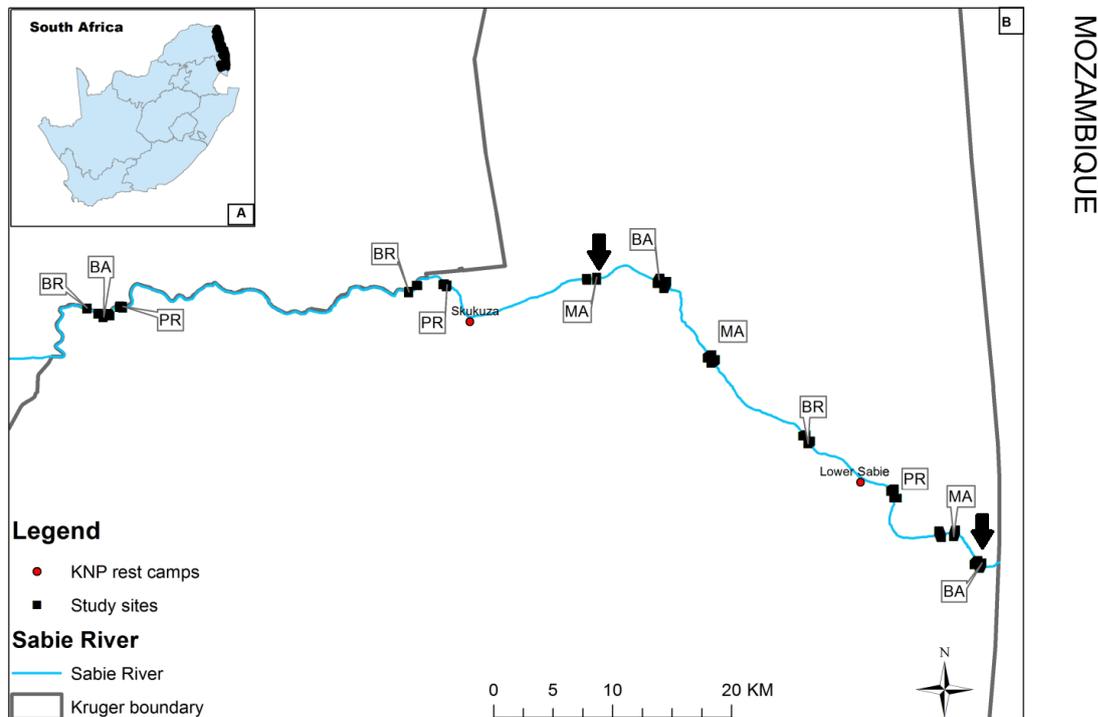


Figure 2.1 The distribution of sampling sites along the Sabie River in the Kruger National Park. Inset (A) indicates the Kruger National Park in relation to South Africa, and (B) the position of the study sites along the Sabie River in Kruger National Park. BR- braided- Widespread sediment bars within the confines of the channel, BA- bedrock anastomosing- Multiple channels flowing through a resistant bedrock base, PR-pool rapid- Deep low energy pools separated by bedrock rapids, MA-mixed anastomosing- Multiple channels flowing through alluvium on bedrock base. (I could not gain access to one BA site (eastern most site) and one replicate at the MA site near Skukuza indicated by black arrow due to various restrictions). Each channel type has six replicates with exception of the BA channel type which has four.

The Sabie River is incised into a bedrock valley referred to as the macro-channel. The active macro-channel floor may have one or more channels that carry water throughout the year and is bounded by the macro-channel banks, which are rarely inundated. The Sabie River is characterised by different channel types (which vary in morphological units) and morphological units (which vary in substrate type) (Rountree et al., 2001). Four channel types, namely the braided, bedrock anastomosing, pool rapid, mixed anastomosing were recorded to delineate the physical environment of each site. The channel types are characterised as i) braided – a channel with widespread sediment bars within the confines of the channel, ii) bedrock anastomosing which comprises multiple channels flowing through a resistant bedrock base, iii) pool rapid has deep, low energy pools separated by bedrock rapids and iv) mixed anastomosing has multiple channels flowing through alluvium on a bedrock base (van Niekerk et al., 1995).

2.3.2 Data collection

The study sites were stratified along the four channel types of the Sabie River (Figure 2.1). Eleven sampling locations from a study conducted in 2004 to 2005 by Parsons et al. (2006) were re-sampled during the months of January and February of 2015. Each sampling location had two sampling sites (i.e. 1A and 1B). Each sampling site had GPS coordinates that were captured with a differential GPS in the 2004 study. In 2015, I used those same sampling points to track the centre points of each site using a differential GPS to ensure that the placement of the sampling plots were the same as those used in 2004 (Parsons et al., 2005). From the centre points, I then measured 25 m on either side to make up the 50 m length of the sampling plot. At each site, the channel type was identified, based on the geomorphological characterisation developed for the Sabie River by van Niekerk et al. (1995).

2.3.3 Plot layout

A modified Nested-sampling plot (Dyakov and Zhelev, 2013) was used to sample the riparian plant communities along the Sabie River (Figure 2.2). Modified Nested-sampling plots are efficient at capturing community composition and structure because species richness data are collected at multiple spatial scales. They provide better estimates of mean species cover and plant diversity patterns at multiple spatial scales (Dyakov and Zhelev, 2013; Stohlgren et al., 1995). The 50 m length of the plot ran parallel to the river and the 20 m width was perpendicular to the channel (running from the channel floor towards the channel bank).

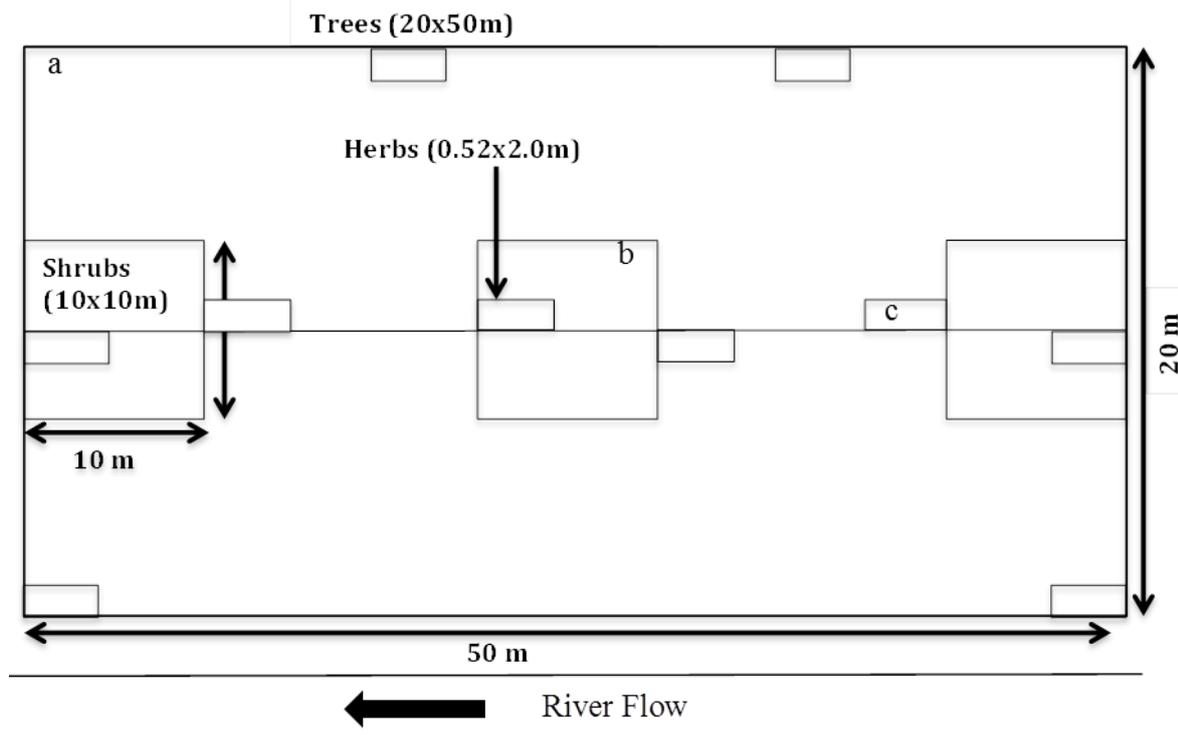


Figure 2.2 Nested sampling plot. Two of these plots were placed at each of the 11 sites: (a) one 20x50 m plot (1000 m²) used for surveying all trees, (b) three 10x10 m plots (300 m²) for surveying all shrubs, and (c) ten 0.5 m x 2.0 m (10m²) for all herbaceous plants. [Adopted from (Dyakov and Zhelev, 2013), based on a modified Whittaker (1956) plot layout]

There was six replicates for channel types (Figure 2.1) of the 50 m x 20 m (1000 m²) tree plots (Figure 2.2 a), containing three 10 m x 10 m (100 m²) shrub plots (Figure 2.2 b) and ten 0.5 m x 2.0 m (1 m²) herb plots (Figure 2.2 c). The total number of plots were 24, 72 and 240 respectively. For the herbaceous layer only individuals with the main stem in the plot were counted for abundances. Within the 1000 m² plot, three 10 m x 10 m (100 m²) shrub plots were set along a fifty meter measuring tape (Figure 2.2 b), running in the centre of the tree 10 m x 10 m plot. Within the 20 m x 50 m (Figure 2.2 a) all woody species with a stem diameter greater than 3 cm or a height greater than 1 m were recorded. I could not gain access to site 12 or sample B at site 04 because of park restrictions, resulting in an unequal sample size (appropriate statistical methods were employed to deal with the unequal sampling, which is detailed below).

2.3.4 Vegetation data

In each of the 21 plots, all native and alien tree, shrub and herbaceous species were recorded within their respective plots and the number of individuals per species recorded as abundance. Voucher specimens of all unknown species were collected and pressed for later identification at the Skukuza herbarium. Biological nomenclature in this study followed the Plants of Southern Africa online checklist (Plants of Southern Africa ver 3.0, 2009); this was cross-referenced with the Germishuizen and Meyer (2003) checklist. For the purpose of this study, woody plants were the growth forms: tree, woody climber and shrub, while non-woody plants (herbaceous species) were herbs, climbers, and dwarf shrubs.

2.3.5 Data analysis

Analyses were carried out in R version 3.3.1 (R Core Team 2016) and the package vegan version 2.4-1, which provides tools for descriptive community ecology, including ordination and the calculation of diversity and dissimilarities indexes (Oksanen et al., 2016). Before any statistical test could be run, the data had to be treated to correct for missing data. This included calculating densities weighted by area: species per site and block-type (i.e. abundance values / actual area surveyed). Using the `decostand {vegan}` function, I standardized the densities based on range (range: standardize values into range 0 ... 1 (default MARGIN = 2)).

Plant density, species richness and diversity

Plant densities were calculated using abundance values divided by actual area surveyed to help correct for unexpected unequal sampling effort/design. Species richness was calculated using `specnumber {vegan}` for the various herbaceous, shrub and tree plots across the different channel types. Alpha diversity was calculated using the Shannon-Wiener index (a diversity index of richness and evenness) using `diversity {vegan}` and represented using a bar graph. Results are visualised using stacked bar graphs, which compare the percentage that each group (alien vs native) contributed to the total density and total species richness and total diversity. To test for statistical significance ANOVAs were carried out for plant density, species richness and diversity by channel type for alien versus native species. A Tukey multiple comparisons test was then conducted to describe the details of these significant differences.

Beta diversity

For beta diversity I used `vegdist {vegan}` to calculate dissimilarities from the standardized data using the default Bray–Curtis method. The Bray-Curtis measure of dissimilarity is a measure of the difference between samples (Clarke, 1993). To visualize beta diversity results, hierarchical clustering with p-values of dissimilarities was produced using the `pvclust` R package (Suzuki and Shimodaira, 2015). Clusters were identified using multiscale bootstrap resampling, with 1000 bootstraps, using average clustering and correlation distance (Suzuki and Shimodaira, 2015). Clusters with approximately unbiased (AU) probability values (p-values) greater than 95% represent channel types with species composition similarities strongly supported by the data (Suzuki and Shimodaira, 2015).

Table 2.1 A list of alien plants recorded on the Sabie River, indicating their abundance, the status of the species and impact in Kruger National Park.

