

**The effects of invasive trees in riparian zones and implications for  
management and restoration:**

**Insights from *Eucalyptus* invasions in South Africa**

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## **Declaration**

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## Abstract

Worldwide, invasive alien plants (IAPs) alter aspects of invaded ecosystems including geomorphology, above-ground vegetation, soil seed banks and soil nutrient regimes, thereby affecting the long-term stability of ecosystems. In many cases these invasions call for various management interventions, including restoration. Effects of alien plant invaders on native ecosystems are widely acknowledged, but compared to terrestrial ecosystems, riparian habitats are poorly studied. Riparian habitats are inherently rich in biodiversity, but are particularly prone to invasion by IAPs because of their dynamic nature and because these ecosystems are affected by many anthropogenic activities. This enhances the proliferation of IAPs, especially trees such as *Tamarix* spp. (e.g. in the southwestern United States), *Salix* spp. (e.g. in Australia), and Australian *Acacia* spp. and *Eucalyptus camaldulensis* (in South Africa). Initiatives such as the Working for Water (WfW) programme in South Africa that are focusing on clearing IAPs, particularly in riparian zones, have reported much success in the short term, but ecosystem recovery remains limited. There is a poor understanding of the nature of the impacts of invasive trees, and of the opportunities that exist for ecosystem restoration. The objective of my thesis was to investigate the effects of the widespread invasions of *Eucalyptus camaldulensis* in riparian zones.

Methodological constraints have been identified as one reason for limited success of restoration projects. Many studies examining the effects of IAPs used a comparative approach of uninvaded (reference) and invaded sites. However, this approach often fails to separate cause from effect. An experimental removal approach has been suggested as an alternative, but it is often inappropriate for large invasive trees owing to time and cost constraints. I used a comparative gradient approach, involving sampling along a continuum from uninvaded sites, and varying *E. camaldulensis* invasion densities categorised as “lightly”, “moderately” and “heavily” invaded (hereafter the gradient of invasion), each with four replicates ( $n = 16$ ). This approach enabled me to detect trends that could be reliably attributed to invasion. Furthermore, my study attempted to provide a comprehensive understanding of the effects of IAPs in invaded ecosystems by considering various components of the ecosystem and integrating their feedback relationships to establish the net effects on ecosystem processes. The riparian zone is a unique ecosystem which provides an opportunity for such a multifaceted study examining and integrating the effects of invasive trees on riparian geomorphology, above-ground vegetation, soil seed banks, and soil properties.

I studied the effects of *E. camaldulensis* invasion in riparian zones along the Berg River in the Mediterranean-type climate zone of the Western Cape, South Africa. I asked the questions 1) Are environmental conditions (i.e. the riparian environment created by geomorphological processes) altered by *Eucalyptus* invasion and if so, are these

conditions less suitable for recruitment of indigenous species? 2. Has *Eucalyptus* invasion altered the composition of indigenous species (potentially limiting post-clearing propagule supply)? 3: How does *Eucalyptus* invasion change the composition of the riparian soil seed bank; and its potential to re-initiate ecosystem recovery? 4: Do soil properties (physical and chemical) change with *Eucalyptus* invasion?

Data for all four questions were collected in the same sites to enable cross comparisons. For the first question, I employed photogrammetry techniques in a GIS and remote sensing environment to analyse repeated aerial photographs (1938 -2010) to reconstruct the invasion history and riparian geomorphology evolutionary dynamics. For the second and third questions, I compared richness, diversity, evenness and composition of resident above-ground and seed bank vegetation between uninvaded sites and the gradient of invaded sites. For the fourth question, I compared a set of variables describing physico-chemical properties in uninvaded sites to the gradient of invaded sites seasonally.

Results of the **geomorphology study** showed that the riparian zone has been very dynamic over the 70 years, with a 13.5% net decrease in area. There was evidence of channel narrowing, riverbank steepening and river bed incision in areas that were densely invaded. No significant trends were detected in hydrometeorological data. The **above-ground vegetation** study revealed that species richness, diversity and structural attributes (e.g. height, relative cover and mean basal diameter) of native species decreased consistently along the invasion gradient. Invasion also altered native and alien plant species composition, both of which showed a high preference for lightly invaded sites. The **seed bank** study revealed that *E. camaldulensis* invasion had no significant effect on total and native species richness, diversity and evenness, however the effects were bigger on native than alien species. Alien species density was significantly higher than native species density. Invasion also influenced the composition of the native seed bank. However, native seed banks were more diverse than above-ground plant assemblages with some native fynbos species occurring only in the seed bank. In the **soil study**, I found that soil pH levels were significantly lower in invaded sites than in uninvaded sites in all seasons. Litter cover and thickness increased significantly with invasion intensity. Soil moisture decreased consistently with invasion intensity while temperature increased in winter and spring. Total macro, micro and available nutrients did not vary significantly along the invasion gradient ( $p > 0.05$ ), but exchangeable cation content was significantly higher in uninvaded than in invaded sites, especially in winter and spring.

Narrowing of river channel and steepening of river banks reduces the suitability of the riparian zone to perform certain ecological functions such as soil seed storage and providing space for vegetation to grow. This reduces opportunities for seedling recruitment and consequently reduces species diversity. Conversely, the reduction of species diversity

in above-ground vegetation reduces seed input into the soil leading to depauperate soil-stored seed banks. The abundance of seeds of *Acacia mearnsii* in the soil-stored seed bank poses a threat of secondary invasions post clearing of *E. camaldulensis* if this is adopted as a management action.

The study was successful in addressing the stated objectives. The transition from a native-dominated riparian plant community to a monoculture of *E. camaldulensis* over c. 50 years has resulted in marked changes to riparian geomorphology and above-ground vegetation, but has yet to radically change the total soil seed bank and soil nutrient concentrations. The findings offer support to the WfW clearing initiatives and show that potential for recovery of native species after removal of the invasive eucalypts still exists. This knowledge not only enhances effectiveness of restoration and long term management of riparian ecosystems, but also advances the field of riparian ecology and restoration. Further experimental work is needed to establish the mechanisms responsible for the changes associated with *Eucalyptus* invasion. The contribution of agriculture in shaping channel morphology also needs to be investigated.

## Opsomming

Die langtermyn stabiliteit van ekosisteme wêreldwyd word bedreig deur uitheemse indringer plante (UIPs) wat, onder andere, die geomorfologie, bo-grondse plantegroei, onder-grondse saadbanke en voedingstofstatus van ekosisteme kan verander. In baie gevalle word bestuursoperasies vir indringer plante vereis, en sluit onder andere herstel (restorasie) in. Die invloed van UIPs op inheemse ekosisteme word wyd erken, maar kennis oor oewerbank-habitatte, in vergelyke met ander terrestriële ekosisteme, skiet steeds tekort. Oewerbank-habitatte is inherent ryk aan biodiversiteit maar uiters sensitief vir indringing deur UIPs. Dit is weens die dinamiese aard van hierdie ekosisteme asook vele menslike aktiwiteite in hierdie tipe habitat. Dit dra by tot die vermeerdering van UIPs, veral bome wat byvoorbeeld insluit *Tamarix* (tamariske) (bv. in die suid-wes van die Verenigde State van Amerika), *Salix* (wilger) (in bv. Australië) en die Australiese *Acacia* (wattel) en *Eucalyptus* spesies (bloekom) in Suid Afrika. Inisiatiewe soos die Werk vir Water (WvW) program in Suid Afrika fokus juis daarop om UIPs vanuit oewerbank areas te verwyder, en alhoewel groot sukses in die kort termyn behaal is, is die herstel van ekosisteme steeds beperk. Daar is dus min inligting beskikbaar oor die impak van indringer bome en gevolglik ook oor geleenthede vir die herstel van hierdie ekosisteme. My tesis ondersoek die impak van die wydverspreide voorkoms van die indringer, *Eucalyptus camaldulensis*, in oewerbank-omgewings.

Beperkte metodes is tans beskikbaar om die impak van indringer plante te ondersoek, en dit is geïdentifiseer as een van die oorsake vir die beperkte sukses van herstelprojekte. Baie studies ondersoek die effekte van UIPs deur natuurlike areas sonder enige indringer plante te vergelyk met areas waar UIPs voorkom. Hierdie tipe benadering kan ongelukkig, in meeste gevalle, nie onderskei tussen die oorsaak en die impak nie. 'n Alternatiewe voorstel is om UIPs eksperimenteel te verwyder, maar is ongelukkig nie van toepassing op groot bome nie weens die tyd en kostes verbonde hieraan. Ek het gebruik gemaak van 'n vergelykende-gradiënt benadering wat steekproefnemings langs 'n geleidelike kontinuum van natuurlike areas sonder enige indringer plante na areas wat effens gematig, en erg ingedring is (hiernaas bekend as die indringer-gradiënt) deur die indringer, *E. camaldulensis*. Die steekproefnemings van elke kategorie van indringing (geen, effens, gematig en erg) is vier keer herhaal ( $n = 16$ ). Hierdie benadering het my toegelaat om neigings te identifiseer wat met sekerheid toegeskryf kan word aan die teenwoordigheid van indringers. My studie het ook verder gemik om 'n omvattende beskrywing van die impak van UIPs in ekosisteme met indringers te verskaf deur verskeie komponente van die ekosisteem, sowel as hul terugvoer-verhoudinge, in ag te neem, en sodoende die totale effek op ekosisteem prosesse te bepaal. 'n Oewerbank is 'n unieke ekosisteem wat 'n geleentheid bied vir 'n veelsydige studie wat die impakte van indringer

bome op oewerbank-geomorfologie, bo-grond plantegroei, grond saadbanke en grondeienskappe, kan bestudeer en integreer.

Ek het die impak van die teenwoordigheid van die indringer, *E. camaldulensis* in oewerbank areas langs die Bergrivier, wat 'n Mediterreense-tipe klimaat het, in die Wes Kaap, Suid Afrika, bestudeer. My studie het die volgende vrae gevra: 1) Is omgewingsomstandighede (bv. die oewerbank-omgewing geskep deur geomorfologiese prosesse) verander deur die teenwoordigheid van die *Eucalyptus* indringing, en indien wel, is hierdie omstandighede minder geskik vir inheemse spesies?; 2) Het die indringing van *Eucalyptus* gelei tot 'n verandering in die samestelling van inheemse spesie gemeenskappe (moontlik beperkte plant voorplantings materiaal nadat die indringer verwyder is)?; 3) Hoe verander die indringing van *Eucalyptus* die samestelling van saad teenwoordig in die grond (saad bank) van die oewerbank en het dit die potensiaal om ekosisteem-herstel weer aan die gang te sit?; 4) Verander indringer *Eucalyptus* grond eienskappe (fisies en chemies)?

Data vir al vier vrae is by dieselfde plek versamel om vergelykings te kan tref. Vir die eerste vraag het ek fotogrammetrie-tegnieke in 'n Geografiese Inligting Stelsel (GIS) en afstandwaarnemings-omgewing toegepas om herhaalde lugfotos (1938-2010) te analiseer om die indringings geskiedenis sowel as die oewerbank se geomorfologiese evolusionêre dinamika saam te stel. Vir die tweede en derde vraag, het ek die aantal, diversiteit, gelykheid en samestelling van die bo-grond en saad bank plantegroei tussen natuurlike (geen indringers) en die gradiënt met indringers vergelyk. Vir die vierde en laaste vraag, het ek 'n stel veranderlikes wat die fisies-chemiese eienskappe van die natuurlike omgewing sonder indringers beskryf, vergelyk met die eienskappe van die indringers gradiënt op 'n seisoenale basis.

Die resultate van die geomorfologiese studie wys dat die oewerbank omgewing baie dinamies was oor die afgelope 70 jaar met 'n totale afname van 13.5% in rivieroewerarea in die gebied wat bestudeer is. Daar is ook bewyse vir 'n vernouing van die kanaal, toename in die steilte van die rivierbank sowel as insnyding in die rivierbedding in areas wat ernstige indringing ervaar. Daar was geen beduidende neigings in die hidrometeorologiese data nie. Die studie van die bo-grondse plantegroei het gewys dat die aantal plantspesies, diversiteit en strukturele kenmerke (bv. hoogte, dekking en gemiddelde basale diameter) van inheemse spesies afneem soos wat die indringings gradiënt toeneem. Indringing verander ook die inheemse sowel as uitheemse plant spesies samestelling. Beide inheemse en uitheemse spesies het areas wat slegs effense indringing wys, verkies. 'n Studie van die saad bank (aantal sade in die grond) het gewys dat die indringer, *E. camaldulensis* geen merkwaardige invloed op die aantal, diversiteit en gelykheid van die totale en inheemse spesies teenwoordig gehad het nie. Die aantal uitheemse spesies was merkwaardig meer as die aantal inheemse spesies. Alhoewel

indringing ook die samestelling van die inheemse saadbank beïnvloed het, was die inheemse saad bank, waarvan sommige spesies slegs daar voorgekom het, meer divers as die bo-grond plant samestellings. 'n Studie van die grond het gewys dat die pH vlakke, afgesien van die seisoen, aansienlik laer is in die areas met indringers in vergelyke met areas sonder die indringers. Die hoeveelheid en dikte van plantmateriaal op die grond neem ook toe met 'n toename in indringers. Die waterinhoud van die grond het afgeneem met 'n toename in indringers en temperatuur het verhoog in beide winter en lente. Die totale makro- en mikrovoedingstowwe het nie merkwaardig gewissel saam met die indringingsgradiënt nie ( $p > 0.05$ ), maar die uitruilbare kation inhoud was aansienlik hoër, veral in die winter en lente-maande, in die areas sonder indringers in vergelyking met die areas met indringers.

Vernouing van rivierkanaal en versteiling van rivieroewers verminder die geskiktheid van die oewersone om sekere ekologiese funksies te verrig soos grond-saadstoring en die verskaffing van ruimte vir plante om te groei. Dit verminder geleenthede vir werwing van saailinge en verminder gevolglik spesiediversiteit. Aan die ander kant, die vermindering van die spesiediversiteit in die bogrondse plantegroei verminder saadinsette in die grond en dit lei tot verarming van grondgestoorde saadbanke. Die oorfloed van sade van *Acacia mearnsii* in die grondgestoorde saadbank hou die bedreiging van sekondêre indringing in na die skoonmaak van *E. camaldulensis* indien dit wel as 'n bestuursaksie aangeneem word.

Hierdie studie het die uiteengesette doelwitte suksesvol aangespreek. Die oorgang van 'n oewerbank-gemeenskap wat hoofsaaklik uit inheemse plante bestaan na 'n gemeenskap wat slegs uit *E. camaldulensis* bestaan, oor 'n periode van ongeveer 50 jaar, het duidelike veranderinge tot gevolg gehad. Hierdie veranderinge is veral opmerklik in die oewerbank-geomorfologie en bo-grondse plantegroei, maar tot op hede is dit nog nie so opmerklik in die saadbank en grond-voedingstowwe konsentrasies nie. Hierdie bevindinge bied ondersteuning aan die WvW verwyderings-ondernemings en wys dat daar wel moontlike herstel van inheemse spesies kan wees na die verwydering van die indringer *Eucalyptus*. Hierdie kennis dra nie net by tot verhoogde effektiwiteit van herstelwerk en langtermyn-bestuursplanne nie, maar ook tot die navorsingsveld van oewerbankekologie en-herstel. Verdere eksperimentele navorsing word benodig om die moontlike meganismes wat verantwoordelik is vir die waargeneemde veranderinge, geassosieer met *Eucalyptus* indringing, te verduidelik. Die bydrae van landbou tot die vorming van kanaal morfologie moet ook verder bestudeer word.

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## **Glossary of terms**

For the purposes of this study, the following simplified working definitions are provided:

Channel width - the width of a river or stream channel between the highest banks on either side of a stream.

Digital elevation model - the representation of continuous elevation values over a topographic surface by a regular array of z-values, referenced to a common datum. DEMs are typically used to represent terrain relief.

Georeferencing - a process of assigning map coordinates to image data to conform to a map projection grid.

Ground control points - one of various locations on a paper or digital map that has known coordinates and is used to transform another dataset—spatially coincident but in a different coordinate system—into the coordinate system of the control point.

Ground sampling distance - in a digital photo is the distance between pixel centers measured on the ground.

Rectification - a process of making image data conform to a map projection

Resolution - level of detail in data.

Riparian zone - riparian buffer zones are vegetated areas along both sides of water bodies that generally consist of trees, shrubs and grasses and are transitional boundaries between land and between land and water environments.

Spatial resolution - is the level of detail in image data (image sampling unit), usually measured in pixel size e.g. 1 pixel - 1m.

Temporal resolution - describes the interval between images taken at the same location.

Tie points - a point in a digital image or aerial photograph that represents the same location in an adjacent image or aerial photograph. Usually expressed as a pair, tie points can be used to link images and create mosaics.

Wet zone - the part of a stream that lies on the flowing water age and usually wet.

## **Glossary of abbreviations**

CARA - Conservation of Agricultural Resources Act

CIB - Centre of Excellence for Invasion Biology

DEM – Digital Elevation Model

DST - NRF Department of Science and Technology - National Research Fund

GCPs - Ground Control Points

GIS - Geographical Information System

GSD - Ground Sampling Distance

IAPs - Invasive Alien Plants

NEMBA - National Environmental Management: Biodiversity Act

SAPIA - South African Plant Invaders Atlas

TPs - Tie Points

WfW - Working for Water

RMSE - Root Mean Square Error

# Chapter 1

## General information

The work presented in this thesis forms part of a research initiative funded by the DST-NRF Centre of Excellence for Invasion Biology (C•I•B) and the Working for Water programme through their collaborative project on “Research for Integrated Management of Invasive Alien Species”. This PhD project set out to investigate changes associated with *Eucalyptus* invasions in a riparian ecosystem. All data chapters are written in the form of papers targeted at various journals. These papers will all be co-authored by my supervisors, hence the use of “we” in many parts of the thesis. Despite this, I was primarily responsible for the conceptualization and design of all work reported on here, I undertook all the field work, did all the analyses, and most of the writing.

### 1.1 Motivation

Riparian ecosystems are inherently rich in biodiversity and provide important functions and services, but are vulnerable to degradation by invasive alien plants (IAPs). Biological invasions threaten habitat diversity and function, and management of invasions in riparian systems is therefore imperative. Relatively little research has been done on plant invasions in these small but important landscape elements. In South Africa, much research has focussed on the effects of invasive tree species in the genera *Acacia* and *Pinus*, but very little on *Eucalyptus* species and much of the evidence on environmental effects of *Eucalyptus* invasions in riparian zones is anecdotal. Methodological limitations (see section 1.7) partly explain the lack of comprehensive information on the effects of tree invasions, especially large trees such as *Eucalyptus camaldulensis*.

The management of IAPs and restoration of degraded riparian habitats is a challenge for managers because of limited financial resources, and a poor understanding of the nature of the invaders' effects. This often results in the application of inappropriate and costly methods and strategies. The lack of a holistic understanding of riparian ecosystems partly explains the limited success of control and restoration activities. The control of biological invasions is most effective when it involves a long-term ecosystem management approach, but this requires comprehensive knowledge of the legacy effects of tree invasions and of the resilience of the native plant communities, i.e. its ability to initiate and support the recovery of functional native vegetation. Riparian zones are a complex of interrelated systems consisting of a geomorphic template, the above-ground vegetation and native soil-stored seed bank, and soil physical and chemical properties.

Studying only one part is not enough to inform management of IAPs and restoration. Because of the complexity of riparian ecosystems, the actual effect of an invader can best be understood as the interplay of these factors. The rationale of this study was therefore to investigate the multiple factors of geomorphology, above-ground vegetation, soil-stored seed bank, and soil properties.

The results of the study will provide knowledge about specific functional relationships among the major riparian ecosystem components under *Eucalyptus* invasion and will be useful for identifying opportunities and constraints for restoration of degraded riparian ecosystems. In the long term, this information will enhance the planning of sustainable clearing (clearing that ensures non-recurrence invasion) and restoration strategies. The study also contributes to the disciplines of invasion ecology and restoration ecology through innovative research methodologies and by proposing a dynamic multidimensional approach to ecosystem management.

## 1.2 Biological invasions as ecosystem disruptors

Biological invasions are increasingly being recognised as a major threat to biological diversity and ecosystem function (Davis, 2003; Gaertner et al., 2009; Vilà et al., 2011, Auerbach et al., In press). They can have a broad range of effects on various aspects of ecosystems including on the physical environment (geomorphology) (Birken and Cooper, 2006; Cadol et al., 2011), above-ground native vegetation [see Gaertner et al. (2009) and Le Maitre et al. (2011) reviews and references therein], soil-stored seed banks (Fisher et al., 2008; French et al., 2011; Marchante et al., 2011), and soil physical and chemical properties [see Ehrenfeld (2003) review and references therein]. Effects of invasive alien plants depend on the traits of the invader, e.g. growth-form, functional traits such as nitrogen fixation and allelopathy (Clifton, 1989).

The Cape Floristic Region (CFR) of South Africa has high levels of biodiversity, but also stands out as one of the areas most affected by IAPs among the world's Mediterranean-type ecosystems (Gaertner et al., 2011). The fynbos biome of the CFR is the most invaded biome in South Africa, with dense invasions in mountains, lowlands and riparian habitats (Richardson and van Wilgen, 2004). About 57% of invasive plant species in the fynbos biome are trees and shrubs in the genera *Acacia*, *Hakea* and *Pinus* (van Wilgen, 2009). *Eucalyptus camaldulensis* is a specialist invader of riparian habitats and constitutes a smaller percentage of invasive trees and shrubs.

Tree invasions can alter the composition and structure of native vegetation (Richardson et al., 2000; Gaertner et al., 2011; Le Maitre et al., 2011); change river geomorphology (Scott et al., 1998; Holmes et al., 2005); increase transpiration leading to

increased water use and reduced water flows (Le Maitre et al., 1996; Görgens and van Wilgen, 2004; McDonald et al., 2009); alter decomposition rates and therefore carbon cycling (Witkowski, 1991; Yelenik et al., 2004; Lindsay and French, 2005); change fire regimes (Forsyth et al., 2004; Ritter and Yost, 2009; Tickner et al., 2001); and reduce wildlife habitat quality (Rejmánek and Richardson, 2011). In riparian ecosystems, tree invasions produce large wood debris which interferes with channel hydraulics and fluvial processes thereby influencing channel morphology (Naiman and Décamps, 1997). Furthermore, invasive alien trees with allelopathic traits, such as eucalypts, have also been reported to suppress the growth of nearby food crops (Rejmánek and Richardson, 2011). Some invasive alien plants shade out entire forest understorey due to higher canopy cover (Brooks et al., 2004; Gaertner et al., 2009; Lowe et al., 2000).

### **1.3 The biogeography and invasion of riparian ecosystems**

Rivers are critical transition zones, serving as conduits for substantial fluxes of materials and energy (Ewel et al., 2001). Riparian zones are ecotones which occupy a unique position in the landscape, forming the interface between aquatic and terrestrial ecosystems (Naiman and Décamps, 1997; Richardson et al., 2007). They are important landscape elements which support distinctive biological communities, and often high plant species richness, in their natural state (Naiman and Décamps, 1997; Hood and Naiman, 2000). Riparian vegetation assemblages fulfil and/or influence various ecosystem functions including the provision of habitat for wildlife and game, provision of food, the moderation of river temperature, stabilization of stream banks and the filtration of sediments and nutrients (Malanson, 1993; Hood and Naiman, 2000; Richardson et al., 2007). Apart from these ecological functions, riparian vegetation also provides important ecosystem services for humans including flood mitigation, ground water recharge, improved water quality, improved water availability for irrigation, and areas for recreational use. Riparian systems, which usually cover only a small part of the landscape, experience high disturbance due to natural processes (fluvial processes – flooding, erosion and deposition) and anthropogenic activities (river damming, land-use in the fringes of rivers), hence susceptibility to invasion (Naiman et al., 2005). Such influences can create novel ecosystems which present numerous challenges for conservation managers (Hood and Naiman, 2000; Richardson et al., 2007; Beater et al., 2008; Pollen-Bankhead et al., 2009). The diversity and abundance of alien plants is typically high in riparian zones worldwide; in some cases this causes substantial changes to the structure and functioning of these ecosystems. In other cases alien plants are passengers of change caused by other factors (Bauer, 2012).

## 1.4 The genus *Eucalyptus*

### 1.4.1 Distribution

The genus *Eucalyptus sensu lato* has c. 800 species that are almost entirely endemic to the Australian continent and a few Pacific islands (Williams and Woinarski, 1997; Brooker, 2000; Tyynelä, 2001; McDonald et al., 2009; Rejmánek and Richardson, 2011). Some taxonomists suggest that eucalypts belong to three genera: *Angophora*, *Corymbia*, and *Eucalyptus* (Rejmánek and Richardson, 2011). Eucalypts include species that grow in temperate rain forests, deserts, humid subtropical areas, and Mediterranean climate regions (Doughty, 2000; McDonald et al., 2009). They range from multi-stemmed shrubs (mallees) to some of the tallest (c. 75m) and largest forest trees on earth (Ritter and Yost, 2009; Rejmánek and Richardson, 2011).

### 1.4.2 Eucalypts in cultivation outside their natural range

Because of their tolerance of a wide range of environmental conditions, eucalypts have been widely planted in many parts of the world, in arid, temperate and tropical countries (Tyynelä, 2001; Forsyth et al., 2004; Butcher et al., 2009; McDonald et al., 2009). They are grown in plantations to provide timber and pulp, to curb deforestation, and for many other purposes including erosion control, wildlife habitat, timber, shelterbelts, ornamentals and honey production (Tyynelä, 2001; Forsyth et al., 2004; Richardson and Rejmánek, 2011). Eucalypts were introduced to South Africa more than two centuries ago, and more than 200 species have been cultivated.

### 1.4.3 Invasiveness of eucalypts in South Africa

Given the extent of dissemination, and their high adaptive capacity to a wide range of physical environments, it is rather surprising that eucalypts are markedly less invasive than other widely cultivated taxa of trees and shrubs, for example species in the genera *Acacia*, and *Pinus*. Seven of the 200 species cultivated in South Africa have been declared invaders in the Conservation of Agricultural Resources Act (CARA) and National Environmental Management: Biodiversity Act (NEMBA) (SAPIA, 2009). Most invasions occur along water courses and on forest margins, in gaps within native forests and plantations, as well as in fynbos and grassland vegetation. *Eucalyptus camaldulensis* is an Australian tree species which is a riparian specialist that can readily invade susceptible riparian zones (Vilà and Gimeno, 2007; Rejmánek and Richardson, 2011). *Eucalyptus camaldulensis* is the greatest threat as it is found throughout much of South Africa and has already transformed long stretches of perennial, seasonal and intermittent rivers and dam shores (Forsyth et al., 2004). It is thus declared a major environmental weed. Other eucalypts that have been found to be invasive include *E. cladocalyx* and *E. conferruminata*.

In many parts of the world where eucalypts are successful invaders, they rarely spread considerable distances from planting sites and their regeneration is frequently sporadic, except in riparian zones where seed dispersal is driven by seasonal floods (Rejmánek and Richardson, 2011). *Eucalyptus* species are fast growing and produce large quantities of seed such that dramatic invasions would have been expected, but recruitment is limited. High rates of seedling mortality and lack of seed dormancy may explain the low rates of invasiveness. Although eucalypts are less successful invaders than some other tree species, the ecological effects of those species that have invaded are of no less concern than those of other invasive taxa such as *Acacia*.

#### **1.4.4 Research on impacts of *Eucalyptus* species on native ecosystems**

Globally, research on the impact of planted *Eucalyptus* species has focussed mainly on ecosystem-level effects such as water consumption (e.g. Le Maitre et al., 2002; Engel et al., 2005; Oumar and Mutanga, 2010), changes to fire regimes (e.g. Dimitrakopoulos and Papaioannou, 2001; McCaw, 2002; van Wilgen, 2009), and allelopathy (e.g. del Moral and Muller, 1970; Khan et al., 2008; Zhang et al., 2010). Fewer studies have investigated community-level effects such as changes in native species diversity (e.g. Tyynelä, 2001; Gaertner et al., 2011; Calviño-Cancela et al., 2012), and soil nutrients (e.g. Adams and Attiwill, 1986; Bernhard-Reversat, 1996; Turner and Lambert, 2008; Jeddi et al., 2009). Almost all the studies cited above were conducted in terrestrial plantation habitats. To my knowledge, no research has examined the effects of self-sown escapees from these planting sites, especially those invading riparian zones. Effective management of invasive *Eucalyptus* species requires urgent research into their effects on native ecosystems. Research in this area has been neglected in South Africa, with most studies focusing on *Acacia* species (Le Maitre et al., 2011). There is a dearth of information on the effects of *Eucalyptus* invasion on native soil-stored seed banks and geomorphological properties of riparian habitats. A rapid assessment study by Forsyth et al. (2004) recommended the clearing of eucalypts by the Working for Water programme (a South African government initiative tasked with clearing of IAPs, especially those that affect water resources, but little knowledge exists on the nature of the effects and possible restoration strategies.

#### **1.5 Research aim and objectives**

The aim of the study was to examine changes in riparian ecosystems associated with the widespread invasion of a large tree species (*E. camaldulensis*), and to determine implications for management and restoration. This is the first attempt to quantify the effects of invasive stands of a *Eucalyptus* species in riparian habitats. The study utilizes

this unique opportunity to undertake multi-dimensional research on various aspects of the invaded ecosystem, including geomorphology, above-ground vegetation, seed bank and soil properties. The specific objectives were to (1) investigate changes in geomorphological characteristics associated with the invasion of *Eucalyptus*, (2) examine changes in above-ground vegetation characteristics associated with *Eucalyptus* invasion; (3) determine whether, and if so then how, *Eucalyptus* invasion has altered the indigenous soil-stored seed bank (potentially limiting post clearing propagule supply); (4) determine changes in soil physical and chemical properties associated with *Eucalyptus* invasion. Each of these objectives constituted a chapter in the thesis.

## **1.6 The conceptual framework**

Plant invaders alter both ecological properties and the physical features of invaded ecosystems (Mack et al., 2000). The geomorphic component of the riparian ecosystem provides the physical template within which riparian ecosystems and their processes exist. The suitability of the environment for germination and survival of riparian plant species depends on alternating processes of geomorphic and hydrologic disturbance and stability in riparian ecosystems (Busch and Smith, 1995). As depicted in Fig. 1, erosion and deposition within the riparian zone determine the vegetation assemblages that can establish, the soil-stored seed bank size and distribution, and resilience, and both soil physical and chemical properties. In turn, vegetation provides anchorage to the soils, preventing erosion, supplies seed for storage in the soil (potentially forming an important buffer), and deposits litter to the soil for nutrient cycling. The soil provides a medium for soil-nutrient processes necessary for growth of above-ground vegetation, as well as storage for seed banks. Fig. 1 conceptualizes the interaction of the components mentioned above.

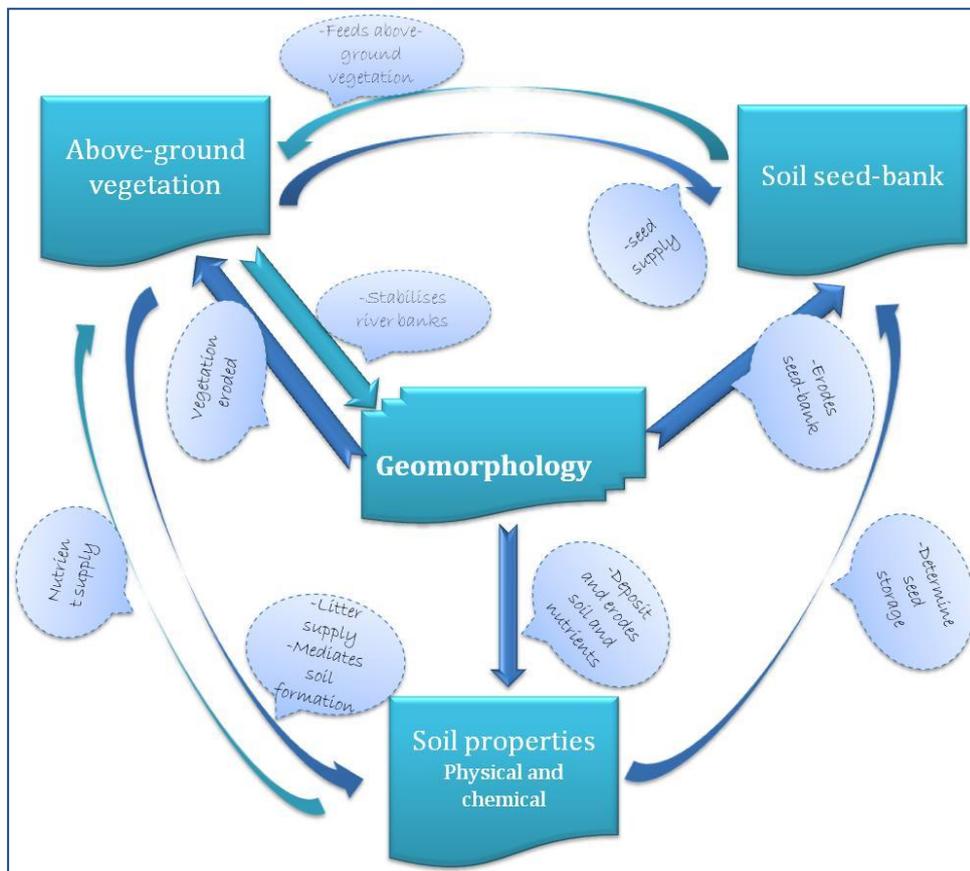


Fig. 1.1. Conceptual framework of the study, providing an overview of the interplay of geomorphology, above-ground vegetation, soil-stored seed bank and soil components of the riparian ecosystem. Changes in each of these components and their interactions were studied with reference to the actual effects brought about by the invasion of riparian systems along the Berg River by the alien tree *Eucalyptus camaldulensis*. The arrows show the various relationships among the components, and the balloons describe the relationships.

Often, wherever IAPs invade in a riparian zone, some physical changes in the structure of the riparian zone can be expected (Rowntree, 1991). Invasion of *E. camaldulensis* has the potential to change many aspects of the ecosystem. Such impacts have been studied for other tree invasions which can contribute to changes in riparian geomorphology (Stallins, 2006; Pollen-Bankhead et al., 2009; Osterkamp and Hupp, 2010), riparian vegetation (above ground and soil seed bank) (Hejda and Pyšek, 2006; Blanchard and Holmes, 2008; Esler et al., 2008; Holmes et al., 2008; Gioria and Osborne, 2009c; French et al., 2011) and soil properties (physical and chemical) (Ehrenfeld, 2003; Corbin and D'Antonio, 2004; Corbeels et al., 2005; Dassonville et al., 2008; Vilà et al., 2011). Riparian areas can be highly dynamic environments that are, to varying degrees, susceptible to invasion. The dynamic nature of this study system presents opportunities for a multi-faceted study. This PhD is unique in that it bases its recommendations for management of *E. camaldulensis* and restoration of the degraded system on a synthesis

of effects on different aspects as opposed perspectives on isolated components of the ecosystem.

### **1.7 Methodological approach and constraints**

Space-for-time substitution or comparative observational studies have been criticized for their failure to separate causes and effects of invasion. Consequently, several studies advocate experimental removal or introductions of the invader, or a combination thereof. An experimental approach was inappropriate for this study for several reasons. Firstly, experimental introductions of known invasive species are unethical (Hejda and Pyšek, 2006) and risky especially in riparian zones where dispersal of *E. camaldulensis* is facilitated by flood pulses (Rejmánek and Richardson, 2011). Secondly, introductions are unrealistic in terms of the time required to get results. Removal of the invader is mainly constrained by cost and insufficient working capacity (Taylor and Hastings, 2004) and the long time it takes for the ecosystem to respond (Hejda and Pyšek, 2006); Furthermore, there are indirect effects following species removal (e.g. soil and native vegetation disturbance) which may obscure the true impact of specific invasive species (Hulme and Bremner, 2006; Truscott et al., 2008).

This study therefore examined changes associated with *E. camaldulensis* invasion in riparian geomorphology, vegetation community, soil-stored seed bank and soil properties along an invasion gradient. This allowed for the detection of trends in these variable characteristics as invasion density increased. The approach was used notwithstanding the uncertainty associated with some aspects of the condition of plots prior to invasion, and the fact that plots may differ in factors other than invasion history; this is a common problem in such comparative studies (Hejda and Pyšek, 2006). My study sites along the Berg River were chosen as close to uninvaded sites as possible - within the same hydro-meteorological unit, and in the same geomorphological zone, and similar soils. All the sites had similar disturbance regimes. As such I believe that the experimental design for the study is entirely appropriate for assessing the effects of *E. camaldulensis* invasion in riparian zones.

### **1.8 Chapter synopsis**

Chapter 1: Introduction

This chapter provides a background to the whole study, including the aims and objectives. It also includes a brief review of the literature on biological invasions as ecosystem

disruptors, riparian ecosystems and invasive alien plants. It describes the main study species, *Eucalyptus camaldulensis*, and how it differs from other invasive tree species.

Chapter 2: Effects of *Eucalyptus* invasion on riparian geomorphology: implications for native vegetation recovery

In this chapter I use geographical information systems and remote sensing (photogrammetry) to examine historical channel morphology properties and invasion dynamics. I then draw inferences from the results as to whether the emerging riparian zone environment is suitable for native species recruitment and establishment following the clearing of *Eucalyptus*. This chapter was written in the format of a paper that will be submitted to a geomorphology journal.

Chapter 3: *Eucalyptus camaldulensis* invasion of riparian zones: effects on floristic diversity, stand structure and composition of native vegetation

I used an observational approach with gradient sampling to establish changes in above-ground vegetation that are associated to *Eucalyptus* invasion. The chapter has been submitted to the journal *Forest Ecology and Management*.

Chapter 4: Resilience of riparian vegetation invaded by *Eucalyptus camaldulensis* and options for restoration: the role of the soil seed bank

In this chapter, soil sampling was conducted in the same plots where the above-ground vegetation study was carried out to facilitate comparison. I used a seedling emergence experimental approach to assess the characteristics of the soil-stored seed bank. Seed banks were compared at two depths and with above-ground vegetation. This chapter has been submitted to the journal *Folia Geobotanica*.

Chapter 5: Effects of *Eucalyptus camaldulensis* invasion on soil physico-chemical properties in riparian zones

I collected soil samples in the same sites in which the vegetation and seed bank studies were conducted. Soil physical (particle size) and chemical (macro, micro and cation exchange) analyses were conducted and compared for various levels of invasion and across seasons. This chapter has been submitted to *Plant and Soil*.

Chapter 6: Conclusions and recommendations

This chapter examines whether the study was able to address the fundamental questions of the study, discusses the problems that were encountered, the contribution of knowledge to the literature on the management of invasive alien plants and restoration. It also discusses outstanding issues and suggests priorities for future research

## Chapter 2: Effects of *Eucalyptus* invasion on riparian geomorphology: implications for native vegetation recovery

This chapter is intended for publication in the journal *Geomorphology*.

Reference: Tererai, F., Gaertner, M., Jacobs S.M., Richardson, D.M. 2012. Effects of *Eucalyptus* invasion on riparian geomorphology: implications for native vegetation recovery. *Geomorphology*.

### Abstract

**Aims:** The invasion of riparian zones by invasive alien trees causes changes in riparian geomorphology. I investigated changes associated with *Eucalyptus camaldulensis* invasion in the riparian zone along the Berg River in the Western Cape Province, South Africa. The main aim of my study was to determine whether it is possible to (1) separate the effects of invasive alien plants from climate and human effects using aerial photogrammetry techniques and (2) to relate specific changes in the riparian geomorphology directly to *Eucalyptus* invasion. I tested the hypothesis: replacement a multi-structural vegetation assemblage by a large tree monoculture will result in river bank stabilization and consequent narrowing of the channel and channel incision. I predicted that agriculture will play a key role in controlling the spatial extent of riparian zones. To increase our confidence that changes detected in the riparian zone are associated with invasion, I examined climate related variables of precipitation and hydrological data.

**Methods:** I used a combination of historical aerial photography, image processing and geographic information system techniques to detect changes in the riparian zone. Field surveys and desk-top analyses of hydrometeorological data were also undertaken. Aerial photos from four years (1938, 1973, 2000 and 2010) were ortho-rectified and used to map extent of the woody riparian vegetation cover, extent of river channel plan-form, and model historical channel morphometry. Mann-Kendall's trend test was used for time series analysis of hydrometeorological data.

**Results:** There was evidence that the detected effects were associated with *E. camaldulensis* invasion. The area of the riparian zone has decreased by about 13.5% between 1938 and 2010. During this period, the riparian zone has been very dynamic with increases and decreases in area at several locations. There is evidence of channel narrowing from an average 22 m by up to 6.8 m in some locations with disappearance of islands and bars. There is also evidence of channel bed incision in areas where narrowing

occurred. No significant trends were detected in time series of precipitation and river flow ( $p > 0.05$ ).

**Conclusions:** It was possible to eliminate the effects of climate from those of invasion and possibly agriculture, and it is considered very likely that changes in vegetation structure due to *Eucalyptus* invasion are a primary cause of the observed changes in river geomorphology. Further work is required to examine interactions between potentially contributing factors. The environment created by widespread invasion of *E. camaldulensis* reduces recruitment and establishment of native species, and the current clearing of invasive stands may destabilize riverbanks causing further disturbance that is conducive for secondary invasions. Further research is also needed to establish the actual contribution of agriculture in influencing channel morphology.

**Key words:** Biological invasions; Channel morphology; Image processing; Restoration; Riparian geomorphology; Riparian vegetation

**Abbreviations:** GIS – Geographical Information System, DEM – Digital Elevation Model, GCPs – Ground Control Points, TPs - Tie Points, RMSE – Root Mean Square Error

## 2.1 Introduction

Riparian habitats support high levels of biodiversity and provide important functions and services (Naiman et al., 1993; Barling and Moore, 1994; Goebel et al., 2003; Décamps et al., 2004; Kondolf et al., 2007). Invasion of riparian habitats by invasive alien plants is acknowledged as a serious problem for biodiversity conservation and ecosystem management (Planty-Tabacchi et al., 1996; Foxcroft et al., 2007; Richardson et al., 2007). Riparian geomorphology forms the physical template on which riparian ecosystems exist (Gregory et al., 1991) and vegetation is an important dynamic component of these ecosystems (Rowntree, 1991). There is an inextricable relationship between riparian vegetation and the physical environment (Hupp and Osterkamp, 1996; Tickner et al., 2001; Osterkamp and Hupp, 2010). Riparian vegetation influences many geomorphological processes (Hupp and Osterkamp, 1996; Rowntree and Dollar, 1996; Bennet and Simon, 2004; Stromberg et al., 2007), while germination and establishment of plant species depends on alternating processes of geomorphic and hydrologic disturbance and stability in riparian ecosystems (Busch and Smith, 1995).

Naturally unstable geomorphologic units such as river bends are susceptible to invasion (Rowntree, 1991). Rowntree (1991) and Abernethy and Rutherford (2001) stressed the need for research on the effects of invasive alien plants on riparian geomorphology. While invasive alien plants alter both ecological properties and ecosystem physical features (Mack et al., 2000), most studies have focused on the biology and biogeography of the spread of invasive species (Tickner et al., 2001). However, despite the strong feedback relationships between riparian plant communities and hydrogeomorphology (Gregory et al., 1991; Stallins, 2006; Stromberg et al., 2007), scant attention has been paid to the interactions between invasions and these physical processes (Tickner et al., 2001; Sandercock et al., 2007).

Geomorphology is the study of the morphology of landforms and the processes responsible for their evolution, while the term riparian refers to landforms within and adjacent to streams, which include the channel bed, banks, and floodplain (Webb, 2008). Riparian geomorphology is the study of the dynamic and complex relationships that exist between vegetation and the formation and morphology of stream channels and floodplains. Erosion and deposition are the active geomorphological processes of streams, and the fringes make up the riparian zone. Riparian vegetation influences river hydrology which plays an important role as the driver of river geometry and processes (Eviner and Chapin III, 2003).

Channel dynamics can manifest as change in cross-sectional geometry, channel gradient, and channel plan-form. These changes are influenced by several variables including climate (precipitation), human activity (agriculture) and vegetation (native and especially invasive alien plants - IAPs) (Décamps, 1993; Rowntree and Dollar, 1996; Anderson et al., 2004; Osterkamp and Hupp, 2010; Cadol et al., 2011; Beschta and Ripple, 2012). Climate has direct (through precipitation and consequent river flow) and indirect effects (e.g. it may promote shift in species composition) on river channels. Changes in vegetation can subsequently influence erosion, sedimentation and deposition (Clifton, 1989; Eviner and Chapin III, 2003). Anthropogenic activities, such as flow regulation can alter the river channel form and the composition and extent of riparian habitat. Agricultural landuse adjacent to the river can increase sediment supply and eutrophication (Richardson et al., 2007 and references therein).