Species	Abundance	Status	Impact	Suggested impact
Climber				
<i>Aristolochia elegans</i> Mast.	1	Invasive	High	Low
<i>Cardiospermum grandiflorum</i> Sw.	69	Invasive	Medium	High
<i>Clitoria ternatea</i> L.	1	Invasive	Low	Low
<i>Ipomoea purpurea</i> (L.) Roth	12	Invasive	Low	Medium
<i>Vicia sativa</i> L.	238			High
Dwarf shrub				
<i>Catharanthus roseus</i> (L.) G. Don.	1	Invasive	Medium	Low
<i>Dicoma tomentosa</i> Cass.	11			Low
Herb				
<i>Acanthospermum hispidum</i> DC.	449	Naturalised	Low	Medium
<i>Ageratum conyzoides</i> L.	19	Invasive	Low	Low
<i>Alternanthera pungens</i>	295	Invasive	Low	Medium
<i>Argemone ochroleuca</i> (GB Ownby)	1	Invasive	High	Low
<i>Bidens biternata</i> (Lour.) Merr. & Sheriff	485	Naturalised	Medium	Medium
<i>Bidens pilosa</i> L.	1	Naturalised	Medium	Low
<i>Cirsium vulgare</i> (Savi) Ten.	1			Low
<i>Commelina benghalensis</i> L.	33	Naturalised	Low	Low
<i>Convolvulus arvensis</i> L.	1	Naturalised	Low	Low
<i>Corchorus trilocularis</i> L.	35	Naturalised	Low	Low
<i>Datura ferox</i> L.	24	Invasive	Medium	Low

<i>Euphorbia heterophylla</i> L.	20	Invasive	Low	Low
<i>Euphorbia hirta</i> L.	22			Low
<i>Gomphrena celosioides</i> L.	3	Invasive	Low	Low
<i>Oxalis corniculata</i> L.	1	Invasive	Low	Low
<i>Parthenium hysterophorus</i> L.	190	Invasive (PT)	Low	High
<i>Richardia brasiliensis</i> Gomes	24	Naturalised	Low	Low
<i>Schkuhria pinnata</i> (Lam.) Cabr.	20	Naturalised	Low	Low
<i>Senna obtusifolia</i> (L.) H.S.Irwin & Barneby	1179	Invasive	Low	High
<i>Senna occidentalis</i> (L.) Link	125	Invasive	Medium	Medium
<i>Stachytarpheta indica</i> sensu auctt.	6	Invasive	Low	Low
<i>Tagetes minuta</i> L.	543	Invasive	Low	High
<i>Tridax procumbens</i> L.	13	Naturalised	Low	Low
<i>Urtica dioica</i> L.	1			Low

Authority- (NEW Plants of Southern Africa ver 3.0, 2017)

Status-of alien plants in KNP (according to Foxcroft et al., 2008, 2003)

PT: potential transformer

Impact – estimate impact based on the species records in KNP by authors (Foxcroft et al., 2008, 2003)

Suggested impact – current estimate impact based on proportion of alien plants relative to total native species abundance and their status in KNP

2.4 Results

Plant density, species richness and diversity

A total of 210 plant species were recorded. Of these 210 species, 40 were alien species and 166 were native species. Thirty-six herbaceous alien plant species were recorded, with the majority (19) considered invasive, one a potential transformer (PT) and the rest naturalized or casual species (Table 2.1). Herbaceous alien plants represented a large amount (70-80 %) of the total herbaceous plant density in the channel (**Error! Reference source not found. A**). Native species were more species rich than alien plants, represented by more than 50% of total herbaceous species, more than 60% of the shrubs, and more than 95 % of tree species were native species (Figure 2.3 B). Woody alien shrubs and trees represented a low percentage of the density, species richness and species diversity of the total. They represented less than 40% of total woody plants across all channel types (Figure 2.3 A-C). Of the woody alien species recorded, two were transformer species *Lantana camara* and *Opuntia stricta* and two were invasive *Sesbania bispinosa* and *Sesbania punicea* (Table 2.1).

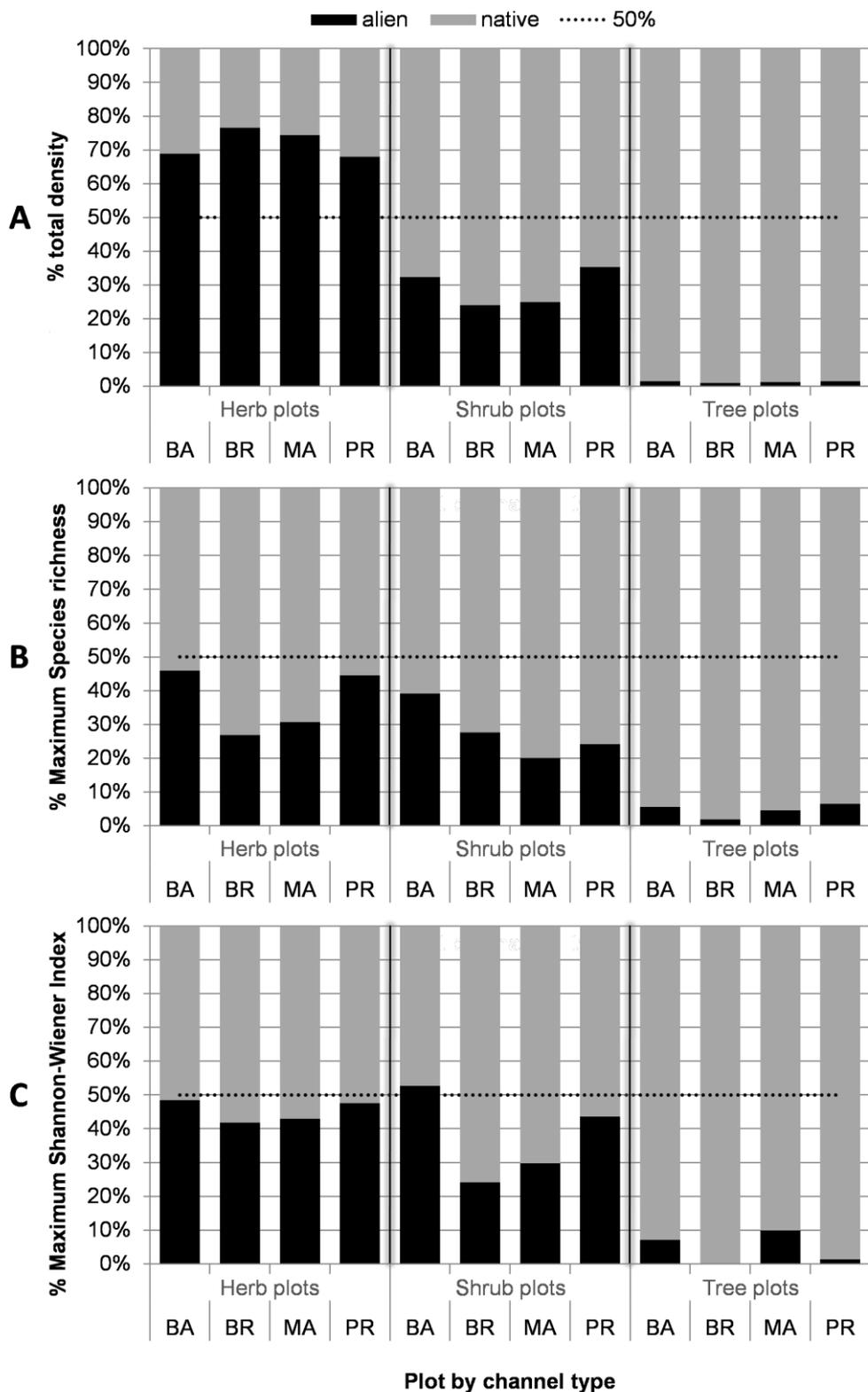


Figure 2.3 Difference in alien (black) and native (grey) plant density (A), species richness (B) and Shannon-Wiener diversity (C) across channel types: BA- bedrock anastomosing, BR- braided, MA-mixed anastomosing, PR-pool rapid. The vertical bars represents density, species richness, and Shannon-Wiener diversity represented in percentage-stacked bar graph to show percentage contribution by each group.

Table 2.2 Factorial ANOVA of density, species richness and alpha diversity for native and alien species (origin) by channel types. Significance: 0 = ‘****’; 0.001 = ‘***’; 0.01 = ‘**’; 0.05 = ‘.’; 0.1 = ‘ ’; 1

Variable	Factor	df	F	p-value
Density	Channel types	3	1.447	0.228
	Origin	1	50.791	0.000000***
	Channel types X origin	3	6.991	0.00013 ***
Species richness	Channel types	3	0.229	0.875
	origin	1	26.386	0.000099 ***
	Channel types X origin	3	0.587	0.632
Alpha diversity	Channel types	3	0.045	0.98693
	origin	1	15.002	0.00135 **
	Channel types X origin	3	0.335	0.8

The ANOVA results showed a significant difference in plant density between alien and native plants [$F(1, 492) = 50.791, p < 0.0001$], however total plant density was not significantly different between channel types [$F(3, 492) = 1.447, p = 0.228$]. Furthermore, there was a statistically significant interaction effect between plant type (origin: native/alien) and channel type on plant density [$F(3, 492) = 6.991, p = 0.0001$] (Table 2.2). Post-hoc Tukey’s HSD tests showed alien plant densities were generally higher than that of native plants (diff = 36.43, $p < 0.0001$). The density of alien plants was statistically different between channel types, but the difference was due density being significantly higher in the braided channel type [$F(3, 492) = 6.991, p = 0.0006$] and mixed anastomosing [$F(3, 492) = 6.991, p = 0.03$]. The density of alien plants by sampling plot showed that herbaceous alien plants contributed the most to alien plant densities followed by shrubs (Figure 2.3 A). Very few woody alien tree species (65) are found in the Park (Foxcroft et al., 2017b), of which only three were recorded throughout our plots (Table 2.1).

Table 2.3 Post hoc TukeyHSD test for differences between native and alien species. The difference (diff) preceded by a negative (-) denotes that the grouped alien was greater than the group native and those without the negative indicate the group native was greater.

Variable	Factors	diff	p-value
Density	Native-Alien	-36.42639	0.0001
Species richness	Native-Alien	23.16667	0.00009
Alpha diversity	Native-Alien	1.636305	0.0014

ANOVA results for species richness and alpha diversity (Shannon-Wiener Index) both showed significant differences between alien and native plants [richness: $F(1,16) = 26.386$, $p < 0.0001$ and diversity: $F(1,16) = 15.002$, $p = 0.0014$] but not between channel types [richness: $F(3,16) = 0.045$, $p = 0.987$ and diversity: $F(3,16) = 0.229$, $p = 0.875$]. The post-hoc Tukey's HSD tests showed native species richness and alpha diversity was mostly higher than that of alien species (Table 2.3). The Bedrock anastomosing and Pool rapid supported higher species richness and alpha diversity of alien species (herbs, shrubs and trees) (Figure 2.3).

Clustering results revealed well-defined differences amongst alien and native species (AU = 100%) (Figure 2.4). The composition of alien plant species within the mixed anastomosing and pool rapid channel types were significantly similar (AU > 95%). However, the composition of alien species within the braided was significantly dissimilar (AU = 90%) to the other channel type. No such significant similarities were seen for native species (AU = 59%).

The alien species in the braided channel type were largely made up of herbaceous species (Figure 2.3). The species that were associated with the bedrock anastomosing channel type were mostly invasive (Table 2.1) (*Datura ferox*, *Euphorbia heterophylla*, *L. camara*, *Oxalis corniculata*, *Sesbania punicea*). Individual woody alien species such as *Lantana camara* and *Sesbania punicea* were associated with bedrock and mixed bedrock channels, which are more broadly the anastomosing channel types. Whereas woody alien shrubs occurred showed no preference for either mixed, bedrock or alluvial influence.

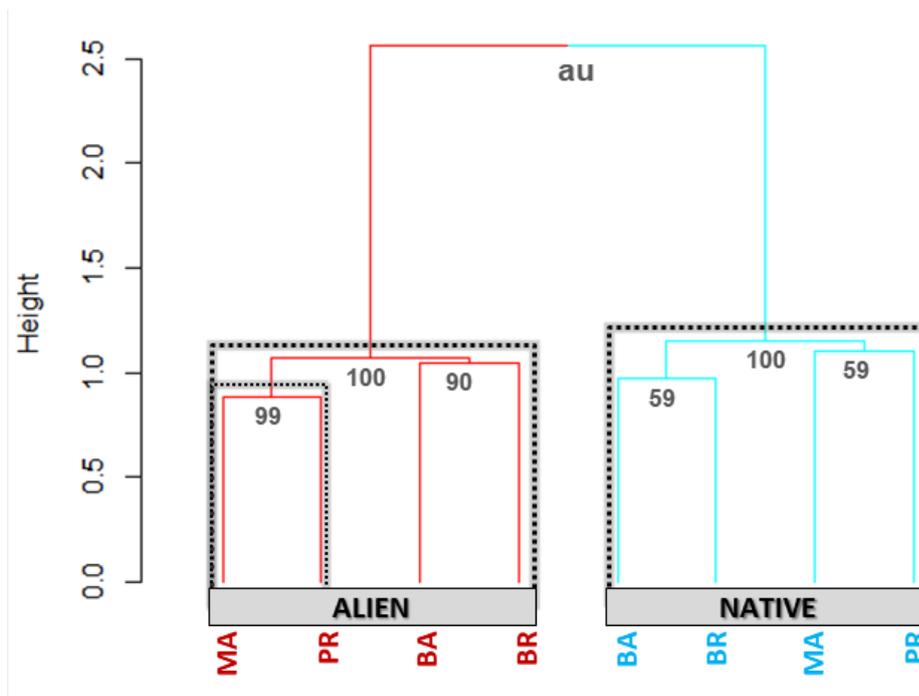


Figure 2.4 Dendrogram of hierarchical clustering with p-values (%) of alien and native species composition using average clustering and correlation distance by channel type (Suzuki and Shimodaira 2015). Clusters with approximately unbiased (AU) probability values (p-values in %) greater than 95% are shown in grey dashed boxes and represent significantly similar channel type groups. The boxes separating alien from native species composition (AU=100%) indicates the two groups significantly distinct from each other.

2.5 Discussion

The distribution of alien plants: plant density, species richness and diversity

This study found that alien species differed in extent and distribution along the Sabie River, indicating that the establishment of alien species is not independent of the riparian template. This is similar to the study by Hood and Naiman (2000), which observed significant differences in the percentage of alien species in the macro-channel floor to the channel bank. The density of alien plants was higher and mostly herbaceous compared to native plants in all the channel types, supporting the notion that riparian zones are vulnerable to plant invasion. These results are in accordance with other studies on KNP's major rivers (e.g. Hood and Naiman, 2000; Myburgh and Bredenkamp, 2005). Foxcroft et al. (2008), however, found contrasting results after the 2000 floods, which was very low abundances of herbaceous and woody alien plant species compared to native species. It is important to note that Foxcroft et al. (2008) were looking at the effect of the large infrequent flood whereas Hood and Naima, (2000), Myburgh and Bredenkamp, (2005) and this study were looking at typical flow conditions of the river. The braided channel type had the highest alien plant density compared to the other channel types, supporting the findings by

Brummer et al. (2016) that braided channels are among the most vulnerable to plant invasions. The braided channel type is characterised as an unstable channel type due to its transient sediment bars and gravel bars (Ward, 1998). Therefore, this result is not surprising given the herbaceous and ruderal nature of the alien species. These species dedicate much of their energy to photosynthesis and reproduction for rapid growth and colonization. Thus, the regular disturbance by floods allows them to colonize, grow quickly and subsequently outcompete native species (Catford et al., 2009). The differences in the distribution of alien plant between channel types may indicate the difference in intensity and frequency of disturbance in the channels.

The high density of alien species in the channel was from a few but widespread alien species. Native species richness and diversity was generally higher than that of alien species across channel types. Alien species richness comprised less than 30% of the total richness, except in the bedrock anastomosing and pool-rapid (bedrock-influenced) channel types, where alien species diversity comprised 40% of the total diversity. An inspection of the results indicates that differences in bedrock and alluvial influence are important for the establishment and the persistence of alien species. This was supported by a higher species richness and diversity of alien species in the bedrock anastomosing and pool-rapid channel type (bedrock-influenced) compared to the braided and mixed anastomosing channel types. Bedrock and alluvial influence are important because they reflect differences in flooding intensity and water availability. The bedrock controlled channels are considered to be stable because of the resistant bedrock template that results in topographically high bars that are largely free of inundation, and water supply is from the water table (Rountree et al., 2001; van Niekerk et al., 1999). The transient sediment bars of the alluvial-influenced channel types make these unstable (more dynamic). Thus, the results suggest there are two types of plant communities where alien species occurred, the first is dominated by herbs (ruderal species driven by disturbance) and the second, is a mix of ruderal and woody species.

Herbaceous alien plants thrived in the highly dynamic braided channel types, and woody species thrived in the more bedrock-influenced channel types. Individual woody alien species such as *Lantana camara* and *Sesbania punicea* were highly associated with the bedrock anastomosing channel type. Overall, there was a low density of woody alien plants. This lower density of woody alien plants along the Sabie River was also observed in other studies (e.g. Hood., 2000; Foxcroft et al., 2008; Vardien et al., 2013) and may, in part, be attributed to the efficacy of management efforts. Vardien et al. (2013) for example observed that clearing of *L. camara* in the upper reach of the Sabie River prevented the down-stream spread of that population to lower reach of the River. The lower Sabie population was genetically distinct from the cleared populations in upper

reach, indicating that different sources of introductions into the park and that clearing was effective in reducing the downstream spread of alien species.

Compositional difference

This study found that most alien plants do not have a strong affinity for specific habitat types, with the exception of a few woody species. Alien species composition had considerable overlap between channel types. This contrasts the study by Myburgh and Bredenkamp (2005), which found that woody and herbaceous alien species significantly differed in habitat preference. They observed that herbaceous alien plants occurred more frequently on low-lying and depositional features, while woody species occurred on less frequently inundated features. It is important to note that their study included smaller landscape elements, which differ further in habitat properties. The high similarity in alien species composition between channel types perhaps reflects the effective dispersal by the river or ruderal nature of alien species. In contrast, native species composition was dissimilar between channel types, which supports the findings by van Coller et al. (1997) that the channel type is a significant determinant of the distribution of native species. A caveat to this study would be that I studied patterns in relation to only channel types. Perhaps other geomorphic features are better predictors of alien species distribution patterns.

Although alien plants represented a large proportion of the vegetation in the riparian zones of Sabie River, woody alien plants, which are controlled in the park i.e. *L. camara* and *O. stricta* (van Wilgen et al. (2017), represented a very low proportion of the density and diversity of the alien plants in the river. Herbaceous alien plants that are not controlled in the park i.e. *Acanthospermum hispidum*, *Tagetes minuta*, *Waltheria indica* represented large proportion of the aliens invading the river. The combined effect of these species has yet to be examined. *A. hispidum*, *T. minuta*, *W. indica* were abundant throughout all channel types, even in bedrock-influenced habitats, which are recruitment areas for *Breonadia salicina*. The native species *B. salicina* depends on characteristic habitat features such as exposed rock fissures for successful recruitment (McLoughlin et al., 2011), and is highly likely to be affected with the smothering of bedrock habitats. Grasses and herbaceous species are suggested to be more effective at reducing erosion because they have dense near surface canopy and form a root mat (Tickner et al., 2001), which may smother bedrock by trapping sediments and reducing bedrock surfaces in the long term. While the previous example may be slow acting, *Parthenium hysterophorus* is an immediate threat to the entire plant community of Sabie River. The allelopathy of *P. hysterophorus*, due to the phyto-toxin sesquiterpene lactone parthenin, may inhibit the recruitment of different plant species in its proximity (e.g. Belz et al., 2009). Land managers may need to take cognisance of

where dense stands of *P. hysterophorus* occurs since it is the most likely to affect native riparian vegetation along the Sabie River.

2.6 Conclusion

This study found that alien species prevalence differed between channel types. This was supported by a significant difference in both alien plant density and species composition between channel types. Alien plants had the highest density in the alluvial dominant braided channel types, followed by the mixed anastomosing channel type. The alluvial-bedrock influence is a proxy for multiple fluvial variables including disturbance intensity and frequency, and water availability. Similar to native species, alien plants are structured along the bedrock and alluvial influence of the channel. The dynamic alluvial landforms provided more opportunities for the establishment of alien species, hence, it was dominated by species that could colonize and grow quickly. The stable bedrock-influenced channel types were more suitable habitat for both herbaceous and woody alien species. The bedrock-influenced channel types are the most likely to be altered by the combined effects of alien plants.

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Chapter 3:

Plant community change in relation to alien plant invasions in the riparian zones of the Sabie River, Kruger National Park.

3.1 Abstract

The proliferation of plant invasions into Kruger National Park (KNP) ranks high on the list of pressing environmental concerns, because of their potential to disrupt the resilience of systems. With the exception of a select few well-known invasive species, the consequences of many and often abundant riparian alien species are largely unknown. Therefore, it is important to determine which species to prioritise for management. Conceptual frameworks for measuring impacts predict that the extent to which an alien species differs in its functional ecology from native species determines its impacts. Therefore, it was predicted that temporal changes in density and diversity of alien species will decrease native plant species richness, density, evenness and species composition. In addition, patterns of plant community change will be mediated by plant strategies where there is competition between alien and native species. Vegetation data were recorded in 2004 at 12 sites along the riparian zones of the Sabie River. Of these, 11 sites were resampled in 2015 and collated with the 2004 data and then assigned categorical trait information. Both native and alien plant density and species richness increased over time. The high densities of alien species correlated with a decline in native species evenness and constrained the recruitment of native species composition. Native plant density decreased when native and alien plants were closer in their combination of plant strategies (life history and growth form plant strategies). This result supports the notion that species with the greatest potential to drive competitive exclusion are those that have a similar combination of traits relative to native species. However, native and alien species differed significantly in their combination of plant strategies. Therefore, results imply that the decline in native species is an indirect consequence of the dominance of alien plants. The effects of alien plants along the Sabie are complex, however alien species with the greatest potential to cause change appear to be those that have a closer combination of plant strategies to native species.

Key words: Alien species, Community change, Fitness differences, Impacts, Niche differences, Plant strategy.

3.2 Introduction

Invasive species are key drivers of global environmental change because of their tendency to facilitate a shift in the dynamics of plant communities (Didham et al., 2005; Gaertner et al., 2014; Longo et al., 2013; Richardson et al., 2007). In doing so, they degrade biodiversity, ecosystem functioning and the resilience of ecosystems (Macdougall et al., 2013). Ecosystems dominated by alien plants are therefore an increasing global concern (Daleo et al., 2009; Price et al., 2011; Richardson et al., 2007). Numerous studies have reported on how even a single alien plant species can potentially alter biodiversity, hydrology, nutrient cycles, soil properties, disturbance and fire regimes (Chamier et al., 2012; Hejda and Pyšek, 2006; Hulme et al., 2013; Levine et al., 2003). By replacing native species and changing vegetation structure and function, alien plants therefore change plant community patterns and alter ecosystem processes (Iponga et al., 2008).

Protected areas, although important for maintenance of key ecosystem processes and the persistence of biodiversity, are not exempt from the dominance of alien plant species (Foxcroft et al., 2013). Therefore, plant invasions rank high on the list of pressing environmental concerns, as has been noted in the Kruger National Park (KNP) (Foxcroft et al., 2013). However, the consequences of alien plant invasions in the KNP are largely unknown, with the exception of a few widespread terrestrial invaders (e.g. *Lantana camara*, *Opuntia stricta*) and aquatic invaders (e.g. *Eichhornia crassipes*) (Foxcroft and Richardson, 2003; van Wilgen et al., 2017). Furthermore, less is known about short-lived alien species that dominate the riparian zone of the major rivers in the park. Consequently, these species tend to rank low on the priority control lists, with the exception of a select few like *Parthenium hysterophorus* that drive significant changes in many other plant communities (van Wilgen et al., 2017). While not all alien plants that establish have negative effects on the native plant community, some can displace native species and transform systems (Warren et al., 2015).