Riparian vegetation controls many geomorphological processes such as erosion and deposition which determine channel form and in-turn vegetation is influenced by geomorphology (Hupp and Osterkamp, 1996; Rowntree and Dollar, 1996; Bennet and Simon, 2004; Stromberg et al., 2007). Woody species in particular are seen as having a significant potential for inducing channel modification (Eviner and Chapin III, 2003). A transformation of vegetation from a mixed native community that includes a range of

vegetation lifeforms (herbs, grasses, shrubs etc.) to a woody monoculture of alien trees may alter channel morphology with far reaching effects on viability of riparian habitats (Rowntree, 1991). Change in channel morphology may be a collective function of all factors (Birken and Cooper, 2006). A change in vegetation structure may drive channel change by altering bank and floodplain characteristics, or the vegetation changes may be a result of channel modification initiated by precipitation and landuse changes or human alterations (Gregory et al., 1991; Stallins, 2006; Osterkamp and Hupp, 2010; Cadol et al., 2011). The challenge is in separating the influence of invasive species from that of native vegetation, climate and various human-mediated activities.

The complexity of interrelated factors influencing effects on riparian geomorphology has resulted in scientific investigations, especially those done before about 1960, typically disregarding vegetation in order to simplify studies (Osterkamp and Hupp, 2010). However, Eviner and Chapin III (2003) argued that vegetation is the main determinant of geomorphology. Since then, significant progress has been made in integrating the effects of vegetation culminating into a discipline called biogeomorphology (Viles, 1988; Stallins, 2006). However, the relationship between vegetation, in particular invasive alien trees, and riparian geomorphology is still poorly understood, and only a few studies have been conducted, e.g. on *Tamarix* in the western United States (e.g. Birken and Cooper, 2006 and Cadol et al., 2011). Some of the constraints to research in this area, especially for examining historical changes in riparian systems associated with plant invasions, have been data and methodological limitations. Analysis of repeated aerial photographs is one method that has been commonly used to attempt to separate the effects of IAPs from those attributable to climate and human effects (Hereford, 1984; Birken and Cooper, 2006; Cadol et al., 2011). However, aerial photos often have a high spatial resolution but typically a low temporal resolution, hence interpretation is improved by ground truthing (Cadol et al., 2011).

My study is one of the first attempts to relate changes in riparian geomorphology to alien plant invasions. The main aim of my study was to determine whether it is possible to (1) separate the effects IAPs from climate and human effects using aerial photogrammetry techniques and (2) to relate specific changes in the riparian geomorphology directly to *Eucalyptus* invasion. The results of the study will help to inform invasive species management and provide useful insights on the potential for native vegetation recovery following removal of the invader.

The study took part in the lower reaches of the Berg River in the Western Cape, South Africa in a human-modified landscape which is predominantly under agricultural use. The native riparian vegetation consists mainly of small tree and shrub species (Geldenhuys, 2008), but the reaches of the Berg River are heavily invaded by invasive alien trees, mainly eucalypt species. I hypothesised that (1) the replacement of a native

multi-structural vegetation assemblage by a large alien tree monoculture will result in river bank stabilization and consequent narrowing of the channel and channel incision, (2) agriculture will play a key role in controlling the spatial extent of riparian zones and 3) there will be no significant changes in climate related variables of precipitation and hydrological data.

## 2.2 Materials and methods

### 2.2.1 Study area

This study was conducted at the Berg River, which is located north-east of Cape Town in the Western Cape of South Africa (Fig. 2.1). The study site was a 32 km stretch of the Berg river from the town of Wellington downstream to the town of Hermon (Fig. 2.1). The study area was chosen because it is a good example of long-established invasions (c. 50 years) (Geldenhuys, 2008) within an agricultural landscape. This stretch was also chosen because it had a complete coverage of aerial photos in the four time steps that were used in this study. The area has a mediterranean-type climate with warm dry summers and cool wet winters with an average rainfall of about 550 mm. The average temperature minima and maxima are 11°C and 22°C respectively. The Berg is a perennial river with high flows and frequent flooding in winter (May to September). While the river is regulated with a large dam which was built in 2007 in the headwaters; this is unlikely to have affected its hydrological regime because environmental flows were taken into account at the design and operation stages of the Berg River Dam according to the International Commission on Large Dams (ICOLD). There are also no distinct hydrogeomorphic river segments within the study area. The geology of the catchment area is dominated by sandstone and quartzites of the Cape Supergroup which have typically nutrient-poor lithologies (Cotter, 2000). Quartzites are associated with sandy soils (Lewis and Illgner 1998). The whole river stretch has been invaded by alien trees, mainly *E. camaldulensis* (which has been present for at least 50 years), but was interspaced with individuals of *Acacia mearnsii* and *Populus* spp. (poplars) in some locations. Dominant native woody riparian vegetation includes small trees and shrubs of *Diospyros glabra*, *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, and *Searsia angustifolia* which are now mainly confined to small pockets or isolated individuals within stands of *E. camaldulensis*.

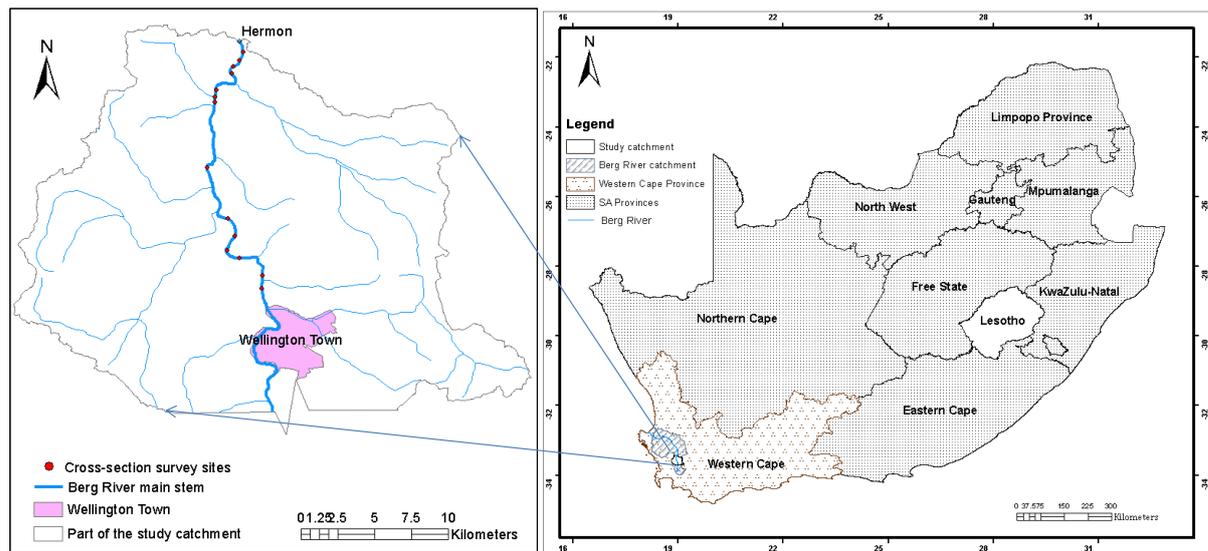


Fig. 2.1. The focus of this study is the riparian zone along the Berg River between the towns of Wellington and Hermon in the Western Cape, South Africa. The red dots show the distribution of the study sites where cross-sections have been surveyed.

### 2.2.2 Data requirements

Raw (1938; 1973; 2000) and orthorectified [2010 - orthorectified using triangulation data and a Digital Elevation Model (DEM) in PCI Geomatica to an accuracy of  $\pm 3\text{m}$ ] aerial photographs covering the Berg river were collected from the South African National Chief Directorate: National Geospatial Information. The scale of the aerial photography ranged from 1:25000 to 1:50000 (Table 2.1). A digital elevation model with a 15 m spatial resolution was downloaded from the Council for Scientific and Industrial Research (CSIR) database. Cross-sectional surveys (from which bankfull width, normal water level width and normal water depth were determined) were conducted in late summer (January and February, 2011) at various sites under varying levels of invasion using a Nikon Total Station DTM500. River flow data (1985 – 2010) from a station at the exit point of the study catchment (at Hermon town) was obtained from the Department of Water Affairs. Rainfall data (1964 – 2010 for the longest record) were collected from ARC Agroclimatology–Institute of Climate, Soil and Water for three stations. During ground surveys, qualitative channel characteristics including river substrate material, river banks and their structure were characterized at all sites where cross-sections were surveyed.

Table 2.1. Year, scale, film type, average number of ground control points (GCP) per photo for the images used in the study of changes in riparian zone of the Berg River, Western Cape, South Africa. GSD means ground sampling distance for colour aerals since 2008 in South Africa.

Year of imagery	Scale	Film type	Average GCPs per photo	Discharge at photo date m <sup>3</sup> /s
1938	1:25 000	Panchromatic	30	unavailable
1973	1:50000	Panchromatic	37	unavailable
2000	1:50000	Panchromatic	39	4.5
2010	GSD – 0.5m	Near infra-red and panchromatic	Used triangulation data	5.6

### **2.2.3 Data processing**

A mosaic of the 2010 orthophotos and a mosaic of the DEM covering the extent of the Berg River between the towns of Hermon and Wellington were created in ArcGIS 10. These two mosaics were used as backgrounds for the orthorectification of the aerial photo time series in PCI Geomatics – OrthoEngine module. The aerial photo sets were orthorectified by ground control points (GCPs) and tie points (TPs). On each photo an average of 35 GCPs and 20 TPs were collected in close proximity to each other to increase accuracy. The root mean square error (RMSE) of the orthophotos at each GCP and TP was smaller than 2m in the X and Y directions. Second- and third-order polynomial transformations were mostly applied for orthorectification because of a lower resultant RMSE as recommended by Hughes et al. (2006). Epipolar DEMs were automatically extracted from the epipolar pairs, geocoded and mosaiced. River plan-forms and riparian zone polygons were digitized from the mosaic of each time step.

### **2.2.4 Aerial photo interpretation**

Aerial photo dates, scales and study sites were selected based on availability of aerial photography. The specific areas analysed from aerial photography and time steps used at any stage of analysis depended on the quality of DEMs generated on aerial photos (Mast et al., 1997). Colour, tone, shape and texture of the vegetation were used to attempt to differentiate between native vegetation and *Eucalyptus*. To detect spatial and temporal changes in the Berg River, I examined the spatial variation in the extent of riparian vegetation, identified changes in channel pattern such as braiding, and the present relative occupation of dense stands of *Eucalyptus* (verified by ground truthing and Google

Earth images). I examined aerial photos for evidence that vegetation colonised channel areas such as bars and islands, stabilising the channel and forcing channel narrowing. Historical cross sections extracted from DEMs only give an indication of the channel profile dimensions because of dense vegetation along the river banks and the perennial flow. Normally the interpretation of changes on older aerial photography is largely limited to visual interpretation (Mast et al., 1997) as photographs were taken using non-metric cameras with only black-and-white panchromatic film.

### **2.2.5 Statistical analysis**

Polygons of riparian zones and river planforms were analysed using the union function in ArcGIS 10 which facilitates detection of changes among shapefile data sets over time. River width (bankfull width) was measured on two aerial photo scenes (1938 and 2010) at 1km intervals. Differences in mean width measurements were determined using a paired t-test since the data were normally distributed. Cross-section points from the field survey were rasterized and crossed with the DEMs of each time step in order to determine the elevation of each DEM time step at that same point. River flow and rainfall data were analysed for trends in Hydrospect 2 (Radziejewski and Kundzewicz, 2000). Point precipitation data for the three stations were first converted to aerial data by averaging. Mann-Kendall test was used to determine if there were any significant trends in hydrometeorological data (Radziejewski and Kundzewicz, 2004). Interdecadal variability analysis for all possible pairs was conducted using independent student t-tests since all data were normally distributed.

## **2.3 Results**

### **2.3.1 Spatial and temporal trends in the riparian zone**

Fig. 2.2 a-d shows parts of the riparian zone with increases (red colour) and decreases (green colour) in riparian zone area. The area of the riparian zone has decreased ( $0.22\text{km}^2$ ) more than it has increased ( $0.19\text{km}^2$ ) by about 13.5% between 1938 and 2010.

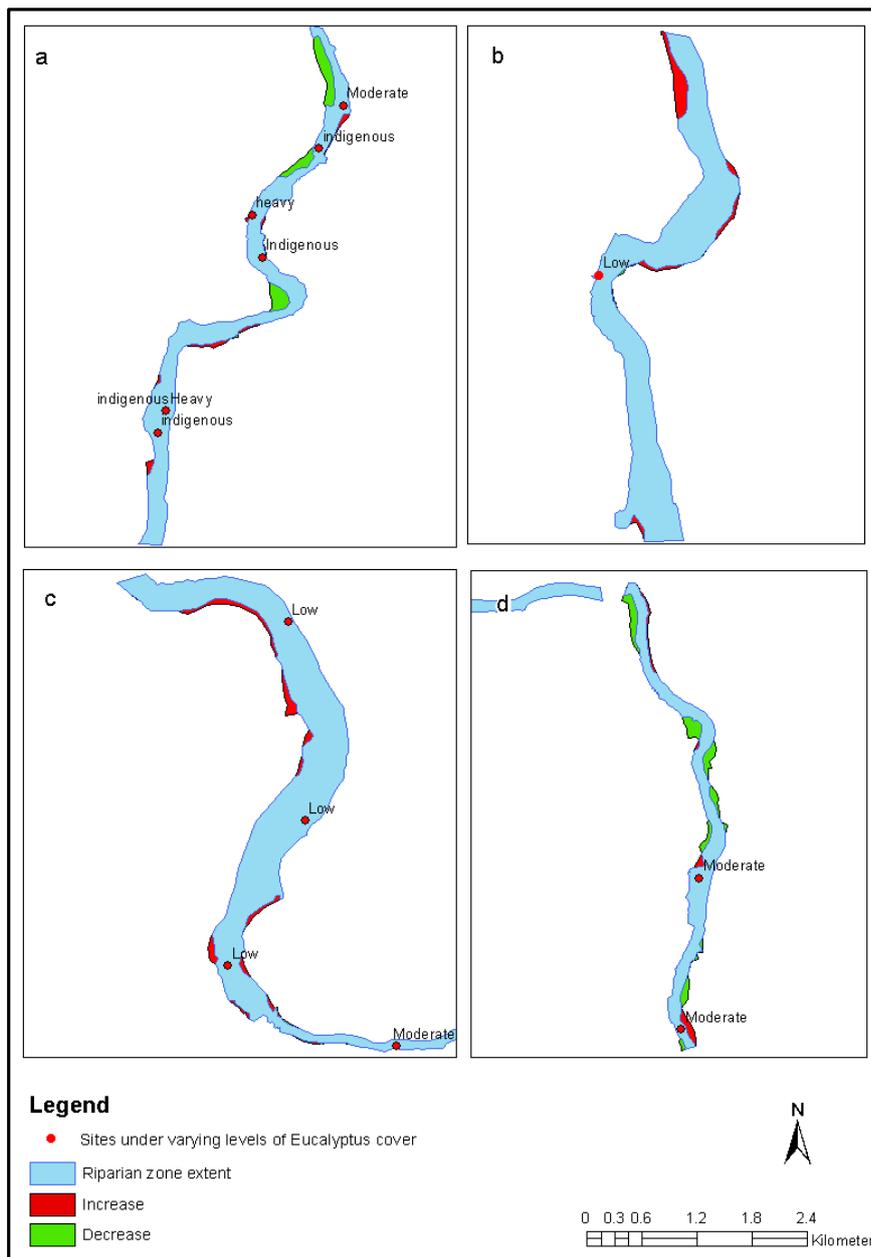


Fig. 2.2. Overall changes in the riparian zone between 1938 and 2010. The blue polygon shows the riparian zone common in both years (1938 and 2010), the green shows areas of decrease, while red shows areas of increase in the area of the riparian zone. Boxes a-d show a continuous river section from a (most downstream) to d (most upstream)

### 2.3.2 Spatial and temporal dynamics in the river channel

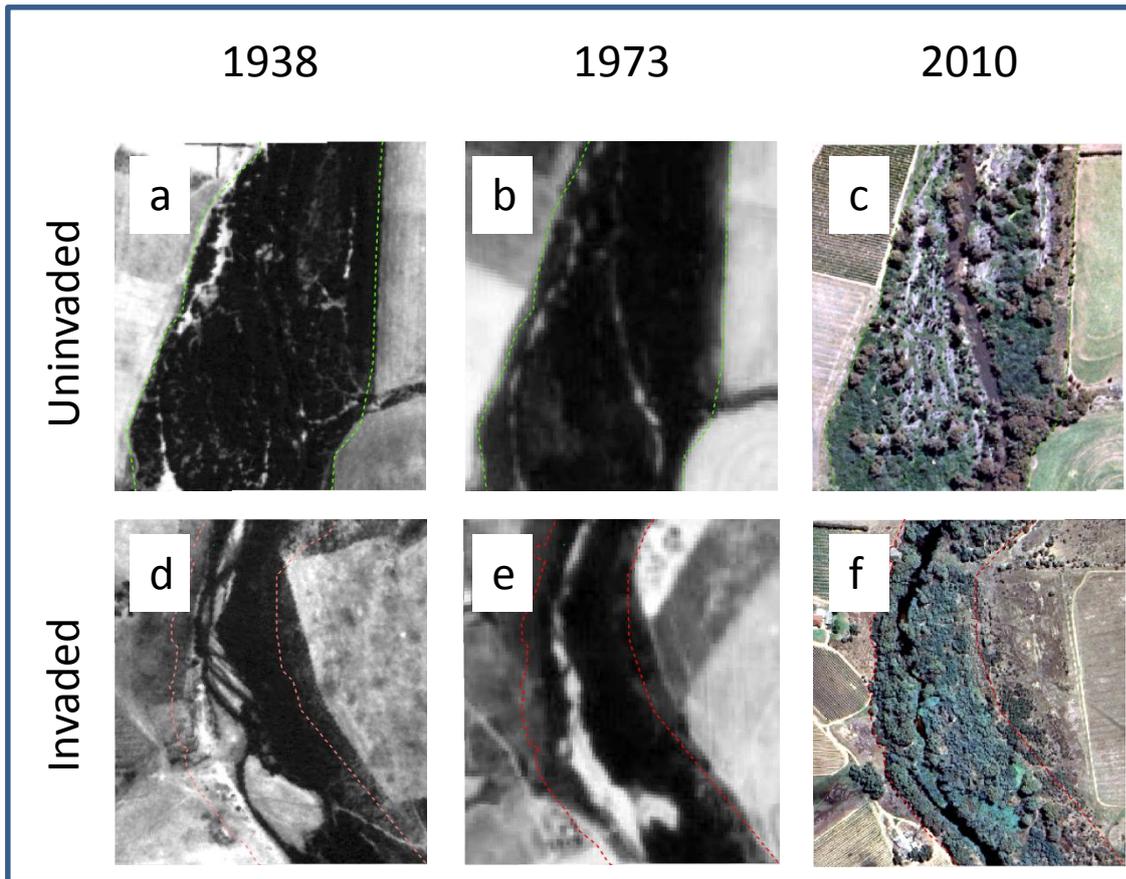


Fig. 2.3. Typical changes in the river channel in uninvaded (a-c) and invaded (d-f) sites over a period of 70 years (1938 – 2010) along the Berg River, Western Cape, South Africa

Little channel changes occurred in sites that had significant amounts of vegetation in 1938 (Fig. 2.3a-c). The 1938 image (Fig. 2.3d) shows a wide river channel with largely bare in-channel landforms. By 2010, such sites were densely invaded by *E. camaldulensis* (Fig 2.3f).

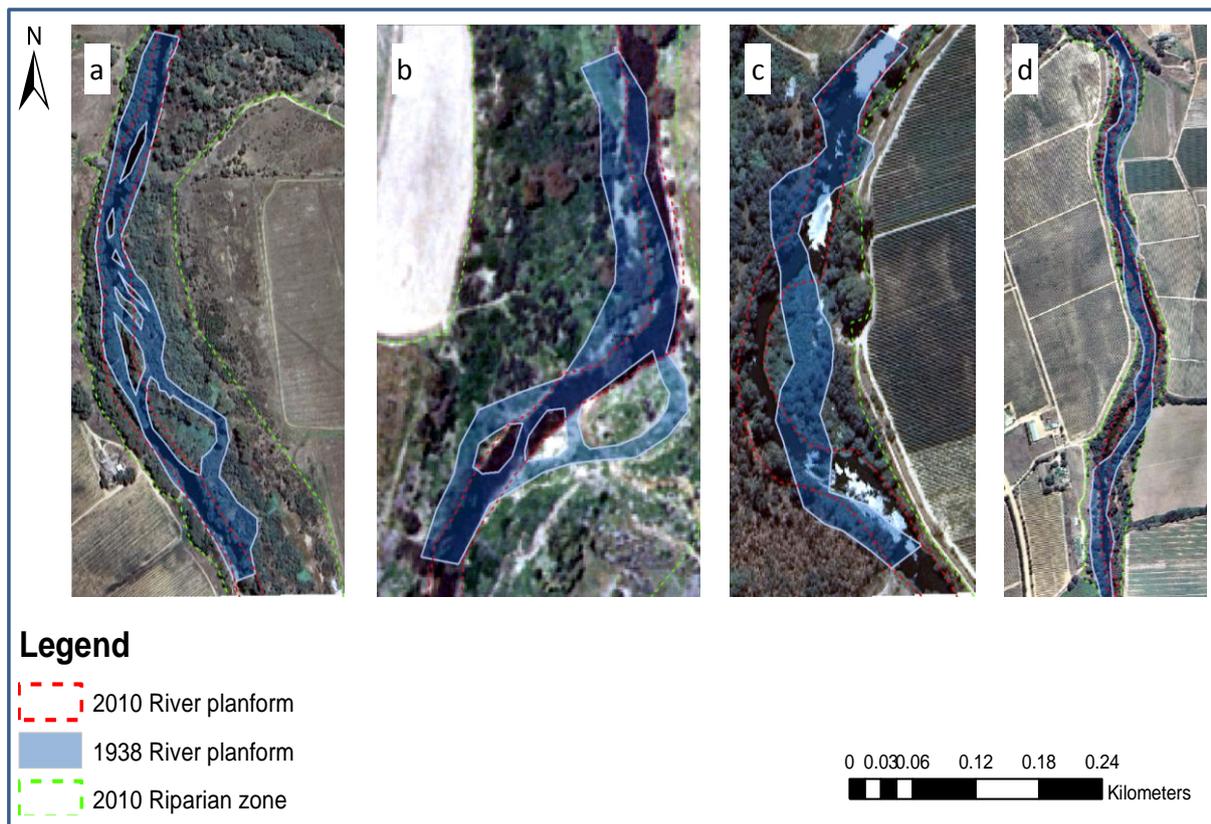


Fig. 2.4. a) and b) present evidence of channel narrowing as the river channel was wider and braided in 1938. c) and d) show evidence of the channel changing path by 2010. All islands and sand bars, and as well as the places where the river used to pass through in 1938 are now occupied by thick stands of *Eucalyptus camaldulensis*. The red dotted line shows the river course in 2010, while the blue transparent polygons show the channel pattern and course in 1938. The green dotted line shows the riparian zone in 2010 along the Berg River, Western Cape, South Africa

The 1938 river channel became narrower by up to 6.8 m by 2010, and parts of the channel that were bare are now occupied by *E. camaldulensis* (Figure 2.4). Fig. 2.4a and b show evidence that *Eucalyptus* is occupying previously bare in-channel islands and sand bars. Fig. 2.4c and d show evidence of the channel changing course between 1938 and 2010.