Because impacts are context dependent, the extent to which alien species have impacted (and can potentially impact) local biota depends on the plant community interactions (González-Moreno et al., 2014; Kumschick et al., 2015; Ricciardi et al., 2013). The scale and extent to which management intervention is required to mitigate these threats are highly debated among scientists and managers (e.g. van Wilgen et al., 2017). Strategic plans for prioritization and intervention aimed at minimizing or preventing impacts of alien plants would benefit managers greatly, however, there is a lack of information in particular on priority species (McGeoch et al., 2016; van Wilgen et al., 2017).

It has been proposed that the dominance and impacts of alien plants are due to their strong competitive ability (Maron and Marler, 2008). However, it is equally argued that alien species take advantage of ecosystem's change, such as disturbance, rather than alien plants being "superior competitors" and the driver of change (Price et al., 2011; Zelnik et al., 2015). Therefore, it is important to differentiate the mechanism of change (Didham et al., 2005). Although it is noted that explicit understanding of mechanisms is best obtained through experimental studies (Bernard-Verdier and Hulme, 2015), patterns from naturally occurring plant communities can also provide insight on the processes driving the correlation (Tomasetto et al., 2013). Conceptual frameworks for measuring impacts highlight the functional ecology (in reference to traits) of an alien species, especially how it differs from the resident community as an important determinant of impact (Cleland, 2011; Hulme and Bernard-Verdier, 2018; Ricciardi et al., 2013; Thompson et al., 2010). More importantly, it is the extent to which an alien species differs from the local native species that determines the magnitude of its impact (Macdougall et al., 2013). It has been posited that limited trait differences between native and alien species drive change via competitive exclusion (fitness differences) and marked differences drive changes through altered ecosystem function (niche differences) (Hulme and Bernard-Verdier, 2018). Thus, evidence of trait differences in relation to plant community change may be important to distinguish the mechanism of change and therefore to determine which introductions to prioritise.

This study addresses some of the challenges described above by examining the response of native plant communities to temporal changes in density and diversity of alien plants and whether the patterns of community change are mediated by plant strategies. Using data from 2004 and 2015, this study examined changes in native and alien riparian plant communities along the Sabie River. It was predicted that 1) the limited control directed towards short-lived invasive alien plants would lead to an increase in density, richness and evenness of alien herbaceous species, 2) a decrease in native plant species density, richness and evenness over time. 3) Native plant decreases will lead to a change in native species composition, and 4) when alien and native species share a high degree of trait similarity, there will be competition, leading to dominance by the superior competitor.

3.3 Materials and methods

3.3.1 Study area

The study area is situated along the riparian zone of the Sabie River in the KNP in the north-eastern region of South Africa (Figure 3.1A). The Sabie River forms the boundary of the park in the west, before bordering Mozambique in the east and Zimbabwe in the north (Venter et al., 2003). The Lowveld region is classified as a semi-arid Savana system with a subtropical climate characterised by dry winters and wet summers (du Toit et al., 2003). The Sabie River is a perennial river that originates on the eastern slopes of the Drakensberg in Mpumalanga Province, at an altitude of about 2200 m a.s.l. (van Niekerk et al., 1999). It flows through KNP and eastwards into Mozambique. The Lowveld region is classified as a semi-arid Savana system with a subtropical climate characterised by dry winters and wet summers (du Toit et al., 2003). Rainfall is highly seasonal causing high flows and periodic flooding in summer (October-March) and low flows in winter (April to September) (du Toit et al., 2003). More than half of the Sabie River catchment drains through a number of different land use types, the most predominant of which is plantation forestry and cultivated land, followed by natural vegetation, degraded land and human settlements (Foxcroft et al., 2007). The remaining half of the catchment falls within the formally protected area of KNP (Figure 3.1).

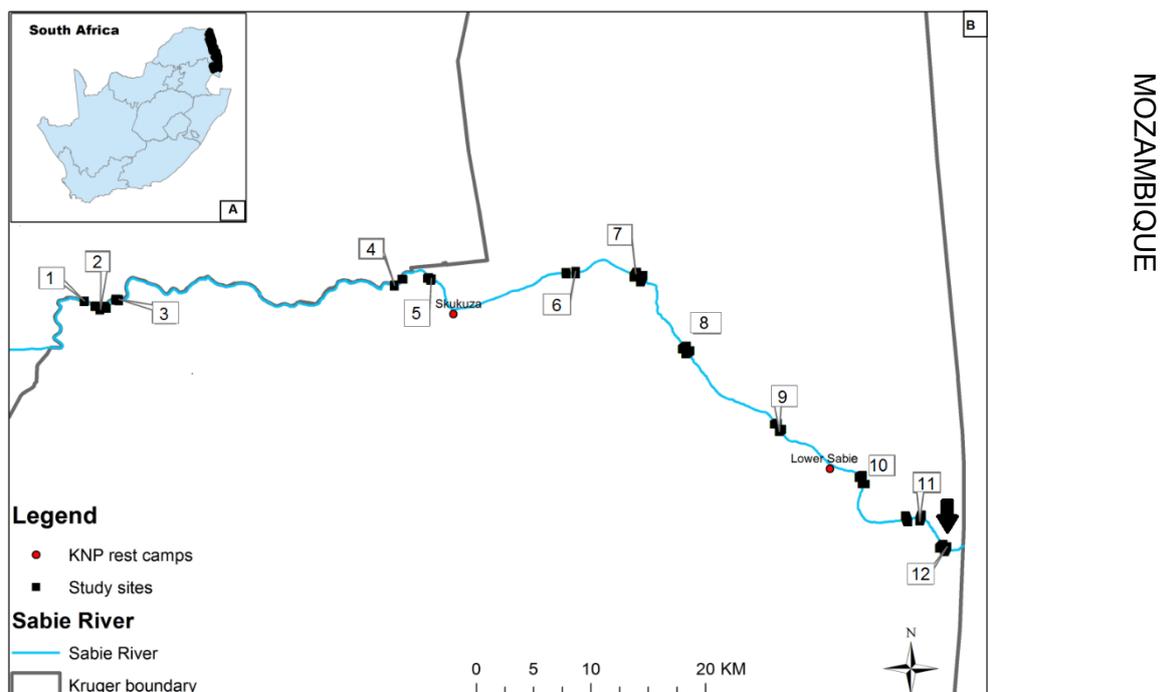


Figure 3.1 The distribution of sampling sites along the Sabie River, based on the sites sampled by Parsons, et al. (2005a). Inset (A) indicates the Kruger National Park (KNP) in relation to South Africa, and (B) the position of the study sites along the Sabie River in KNP. The black arrow indicates site 12, which could not

be accessed in 2015 due to law-enforcement restrictions, leaving a total of 11 sites sampled in 2015 and 12 in 2004. Sites start from the western boundary and end near the east boundary bordering Mozambique. Redrawn from Parsons et al. (2005a).

3.3.2 Study design and plot layout

Sampling in 2004/5

The 2004 woody plant data were collected by Parsons et al. (2005) in June-October of 2004. The data were collected in 2004 after a large infrequent flood in 2000 to understand the effects of large infrequent disturbances on riparian vegetation. These data were collected at 12 sites using contiguous belt transects (two transects at each site totalling 24 transects) of 50 m² that ran the width of the channel form and stretched from channel bank to channel bank (Figure 3.2, see also Parsons et al., (2006) for additional details). The 2004 transects were stratified by channel type. Specifically, Parsons et al. (2006) used belt transects to measure the effect of a large infrequent flood event. Belt transects are more efficient at detecting changes in plant communities along an environmental gradient (Parsons et al., 2005b). The GPS coordinates of every woody species (shrub and tree), with a diameter of ≥ 3 cm, were captured using a differential GPS.

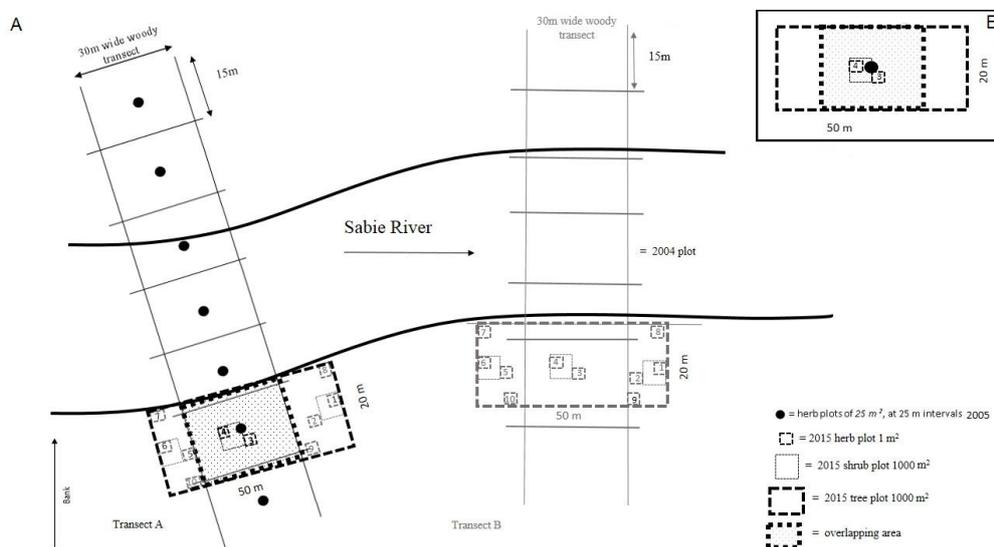


Figure 4.8 Layout of the study area. Line transects A and B were established in 2004. The 15 m x 30 m (450 m²) squares represent the 2004 woody plots (panel A). The 2004 herbaceous plots sampled with 5 m x 5 m (25 m²) square plots, represented as solid circles, were placed only at the centre of the woody transect A (panel A). In 2015 the data was resampled at both line transects using Whittaker plots represented by the rectangle sampling plots. Trees were sampled in 20 m x 50 m (1000 m²) plots, shrubs in three plots of 10 m x 10 m (100 m²), herbs in 10 plots of 2 m x 0.52 m (1.04 m²). Plots omitted from the analysis are in 48

grey these include all the plots recorded in transect B (due to no herbaceous plots being done in 2005) and transect A plots transect A plots that fell outside of the overlapping area (panel A). The final reduced sampling area is indicated in the smaller black square (panel B), i.e. an area of 20 m x 30 m (600 m²) for trees, 10 m x 10 m (100 m²) for shrubs, 2 m x 0.52 m (1.04 m² x 2), was used for comparing between 2004 and 2015.

Herbaceous plant data were sampled in 25 m² plots at 25 m intervals placed at the centre of woody transect A only. Only 12 of the 24 woody belt transects had herbaceous plots in 2004. Herbaceous plants were sampled between April and July of 2005 in plots that ran along the same transect from the one macro-channel bank to the other. Herbaceous plot counts (1-22 from bank to bank) varied with channel type width. For the herbaceous layer, the number of individuals and species names of all plants with their main stem in a plot were recorded. The categorical trait information for each species was collated, namely life history (annual, biennial and perennial), origin (alien or native), and growth form (climber, dwarf shrub, herb, shrub, scrambler, tree, woody climber). All trait information was derived from Germishuizen (2003) and the Plants of Southern Africa ver 3.0 (2009).

Sampling in 2015

Eleven of the 12 sites sampled in 2004 were resampled in 2015 for comparison (site 12 could not be sampled due to law enforcement activities). These plots were placed at the centre coordinates of the 2004 woody plots using a differential GPS. Sampling in 2015 was carried out using a modified version of Whittaker's nested sampling plot design (Stohlgren et al., 1995). This plot design was specifically used because it is more efficient at capturing community composition and structure since species richness data are collected at multiple spatial scales (Dyakov and Zhelev, 2013). In particular, they provide better estimates of mean species cover and plant diversity patterns at multiple spatial scales (Dyakov and Zhelev, 2013; Stohlgren et al., 1995). Consequently, one replicate of each 50 m x 20 m (1000 m²) tree plot contained three 10 m x 10 m (100 m²) shrub plots and ten 0.52 m x 2.0 m (1.04 m²) herbaceous (herb) plots (Figure 3.2). Within the 1000 m² plots, three 100 m² shrub plots and six 1.04 m² herb plots were set along a 50 m measuring tape running through the centre of the tree plot. The categorical trait information for each species was also collated, namely life history (annual, biennial and perennial), origin (alien or native), and growth form (climber, dwarf shrub, herb, shrub, scrambler, tree, woody climber). Trait information was derived from Germishuizen (2003) and Plants of Southern Africa ver 3.0 (2009).

Data standardisation 2004/5 – 2015

To determine the overlap between plots, the 2004 GPS coordinates for individual woody plants were imported into a GIS (ESRI ArcGIS 10.1), together with the centre coordinates of the 2015 sampling plots as points. The centre points of the 2015 plots were buffered by 50 m x 20 m (woody plots) and 0.52 m x 2.0 m (herbaceous plots) respectively using ArcGIS' Proximity toolset, in the Analysis toolbox, to produce 22 polygons. The Select by Location tool in the Layers and Table Views toolset were used to select the woody and herbaceous points that were within the 22 polygons. The individual plant points were exported as a database table and to check the data for errors, species name changes and assigning attributes (i.e. life history) for the 2004 data.

3.3.3 Data analysis

Analyses were carried out in Rstudio version 1.1442 and the R package *vegan* version 2.5-1, which provides tools for descriptive community ecology, including ordination and the calculation of diversity and dissimilarity indices (Oksanen et al., 2016). Because the data were unbalanced, before statistical tests could be performed count data were converted into densities of species per site (i.e. count values / actual area surveyed). Data were log transformed to make it within the acceptable limits of normality and to reduce the spread (range) in the dataset.

Plant density, species richness and evenness

Plant density was calculated using count values divided by actual area surveyed to correct for unequal sampling effort/design between 2004 and 2015. Density was calculated for the native and alien communities across the various sites for 2004 and 2015 data, respectively. Results were represented using boxplots generated in R. To examine change in native plant density in relation to change in alien plant density, log-transformed density was adjusted by the number of years since measured. The results were represented using a scatter plot in Microsoft Excel (2013). Deviation (or change) was calculated by subtracting alien or native plant density within a site between the sampling periods, then divided by the number of years since sampling (density/number of years).

Species richness (the number of species per plot) and evenness (Pielou's evenness) were calculated using *specnumber* {*vegan*}, along with various diversity indices (i.e. Shannon-Wiener, Simpson, and Fisher diversity indices and species richness) (Clarke, 1993). Pielou's evenness is

a measure of equitability, a measure of how evenly distributed individuals are among the different species (Clarke, 1993). Species richness and evenness were calculated separately for the native and alien communities across the various sites for 2004 and 2015 data. Results were represented with a boxplot using R, comparing changes in the native or alien plant community between sampling years.

Log-transformation was applied (\log_{10}) to plant density, species richness and evenness before performing the ANOVAs. To test for statistical significance within the various sites between years, one way ANOVA and two way ANOVA factorial design (Vikneswaran, 2006) were run in R for plant density, species richness and evenness for alien and/or native species. A Levene's test was done to test for homogeneity of variance across groups in R using *Levene.test* {car}. A post hoc Tukey multiple comparisons test was later run to identify where differences were most significant.

Plant trait strategy and species composition similarity

To assessing whether differences in plant trait strategies (growth form and life history) between native and alien species are important to understand the assembly and interactions of an invaded riparian plant community; regardless of species identity within the native and alien communities, I created a plant strategy (growth form and life history) matrix. The matrix was calculated by summing counts of all native or alien species for the different categorical plant strategies. The sums were then calculated into density, weighted by areas (i.e. count values / actual plot area surveyed), for the different sites within each year of data collection. By creating community-aggregated measures of plant strategies, I avoid any potential bias that could be imposed by too many rare species. This method is similar to the trait matrix created by Cleland et al., (2011). To test for significant differences, square root transformation was applied to down-weight the importance of the more abundant species. The data was analysed the same way as the species composition matrix and method is listed below.

For species composition, densities for each species in the matrix were calculated for the different sites, and then a square root transformation was applied to down-weight the importance of the more abundant species. Dissimilarity indices, *vegdist* {vegan} Bray–Curtis index (Oksanen, 2015), were then calculated separately for the transformed species composition and plant strategies matrixes in R. A PERMANOVA using *adonis* {vegan} is an analysis of variance which fits linear models to distance matrices and uses permutation tests ($n = 999$) with Pseudo F-ratios to inspect significances (Clarke 1993). Results are analogous to a multivariate analysis of

variance where significant differences between treatments are assessed. Betadisper {vegan}, a multivariate analogue of Levene's test for homogeneity of variances, was used to test for homogeneity. A SIMPER analysis (Clarke 1993) was also done for the plant strategy (growth form and life history) matrix, to decompose the contribution of each plant strategy to overall differences. The SIMPER function performs a pairwise comparison of groups of sampling units and finds the average contributions of each species to the average overall Bray-Curtis dissimilarity.

Similarity graphs

Bray-Curtis similarity

Eqn (1)

$$S_{jk} = \frac{\sum_{i=1}^p 2\min(Y_{ij}, Y_{ik})}{\sum_{i=1}^p (Y_{ij} + Y_{ik})}$$

The general formula for calculating the Bray-Curtis similarity between samples used to draw similarity graphs (from Somerfield 2008)

- J & K are the two sites
- y_{ij} represents the count in the i th row and j th column of the data matrix
- y_{ik} is the count for the i th row in the k th column
- $\sum_{i=1}^p \min(.,.)$ term is the sum of the minimum of the 2 counts.

To create similarity graphs, Bray–Curtis similarity was calculated using the similarity index, equation (1), by site between years using Microsoft Excel (2013), for the native and alien plant community using density. Plant densities was calculated using abundance values divided by actual area surveyed to help correct for sampling effort. Data standardization must be done prior using Bray and Curtis similarity index (Somerfield 2008). The Bray-Curtis similarity index is a measure of the difference between samples (Clarke, 1993). In this study, samples were the various sites in the different sampling years. The results are represented using scatter plots produced in Microsoft Excel (2013). Bray-Curtis similarity denotes similarity between the varies sites between the sampling years, with values close to one indicating high similarity and those close to zero indicating low similarity in shared species.

3.4 Results

Change in native species density in relation to change in alien plants density, Species richness, Evenness

A total of 157 species was recorded across all sampling years; of that, a total of 93 species were recorded in 2004 and 112 species in 2015. In 2004, 13 alien species (and 162 individual plants) were recorded, representing about 13 % of the number of individual plants that were recorded in 2004. In 2015, 21 alien species accounted for 23% of the total number of individual plants that were recorded in 2015. A total of 80 native species were recorded in 2004 and 91 species recorded in 2015. Native species decreased from 87% of the total number of individuals in 2004 to 77% of the total.

Alien plants had higher densities (two times more dense) compared to native species within and between the sampling years (origin $df= 1$, $df= 10.366$, $p= 0.003$). Both alien and native plant density increased over time. One way ANOVA on alien plant density showed that alien plant density increased significantly between years (year $df= 1$, $F= 4.489$, $p= 0.049$, Figure 3.3A), although native plant density also increased between the sampling years. The increase was not significant for native species (year $df= 1$, $F= 0.666$, $p= 0.424$, Figure 3.3A). The interaction between year with native and alien plant density was significant (origin x year $df= 1$, $F= 5.853$, $p= 0.020$).

Generally, the native plant community had higher species richness compared to alien plants, (origin x year $df=1$, $F=97.540$, $p<0.05$, Figure 3.3B). Overall species richness was significantly higher in 2015 than 2004 ($p=0.027$). Native species richness was not significantly different between 2004 and 2015 ($p=0.734$). Species richness for alien species increased from 2004 to 2015 but the increase was not significant ($p=0.120$). Overall evenness was significantly different between 2004 and 2015 (Year $df= 1$, $F= 6.078$, $p= 0.018$, Figure 3.3B). While alien species evenness increased significantly from 2004 to 2015 ($p=0.001$, Figure 3.3C), native species evenness decreased slightly and not significantly from 2004 to 2015 ($p=0.829$, Figure 3.3C). Change in native plant density had a positive correlation with change in alien plant density. Native plant density increased with an increase in alien plant density over time. Sites with high native plant density had high alien plant density ($R^2 =61\%$) (Figure 3.4).

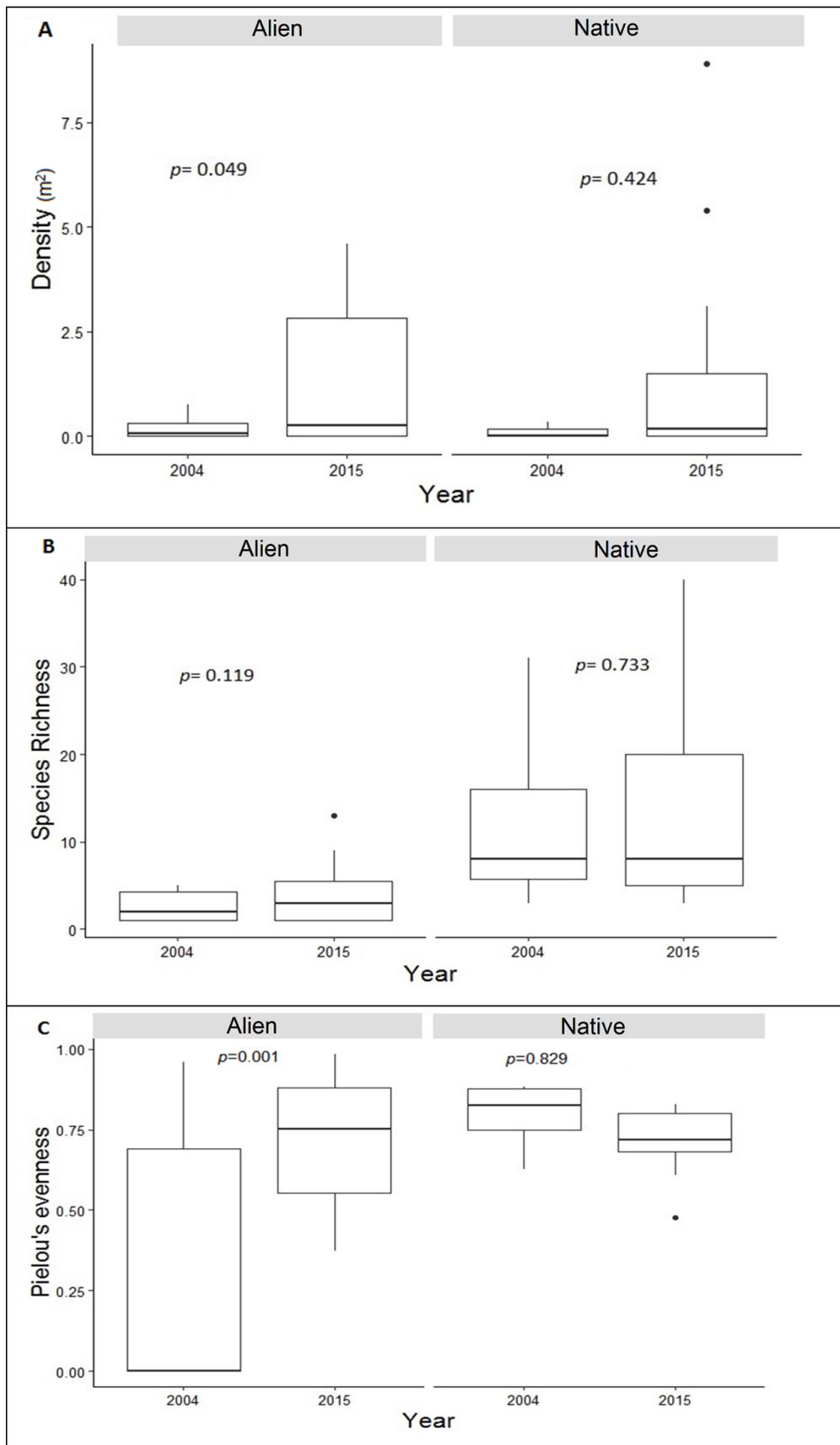


Figure 3.3 Differences in native and alien plants density (A), species richness (B), evenness (C) between 2004 and 2015. The values on the graphs are ANOVA statistics done in R. Native and alien plant density

(A) and species richness (B) increased from 2004 to 2015. Alien plant community increased in evenness (C) of frequencies