### 2.3.4 Typical cross-sectional changes

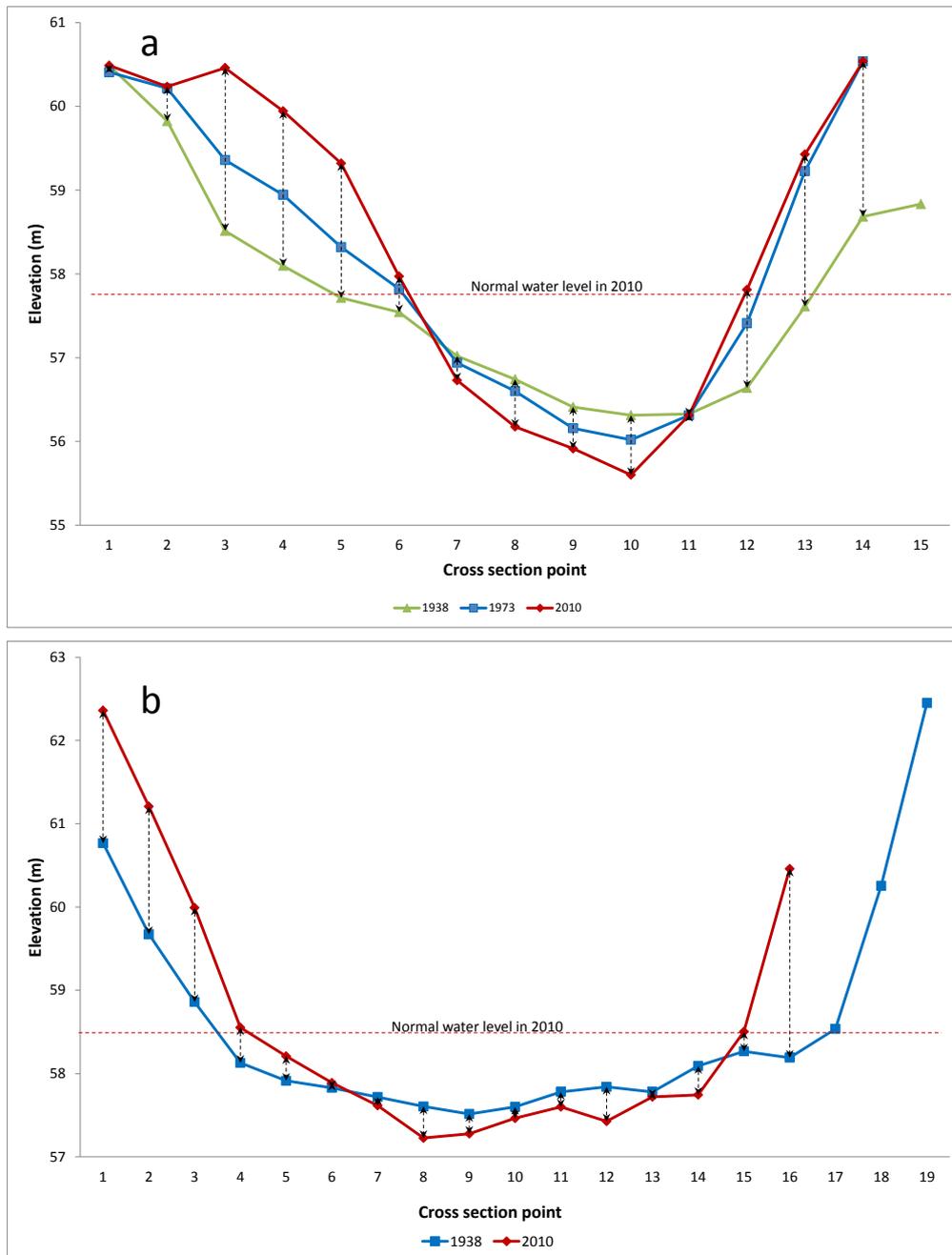


Fig. 2.5. a) Variations in cross sectional profile at a currently invaded site from 1938, 1973 and 2010; b) variation in cross sectional profile at a currently invaded site between 1938 and 2010 along the Berg River, Western Cape, South Africa. The red line shows a cross-section that was surveyed in 2010, and the blue and the green show cross-sections extracted from 1973 and 1938 DEMs. Fig b does not show a profile for 1973 because the DEM was not accurate enough. The red dotted line shows water level at the time of the survey in 2010.

The cross sections from these two sites show that the cross sections became narrower (Fig. 2.5 a and b) and the channel banks became steeper (Fig. 2.5a).

In 1938, on average the riparian zone was significantly wider than that of 2010 ( $p < 0.01$ ) (Fig. 2.6).

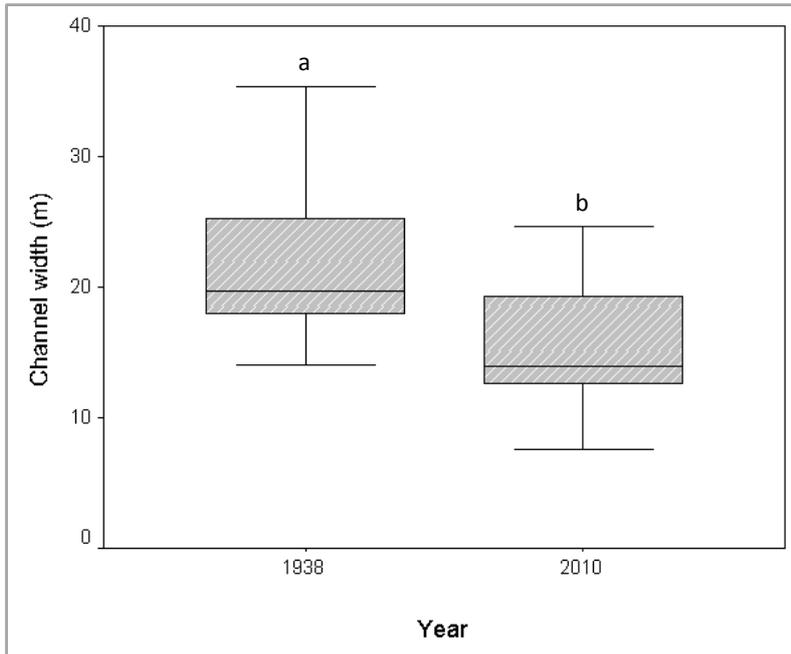


Fig. 2.6. Average channel width in 1938 and 2010 along the Berg River, Western Cape, South Africa. Significant differences were tested using a paired t-test since data were normally distributed, and the letters a and b show that the 1938 channel width was significantly higher in 1938.

### 2.3.5 Precipitation and flow variation through time

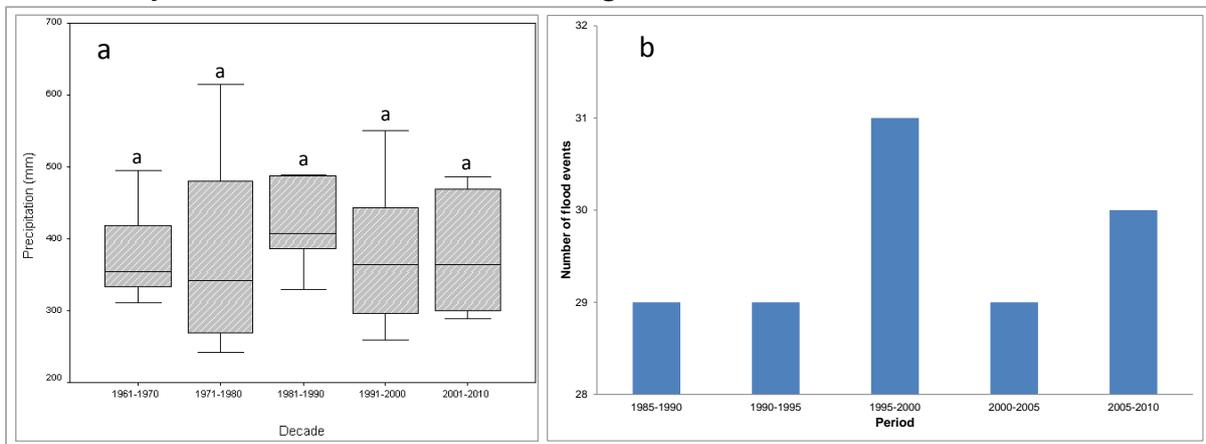


Fig. 2.7. a) Interdecadal variability in rainfall from 1961-2010; The whiskers of each bar represent the non-outlier range, the bar represents the 25<sup>th</sup> to the 75<sup>th</sup> percentile and horizontal line within the bar represents the mean. b) Number of flood events within 5 year periods (flood described as any flow event that exceeds the rating capacity of the flow measurement structure). There were no significant differences between decadal pairs of precipitation and flood events did not increase considerably over time.

Trend analysis using Mann-Kendall's trend test did not detect any significant trends in both precipitation (Fig 2.7a) and flood events data (Fig 2.7b) ( $p > 0.05$ ). Interdecadal

variability analysis on precipitation data showed no significant differences between all pairs of decades ( $p > 0.05$ ).

## 2.4 Discussion

### 2.4.1 Spatial and temporal trends of the riparian zone

Over the four time steps, the riparian zone has been changing at every time step, widening in some parts and narrowing in others. In all areas where decreases in the riparian zone were detected, the land has been confirmed (through satellite imagery and ground truthing) to have been cleared for agricultural purposes. Agriculture is a key control of riparian zone dynamics along the Berg River, and has resulted in a net decrease of about 13.5% in area over 70 years. The widening of the riparian zone (i.e. the expansion of woody cover) can be attributed to *E. camaldulensis* invasion as these areas were confirmed by ground truthing to have dense stands of eucalypts. However, the lateral expansion of *E. camaldulensis* invasion is limited by the encroachment of agricultural land. For the Berg River, as with rivers in many parts of the world (Stromberg, 2001), conversion to cropland has been the primary cause of riparian loss and degradation. As in the findings of Birken and Cooper (2006) in their study of *Tamarix* invasions in riparian zones (occurring in a pristine landscape) in the southwestern United States, it would have been expected that *E. camaldulensis* invasions would result in widening of the riparian zone.

### 2.4.2 Spatial and temporal dynamics in the river channel

Our first hypothesis that invasion by large *Eucalyptus* trees will result in river bank stabilization and consequent narrowing of the channel and channel incision was supported. Over the past 70 years, several changes have happened to the river channel. There has been consistent channel narrowing and this result concurs with that of Osterkamp and Hupp (2010) and Cadol et al. (2011). Among the factors that can explain this, are climate (hydrology and rainfall), human activities (flow regulation and abstraction) and changes in vegetation (invasion) (Birken and Cooper, 2006; Cadol et al., 2011). Unlike in other studies where climate and flow regulation were confounding factors (Birken and Cooper, 2006), these appeared to have little influence since no significant trends were detected. This suggests that changes in channel morphology are associated to changes in vegetation structure, composition and function. Native vegetation of the Berg River includes shrubs and relatively small trees, which have been replaced by a large tree, *E. camaldulensis*. The replacement a multi-structural vegetation assemblage by a large *Eucalyptus* tree monoculture resulted in river bank stabilization and consequent

narrowing of the channel. Such changes have been reported to cause alterations in river morphology (Hereford, 1984; Rowntree, 1991). *Eucalyptus camaldulensis* has been reported to have an extensive root system that reinforces riverbanks in Australia (Abernethy and Rutherford, 2001). Similar observations have been made with *Tamarix* invasions of riparian ecosystems in the western United States (Birken and Cooper, 2006; Cadol et al., 2011). Narrowed reaches often incise river channel bed since lateral fluvial action is restricted by vegetation (Cadol et al., 2011). It was difficult to measure historical channel incision in the Berg River because it is perennial, so the water surface prevents modeling of channel bed from aerial photographs. In sites where narrowing had occurred channel bed incision has been observed (Cadol et al., 2011), meaning that the erosive power of the river gets redirected to concentrate vertically as opposed to being distributed vertically and laterally. The result is narrow deep channels such as in the Berg River (average bankfull width of 14m and up to 4 m deep) in several locations that were heavily invaded. In heavily invaded sites, the river bed was rocky as opposed to sandy alluvium in the river beds of uninvaded sites, and this is evidence for river bed incision in the former.

*Eucalyptus* invasion can have two contrasting effects on the river banks: The steep river banks expose tall *Eucalyptus* trees to falling; especially those hanging precariously on the steep riverbanks get toppled through fluvial scour and undercutting causing bank collapse (Rowntree, 1991). In such cases, these fallen trees obstruct the channel, resulting in temporal lateral erosion (Keller and Swanson, 1979). This kind of disturbance creates opportunities for seed deposition and recruitment, especially of *Eucalyptus*. *Eucalypts* are more likely to fall onto the channel in this way due to their weight and height (average – 35m) compared to native trees (average 15m) (F. Tererai, unpubl. data). The second effect that *Eucalyptus* has is to stabilize the river bank. As a result river banks of the Berg River drop steeply into the water, with no wet zone. This reduces the capacity of river banks as native seed reservoirs, thereby depleting the soil-stored seed banks (Henderson and Wells, 1986; Rowntree, 1991). These effects distinguish *Eucalyptus* as tall tree invaders from native vegetation (shrubs and small trees), although in rare occasions native trees can have similar effects.

In the process of narrowing, river landforms such as sand bars and islands have disappeared, and in some cases the channel has changed its course. The narrowing of the river channel could have different causes (e.g. expansion of agricultural lands), but I assume that in this case *Eucalyptus* invasion has caused the changes because all formerly bare in-stream sand deposits such as islands and bars are now covered by dense eucalypt stands. Spontaneous vegetation establishment has been found to favour these in-stream landforms (Cooper et al., 2003; Kondolf et al., 2007; Osterkamp and Hupp, 2010). The observed changes in channel morphology appear to be vegetation

driven, as dense *Eucalyptus* stands tend to have established on areas formally occupied by the islands, sand bars or the channel itself. The mechanism of channel narrowing could have been accretion (Carter and Rogers, 1989; Birken and Cooper, 2006) as evidenced by bank advancement at sites that were heavily invaded. Similar trends have been observed with the establishment of other invasive trees such as *Tamarix* in western United States (Birken and Cooper, 2006; Cadol et al., 2011).

## 2.5 Implications for restoration and research need

The invasion of *E. camaldulensis* for c. 50 years is associated with changes in the riparian zone environment along the upper Berg River. The stabilization and narrowing of the river channel resulting in steep river banks has been reported to cause a reduction in the seed storage capacity of the river banks elsewhere (Henderson and Wells, 1986; Sandercock et al., 2007). This reduces the capacity of the soil-stored seed bank to reinitiate autogenic native vegetation recovery after clearing of the invader (Henderson and Wells, 1986). If removal of *Eucalyptus* is adopted as a management option, this may promote bank destabilization and lateral erosion resulting in channel widening in some areas (Beschta and Ripple, 2012). This kind of disturbance promotes the spontaneous recruitment of invasive alien plants, especially *Eucalyptus* and *Acacia mearnsii* which are abundant in the soil-stored seed bank (F. Tererai, unpubl. data).

Currently, historical photos are the most commonly used source of data for tracking invasion over time and associated changes in the environment (Mast et al., 1997). There is need for further research to establish the actual contribution of agricultural activities in shaping river morphometry. There is also need for ongoing field monitoring of geomorphological changes over time as these are often constrained by insufficient spatial and temporal resolutions. The river channel is densely invaded such that terrain modeling for the purposes of reconstructing historical changes is difficult. The current results are only indicative of change, but accurate quantification of the change requires long-term field measurements and monitoring.

## 2.6 Conclusions

In contrast to the other literature on the impacts of invasive alien trees on riparian geomorphology, my study was conducted on a relatively small perennial river that is densely invaded with a large tree right to the water edge. Importantly, the river flows through a landscape profoundly influenced by agriculture. The study aimed to investigate

the changes in riparian geomorphology associated with invasive *E. camaldulensis* and with agricultural landuse to test whether it was possible to distinguish between the effects of invasion and those of human activity. It was possible to separate the effects of climate from the combined effect of invasion and human activity in this study. I attributed the changes detected in the riparian zone to the invasion and human activity because hydrometeorological data showed no significant trends. Agriculture appears to have significant influence on the riparian zone, especially the spatial extent of the riparian area. There was some evidence that the detected changes in channel morphology were related to invasion of *E. camaldulensis*. I could not establish whether agriculture co-influenced channel morphology with invasion and this requires further research. Findings of this study supported all three proposed hypothesis.

## **2.7 Acknowledgements**

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### **Chapter 3: *Eucalyptus* invasions in riparian forests: floristic diversity, stand structure and compositional changes in native vegetation**

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#### **Abstract**

Effects of alien plant invaders on native ecosystems are widely acknowledged, although the evidence is sometimes speculative, especially in riparian zones. We examined the changes in floristic diversity, stand structure and composition of resident species associated with invasions of *Eucalyptus camaldulensis* in riparian zones of the Western Cape, South Africa. Using a gradient comparative approach, we compared the richness, diversity ( $H'$ ) and evenness ( $J$ ) of resident vegetation in a riparian forest under varying levels of *E. camaldulensis* percentage cover. We found that species richness, diversity and structural attributes (e.g. height, relative cover and mean basal diameter) of native species decreased consistently along the invasion gradient. However, evenness did not change significantly with increasing *Eucalyptus* invasion. *Eucalyptus camaldulensis* invasion was associated with changes in native plant species composition; although some native species occurred in alien invaded sites, they were more abundant in uninvaded sites. Our results indicate that the invasion of *E. camaldulensis* may cause alterations to native plant communities. Further experimental work is needed to determine the mechanisms responsible for changes attributed to *Eucalyptus* invasion.

**Key words:** Biological invasions; Community-level effects; Fynbos biome; Invasive alien plants; Management; Mediterranean-type ecosystems

### 3.1 Introduction

Many invasive species change the composition, structure and functioning of native ecosystems (Vitousek et al., 1996; Hejda and Pyšek, 2006; Truscott et al., 2008; Gooden et al., 2009), and some cause significant declines in native species diversity (Davis, 2003; Gaertner et al., 2009; Vilà et al., 2011). In extreme cases, invasions may transform the character or form of entire landscapes (Busch and Smith, 1995) through dominance, superior competitive ability and the modification of ecosystems (Hejda and Pyšek, 2006).

Riparian zones, the fringes of rivers or streams, form the interface between aquatic and terrestrial ecosystems and are often characterised by a distinctive flora that differs in structure and function from adjacent terrestrial ecosystems (Naiman and Decamps, 1997). The flora of these ecosystems provide important functions (e.g. stabilizing stream banks, controlling nutrients, and providing habitat) and services such as flood mitigation and ground water recharge (Barling and Moore, 1994; Hood and Naiman, 2000; Hooper et al., 2005). However, riparian forests are highly prone to invasion by alien plants, largely because of their dynamic hydrology and because rivers disperse propagules (Pyšek and Prach, 1993; Planty-Tabacchi et al., 1996; Naiman and Decamps, 1997; Hulme and Bremner, 2006; Foxcroft et al., 2007). Furthermore, riparian zones are associated with intense anthropogenic activity which promotes proliferation of invasive species driving drastic ecosystem changes (Hejda and Pyšek, 2006; Jäger et al., 2007; Meek et al., 2010). Common invasive alien tree invaders of riparian forests include *Tamarix* spp. in the south-western USA and *Acacia* spp. and *Eucalyptus camaldulensis* Dehn. in South Africa (Galatowitsch and Richardson, 2005; Nagler et al., 2011).

The potential impacts of invasive alien plants are widely acknowledged worldwide, but detailed quantitative assessments of impacts are rare (Hulme, 2003; Hulme and Bremner, 2006; Jäger et al., 2007; Pyšek and Richardson, 2010). Ecosystem-level impacts such as nutrient enrichment (Ehrenfeld, 2003; Gaertner et al., 2011), effects on hydrology (Le Maitre et al., 1996; Scott and Lesch, 1997) and changes in fire regimes (Brooks et al., 2004) are well documented for some woody invasive species, but studies measuring community-level impacts, for example, through suppression of native plants due to the dominance of invasive alien species are scarce (Tickner et al., 2001; Hejda et al., 2009). The lack of detailed assessments of impacts has in many cases thwarted the implementation of effective management strategies for invasive alien plants (Starfinger et al., 2003).

In South Africa, *Eucalyptus camaldulensis* invasions have been recognized as a problem (Forsyth et al., 2004), but our understanding of the extent and impact of these invasions is limited. No research has been done to determine community-level effects of *E. camaldulensis* in riparian forest ecosystems, yet, irrespective of whether they are

invasive or not, eucalypts have attracted more criticism for environmental impacts than most other widely planted alien species (Evans, 1992; Doughty, 2000; Tyynelä, 2001; Rejmánek and Richardson, 2011). *Eucalyptus camaldulensis* is widespread in riparian zones of South Africa (Forsyth et al., 2004). However, the evidence for impacts is often anecdotal, controversial and context dependent (Rejmánek and Richardson, 2011).

Methodological constraints have in part been cited as limiting community level research (Hejda and Pyšek, 2006). Several studies have examined community and ecosystem-level impacts using observational approaches (Levine et al., 2003; Hulme and Bremner, 2006; Jäger et al., 2007; Truscott et al., 2008), but recent studies present an alternative approach to quantifying impacts of invasive alien plants. The alternative approach involves the experimental introduction or removal of invasive species. Experimental introductions into semi-natural habitats are not encouraged (Hejda and Pyšek, 2006; Hulme and Bremner, 2006) and are often inappropriate or prohibited in ecologically sensitive areas (Truscott et al., 2008). Removal is mainly constrained by practicality, cost and time, especially with large tree invaders (Starfinger et al., 2003; Shafroth and Briggs, 2008; Davis et al., 2011).

In this study, we seek to determine changes in native vegetation communities associated with the invasion of *E. camaldulensis* in riparian zones by comparing “uninvaded” sites with sites under varying levels of invader canopy cover. More specifically, we ask the questions: (1) Is invasion associated with changes in diversity, structure and composition of riparian resident communities? (2) Does a gradient sampling comparative approach yield satisfactory results in assessing alterations in native vegetation communities associated to *E. camaldulensis*? The results of our study are envisaged to inform efforts to manage invasive alien trees threatening riparian forests and to guide future research.