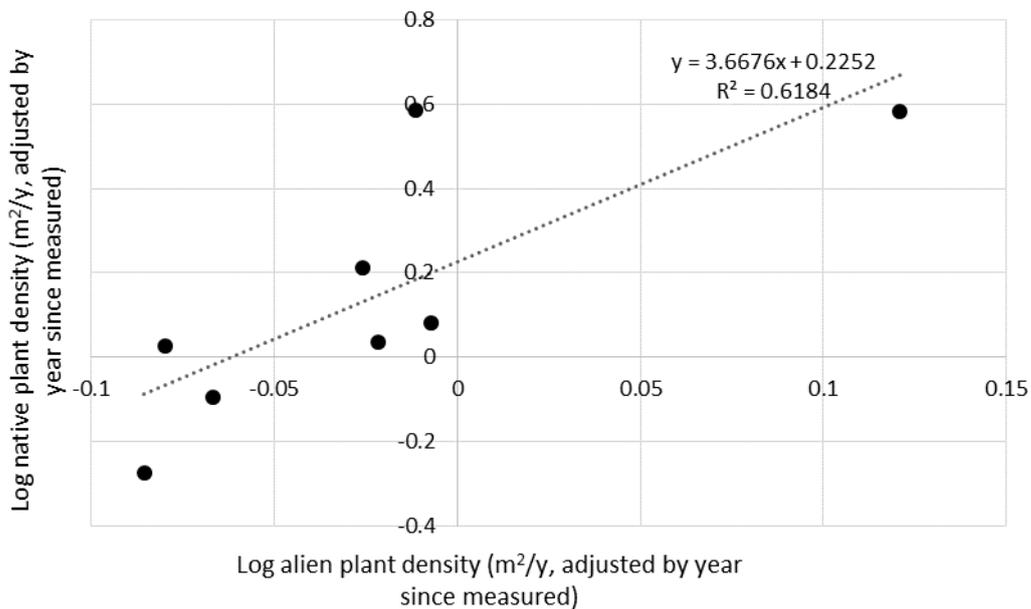


Figure 3.4 The relationship between change in log alien plant density with change in log native plant density within the various sites. Change in alien plant density has a positive correlation with change in native plant density.

Change in species composition

Species composition was significantly different between sampling years (total community: Year $df=1$, pseudo-F= 1.8122, $p=0.029$). Alien species composition was more dissimilar than native species composition within the various sites between the sampling years (Appendix Figure 1). However, alien and native species composition, respectively, was not significantly different between years (Alien: Year $df= 1$, pseudo-F =2.055 $p=0.054$; Native Year $df= 1$, pseudo F =1.57 $p=0.054$). The composition of alien species in 2004 shared less than 10% similarity with the composition of alien species in 2015 (Appendix Figure 1). Only one site (site 2) had a 50% similarity in alien species composition (Appendix Figure 1). Sites with no alien species were more dissimilar in native species composition than sites with medium and high alien plant density (Figure 3.5). Species composition similarity within sites between sampling years for native species increased with the increase in alien plant density within a site ($R^2= 67\%$). In sites where alien plant density was high, native species composition was similar between the sampling years (Figure 3.5).

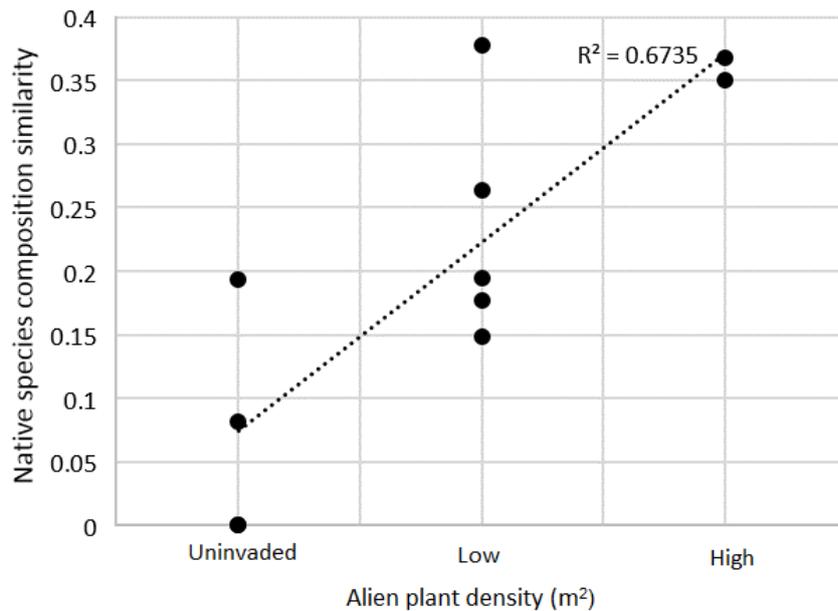


Figure 3.5 A scatter plot showing the relationship between native species composition similarity across sampling years arranged by degree in alien plant density; Uninvaded= sites that had no alien species, Low= sites with less than 10% alien plant density, and High= sites with greater than 16% alien plant density. Bray-Curtis similarity measure denotes similarity between samples, where measures close to one indicate high similarity, close to zero indicates low similarity in shared species. Areas with a high density of alien plants had high similarity in native species composition between the sampling years than sites with a low density of alien plants.

Plant strategy similarity

Alien and native plants were dissimilar in their proportion of plant strategies (Origin df= 1, pseudo-F= 2.717, $p=0.027$) and there was no significant interaction between origin and year (Origin x Year df= 1, pseudo F= 0.313, $p= 0.965$). The plant strategies that contributed the most to the dissimilarity between alien and native species across years were herbs (27%), annuals (25%) and perennials (25%) (See Appendix Table 1). The plant strategies that contributed to the dissimilarity within the native plant community across years were perennials (18%) and dwarf shrubs (17%) (66% cumulative contribution to dissimilarity), within the alien plant community it was the herb (34%) and annual (34%) plant strategies. When comparing plant strategy similarity between native and alien plant communities across the years with native plant density, the results yielded a negative correlation (Figure 3.6). The pattern is even more noticeable when comparing plant strategy similarity between native and alien plant communities with total plant density (see Appendix Figure 2).

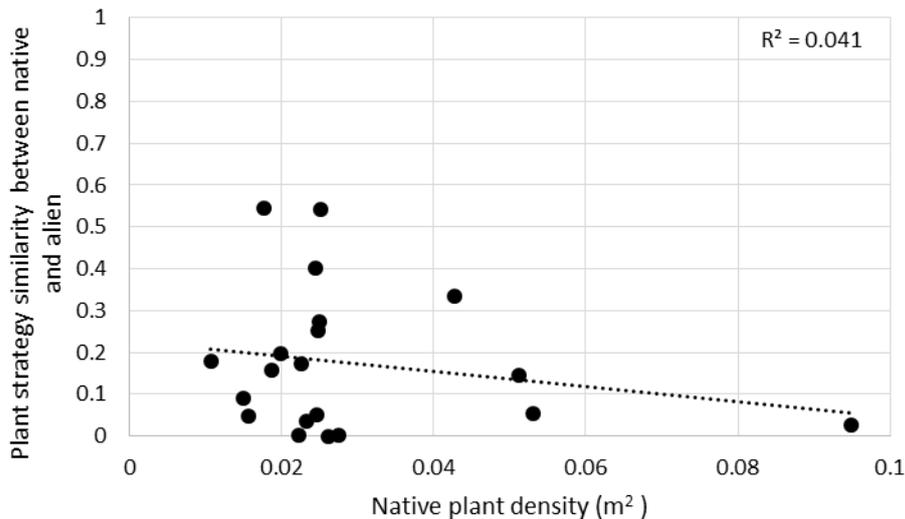


Figure 3.6 The relationship between Bray-Curtis similarity of plant strategies between native and alien plants with native plant density across sampling years was non-linear. Bray-Curtis similarity index denotes similarity in plant strategies between native and alien in relation to native plant density across sampling year between the different sites. A measure close to one denotes high similarity in shared plant strategies, while close to zero means fewer shared plant strategies.

3.5 Discussion

Plant density, species richness and evenness

As expected, alien plant density was significantly higher than native species across years. The higher densities of alien plants may be due to their ability to grow rapidly and reproduce more quickly than natives, since they were able to invade and increase in the presence of high native plant abundance and species richness. For example, Parsons et al., (2005) reported that native plants were substantially more abundant four years after the 2000 flood stripped the river of vegetation. Foxcroft et al. (2008) and Morris et al. (2008) observed that alien species comprised less than 6% of the total plant abundance in the channel 2004/5, and increased to 97% in 2006. Similarly, in this survey, alien plants went from comprising 32% of the total density in 2004 to 53% of the total density in 2015. The observed pattern may also be due to the plant strategy (growth form and life history) differences between native and alien species. In this survey, the alien plant community was mostly annual and short-lived perennial species, which invest in rapid development and reproduction to produce large amounts of seed (Brock, 1983), while native species were largely long-lived perennials. Therefore, the high density of alien species may be due to their ability to grow quickly and increase their propagule pressure.

Contrary to expectations, the increase in alien plant density did not result in the decrease in native plant density over time. Rather, both alien plant density and native plant density showed a trend towards an increase over time, however increases were not significantly different. Similarly, species richness for both alien and native species appeared to increase over time however, the increase was not significantly different. Fridley et al. (2007), suggest that positive native-alien species richness relationships should be expected in disturbance driven systems such as riparian zones. Disturbances causes shifts in composition and structure in communities, which in turn, increases the incidence of invasion (Fridley et al., 2007). Therefore, patterns may be also mediated by the disturbance regime facilitating the addition of new alien species and recovery of native species richness and density.

Consistent with this study's predictions, native plant evenness trended to decrease with the significant increase in alien plant evenness from 2004 to 2015. This indicates that while some native species became very abundant some species declined. In contrast to native species, all alien species similarly increased in abundance over time. Therefore, these results suggest that alien plants may have a negative effect on the diversity of the native plant community. This would be congruous to the study by Morris et al. (2008) along the Sabie river, who reported that significant increases in densities of annual or short-lived perennial alien species (e.g. *Senna obtusifolia*, *Senna occidentalis*, *Tagetes minuta*, and *Xanthium strumarium*), reduced the alpha diversity and species evenness of herbaceous and woody native species. Beater et al. (2008), studying the impacts of clearing invasive alien plants in the upper reaches of the Sabie River, reported a decrease in the aerial cover of woody indigenous plants with the increase in aerial cover of woody alien species (e.g. *Eucalyptus grandis*). Over time, the nature of the invasive alien plant problem has changed from dealing with large trees to addressing a suite of alien species with numerous individuals at various stages of regeneration (Beater et al., 2008).

Change in species composition

The total species composition increased significantly from 2004 to 2015, and alien species contributed more to the differences than native species. Only 10 % of the alien species that were present in 2004 (a total of 13 alien species) were present in 2015 (a total of 21 alien species), showing that eight new alien species were introduced along the Sabie (including *Acanthospermum hispidum*, *Parthenium hysterophorus*, *Cardiospermum grandiflorum*, *Xanthium strumarium*). This result indicates that although there was some recruitment of new alien species, there was also recovery of species that were already in the system. Some alien species such as

Chromolaena odorata and *Senna septemtrionalis* (see Appendix Table 2) disappeared from the alien plant community. *Chromolaena odorata*, among other perennial alien species, underwent intensive post-flood clearing, so it is possible its absence is a result of clearing efficacy (see van Wilgen et al. (2017) for comprehensive list of species that were targeted). For the native plant community, 50 % of native species that were present in 2004 were also present in 2015. However, alien or native species composition was not significantly different between 2004 and 2015. An examination of the recovery of native species composition in relation to varying densities of alien plants showed that native species composition was lower in sites that had higher densities of alien plants. This indicates that sites that had no alien species had a more diverse composition of native species than areas with high alien plant density. Therefore, this suggests that alien plant density has a negative effect on the recruitment of native species composition along the Sabie. Therefore, the current density of alien species may be resulting in reduced native species composition. Alien plants may be excluding the less common or habitat specific native species, for example, *Breonadia salicina*. In Chapter 2 of this study, the Bedrock anastomosing and Pool rapid reaches suitable for *Breonadia salicina* recruitment generally supported higher species richness and alpha diversity of alien species (herbs, shrubs and trees). Additionally, the bedrock anastomosing channel type was also mostly associated with species that are considered invasive, such as *Datura ferox*, *Euphorbia heterophylla*, *Lantana camara* and *Sesbania punicea* (see chapter 2). However, this effect of the current suite of alien species on the less common native species may need to be investigated further.