## **3.2 Materials and methods**

### **3.2.1. Study area**

The Berg River is located north-east of Cape Town in the Western Cape Province of South Africa (Fig. 3.1). It is approximately 294 km long from source to mouth, with a catchment area of 7715 km<sup>2</sup>. The study was conducted along the Berg River main stem in the upper catchment, between the towns of Hermon and Franschoek - a distance of about 92 km (Fig. 3.1). The study area was chosen because it is a good example of old invasions (c. 50 years) (Geldenhuys, 2008) in which impact can be reasonably assessed

and associated with *E. camaldulensis* invasion with relatively high levels of confidence (Ruwanza et al., 2012).

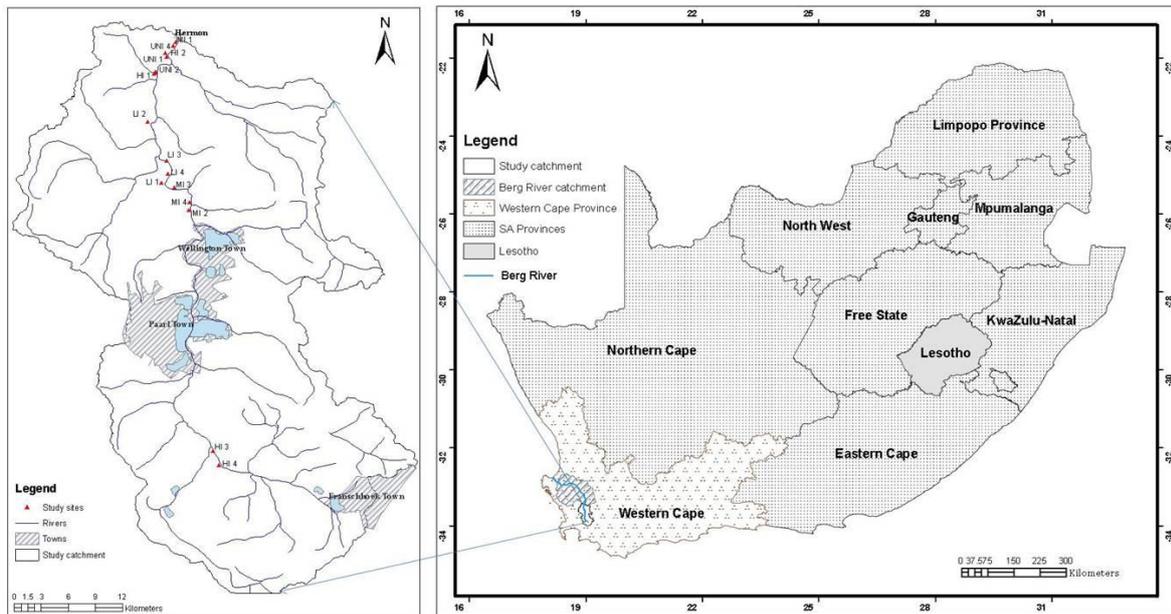


Fig. 3.1. Distribution of study sites (UNI – Uninvaded; LI – Light invasion; MI – Moderate invasion; HI – Heavy invasion) along the Berg River stretch between the towns of Hermon and Franschhoek; Western Cape, South Africa.

The study area falls within the Mediterranean-climate region of South Africa which has warm dry summers and cool wet winters. The average rainfall within the Berg river catchment is about 550 mm. The average temperature minima and maxima are 11°C and 22°C respectively. Altitude ranges from 247 m at Franschhoek to 66m at Hermon. The Berg is a perennial river with high flows and frequent flooding in winter (May to September).

The geology of the study catchment area is dominated by sandstone and quartzites of the Cape Supergroup which have typically nutrient-poor lithologies. The whole river stretch has been invaded by alien trees, mainly *E. camaldulensis* (which has been present for at least 50 years), but was interspaced with individuals of *Acacia mearnsii* and *Populus* spp. (poplars) in some locations. Native woody riparian vegetation (dominated by the trees and shrubs *Diospyros glabra*, *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, and *Searsia angustifolia*) now occurs mainly in small pockets or isolated individuals within *E. camaldulensis* stands.

About 65% of the Berg river catchment is under agriculture, mainly vineyards, fruit orchards and wheat fields (Geldenhuys, 2008). This may have influenced invasion dynamics through nutrient runoff into the riparian zone. The Berg River hydrological regime is regulated by irrigation flow abstraction and dams (the most important being the Berg Dam in the headwaters which was built in 2007) which may have an influence on

proliferation of invasive plants (Bacon et al., 1993; Busch and Smith, 1995). Other major agents of human ecological disturbance are clearing or harvesting of *E. camaldulensis* and *A. mearnsii*; while natural disturbance results from flooding, erosion and deposition. Fire seldom penetrates the riparian zone in the study area.

### **3.2.2. Study species**

*Eucalyptus camaldulensis* Dehn. has one of the widest natural distributions of any Australian tree species. It is a riparian species occurring in most climatic zones and the majority of river systems across mainland Australia (McDonald et al., 2009). Like many of the c. 800 eucalypt species (taxa in the genera *Angophora*, *Corymbia* and *Eucalyptus*), *E. camaldulensis* has been widely planted in many parts of the world outside its native range (Rejmánek and Richardson, 2011). Besides pines, eucalypts are the most commonly and widely cultivated exotic trees because of their tolerance of a wide range of conditions (Mensforth et al., 1994; Tyynelä, 2001; Forsyth et al., 2004; Butcher et al., 2009). *Eucalyptus camaldulensis* favours areas of deposition along watercourses in its native range (Mensforth et al., 1994; Butcher et al., 2009; McDonald et al., 2009), and outside the native range where it has become a successful invader (Forsyth et al., 2004; Rejmánek and Richardson, 2011). Eucalypts were introduced to South Africa in the late 19<sup>th</sup> century for several purposes including timber, fuelwood, shelterbelts; they are also valuable sources of nectar and pollen for the apiculture industry (Tyynelä, 2001; Forsyth et al., 2004; Rejmánek and Richardson, 2011). *Eucalyptus camaldulensis* is now considered invasive in many parts of South Africa, and self-sown stands are especially widespread and dense in riparian zones of the Western Cape province (Forsyth et al., 2004).

### **3.2.3. Study design**

Study sites were established along a continuum of invasion (hereafter invasion gradient), and were grouped into four “invasion condition classes”, each with four replicates (n=16 sites): “uninvaded” (0% – 24% cover of *E. camaldulensis*), “light” (25% – 49% cover), “moderate” (50% – 74%), and “heavy” (≥75% canopy cover). Most of the invaded sites were predominantly *Eucalyptus* except in a few unavoidable cases where isolated individuals of *Acacia mearnsii*, an invasive tree native to Australia, occurred. Sites measured 10 m along the river and spanning the whole riparian zone, with contiguous plots in 5 m widths perpendicular to the river. The sites were randomly and longitudinally located on both sides of the river. Proximity of invaded and uninvaded sites ensured that sites had similar conditions (soil type, nutrient levels, pH, elevation, precipitation, temperature) with reasonable level of confidence. In two of the “uninvaded” sites a few

individuals of *E. camaldulensis* occurred as no suitable sites totally free of this species could be found. Many studies have found that “pristine” (i.e., non-invaded and non-degraded) reference sites in riparian ecosystems are extremely rare or simply do not exist (Rosgen 1994; Busch and Smith, 1995; Prins et al., 2005; Richardson et al., 2007; Brewer and Menzel, 2008). However, this was envisaged not to exert significant impact on the species diversity of resident vegetation because most invasive plant species have little effect on native vegetation composition and structure when they occur at very low densities (Hejda and Pyšek, 2006; Catford et al., 2012).

#### **3.2.4. Data collection**

To examine species composition across a gradient of *E. camaldulensis* invasion, we recorded species (native and alien) percentage cover (in four height classes), counts, height (average and maximum), and diameter (basal and breast height) data in 10 m x 5 m plots from the 16 sites in the spring season (September and October) of 2010. We also recorded ground cover in terms of litter, bare soil, and rock material within the same plots. Plot numbers varied from four to nine per site depending on the width of the riparian zone ( $n = 99$ ). Voucher specimens were collected for species that could not be identified in the field and were sent to a local herbarium for identification. Follow-up surveys were conducted in spring season of 2011 to capture plants that may have been missed.

#### **3.2.5. Statistical analysis**

All analysis was based on number of plots at each in each invasion condition, that is uninvaded (30), light (19), moderate (25) and heavy (25). Species richness ( $S$ ), Shannon-Wiener's diversity index ( $H'$ ), and species evenness ( $J$ ) were used to measure changes in community characteristics associated with invasion. Evenness was calculated as  $H'/\ln S$ , where  $S$  is the number of species (Kent and Coker, 2002). Differences among the four invasion conditions were tested with Kruskal-Wallis ANOVA and the respective pairs of uninvaded and invaded sites were tested with Mann-Whitney U test, both of which are non-parametric statistics as the data exhibited strong deviations from the normal distribution. The difference in total number of native species recorded in all plots of reference and invaded sites was used as an indicator of the change associated with invasion at each level of *E. camaldulensis* cover, at the river segment scale. *Eucalyptus camaldulensis* cover was used to assess changes associated with the invader on native species diversity at the plot scale. Density of each plant species was calculated as mean number of individuals ( $N$ ) per unit area (plot), and projected to number of individuals per hectare (ha).

To evaluate the differences in species composition, permutational multivariate analysis of variance (PERMANOVA) and direct gradient analysis were used. Based on the length of the main gradient in the data, estimated by use of indirect gradient analysis (DCA) (Table 3.2), either canonical correspondence analysis (CCA) or redundancy analysis (RDA) was used. The Monte-Carlo permutation tests (499 permutations) were used to determine the significance of the invasion gradients (measured as percentage aerial cover of *E. camaldulensis*). Data were tested for normality, transformed accordingly and split into: i) major species (species with at least 1% cover in one treatment – 47 species); ii) native species; iii) alien species; iv) tree and shrub species; and v) other growth forms (forbs, graminoids, geophytes, and vines) in order to clarify observed differences. Major species data were analysed using a two-step approach (Hejda and Pyšek, 2006): (i) presence/absence data were used to test for compositional changes associated with invasion; (ii) species cover (%) was used to ascertain the shifts in dominance of species associated with invasion (Hejda and Pyšek, 2006). Similarity percentages analysis (SIMPER) was used to identify species contributing strongly to within group similarities, as well as dissimilarities among invasion categories (Gooden et al., 2009). Richness and diversity multivariate statistics were computed using multivariate ecological research software, Primer (version 6, PRIMER-E Ltd, Plymouth, UK), while ordination analysis was done in multivariate ecological software Canoco 4.5 (Lepš and Šmilauer, 2003).

Since the presence and abundance of *E. camaldulensis* was the primary distinguishing factor between uninvaded and invaded sites, this species was excluded from the input data for analysis of species richness and all multivariate tests (Hejda and Pyšek, 2006; Jäger et al., 2007).

### **3.3 Results**

#### **3.3.1 Floristic diversity**

##### *Species richness*

A total of 75 species from 62 genera and 36 families were recorded in all sites along the invasion gradient. Of the 75 species, 32 were native (including 56.3% trees and shrubs, 25% geophytes and 6.3% grasses), while 43 were alien plant species (including 55.8% forbs, 16.3% grasses, and 11.6% trees and shrubs). Total number of native species recorded in uninvaded (21), lightly (19), moderately (15) and heavily (13) invaded sites decreased consistently. The low invasion plots had significantly higher species richness than the high invasion plots ( $Z = -3.38$ ;  $df = 55$   $p < 0.001$ ). Differences in total plant species richness among plots in uninvaded, lightly, moderately and heavily invaded sites

were statistically significant (Kruskal-Wallis ANOVA:  $H_{3,99} = 18.51$ ,  $p < 0.001$ ). However, pair-wise comparisons revealed that, only uninvaded and heavily invaded plots exhibit significant differences in total plant species richness ( $Z = -3.38$ ,  $df = 55$ ,  $p < 0.001$ ) (Fig. 3.2).

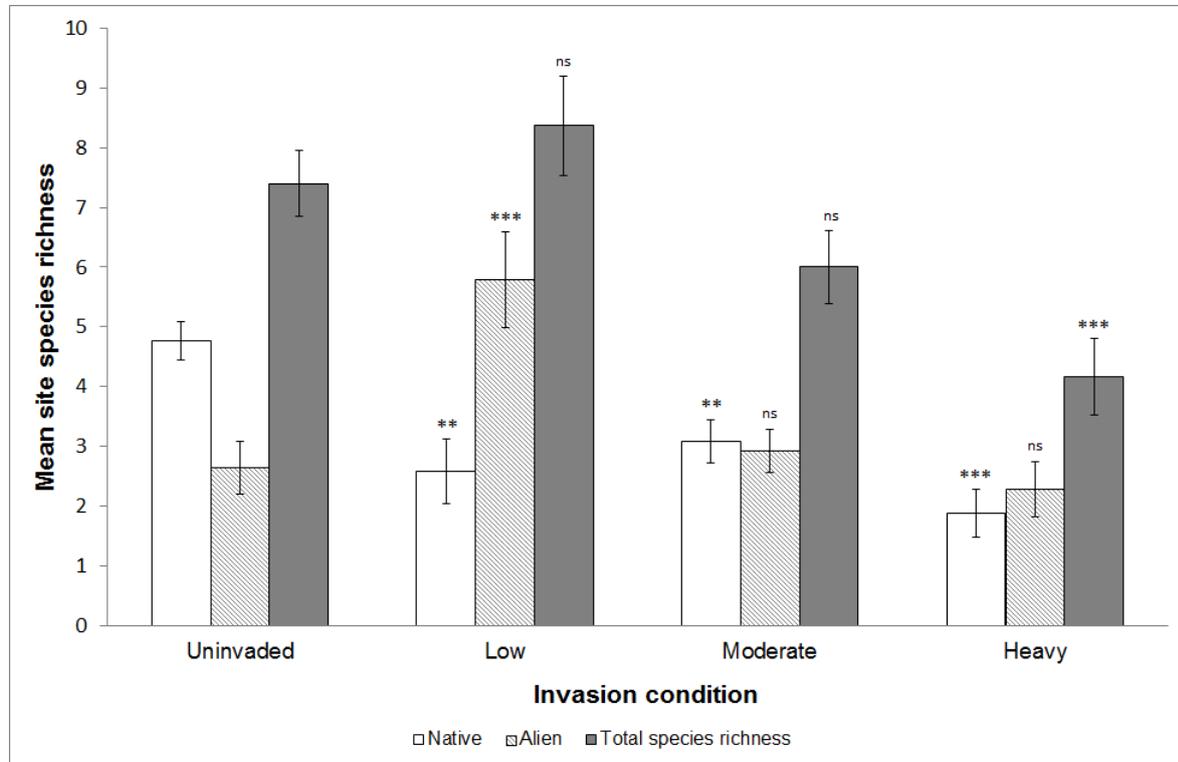


Fig. 3.2. Native and alien plant species richness (mean  $\pm$  SE) of plots in uninvaded ( $n = 30$ ) sites compared to plots in lightly ( $n=19$ ), moderately ( $n=25$ ) and heavily ( $n=25$ ) invaded sites along the Berg River, Western Cape province, South Africa (significant differences between uninvaded and, lightly, moderately and heavily invaded sites were tested by the non-parametric Mann Whitney U test, since all data were not normally distributed). The measure of variance is the standard error. Significance level \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ , ns – not significant.

There was a significant difference in native species richness among the four invasion conditions (Kruskal-Wallis ANOVA:  $H_{3,99} = 27.41$ ,  $p < 0.001$ ). Pair-wise comparisons showed that there is a significant decline in native species richness for low and moderate invasion and a greater decline for heavy invasion (Fig. 3.2). There were also significant differences in alien species richness among the four invasion conditions ( $H_{3,99} = 15.48$ ,  $p < 0.01$ ). Pairwise comparisons for alien species richness between uninvaded sites and the other invasion conditions showed that, only the lightly invaded plots exhibited significantly higher mean alien species richness ( $Z = -3.23$ ,  $df = 44$ ,  $p < 0.001$ ) (Fig. 3.2).

#### *Diversity and evenness*

Differences in diversity among uninvaded, lightly, moderately and heavily invaded plots were statistically significant ( $H_{(3,99)} = 9.97$ ,  $p = 0.02$ ). However, the difference in species

evenness among these plots was not statistically significant ( $H_{3,99} = 1.83$ ,  $p = 0.61$ ). While diversity of both native and alien species varied significantly ( $H_{3,99} = 20.06$ ,  $p < 0.001$  and  $H_{3,99} = 11.77$ ,  $p < 0.01$  respectively) among invasion conditions, evenness did not vary significantly ( $H_{3,99} = 1.12$ ,  $p = 0.77$  and  $H_{3,99} = 1.69$ ,  $p = 0.64$  respectively).

Uninvaded plots exhibited significantly higher values of Shannon diversity index  $H'$  for native species when compared to the lightly ( $df = 49$ ), moderately ( $df = 55$ ) and heavily ( $df = 55$ ) invaded plots (Table 3.1). Native and alien mean species evenness was  $0.57 \pm 0.04SD$  and  $0.52 \pm 0.06SD$  respectively, and differences between the reference (uninvaded) sites and, lightly, moderately and heavily invaded sites were not statistically significant ( $p > 0.05$ ) (Table 3.1).

Table 3.1. Native and alien species diversity ( $H'$ ) and evenness ( $J$ ) based on species abundance (% cover) data in all 10 m x 5 m plots within an invasion gradient from uninvaded, lightly, moderately and heavily invaded sites along the Berg River, Western Cape, South Africa (significant differences between uninvaded and, lightly, moderately and heavily invaded sites were tested by the non-parametric Mann Whitney U test, since all data were not normally distributed). The measure of variance is the standard error. Significance level \*  $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; and \*\*\*  $p \leq 0.001$ ; ns – not significant.

Index	Uninvaded		Light		Moderate		Heavy	
	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>
Shannon Index ( $H'$ )	0.83±0.07	0.40±0.09	0.47±0.12	0.83±0.11	0.52±0.09	0.44±0.10	0.30±0.09	0.35±0.09
Mann-Whitney U test value			-2.66**	-2.78**	-2.49*	-0.67ns	-4.32***	-0.36ns
Evenness ( $J$ )	0.55±0.04	0.52±0.07	0.60±0.07	0.60±0.06	0.52±0.06	0.46±0.08	0.60±0.08	0.50±0.08
Mann-Whitney U test value			-0.80ns	-0.40ns	-0.24ns	-0.74ns	-0.52ns	-0.08ns

Table 3.2. Results of ordination analysis performed on presence/absence and species cover (%) data of major, native, alien, tree and shrub, and forb/vine/graminoid/geophyte species along the Berg River, Western Cape, South Africa

Data set	Data	Analysis	Cumulative explained variance		f-ratio	p-value	Length of gradient
			1 <sup>st</sup> axis	2 <sup>nd</sup> axis			
Major species	Presence/absence	CCA	42	66.7	1.69	<0.001	4.08
Major species	Cover	CCA	38	62.4	1.96	<0.01	5.23
Natives	Cover	RDA	47.7	78.3	1.41	0.04	0
Aliens	Cover	RDA	32.7	63.9	1.31	0.11	2.17
Tree and Shrub	Cover	CCA	43.2	71.4	1.91	<0.01	4.92

Forbs, vines and graminoids	Cover	CCA	38.1	73.6	1.98	<0.001	5.33
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Percentages of variance explained by the first two canonical axis, and the statistics of Monte-Carlo permutation tests (F,p) are shown. The selection of the method used was based on the length of the gradient of the first two ordination axis as obtained by the DCA analysis. Note that *Eucalyptus camaldulensis* was excluded from this analysis.

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### 3.3.2. Stand structure

The height of native tree and shrub species consistently decreased with increasing height of *E. camaldulensis* (Fig. 3.3a). There were no other alien trees or shrub species in uninvaded sites. Height of other alien tree and shrub species (including *Acacia mearnsii*) among lightly, moderately and heavily invaded sites did not vary significantly (Fig. 3.3a).

Relative cover of *E. camaldulensis* and that of native species varied significantly along the invasion gradient ( $H_{3,55} = 25.39$ ,  $p < 0.001$ ) and ( $H_{3,138} = 8.16$ ,  $p = 0.04$ ), respectively (Fig. 3.3b). Plant species density per hectare did not vary significantly for either native species, *E. camaldulensis* or other alien tree and shrub species (Fig. 3.3c).

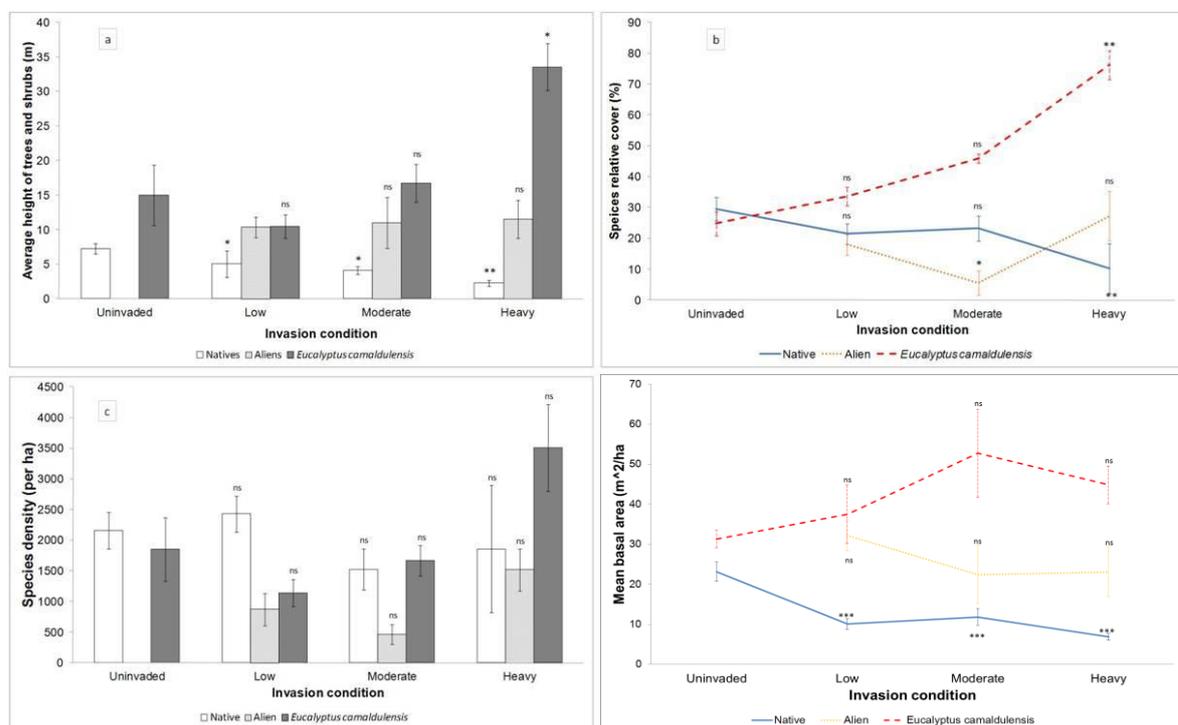


Fig. 3.3. (a) Mean height of trees and shrubs >1.3 m; (b) Species relative cover (%); (c) Mean density of trees and shrubs >2 m; and (d). Mean area (measured at 30 cm above ground and converted to basal area) of alien and native plants >2 m in height. All pairwise comparisons are made against the uninvaded (reference) plots observed in the riparian zone of the Berg River of Western Cape, South Africa. significant differences between uninvaded and, lightly, moderately and heavily invaded sites were tested by the non-parametric Mann Whitney U test, since all data were not normally distributed. The measure of variance is the standard error. Significance level \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ , ns – not significant.