A potential criticism here may be that the current alien plants are mostly short-lived species, therefore they should not affect the recruitment of trees and shrubs unless their timing of germination and establishment is such that it affects the critical timing of native trees and shrubs. Riparian vegetation often requires specific microsite conditions such as soil moisture levels, light conditions and temperature fluctuations before a seed can germinate (Naiman et al., 2010). In addition, riparian species seed viability is generally very short (1 to 2 weeks) (Manders, 1990; Naiman et al., 2010), hence timing of seed production and release with flooding season is a common strategy for riparian plants. The alien species, however, can germinate at any time of year provided they receive enough moisture (Parsons and Cuthbertson, 1992). Alien species, therefore, have a competitive advantage over natives since they can establish first and grow faster compared to natives. Morris et al. (2008) for example, reported that clearing alien species that were mostly annual species along the Sabie River also resulted in a significant increase in native plants, including trees and shrubs. Morris et al. (2008) therefore concluded that clearing of these short-lived species reduces their shading effect. The decline in native species here may be due to the combined effect of the suite of alien species that have numerous individuals at various stages of regeneration (Beater et al., 2008).

Differences in plant strategies between native and alien species

Consistent with this study's predictions, high similarity in plant strategies between native and alien species lowered native plant density. This implicates competition via niche differences as an important factor structuring the interaction between native and alien species along the Sabie River. Niche differences are those that cause species' per capita population growth rates to increase as species become rare (predict competitive dominance) (MacDougall et al. 2009). This result is supported by the gentle slope of the correlation between native plant density and life history similarity. Therefore, the changes in native species may be an indirect consequence of the dominance of alien species.

Because observational studies cannot control for other confounding factors (e.g. water availability, disturbance, the rate of decline of the water table). It is possible patterns may also be in part due to changes in water availability or disturbance in combination with competition. Diez et al. (2012) explains the disturbance brings species closer to their physiological tolerance limit. To add further, MacFadyen et al. (2018) in a study of long-term patterns of rainfall in KNP, explains seasonality in KNP has changed. MacFadyen et al. (2018) observed that high-rainfall seasons are now receiving more rainfall and low-rainfall seasons receiving less. This would be congruous with other studies where competition was always mediated by other factors (water availability or disturbance) in the plant community (Cleland et al., 2011; McIntyre et al., 2005; Price et al., 2011). For example, Price et al. (2011) in an experimental study, evaluated competition and disturbance as mechanisms governing dominance in floodplain wetlands of eastern Australia. Price et al. (2011) found that the dominance of the non-native *Phyla canescens* (Ippia) and *Paspalum distichum* (water couch) was driven by competition, but the most successful of the two species was determined by water availability.

A potential criticism of this study is that it relies on very broad categorical traits to imply interactions or competition (Hulme and Bernard-Verdier, 2018). However, there is a lack of universal traits used in comparisons of native and alien species differences, as most traits (phylogenetic distance or continuous traits) are also limited in their ability to infer mechanisms related community assembly (MacDougall et al., 2009).

3.4 Conclusion

This study investigated the response of native plant communities to temporal changes in alien plant density and diversity. The study observed that high densities of alien species did constrain the recruitment of native plant density, species evenness and composition. The high density of alien species correlated with a reduction in native species evenness and constrained recruitment in native species composition. The decline in native plant density when native and alien species shared a closer combination of plant strategies indicates that species with the highest potential to drive change are those that are similar in trait combinations. Native and alien species were significantly dissimilar in their combination of plant strategies; implying that the interaction between native and alien species is driven by trait differences (competition via niche differences). Therefore, the decline in native species with an increase in alien species may be an indirect consequence of the dominance of alien species. These results imply that effects of alien plants along the Sabie are complex, and managers should focus on alien species that have a closer combination of plant strategies to native species, as they have a high potential to drive competitive exclusion.

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Chapter 4: Discussion and conclusion

4.1 Introduction

The nature of the invasion problem in the Sabie River

Invasive alien species disrupt ecosystems and the flow of system processes. Because of their ability to replace native species and alter vegetation structure, invasive species are competitively superior to native species and therefore major drivers of environmental change. Thus, controlling their spread and impacts is essential for biodiversity conservation. Plant invasions are a high priority for protected areas, and riparian zones are especially vulnerable to invasions. This is because rivers are conduits of propagules; consequently, riparian zones in savanna systems tend to be the most invaded areas in the landscape.

This study aimed to examine patterns of alien plants, their effect on the native plant community and their pathways of impact. This was to determine whether alien plant species are independent of geomorphology (chapter 2) and to examine the response of native plant communities to temporal changes in density and diversity of alien plants (chapter 3), which could help management determine which plant invasions to prioritize.

4.2 Key findings - Alien plant distribution and habitat association along the channel types of the Sabie River.

The main aim of Chapter 2 was to determine if the distribution of alien plants along the riparian zone of the Sabie River was independent of the channel's geomorphology. Although alien species occurred in high densities on all the channel types, which reflects the dispersal capabilities of the rivers. The results indicate that alien plants are not independent of the channel geomorphology. The extent and distribution of alien plants differed across channel types, indicating that some channel types are more suitable than others for alien plant establishment. Overall, alien plant density was higher in channel types of alluvial influence than of bedrock influence. The braided channel type (alluvial influence) had the highest density of alien plants compared to the other channel types and many of those alien species were annuals and short-lived perennials. The bedrock dominant areas supported a higher alien species richness. Therefore, these results indicate that there are two types of alien plant communities established along the Sabie River.

The first is a plant community dominated by ruderal or early successional alien species (e.g. annuals or herbs), which are disturbance driven. The second is a community of woody species mixed with ruderal species where water availability is determined by the rise and fall of the water table. The results showed that herbaceous alien plants thrive in the highly dynamic braided channel types and woody species thrive in the bedrock-influenced channel types. Although herbaceous species (specifically herbaceous ruderals) showed no evidence for habitat affinity, individual woody alien species were strongly associated with the bedrock anastomosing channel type (these were *Lantana camara* and *Sesbania punicea*, which are priority species for control in KNP). Since the bedrock-influenced channel types are suitable for both herbaceous and woody alien species, native species associated with these channel types appear to be more vulnerable to the impacts of plant invasions.

4.2.1 Shortcoming and opportunities

A caveat to this study would be that it only considered patterns in relation to channel types. Future studies could benefit by adding other environmental features, including geomorphic unit (e.g. lateral bar or island) and substrate type (e.g. coarse alluvial sand or exposed bedrock), which can determine the distribution patterns of riparian species. The exclusion of geomorphic units may explain why most alien species did not show an association with specific habitat types that has been observed in other studies (i.e. Chytrý et al., 2008; Hood and Naiman, 2000; Myburgh and Bredenkamp, 2005). However, it is important to note that these studies included smaller scale elements (e.g. depositional bars, channel bars and channel floor), which differ further in habitat properties and flow patterns from the bigger channel type. For example, degree of bar development to be an important influencing factor influencing vegetation pattern, noting a close relationship with age of the fluvial surface. This study was, however, congruent with Chytrý et al. (2008), Hood and Naiman (2000) and Myburgh and Bredenkamp (2005) in their conclusions that alien species distribution is not independent of the habitat characteristic of the channel. Hood and Naiman (2000) observed a difference in the presence of alien species in the macro-channel floor to the channel banks, while Myburgh and Bredenkamp (2005) observed that herbaceous alien species were associated with depositional features and woody species occurred on less frequently inundated features in the Olifants River, KNP. My study also found that bedrock and alluvial influence is key, which van Coller et al. (1997) found to be an important component for structuring distribution patterns of indigenous vegetation. A possible caveat is the short time frame of the study, reflecting one snapshot in time. Vegetation patterns change over time and any spatial pattern in time is the result of dynamic processes playing out over potentially long periods. There may be merit in a follow-up study to complement the results of this study.

4.3 Key findings - Plant community change in relation to alien plant invasions in the riparian zones of the Sabie River, Kruger National Park.

In Chapter 3, I investigated 1) the response of native species to density and diversity of alien plants, and 2) whether these patterns are correlated to different combinations of plant strategies. The results found that high densities of alien plants resulted in the decline of native species evenness. Native plant evenness decreased with the significant increase in alien plant evenness between 2004 and 2015. The study also found that high densities of alien plants constrained the recruitment of native species composition among sites. This study observed that recruitment of native species composition in 2015 decreased where there was higher alien species density in 2004. Therefore, high density of alien species may be facilitating homogenisation in the native community in the riparian zones, by excluding the less common native species. Finally, the observed differences in plant strategies between native and alien species suggest that competition via niche differences (or stabilizing trait strategies) may be the mechanism behind the observed pattern. This is because alien plants were mostly annual and herbaceous, which are plant trait strategies that facilitate population growth. Therefore, I concluded that impacts by alien plants arose from their competitive dominance, being able to grow quickly and access resources at the expense of natives. Where native and alien species had a close combination of plant strategies, alien plant density was lower, indicating that there were a few instances where native and alien plants were in direct competition. Therefore, I propose that managers target those alien species that have a similar combination of plant strategies to native species as they are the most likely to drive competitive exclusion. These include, for example, the woody perennial species that can directly compete with native woody species.

4.31 Shortcoming and opportunities

The need to measure impacts stems from the need to prioritise management efforts (McGeoch et al., 2016). The lack of a general framework for interpreting impacts imposes a challenge for managers looking to assess risks associated with alien plants. Given the complexity of mechanisms and mediators that affect impacts, it is not surprising that ecological impacts are context dependent. Therefore, baseline studies such as this are important for providing context-specific information. A potential criticism to this study is that most of the alien species are herbaceous annuals and short-lived perennials species, which are not known to compete with trees and shrubs for resources. However, these alien species become very dominant in the presence of high native species, indicating competitive superiority.

Given the context-dependence of impacts, which can vary under different abiotic and biotic influences. Disturbance, which is a major driver of community dynamics in riparian zones, can modify the performance, magnitude, and direction of impact of an alien species. It raises the question of how the results provide evidence of impacts on alien presence and abundance and the management implications thereof. A large number of studies have demonstrated how disturbance facilitates invasion, and there is no doubt that disturbance facilitated the invasion success of some alien species in the Sabie River. Alien plant density was highest in the most dynamic channel type, indicating that disturbance is a driver of alien species presence and perhaps abundance in that channel. Furthermore, change in alien plant density over time had a positive correlation with change in native plant density over time, which further supports that disturbance played a role in the invasion success of alien species. However, alien species richness and diversity was highest in the in the bedrock-anastomosing channel type, which is characterised by topographically high bedrock bars that are rarely inundated, indicating that alien species did not require disturbance to weaken invasion resistance, (clearing already established native species or to establish. An analysis of species evenness showed that native species evenness decreased while alien species evenness increased. This indicates that although some native species were able to recruit, some alien species became less abundant over time. Furthermore, species composition showed that sites with high alien plant density in 2004 had a similar composition of native species the sampling years. This indicates that high density of alien plants affected the recruitment of native species between the sampling years. Therefore, I conclude that alien species exerted a negative effect on native species. Disturbance provided opportunity for alien plants to establish in areas where frequent inundation was a driver of habitat conditions. However, alien species also had plant trait strategies that allowed them to grow quickly and become denser even in the presence of high native plant abundance and richness. This indicates alien species are competitively superior to native species. A recommendation for managers is to clear areas with high-density of alien plants where alien species threaten the recruitment of native species, notably habitat specific native species.

4.4 Conclusion

Rivers are the most invaded landscapes within protected areas. In KNP, this is worsened further by the orientation of the park to potential sources of propagules. The park is therefore, highly vulnerable to the spread and impacts of alien species. Thus, understanding the risk associated with plant invasions is important for protecting biodiversity. By investigating the distribution

patterns of alien species along the river, this study showed that the establishment of alien plants is not uniform along riparian habitats. Habitat properties in riparian zones are important in determining the distribution of alien species. Therefore, this study has provided insight into areas of higher concern for the spread of problematic aliens. By examining the response of natives to changes in alien plant densities, richness and composition, the study has found that high densities of alien exerted a negative effect on native species recruitment and compositions. The study also found that native and alien species differ in their combination of plant trait strategies, allowing alien species to respond better to disturbance and outperform natives. Therefore, this suggests that the decline in native species is an indirect consequence of the dominance of alien species.