There were no significant differences in basal area of *E. camaldulensis* along the invasion gradient ( $H_{3,55} = 1.02$ ,  $p = 0.8$ ). Pairwise comparisons also showed no significant differences between uninvaded, and lightly, moderately and heavily invaded sites ( $p > 0.05$ ) (Fig. 3.3d) in terms of *E. camaldulensis* basal diameter. However, basal diameter of native

tree and shrub plant species decreased significantly as basal diameter of eucalypts increased (Fig. 3.3d) along the invasion gradient ( $H_{3,138} = 19.47$ ,  $p = 0$ ).

### 3.3.3 Relationship between *E. camaldulensis* and, native and alien plant species characteristics

Correlative assessments revealed that total species richness, total diversity ( $H'$ ), and richness and diversity of native plant species significantly decreased with increasing *E. camaldulensis* relative cover ( $p < 0.05$ ) (Fig. 3.4). There was, however, no significant correlation between *E. camaldulensis* density and native plant species density per ha (Spearman  $r = -0.21$ ;  $p = 0.12$ ). This means that the aerial cover of *E. camaldulensis* is more influential than its abundance (individual count ( $N$ ) per unit area) in reducing abundance of other plant species (Pearson  $r = -0.52$ ;  $p < 0.001$ ).

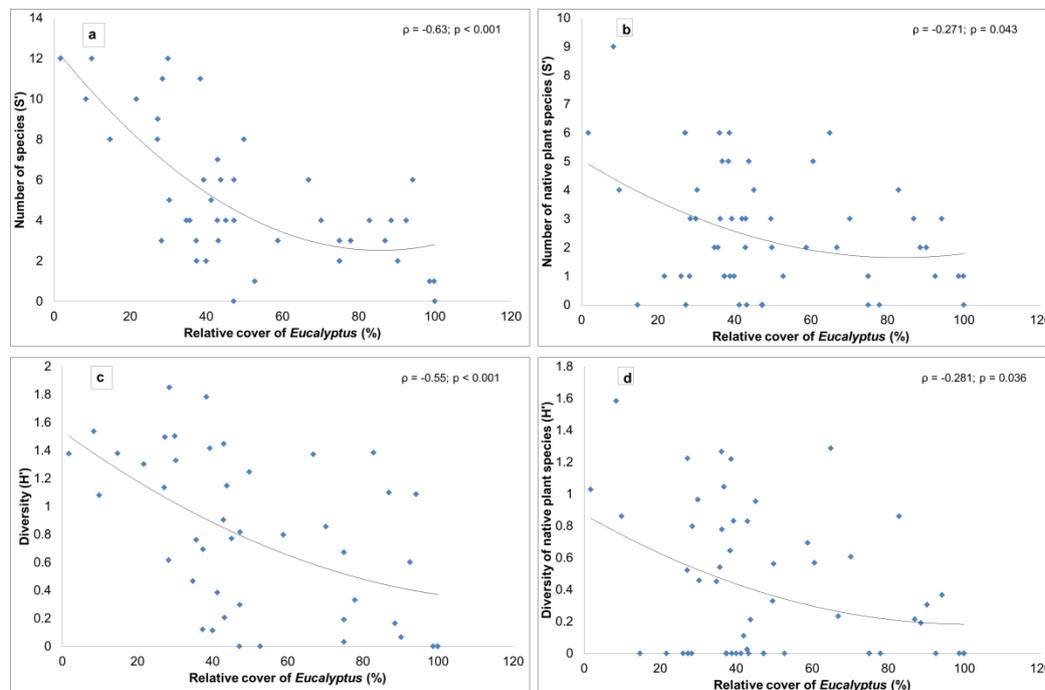


Fig. 3.4. Relationship between *Eucalyptus camaldulensis* relative cover and: (a) richness of all plant species; (b) richness of native plant species; (c) diversity of all plant species ( $H'$ ); and (d) diversity of native based on species abundance data in all 10 m x 5 m plots containing *Eucalyptus camaldulensis* along the Berg River, Western Cape, South Africa.

### 3.3.4 Floristic composition

*Eucalyptus camaldulensis* invasion was associated with significant changes in plant species composition as demonstrated by the results of CCA ordination on major species (species with at least 1% cover in one treatment) presence/absence data ( $p < 0.001$ , Table 3.2). In the CCA of major species cover, the first axis ( $\lambda$ ) separated the species according to their

response to invasion and accounted for 38% of the variation in the data. The Monte-Carlo permutation test for the axis was significant ( $p < 0.01$ , Table 3.2). Differences in species composition along the invasion gradient were confirmed by PERMANOVA of major (Bray Curtis;  $F = 4.417$ ;  $p < 0.001$ ) and native (Bray Curtis;  $F = 4.42$ ;  $p < 0.001$ ) species.

In the CCA of tree and shrub species, and other growth forms (forbs, graminoids, vines, and geophytes), the first axis ( $\lambda$ ) explained an average 40%, while the second axis explained a cumulative average of 72.5% of the variation in species data (Table 3.2). The Monte-Carlo permutation test for the significance of the gradient was statistically significant ( $p < 0.05$ , Table 3.2). Most species, especially native, are negatively correlated to high levels of *E. camaldulensis* invasion (Fig. 3.5a-d). Of the native tree and shrub species, *D. glabra*, *S. angustifolia*, *K. africana* and *P. elongatus* showed some tolerance of *Eucalyptus* invasion (Fig. 3.5a), but still exhibited high association with uninvaded plots. Alien plant species distribution is also negatively correlated to heavy invasion of *E. camaldulensis* with *A. mearnsii* showing an inverse association with increasing invasion (Fig. 3.5b).

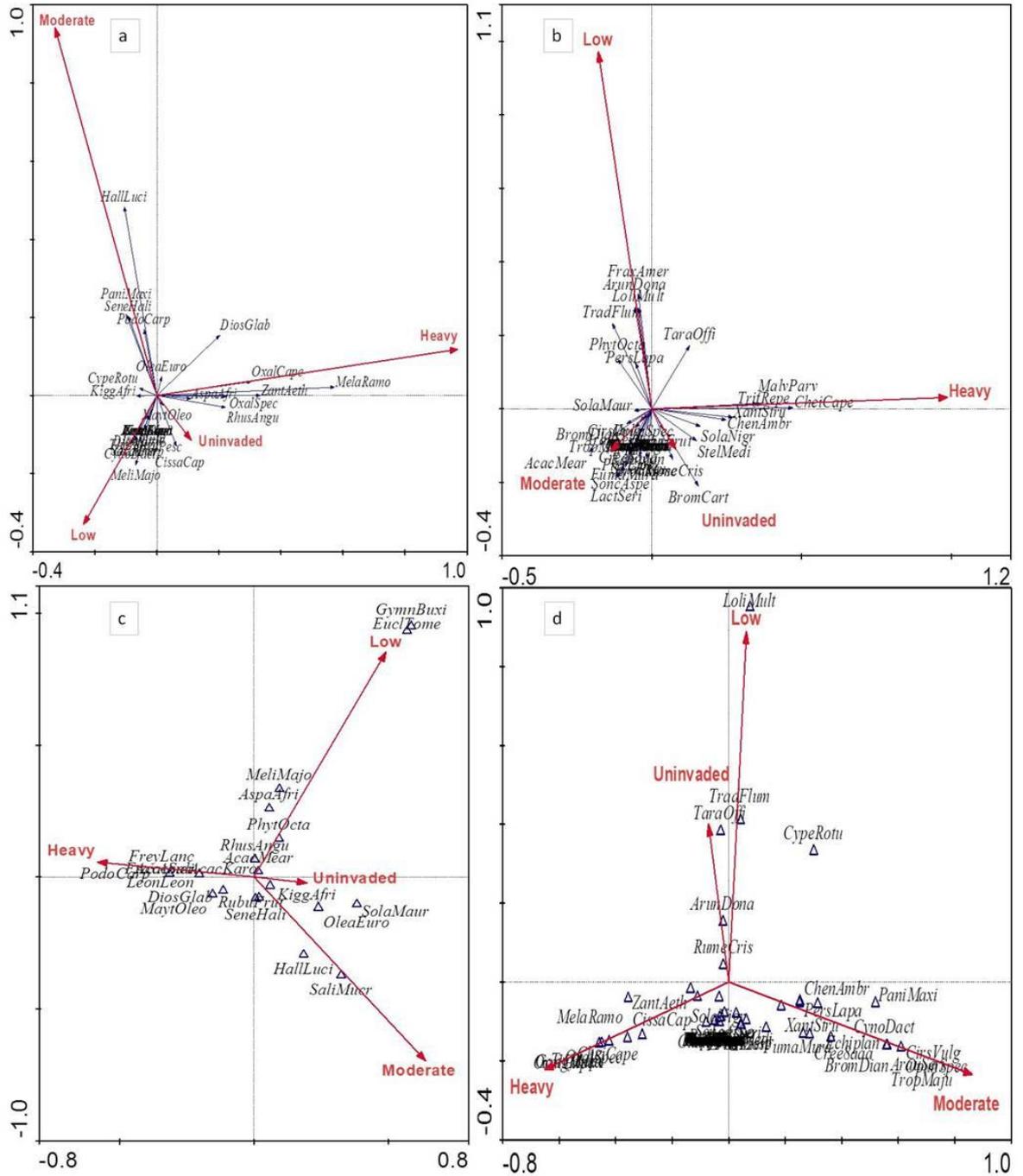


Fig. 3.5. Canonical correspondence analysis and redundancy analysis ordination diagrams showing the response of (a). native, (b). alien, (c). tree and shrub, and (d). forbs/graminoids/geophytes/vine species to the invasion by *E. camaldulensis* based on species covers. *Eucalyptus camaldulensis* was not included in the Monte-Carlo test, and species names are abbreviated, see Appendix 3.1 for full names. Data were split into groups to clarify differences among sites.

Similarity percentages (SIMPER) test showed an overall dissimilarity of 84% among the uninvaded, lightly, moderately and heavily invaded sites. The species contributing up to 90% of the observed differences in composition in the various invasion conditions are shown in Appendix 3.2, Supplementary material. *Kiggelaria africana* and *Zantedeschia aethiopica*

contribute up to 83% to the observed differences in heavily invaded sites, and are common in all the invasion conditions.

### 3.4. Discussion

#### 3.4.1 Relationships between invasion and, floristic diversity and structure

This paper aimed at determining changes in native species diversity, community structure and composition associated with invasion of *E. camaldulensis* in riparian forests by comparing uninvaded sites and sites under varying levels of invader percentage cover. Total and native species richness and diversity have been shown to progressively decrease with increasing levels of invasion. The structural attributes of native plant species; height, diameter at breast height, basal diameter, and percentage canopy cover, were negatively correlated with the same attributes of *Eucalyptus*. *Eucalyptus* invasion, however, was not associated with alterations in the native community characteristics of evenness and density.

While we know of no other studies on effects of *E. camaldulensis* in riparian forest ecosystems, our findings concur with a comparative study of *E. camaldulensis* in woodlots in northeastern Zimbabwe where the *E. camaldulensis* plantation had significantly lower native species richness and diversity than in native miombo woodlots (Tyynelä, 2001). Similar results have been found for *Acacia* spp. in South Africa and Portugal (Holmes and Cowling, 1997; Marchante et al., 2003), and *Tamarix* spp. in the United states (Shafroth et al., 2005; Stromberg et al., 2012).

Both uninvaded and heavily invaded sites had very few understorey species and in both sites, the vegetation formed closed canopies. It has been argued that shading could be one of the causes for declines in native species richness in heavily invaded areas, as well as areas with native vegetation forming dense canopies (e.g. Jäger et al. (2007); Reynolds and Cooper (2010)). *Eucalyptus camaldulensis* casts sparse shade (Bone et al., 1997) because its leaves hang vertically and they tend to become smaller as the species becomes mature (Doughty, 2000). However, our observation in the riparian zone is that *Eucalyptus* achieves over 75% canopy cover, and this, coupled with its medium height, limits light penetration to the forest floor, thus limiting undergrowth. This is a special attribute for *E. camaldulensis* in riparian zones, as riparian *E. camaldulensis* forests benefit from relatively frequent flooding which increases xylem pressure potential thereby increasing leaf size and ultimate tree growth rate (Bacon et al., 1993).

Allelopathy could be another reason for limited undergrowth (or reduced species richness) underneath eucalypts. Allelopathic potential of *Eucalyptus* has been reported to cause low species diversity and altered structural attributes of resident vegetation communities in various ecosystems, including naturalised stands and plantations (del Moral

and Muller, 1970; May and Ash, 1990; Khan et al., 2008). Allelopathy distinguishes *Eucalyptus* from other common tree invaders of riparian zones such as *Tamarix* spp. which are non-allelopathic (Lesica and DeLuca, 2004), besides other shared attributes such as fast growth rate (Doughty, 2000) and ability to access multi-water sources (Engel et al., 2005). *Eucalyptus* species are also known for their characteristic thick litterfall (Bacon et al., 1993) which has in some cases been implicated in inhibiting the germination, growth and establishment of native species (Bacon et al., 1993; Barbier et al., 2008). Furthermore, *Eucalyptus* has been associated with altering nutrient cycling regimes (del Moral and Muller, 1970; Gaertner et al., 2011). Changes in nutrient cycling may alter the species competitive regime, and lead to reduction in native species diversity or stunted undergrowth (Jäger et al., 2007).

It has been argued that dominant native species share certain characteristics with invasive alien species and may therefore have similar effects on less competitive understorey species (Thompson et al., 1995; Daehler, 2003; Davis et al., 2011). Our results support this argument. Both invaded and uninvaded sites were dominated by a few tree and shrub species. Invaded sites are dominated by *E. camaldulensis*, while uninvaded sites along the Berg River were dominated by tree and shrub species such as *K. africana*, *P. elongatus*, *O. europaea* subsp. *africana*, *D. glabra*, and *S. angustifolia* (see Appendix 3.2 in Supplementary material). The prevalence of highly competitive or shade tolerant species in uninvaded and heavily invaded sites could be related to the “colonization-based saturation” of richness effect (Sax and Gaines, 2008) where further colonization is inhibited by the established species. Thompson et al. (1995) and Daehler (2003) argue that in situations where native and alien species have similar effects, the latter might well be accepted as a new and equally valuable ecosystem. However, for *E. camaldulensis*, if one considers both community and ecosystem-level effects, it becomes apparent that management actions are needed.

#### **3.4.2. Relationships between invasion and floristic composition**

Community composition of all growth forms in riparian zones changed with increasing abundance of *E. camaldulensis*. This accords with floristic diversity results, which showed that *E. camaldulensis* is associated with changes in diversity and composition of native species in riparian zones. While some native plant species showed tolerance of invasion, most exhibited a higher affinity for uninvaded sites. Native tree and shrub species such as *K. africana*, *O. europaea* subsp. *africana*, and *D. glabra*, while dominant in uninvaded sites, still persisted within *Eucalyptus* stands. However, their growth form was mainly shrubby, as

opposed to trees in uninvaded sites. Herb and graminoid species were the most affected, as they disappeared completely in heavily invaded sites.

*Eucalyptus camaldulensis* invasion in riparian zones does not result in total exclusion of resident species, and this agrees with diversity results which showed no change in native species evenness. This is confirmed by Reynolds and Cooper (2010) who stated that decrease in light levels creates opportunities for shade tolerant species. Hejda and Pyšek (2006) also found a marginally significant difference in evenness between uninvaded plots and plots invaded by *Impatiens glandulifera*. While our results may not be directly comparable to those of this study because *I. glandulifera* is an annual herb, and *E. camaldulensis* is a tall tree, the trends exhibited by these invaders are similar. The fact that *E. camaldulensis* does not cause total exclusion makes it rather unique when compared to other major invasive tree species normally occurring in riparian zones such as *A. mearnsii* and *Tamarix* spp. that are prominent in South Africa, and the United States respectively, as these species result in total exclusion of natives in most situations. This could be because, the other invasive tree species are not as tall as eucalypts, thus allow relatively less light penetration to undergrowth. Furthermore, *A. mearnsii* is a nitrogen-fixing tree that causes nutrient enrichment, which may be unfavourable for other native species (Witkowski, 1991; Yelenik et al., 2004). However, the fact that natives are not completely excluded underneath eucalypts may be a matter of time, in which case eucalypts may be viewed as being a relatively slow ecosystem engineer.

Of importance to note is that, *E. camaldulensis* co-existed with a few isolated individuals of other invasive species such as *Acacia longifolia* and *A. mearnsii*. The fact that *A. mearnsii* contributed 59% to observed differences between composition of heavily invaded sites and other invasion conditions, positions it as a potential early opportunist successor after *E. camaldulensis* clearing. This is also evidenced by its presence already in the lightly invaded sites as the biggest contributor (35.6%) to differences observed between lightly invaded sites and other invasion conditions. Interestingly, even other alien plants including some taxa of *Acacia*, especially *A. mearnsii*, decreased with increasing abundance of *Eucalyptus*, and this finding concurs with that of Alvarez and Cushman (2002) who reported a similar effect with the invasive climber *Delairea odorata* in coastal California. Most of the detected change in native plant species is envisaged to be associated with *Eucalyptus* since it is the dominant invader (Hejda and Pyšek, 2006; Catford et al., 2012), but it is also possible that eucalypts may be benefiting from interspecific facilitation of other invasive plants it exists with, to the disadvantage of native species (Simberloff, 2006).

### **3.4.3. Methodological constraints and approach**

Space for time substitution or comparative observational studies have been criticized for their failure to separate causes and effects of invasion. Consequently, several studies advocate experimental removal or introductions of the invader, or a combination thereof. An experimental approach was inappropriate in our case because firstly, experimental introductions of known invasive species are unethical (Hejda and Pyšek, 2006) and risky especially in riparian zones where dispersal of *E. camaldulensis* is facilitated by flood pulses (Rejmánek and Richardson, 2011); and secondly, introductions are unrealistic in terms of the time required to get results. Removal of the invader is mainly constrained by cost and insufficient working capacity (Taylor and Hastings, 2004) and the long time it takes for the ecosystem to respond (Hejda and Pyšek, 2006); Furthermore, there are indirect effects following species removal (e.g. soil and native vegetation disturbance) which may obscure the true impact of specific invasive species (Hulme and Bremner, 2006; Truscott et al., 2008).

This study therefore evaluated the riparian vegetation community along an invasion gradient. This allowed for the detection of trends in native plant community characteristics as invasion increased. The approach was used notwithstanding the uncertainty associated with character of plots prior to invasion, and the fact that plots may differ in factors other than invasion history which is a common problem in such comparative studies (Hejda and Pyšek, 2006). Our study sites were chosen as close to uninvaded sites as possible - within the same hydro-meteorological unit, and in the same geomorphological zone. All the sites had similar disturbance regimes. As such we believe that the experimental design for the study is entirely appropriate for assessing the potential effects of *E. camaldulensis* invasion in riparian zones. However, while the gradient sampling gives a higher confidence that the detected changes in the various riparian ecosystem variables are indeed associated with invasion, than a simple comparative study of invaded and uninvaded sites, we acknowledge that we still cannot be absolute in assigning causation.

### **3.5 Implications for management**

The results suggest that invasion of *E. camaldulensis* in riparian zones is a major problem for the conservation of native biological diversity. Prediction of the trend of effects and dominance of invasions over extended periods of time is often challenging (Starfinger et al., 2003). However, given that eucalypts can reach ages of 500 – 1000 years (Jacobs, 1955), the continued presence of this species is likely to transform riparian ecosystems into a monoculture. Management to reduce the density of invading eucalypts seems more feasible

than the potentially better, but probably untenable, option of eradication (Ogden and Rejmánek, 2005).

This goal is considered achievable because established stands appear to comprise only mature individuals with little recruitment, since seedlings are not shade tolerant and the seed bank is short-lived (Rejmánek and Richardson, 2011). This is contrary to other major invasive species in these ecosystems such as *A. mearnsii* which has a persistent seed bank and for which massive seedling establishment occurs even in dense stands (Rascher et al., 2011). However, success of removal relies on the choice of the right combination of methods and their application over sufficient time (Starfinger et al., 2003).

South Africa initiated one of the world's largest programmes, the Working for Water, focussed on clearing invasive alien plants, mostly targeting riparian zones (Esler et al., 2008; van Wilgen et al., 2011). Significant progress has been made in clearing, but native vegetation recovery is still limited. *Eucalyptus camaldulensis* coexists with individuals of other invasive trees, notably *Acacia* spp.; secondary invasions of these species following clearing of eucalypts are a major problem. Secondary invasion can however be managed by minimisation of soil disturbance during clearing and effective follow up to deal with resprouting and seedling recruitment of *Eucalyptus* and other known invasive species which are abundant in the soil-stored seed bank (F. Tererai, unpubl. data).

Although the gradient-sampling comparative approach used in this study yielded satisfactory results and is considered appropriate for assessing potential effects of tree invasions on native vegetation communities, there is potential for application of an experimental removal approach to complement the findings of the present study (Hejda and Pyšek, 2006; Hulme and Bremner, 2006; Truscott et al., 2008). Some of the heavily invaded sites used in this study have already been cleared or are targeted for clearing in the near future (Ruwanza et al., 2012). These could serve as experimental removal sites for future studies measuring native vegetation response to *E. camaldulensis* removal.

### **3.6 Acknowledgements**

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technical support and assistance in liaising with landowners, and Sheunesu Ruwanza for general assistance.

### 3.7 Appendices

The following supplementary Information may be found in the supplementary files accompanying this thesis:

**Appendix 3.1:** Species composition in plots along the invasion gradient from “uninvaded”, “lightly”, “moderately” and “heavily” invaded plots along the Berg River, Western Cape, South Africa. Mean relative species covers are shown (n = 30 uninvaded plots; 19 lightly invaded plots; 25 moderately invaded plots; and 25 heavily invaded plots). Only species with at least 1% mean cover in one treatment are shown. Aliens are indicated by (\*)

**Appendix 3.2:** Results of similarity percentages analysis (SIMPER) summarizing the species contributing significantly to observed differences uninvaded (n=30); lightly (n=19); moderately (n=25); and heavily (n=25) invaded plots based on species abundance measure from the 10 m x 5 m plots along the Berg River, Western Cape, South Africa. For full species names see Appendix 3.1.

## Chapter 4: Resilience of riparian vegetation invaded by *Eucalyptus camaldulensis* and options for restoration: the role of the soil-stored seed bank

A version of this chapter was submitted to the journal *Folia Geobotanica*.

Reference: Tererai, F., Gaertner, M., Jacobs S.M., Richardson, D.M. 2012. Resilience of riparian vegetation invaded by *Eucalyptus camaldulensis* and options for restoration: the role of the soil-stored seed bank. *Folia Geobotanica* (submitted).

### Abstract

Riparian zones are highly vulnerable to alien plant invasion. In densely invaded habitats recovery following clearing largely relies on soil-stored seeds, but the propagule pressure of native species is often low. We investigated the potential role of soil-stored seed banks for native species recovery. We asked: Does the richness, diversity and composition of native soil-stored seed banks change with *Eucalyptus camaldulensis* invasion? Does the native seed bank match the above-ground native vegetation? Is the native soil-stored seed bank sufficient to initiate recovery of native vegetation after removal of *E. camaldulensis*? We conducted our study in riparian habitats along the Berg River in the Western Cape Province, South Africa. A seedling-emergence approach was used to assess the soil-stored seed banks in two layers: 0-10cm and 10-20cm. We compared seed density, richness, diversity ( $H'$ ) and evenness ( $J'$ ) under varying levels of *E. camaldulensis* percentage cover, and the seed banks at the two depths with each other and with the above-ground vegetation. *Eucalyptus camaldulensis* invasion had no significant effect on total and native species richness, diversity and evenness. Although not significant, invasion had a bigger effect on native species richness and diversity than on alien species richness in the top 10cm. Alien species density was significantly higher than native species density across all invasion classes. Invasion influenced the composition of the native seed bank, with native species showing preference for uninvaded sites at both soil depths. Native seed bank assemblages were more diverse and species similarity between invaded and uninvaded sites was higher in the seed bank than in above-ground plant assemblages. There is good potential for recovery of native species after *Eucalyptus* removal but more from surviving plants in the above-ground vegetation, than from immediate seed recruitment because of the threat of secondary invasions. Although up to 50 years of invasion by *E. camaldulensis* did not have

significant effects on the native seed bank, research is needed to elucidate possible effects on successional pathways following its removal.

**Key words:** Biological invasions; Community recovery; Ecosystem resilience; Restoration; Secondary invasions; Seed recruitment

#### 4.1 Introduction

In many parts of the world invasive alien plants have changed the composition of native plant communities (Richardson et al., 1989; Vitousek et al., 1996; Levine et al., 2003; Pyšek and Richardson, 2010; Vilà et al., 2011). Most studies of such changes have applied comparative approaches of invaded and uninvaded sites to assess effects on the diversity of standing vegetation (Vilà and Gimeno, 2007; Gioria and Osborne, 2009a). However, above-ground vegetation forms only part of the overall plant diversity (Vilà and Gimeno, 2007). The seed bank is an important consideration in restoration ecology as it represents a reservoir of biodiversity to initiate regeneration of native vegetation following removal of the stressor (Holmes and Richardson, 1999). The study of soil-stored seed banks is needed to give a full insight into possible impacts of disturbance and community dynamics such as succession (Fisher et al., 2008; Gioria and Osborne, 2009a), hence providing the opportunity to predict restoration potential in invaded areas (Holmes, 2002).

“Clearing” is a common management action for the control of invasive alien plants in many parts of the world (Manchester and Bullock, 2000; Richardson et al., 2007; Beater et al., 2008; Shafroth and Briggs, 2008). However, simply removing existing invasive species often fails in enhancing the recovery of native species and restoring aspects of functionality in degraded ecosystems (Galatowitsch and Richardson, 2005; Le Maitre et al., 2011). After removal of invasive alien plants native vegetation mainly regenerates from remnant native species, seed bank and dispersed seed input from external sources (French et al., 2011). There are several factors that could account for recruitment limitation post-clearing of the invader. In densely invaded habitats, including riparian zones, which are often associated with suppressed native vegetation, recovery relies on soil-stored seeds (Musil and De Witt, 1990). However, native species propagule pressure (both density and abundance) is often low and some species may not be represented in the seed bank (Richardson et al., 2007; Fourie, 2008; Vosse et al., 2008). Invasive trees often form almost complete monocultures, thereby disrupting inputs to the soil-stored seed bank by native species and, over time, leading to the attrition of previously deposited native seed stores. Native plants that occur in heavily invaded ecosystems die prematurely or produce little to no seeds at all (del Moral

and Muller, 1970; Holmes and Cowling, 1997; Levine et al., 2003; Vilà and Gimeno, 2007). This often translates into a depauperate seed bank over time, which limits recruitment (Gioria and Osborne, 2009b; French et al., 2011). The rationale of our study is to understand the role of soil-stored seed banks in riparian habitats in driving autogenic native vegetation regeneration which is crucial for restoration (Fourie, 2008; Vosse et al., 2008).

Riparian zones are inherently rich in biological diversity (Naiman et al., 1993; Kauffman et al., 1995; Décamps et al., 2004), but are highly vulnerable to invasion by alien plant species. Major invasive alien tree invaders of riparian zones include *Tamarix* spp. in the south-western USA, *Salix* spp. in Australia (Stokes, 2008), and Australian *Acacia* spp. and *Eucalyptus camaldulensis* Dehn. in South Africa (Galatowitsch and Richardson, 2005). Riparian zones are especially prone to invasion because of their dynamic hydrology and opportunities for recruitment following natural and anthropogenic disturbances (Holmes et al., 2005; Sîrbu et al., 2012). The maintenance and restoration of degraded riparian habitats is therefore crucial in order to maintain biological diversity and ecosystem function. Notwithstanding the strong resilience of most riparian ecosystems (Kauffman et al., 1995), there is need for enhanced understanding of the effects of individual invaders on the total species pool, including the soil-stored seed bank (Vilà and Gimeno, 2007). Most research on seed bank dynamics has focussed on terrestrial ecosystems and little information is available on seed banks in riparian habitats (Vosse et al., 2008). Because of their richness in biological diversity and proneness to invasion, it is imperative to examine the dynamics of seed banks in riparian zones (Richardson et al., 2007).

*Eucalyptus camaldulensis* is an Australian tree species which is a riparian specialist that can readily invade susceptible riparian zones (Vilà and Gimeno, 2007; Rejmánek and Richardson, 2011). It has already invaded long stretches of rivers in South Africa, especially in the Western Cape Province (Forsyth et al., 2004). *Eucalyptus camaldulensis* is very successful at competing for resources including light, water, and space; other studies have cited its allelopathic effects (Khan et al., 2008) as jointly working to exclude native plants, as well as disrupting seed input into the soil. The effects of invaders could be direct, by reducing seed rain as the invader outcompetes native species (Holmes and Cowling, 1997), or indirectly by altering disperser media dynamics such as resultant competition for bird dispersed species (Vilà and Gimeno, 2007). *Eucalyptus camaldulensis* seeds are short lived and only released annually (Pettit & Froend, 2001; Rejmánek and Richardson, 2011), we therefore expect a transient seed bank for the species. However, the climate and ecotype of origin of *E. camaldulensis* in its native range, which are very different between northern and southern Australia may determine whether or not it releases seed annually.

We studied changes in soil-stored seed banks associated with invasive tree species in riparian zones. The aim of the study is to assess the effects of *E. camaldulensis* invasion in riparian zones on the soil-stored seed bank of native species. More specifically we ask: 1) Does the richness, diversity and composition of the soil-stored seed bank change with invasion of *E. camaldulensis*? 2) Does the richness, diversity and composition of native seed bank match above-ground native vegetation characteristics? 3) Does the seed bank under stands of invasive *E. camaldulensis* invasion have potential to initiate autogenic recovery of native species following removal of *E. camaldulensis* stands?

## 4.2 Materials and methods

### 4.2.1 Study site

Our study was conducted at the Berg River, which is located north-east of Cape Town in the Western Cape of South Africa (Fig. 3.1). The study was conducted along the main stem of the Berg River in the upper catchment, between the towns of Hermon and Franschoek - a distance of 92 km (Fig. 3.1). The study area was chosen because it is a good example of long-established invasions (c. 50 years) (Geldenhuys, 2008) where any observed effects can be reliably attributed to the influence of *E. camaldulensis*. The area has a mediterranean-type climate with warm dry summers and cool wet winters with an average rainfall of about 550 mm. The average temperature minima and maxima are 11°C and 22°C respectively. The Berg is a perennial river with high flows and frequent flooding in winter (May to September). The whole river stretch has been invaded by alien trees, mainly *E. camaldulensis*, but was interspaced with individuals of *Acacia mearnsii* and *Populus* spp. (poplars) in some locations. Dominant native woody riparian vegetation includes trees and shrubs of *Diospyros glabra*, *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, and *Searsia angustifolia* which are now mainly confined to small pockets or isolated individuals within stands of *E. camaldulensis*.

### 4.2.2 Study species

*Eucalyptus camaldulensis* Dehn. has one of the widest natural distributions of any Australian tree species. It occurs in most climatic zones and the majority of river systems across Australia (McDonald et al., 2009). Like many other of the c. 800 eucalypt species (taxa in the genera *Angophora*, *Corymbia* and *Eucalyptus*), *E. camaldulensis* has been widely planted in many parts of the world outside its native range (Rejmánek and Richardson, 2011). This is because of its ability to grow in a wide range of sites (Butcher et al., 2009). *Eucalyptus camaldulensis* favours areas of deposition along watercourses in its native range (Butcher et al., 2009; McDonald et al., 2009), and in areas outside its native range where it has become

a successful invader (Forsyth et al., 2004; Rejmánek and Richardson, 2011). Eucalypts were introduced to South Africa in the late 19<sup>th</sup> century (Forsyth et al., 2004) for several purposes including timber, fuelwood, and shelterbelts; they are also valuable sources of nectar and pollen for the apiculture industry (Rejmánek and Richardson, 2011). *Eucalyptus camaldulensis* is now invasive in many parts of South Africa, and self-sown stands are especially widespread and dense in riparian zones of the Western Cape province (Forsyth et al., 2004; Meek et al., 2010).

#### **4.2.3 Study design**

We studied soil-stored seed banks and above ground vegetation changes along a continuum of invasion density (hereafter invasion gradient), and study sites were grouped into four “invasion condition classes”, each with four replicates (n=16): “uninvaded” (0% – 24%), “Light” (25% – 49%), “moderate” (50% – 74%), and “heavy” ( $\geq 75\%$  cover of *E. camaldulensis*). Most of the invaded sites were predominantly *Eucalyptus* except in a few unavoidable cases where isolated individuals of *Acacia mearnsii*, an invasive tree native to Australia, occurred. Sites measured 10 m along the river and spanning 20m of the riparian zone, with plots in contiguous 5 m widths perpendicular to the river. The sites were randomly and longitudinally located on both sides of the river. Care was taken to locate plots across a range of conditions (various soil types and slopes) and vegetation types (such as grass patches, shrub and forest) in which *E. camaldulensis* achieved dominance. Proximity of invaded and uninvaded sites ensured that sites had similar conditions with reasonable level of confidence. A few individuals of *E. camaldulensis* occurred in two of the “uninvaded” sites as no suitable sites could be found that were totally free of this species. “Pristine” reference sites, completely free of alien species are extremely rare or simply do not exist in most ecosystems, including riparian habitats (Rosgen, 1994; Richardson et al., 2007; Brewer and Menzel, 2008). Previous work in different parts of the world has shown that major impacts of invasive trees, including effects on soil properties, are generally only realized when the invader becomes abundant or dominant (Hejda and Pyšek, 2006; Vilà et al., 2011; Catford et al., 2012). Data collection and analysis of above-ground vegetation data formed part of a separate study (F. Tererai, unpublished data) and only results on the comparison between seed bank and above-ground vegetation are presented here.

#### **4.2.4 Data collection**

Soil samples were collected along the invasion gradient. Sampling was done late summer (February) of 2011, after the seed rain in order to capture both the transient and the persistent components of the seed bank (Walck et al., 2005; Vilà and Gimeno, 2007; Fisher

et al., 2008). Soil sampling was deliberately conducted on the same sites as the above-ground vegetation study (hereafter “the vegetation study”) (F. Tererai, unpubl. data). This allowed a comparison to be made between characteristics of soil-stored seed banks and vegetation characteristics. At each site, we sampled the first four - 5 m x 10m plots. Three-4m<sup>2</sup> quadrats were randomly located in each plot. Five sampling points (15cm diameter) were randomly selected, and five soil cores (5cm x 20cm) were extracted. The top 10cm of the cores from each quadrat were bulked to constitute a sample, and similarly with the bottom 10 cm cores of all sites (tray; n = 384). Sample bulking was done to reduce variability due to seed clustering or irregular distribution in the soil (Fisher et al., 2008).

#### **4.2.5 Seedling emergence assessment experiment**

A seedling-emergence approach was used to estimate species richness and abundance per unit area (Holmes and Cowling, 1997; Holmes, 2002; Vosse et al., 2008). The experiment was set up in an ambient greenhouse in early autumn. The soil was passed through a 10mm mesh to remove large stones, roots and litter (Vilà and Gimeno, 2007). The soils were placed in trays lined with hessian material to prevent seed and soil from washing out. The trays were given a smoke treatment in February to simulate a late summer fire. The treatment was conducted by burning native plants in a drum and the smoke pumped into the tent containing the trays. The treatment has been shown to significantly enhance germination response in a variety of Western Cape plant taxa (Holmes and Cowling, 1997; Holmes, 2002). The trays were kept moist by regular watering. Seedling emergence was recorded every fortnight for nine months. For species that could not be identified immediately, duplicates were removed, and the species were grown until identifiable or until they flowered. Plants that had not flowered at the end of the experiment were compared with field herbarium specimens and identified to species level where possible.

#### **4.2.6 Analysis**

Germinants from the soil-stored seed bank were categorised into trees and shrubs, forbs and graminoids. To determine the effect of invasion on the transient and more persistent component of the soil-stored seed bank permutational multivariate analysis of variance (PERMANOVA) was performed. Similarity percentages analysis (SIMPER) was used to identify the species that contributed most to the differences between uninvaded and invaded sites. Species richness ( $S$ ), Shannon-Wiener's diversity index ( $H'$ ), and species evenness ( $J$ ) were used to measure the effect of invasion on seed bank community characteristics.

To evaluate differences in species composition, we used direct gradient analysis. Based on the length of the main gradient in the data, estimated by use of indirect gradient analysis (DCA) (Table 4.1), we used redundancy analysis (RDA) (Lepš and Šmilauer, 2003). Monte-Carlo permutation tests were used to determine the significance of the invasion gradients (measured as percentage aerial cover of *E. camaldulensis*). Data were split into: i) top 10cm - all species ii) top 10cm - native species; iii) bottom 10cm all species and, iv) bottom 10cm native species. Richness and diversity multivariate statistics were computed using multivariate ecological research software, Primer (version 6, PRIMER-E Ltd, Plymouth, UK), while ordination analysis was done using Canoco 4.5 software package (Lepš and Šmilauer, 2003).

Table 4.1. Results of redundancy analysis of species count data (all and native species) of the top and bottom 10cm of the soil profile for 16 sites along the Berg River, Western Cape, South Africa. Percentages of variance explained by the first two canonical axes, and the statistics of Monte-Carlo permutation tests ( $F, P$ ) are shown. The selection of the method used was based on the length of the gradient of the first two ordination axis as obtained by the DCA analysis.

Data set	Cumulative explained variance		f-ratio	P-value	Length of gradient
	1 <sup>st</sup> axis	2 <sup>nd</sup> axis			
Top 10cm all species	51.5	76.8	5.177	0.002	3.621
Top 10cm native species	42.2	73	5.075	0.014	3.448
Bottom 10cm all species	55.1	84.3	6.224	0.002	2.675
Bottom 10cm native species	54	82.6	6.462	0.012	2.206

To determine whether the seed-bank matches above-ground vegetation, parametric (student t-test) and/or non-parametric statistics (Mann-Whitney U test) were used depending on whether or not the data were normally distributed. Since the aim was to establish the effects of invasion on seed bank characteristics; all comparisons were made between uninvaded plots (reference) and, the lightly, moderately and heavily-invaded plots. Comparisons were made based on the assumption that diversity and abundance of uninvaded and invaded (light, moderate and heavy) communities were similar prior to invasion (Vilà and Gimeno, 2007; Gioria and Osborne, 2009b).

### 4.3 Results

#### 4.3.1 Seed bank species density and richness

The top 10 cm generally had higher seed densities as shown by the difference in the vertical scales (Fig. 4.1a and b). There was no significant variation in the density of native germinants along the invasion gradient ( $H_{3,64} = 5.08$ ,  $P = 0.166$ ) although the density decreased with increasing cover of *E. camaldulensis* in the top 10cm. In the top 10cm, all invasion conditions except heavily invaded sites exhibited significantly higher density of alien germinants than uninvasion sites (Mann Whitney U test,  $P < 0.05$  – Fig. 4.1a). The number of *E. camaldulensis* germinants averaged 5 m<sup>-2</sup> in all invasion conditions, with no significant variation ( $H_{3,64} = 5.55$ ,  $P = 0.136$ ). Heavily invaded sites had the fewest *E. camaldulensis* germinants in the top 10 cm. In the bottom 10 cm, *E. camaldulensis* germinants did not vary significantly along the invasion gradient ( $H_{3,64} = 3.797$ ,  $P = 0.284$ ) and averaged 0.8 m<sup>-2</sup>.

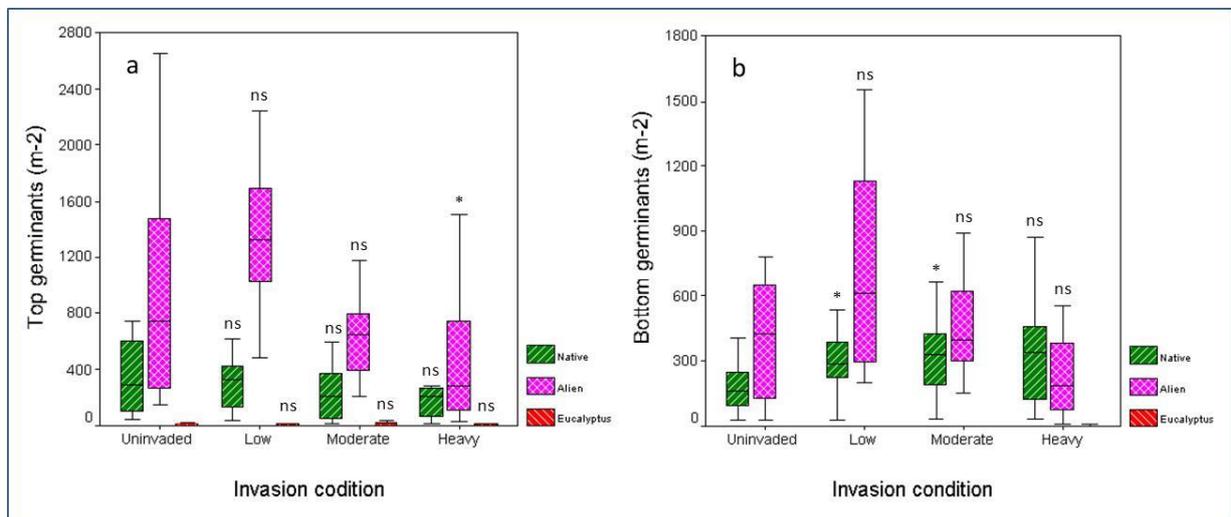


Fig. 4.1. Density (number of germinants m<sup>-2</sup>) of germinants (native, alien and *Eucalyptus camaldulensis*) in (a) the top 10cm and (b) the bottom 10cm soil samples collected from uninvaded, lightly, moderately and heavily invaded sites along the Berg River of Western Cape, South Africa. The whiskers of each bar represent the non-outlier range, the bar represents the 25<sup>th</sup> to the 75<sup>th</sup> percentile and horizontal line within the bar represents the mean. Significant differences between uninvaded and lightly-, moderately- and heavily-invaded sites were tested by the non-parametric Mann Whitney U test, since all data were not normally distributed. Significance levels: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; and \*\*\*  $P < 0.001$ , ns – not significant.

Overall, in the top 10cm of the soil profile 8% more species were recorded than in the bottom 10cm (Table 4.2). A total of 20 and 15 native species were recorded in the top and bottom 10 cm respectively. All the alien species occurring in the top 10cm were found in the bottom 10cm, except for one (Table 4.2). Of all the species occurring in the seed bank, 62% were forbs. The native, alien and total species richness in the top and bottom 10cm varied significantly along the invasion gradient (Kruskal-Wallis ANOVA,  $P < 0.05$ ).

Table 4.2. Summary of the germinant species recorded in the top 10cm and bottom 10cm of the soil profile of the 16 sites situated along the Berg River, Western Cape, South Africa

Component		Top 10cm	Bottom 10cm
<b>Total species recorded</b>		61	56
<b>Genera</b>		50	46
<b>Families</b>		30	26
<b>Native</b>	<i>Trees and shrubs</i>	9	6
	<i>Forbs</i>	4	3
	<i>Graminoids</i>	7	6
<b>Alien</b>	<i>Trees and shrubs</i>	7	8
	<i>Forbs</i>	25	25
	<i>Graminoids</i>	8	8

Pairwise comparisons revealed that the variation in the top 10 cm was explained by significantly fewer native, alien and total species richness in heavily invaded sites than in uninvaded sites ( $P > 0.05$  - Fig. 4.2a). In the bottom 10 cm, lightly invaded sites had significantly higher native, alien and total species richness than uninvaded sites (Fig. 4.2b).