Appendices

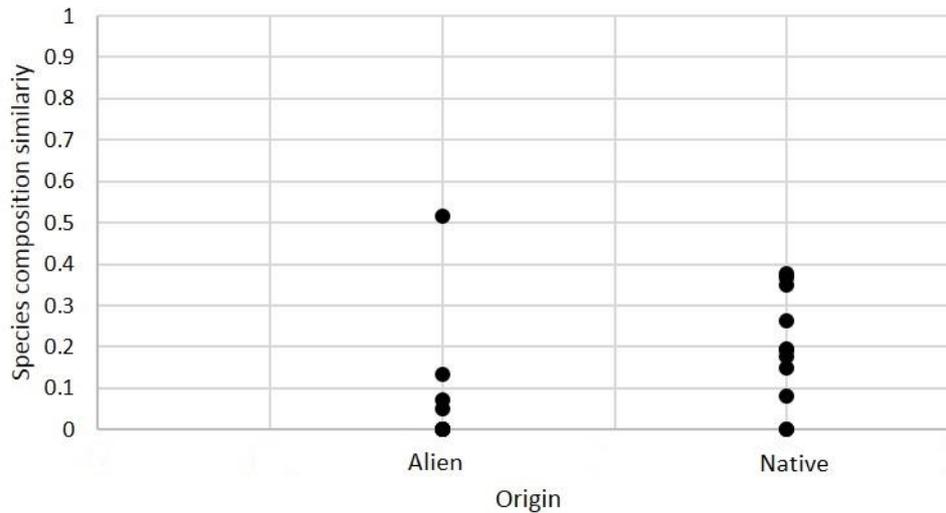
Appendix A

Appendix Table 1 SIMPER analysis showing the dissimilarity in growth form and life history strategies in native and alien plant communities. Native and alien plant communities differ significantly in plant strategies. The plant strategies are ordered by descending contribution of dissimilarity up to 100. For example, herbs have a 27 % difference with annual life history (Bray-Curtis 0.229), and 19% difference from perennial (first two entries of the table). Indicating that herbaceous were annual and perennial, however herbaceous annuals were more than herbaceous perennials.

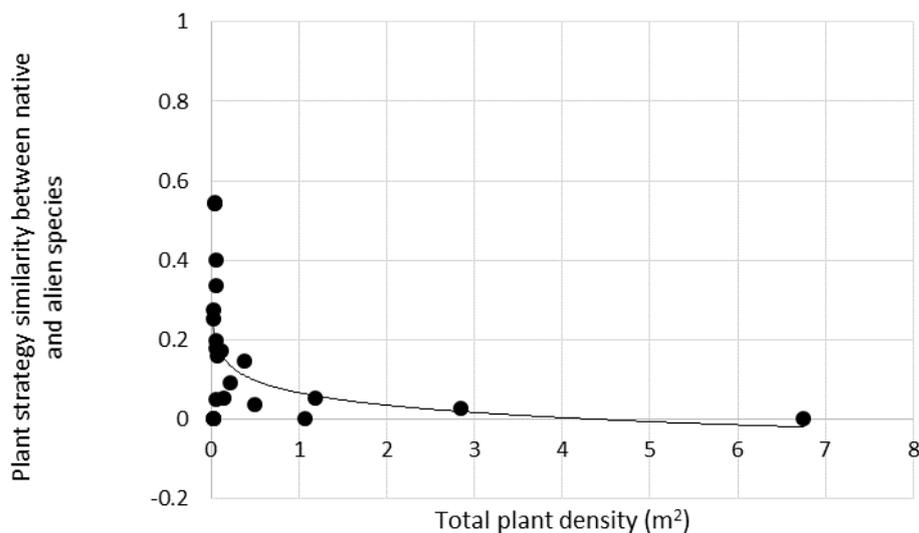
Life history and growth form	Bray-Curtis dissimilarity	Alien species density	Native species density	Cumulative contribution
Herb	0.229	0.738	0.428	0.274
Annual	0.213	0.642	0.232	0.528
Perennial	0.160	0.231	0.428	0.720
Dwarf shrub	0.070	0.016	0.203	0.804
Shrub	0.064	0.005	0.181	0.879
Tree	0.042	0	0.0026	0.929
Climber	0.030	0.121	0.025	0.966
Biennial	0.025	0.006	0.180	0.996
Woody climber	0.003	0	0.00095	0.999
Scrambler	0.000	0	0.000006	1

Appendix Table 2 The total list of alien species recorded in 2004 (n=12) and 2015 (n=16) and their life history. There were more perennials in 2004, while there were more annuals in 2015. Perennials decreased over time while annuals increased with time. Intensive post-flood alien plant control was implemented after the 2000 flood on high priority perennial alien species. These included species like *Chromolaena odorata*, which was only found in a few plots and *Lantana camara* that had dense stands prior to the 2000 floods. The decline of perennials from 2004 to 2015 may reflect the efficacy of management interventions towards these high priority perennial species. High priority species, based on van Wilgen et al. (2017), list are highlighted in bold.

2004 Alien species	2015 Alien species	Life history
Not recorded	<i>Acanthospermum hispidum</i>	Annual
Not recorded	<i>Alternanthera pungens</i>	Perennial
Not recorded	<i>Aristolochia elegans</i>	Perennial
Not recorded	<i>Bidens bipinnata</i>	Annual
<i>Caesalpinia decapetala</i>	Not recorded	Perennial
<i>Cardiospermum grandiflorum</i>	Recorded	Perennial
Not recorded	<i>Catharanthus roseus</i>	Perennial
<i>Chromolaena odorata</i>	Not recorded	Perennial
Not recorded	<i>Commelina benghalensis</i>	Annual
Not recorded	<i>Corchorus trilocularis</i>	Biennial
Not recorded	<i>Euphorbia heterophylla</i>	Annual
Not recorded	<i>Ipomoea purpurea</i>	Annual
<i>Gomphrena celosioides</i>	Recorded	Perennial
<i>Hyptis pectinata</i>	Not recorded	Perennial
<i>Lantana camara</i>	Recorded	Perennial
Not recorded	<i>Parthenium hysterophorus</i>	Annual
<i>Persicaria lapathifolia</i>	Not recorded	Annual
Not recorded	<i>Richardia brasiliensis</i>	Perennial
Not recorded	<i>Schkuhria pinnata</i>	Annual
Not recorded	<i>Senna obtusifolia</i>	Annual
<i>Senna occidentalis</i>	Recorded	Annual
<i>Senna Septemtrionalis</i>	Not recorded	Perennial
<i>Sesbania punicea</i>	Not recorded	Perennial
Not Recorded	<i>Tagetes minuta</i>	Annual
<i>Tridax procumbens</i>	Recorded	Annual
<i>Verbena bonariensis</i>	Recorded	Annual
Not recorded	<i>Vicia sativa</i>	Annual
Not recorded	<i>Xanthium strumarium</i>	Annual

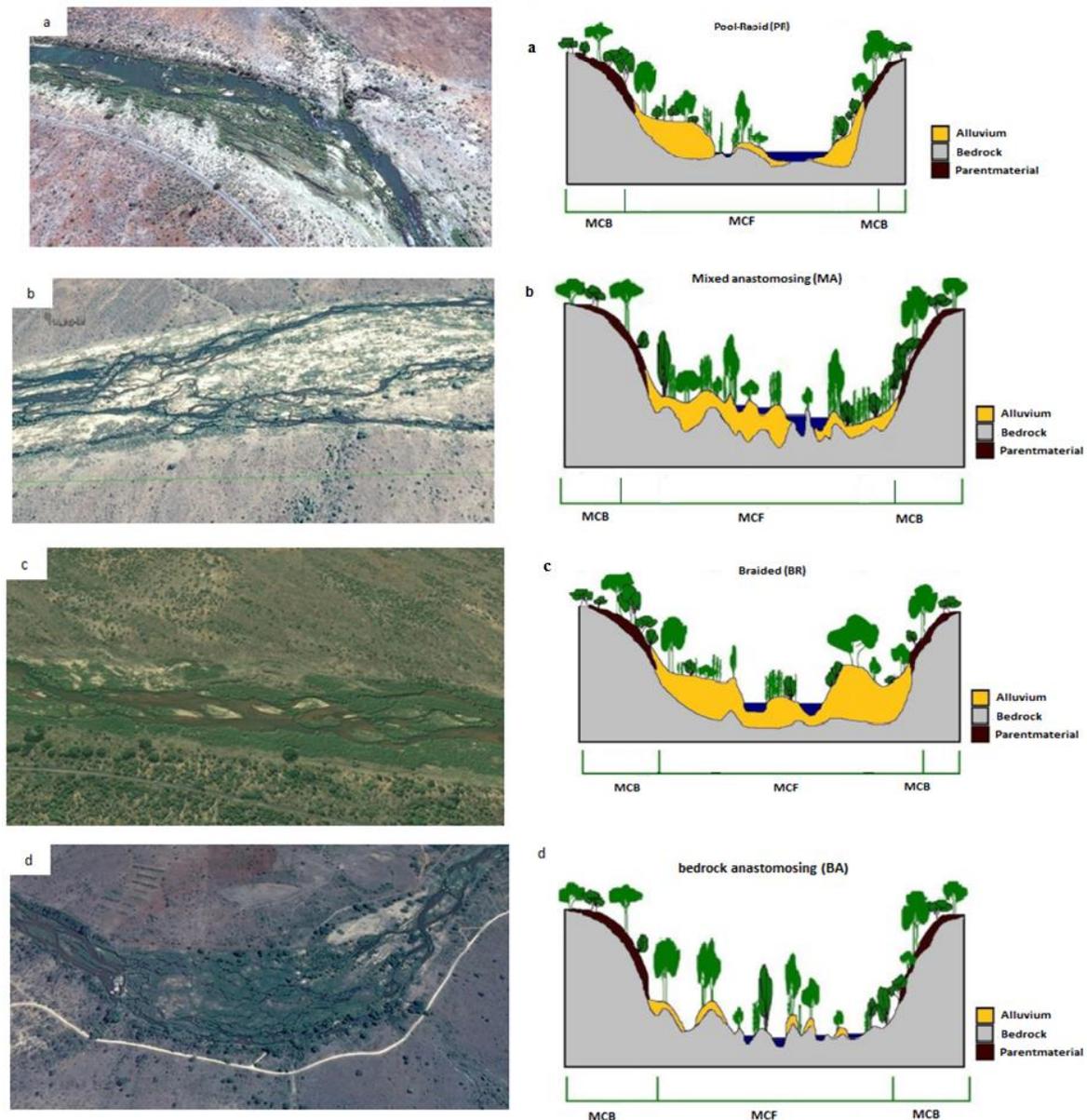


Appendix Figure 1 Species composition similarity for native and alien plant community across sampling years, calculated in Microsoft Excel (2013) using Bray-Curtis similarity formula. The points represent Bray-Curtis similarity measures across the sampling years and various sites. Measures close to one indicate similarity, and close to zero means dissimilarity in shared species. Alien species composition was more dissimilar than native species composition between 2004 and 2015 (alien: $p=0.54$; native: $p=0.078$). With the exception of site 2a (similarity = 50%), a bedrock anastomosing site where the river forms the boundary of the park and border to adjacent subsistence farming land. Parsons et al. (2006) reported that the bedrock anastomosing suffered small losses of herbaceous cover compared to other channel types.



Appendix Figure 2 The relationship between native and alien plant life history similarity in relation to total plant density is non-linear. Bray-Curtis similarity index denotes life history similarity between native and alien within the various sites in relation to total plant density across sampling year. Measures close to one denote similarity in shared plant strategies, close to zero means fewer shared plant strategies. Therefore, total plant density has a negative relation when native and alien plant share a closer combination in plant

strategies. Therefore, native and alien plants community along the Sabie River diverged from being too similar. This further support that competition is highest between functionally similar species because they are likely going compete for the same resources.



Appendix Figure 3 A cross section and aerial view of the four principle channel types within the Sabie River, KNP. a – Pool-rapid; b – Braided; c – Mixed anastomosing; d – Bedrock anastomosing (Adapted from McLoughlin et al., 2007) (aerial imagery Source Google Earth Pro©2017CNES/Airbus).