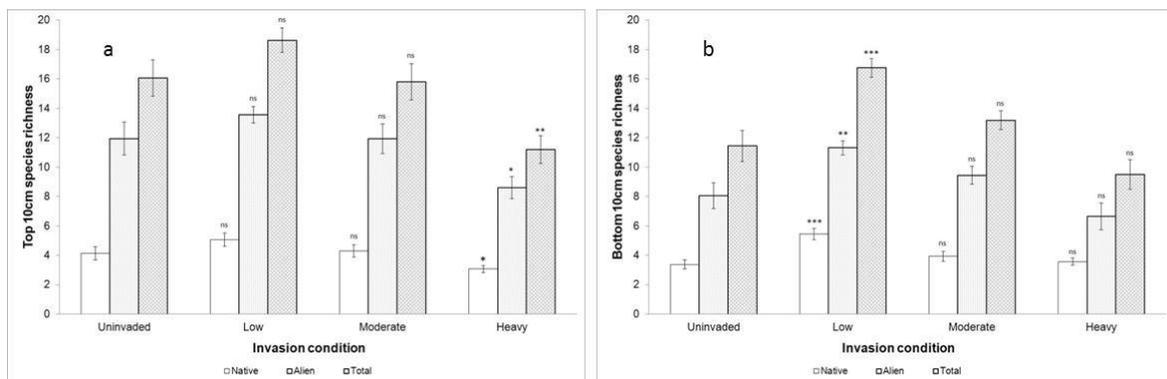


Fig. 4.2. Native and alien plant species richness (mean  $\pm$  SE) of soil samples collected from (a) the top 10cm and (b) the bottom 10cm of the soil profile of uninvaded sites ( $n = 16$ ) compared to lightly ( $n=16$ ), moderately ( $n=16$ ) and heavily ( $n=16$ ) invaded sites along the Berg River, Western Cape, South Africa. Significant differences between uninvaded and, lightly, moderately and heavily invaded sites were tested using the non-parametric Mann Whitney U test, since all data were not normally distributed. The measure of variance is the standard error. Significance levels: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; and \*\*\*  $P < 0.001$ , ns – not significant.

#### 4.3.2 Seed bank species diversity

Diversity and evenness of native and alien species in the top 10 cm did not vary significantly along the invasion gradient (Kruskal-Wallis ANOVA,  $P > 0.05$ ). Pairwise comparisons showed no significant differences between uninvaded and invaded (light, moderate, and heavy) plots (Table 4.3). The diversity of native and alien species in the bottom 10 cm varied significantly along the invasion gradient (Kruskal-Wallis ANOVA,  $P < 0.05$ ). The variation is

explained by lightly invaded sites that were significantly richer in both native and alien species than uninvaded sites ( $P < 0.05$  - Table 4.3). Evenness of native species increased with invasion in the top 10 cm while it decreased for both native and alien species with invasion in the bottom 10 cm, although not significantly.

Table 4.3. Native and alien species diversity ( $H'$ ) and evenness ( $J'$ ) of soil samples collected from the top and bottom 10 cm of the soil profile based on species abundance (species count) data in all 10 m x 5 m plots within an invasion gradient from uninvaded, lightly, moderately and heavily invaded sites along the Berg River, Western Cape, South Africa. The measure of variance is the standard error. Significance levels: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; and \*\*\*  $P < 0.001$ , ns – not significant. The grey coloured block (Uninvaded) is the basis of comparison for all the other invasion conditions

Top 10 cm								
Index	Uninvaded		Light		Moderate		Heavy	
	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>
Shannon Index ( $H'$ )	0.718±0.124	1.60±0.100	0.920±0.080 <sup>ns</sup>	1.610±0.110 <sup>ns</sup>	0.904±0.112 <sup>ns</sup>	1.694±0.124 <sup>ns</sup>	0.690±0.070 <sup>ns</sup>	1.440±0.010 <sup>ns</sup>
Evenness ( $J'$ )	0.487±0.072	0.671±0.038	0.600±0.060 <sup>ns</sup>	0.620±0.040 <sup>ns</sup>	0.634±0.055 <sup>ns</sup>	0.686±0.037 <sup>ns</sup>	0.650±0.060 <sup>ns</sup>	0.686±0.030 <sup>ns</sup>
Bottom 10 cm								
Index	Uninvaded		Light		Moderate		Heavy	
	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>	<i>Native</i>	<i>Alien</i>
Shannon Index ( $H'$ )	0.843±0.081	1.353±0.092	1.12±0.070 <sup>**</sup>	1.610±0.121 <sup>*</sup>	0.750±0.070 <sup>ns</sup>	1.541±0.082 <sup>ns</sup>	0.710±0.050 <sup>ns</sup>	1.120±0.140 <sup>ns</sup>
Evenness ( $J'$ )	0.708±0.049	0.698±0.036	0.690±0.040 <sup>ns</sup>	0.670±0.040 <sup>ns</sup>	0.634±0.045 <sup>ns</sup>	0.700±0.032 <sup>ns</sup>	0.590±0.040 <sup>*</sup>	0.640±0.060 <sup>ns</sup>

### 4.3.3 Species composition of seed banks

*Eucalyptus camaldulensis* invasion had a significant effect on the species composition of seed banks in both top and bottom 10cm-levels as demonstrated by the results of RDA ordination ( $P < 0.05$ , Table 4.1). In the RDA, the first axis ( $\lambda$ ) separated the species according to their response to invasion and accounted for an average 51% and cumulative average maxima of 79% (with the second axis) of the variation in all datasets (Table 4.1).

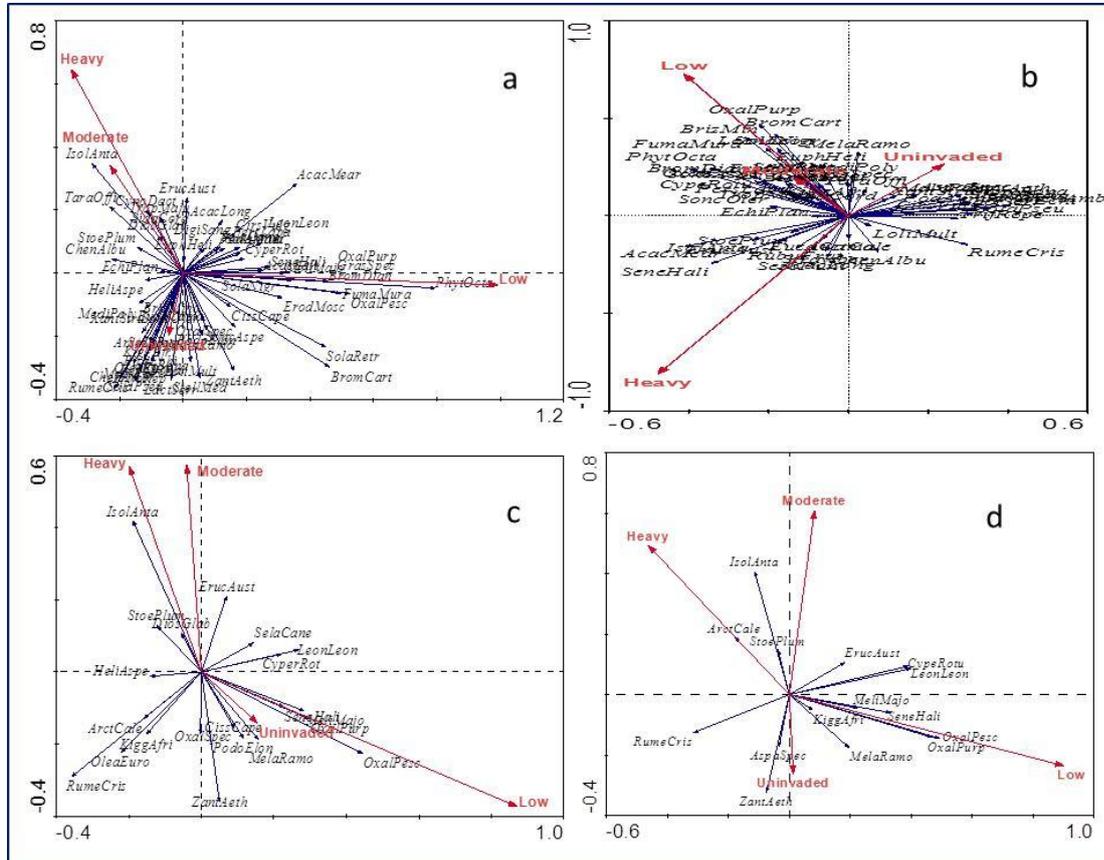


Fig. 4.3. Redundancy analysis ordination diagrams showing the response of (a) top 10cm, all species; (b) bottom 10cm, all species; (c) top 10cm, native species; and (d) bottom 10cm native species to the invasion by *Eucalyptus camaldulensis* along the Berg River based on species count. Codes for species names refer to taxa in Appendices 4.1 and 4.2. Data were split to clarify differences among groups.

Most species, especially native taxa, decreased in abundance with an increase in the level of invasion by *E. camaldulensis* (Fig. 4.3a-d). Species abundance (density) appears to have been influenced more by invasion than presence/absence. Common tree and shrub species such as *Kiggelaria africana*, *Diospyros glabra*, and *Olea europaea* ssp. *africana* that were present in the top 10cm of the soil profile were not present in the bottom 10cm. A few native fynbos species, such as *Stoebe plumosa* (occurring in all invasion conditions and in both top and bottom 10cm layers) and *Aspalathus* species (only occurring in uninvaded and heavily invaded sites, and only bottom 10cm) were present in the seed bank (Fig. 4.3c and d, and Appendix 4.1 and 4.2). Alien tree and shrub species were represented mainly by three *Acacia* species, the most abundant being *A. mearnsii* which was present in similar numbers

in top and bottom 10cm layers. *Eucalyptus camaldulensis* occurred in very small numbers in the seed bank, and even smaller numbers in the bottom 10cm.

#### **4.3.4 Seed bank –vegetation comparison**

The vertical scales of total richness and diversity graphs (Fig. 4 a and b) are about double those of native richness and diversity (Fig. 4c and d). Although the top 10 cm consistently showed higher species richness and diversity than the bottom 10 cm, the difference was not significant (Fig. 4.4 a and b). There were generally no significant differences between total and native species richness and diversity of the top 10cm and bottom 10cm layers of the soil-stored seed bank ( $P > 0.05$ ; Fig. 4.4a and b). However the seed bank richness and diversity of both top and bottom 10cm was significantly higher than that of aboveground vegetation ( $P < 0.05$ ; Fig. 4.4a and b). A similar trend was observed with the richness and diversity of native species for the bottom 10 cm, except in uninvaded sites (Fig. 4.4d). Generally, the top and bottom 10cm of the lightly invaded sites exhibited significantly higher ( $P < 0.05$ ) richness and diversity for both total and native species than the above-ground native vegetation richness and diversity which consistently declined with increasing invasion (Fig. 4.4a-d).

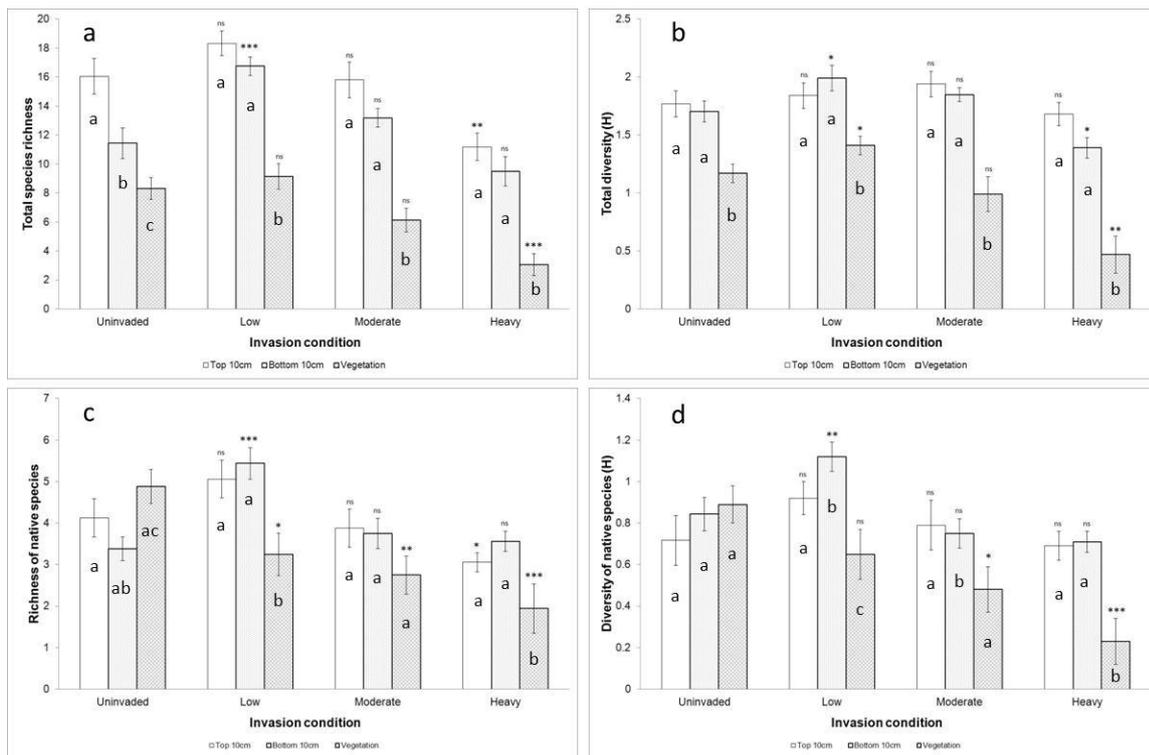


Fig. 4.4. Seed bank and vegetation characteristics (a) total species richness, (b) total diversity, (c) richness of native species and (d) diversity of native species recorded in the seed bank experiment (top 10cm and bottom 10cm) and above-ground vegetation study both conducted on 16 sites along the Berg River, Western Cape, South Africa. Significant differences between uninvaded and, lightly, moderately and heavily invaded sites were tested using the non-parametric Mann Whitney U test, since all data were not normally distributed and are depicted by \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; and \*\*\*  $P < 0.001$ , ns – not significant. The measure of variance is the standard error. Significant values for comparisons between seed bank (top and bottom 10cm) and above-ground vegetation characteristics are shown by letters a, b, and c.

PERMANOVA revealed that species composition of both vegetation and seed bank varied significantly along the invasion gradient ( $P < 0.001$ ). Species similarity between invaded and uninvaded sites was, however, higher in the seed bank (average of top and bottom 10cm, 44%) than in vegetation (23.61%). Native tree and shrub species such as *Asparagus africana*, *Freylinia lanceolata*, *Halleria lucida*, *Maytenus oleoides*, and *Salix mucronata* that are known to be able to recruit from seed were not recorded in the seed bank, but were present in above-ground vegetation. Conversely the native shrubs *Erucastrum austroafricanum*, *Selago canescens*, *Stoebe plumosa*, and *Helichrysum asperum* were found in the seed bank but not in vegetation.

## 4.4 Discussion

### *Richness and diversity*

The results of this study show that the transition from a native-dominated riparian plant community to a *E. camaldulensis* monoculture over around 50 years has not yet resulted in marked changes to the total soil-stored seed bank. This may possibly be explained by soil-stored seed bank longevity as it has been observed that seed production by native plants that co-exist with eucalypts is limited (F. Tererai, pers. Obs.). *Eucalyptus camaldulensis* invasion, however, had stronger effects on the native seed bank than on the alien seed bank, with native richness declining with invasion. This agrees with the findings of Holmes and Cowling (1997) who compared uninvaded and *Acacia* invaded sites in the fynbos biome of South Africa. The seed bank species pool also varied with depth, although differences were not significant overall. This variation was accounted for by native species, in particular native tree and shrub species which exhibited the biggest decrease. This is of special concern because native tree and shrubs have been identified as key species for restoration of riparian vegetation, given their above-ground dominance in uninvaded sites in comparison to other growth forms (Meek et al., 2010; F. Tererai, unpubl. data). These findings concur with those of Fisher et al. (2008) in their study of a Mediterranean woodland invaded by the South African species *Ehrharta calycina* and *Pelargonium capitatum* in Western Australia and Holmes (2002) who studied *Acacia saligna* invasions in the Western Cape.

### *Seed bank density*

Native seed bank density was higher in uninvaded sites and declined along the invasion gradient in the top 10cm, while native geminants increased significantly along the invasion gradient in the bottom 10cm except in heavily invaded sites. This suggests that invasion depletes the relatively shallower seed bank faster than the deeper more persistent component. The finding that native seed density did not decline with soil depth as reported in other studies (e.g. Holmes, 2002) is surprising, but may be indicative of the fast rate of soil turnover in riparian ecosystems. Many processes in riparian ecosystems are implicated in burying seeds in the soils, for example floodwaters can disperse propagules and bury them under sediment (Richter and Stromberg, 2005; Vosse et al., 2008).

The preserved seed in the deeper soil layers is envisaged to facilitate natural ecosystem recovery following control of the invader. However, the abundance of annual forbs in both the transient and the persistent seed bank poses a serious challenge for the management of *E. camaldulensis* and the restoration of ecosystem functioning. While native tree and shrub species that are dominant in established vegetation disappeared completely

in the bottom 10 cm, the alien seed bank persisted suggesting that the native seed bank is not as resilient as the alien seed bank, especially *Acacia mearnsii*. High numbers of *A. mearnsii* in the soil-stored seed bank will probably result in a secondary invasion of this species once *E. camaldulensis* abundance is reduced. There were very few *E. camaldulensis* germinants, and these even declined to negligible levels with depth in the soil, an indicator that the seed bank is small and short-lived, which reduces the potential for reinvasion through seedling recruitment. This is consistent with the reported lack of seed dormancy in the genus *Eucalyptus* (Rejmánek and Richardson, 2011). *Eucalyptus camaldulensis* does however resprout (Nicolle, 2006; Rejmánek and Richardson, 2011), making regular and consistent follow-up operations crucial in ensuring local eradication.

### *Seed bank composition*

The composition of the soil-stored seed bank is an important indicator of potential future plant community response to environmental change (Fisher et al., 2008). The composition of alien species in the seed bank has been affected by *E. camaldulensis* invasion but not to the same extent as native species composition. This finding concurs with the findings of Holmes and Cowling (1997), Holmes (2002) and Vosse et al. (2008) who studied fynbos seed banks under Australian acacias in the Western Cape. The shifts in aboveground species dominance appear to have less control on the composition of deeper and persistent soil-stored seed banks. This means that native species propagules still persist for future restoration activities, though in reduced numbers.

The fact that dominant species in the above-ground vegetation (e.g. *Kiggelaria africana*, *Diospyros glabra*, and *Olea europaea ssp. africana*) only occur in small numbers in the soil-stored seed bank indicates suppressed reproductive capacity of native species, seed and seedling mortality due to possible competition for resources (light, water and nutrients) and allelopathy (Vilà and Gimeno, 2007). Native species in heavily invaded sites have been observed to produce little or no seed at all (del Moral and Muller, 1970; Holmes, 2002; F. Tererai, pers. obs.). This is also evidenced by the presence of a number of native shrub species in the established vegetation but not in the soil-stored seed bank.

### *Seed bank – Vegetation comparison*

The above-ground vegetation does not match the seed bank, either in the top or bottom 10cm layers. Many more species were recorded in the seed bank than were present in the above-ground – agreeing with findings in other parts of the world, e.g. in a comparative study

of vegetation and seed bank composition in Mediterranean Spain (Díaz-Villa et al., 2003). This result also concurs with the findings of Holmes and Cowling (1997) for the fynbos biome of South Africa and French et al. (2011) in the Australia coastal dunes. However, most of the seed bank richness and diversity consisted of alien forb species, which may hamper the establishment of native species (Esler et al., 2008). The presence of some native shrub plant species only in the seed bank and not in above-ground vegetation, consistent with the findings of Fisher et al. (2008), is evidence of the persistence of some native plant species in the seed bank. While the presence of these fynbos species in the seed bank indicates that fynbos seed banks are reasonably long-lived (Holmes and Cowling, 1997), seeds of these species are likely to reduce in numbers with increase in time and density of invasion by *E. camaldulensis*. The seed bank was significantly more diverse than above-ground vegetation in the top 10 cm of uninvaded and heavily invaded sites. This may be explained by the fact that the vegetation of uninvaded sites is similar in structure to that of heavily invaded sites with native species seed production declining with vegetation age (F. Tererai, unpubl. data) and would have a similar effect on native seed production.

#### **4.5 Implications for restoration of native plant communities**

Potential for natural riparian vegetation recovery exists, but probably not immediately following *Eucalyptus* removal. Autogenic ecosystem recovery from seed recruitment may be hampered by low native seed densities and the challenge of secondary invasions (French et al., 2011). Furthermore, the native plant species might require soil disturbance (mechanical if necessary) to re-emerge from seed which is buried up to 20cm deep in the soil (Holmes and Cowling, 1997; Holmes, 2002). However, natural processes in the riparian ecosystem such as flooding and uprooting of trees may be sufficient to bring up soils from greater depths. We propose that in light of these facts, potential for recovery lies in the above-ground remnant native species (French et al., 2011) that currently co-exist with *E. camaldulensis* and will remain after clearing. These remnant species may regain dominance following removal of invader canopy, and consequently start seed production and recruitment. Thus we recommend sparing remnant native individuals during *Eucalyptus* clearing to facilitate recovery.

Regardless of the stage of *Eucalyptus* invasion and depth in the soil, the seed mass, richness and diversity of alien species (besides *Eucalyptus*) is higher than that of native species, hence the need to closely monitor and control secondary invasions following *Eucalyptus* removal. These alien plant species are “sleeper cells” awaiting ecological perturbation (Fisher et al., 2008); hence follow up clearing should be an integral part of the restoration programme of riparian zones. Keeping fire out may also help to prevent

spontaneous seed recruitment of IAPs, especially of *Acacia mearnsii* which is abundant in the soil-stored seed bank and whose germination is known to be stimulated by fire.

In conclusion, it is also noteworthy that while *Eucalyptus* invasion may not have significant effects on the native seed bank, it may alter successional pathways (Fisher et al., 2008), and further research is required in this area. Galatowitsch and Richardson (2005) also reiterated the need for research on recruitment dynamics of disturbed riparian zones. The knowledge generated in this study contributes to formulation of adaptive management strategies that enhance conservation of the biological diversity of riparian ecosystems.

#### 4.6 Acknowledgements

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#### 4.7 Appendices

The following supplementary Information may be found in the supplementary files accompanying this thesis:

**Appendix 4.1** Table 4: Plant species and their percentage frequency recorded in the germination greenhouse experiment on soils collected from top 10cm of the mineral soil profile of the Berg River riparian zone along a gradient of *Eucalyptus camaldulensis* invasion from uninvaded, light, moderate and heavy. Species with an asterisk are alien

**Appendix 4.2** Table 5: Plant species and their percentage frequency recorded in the germination greenhouse experiment on soils collected from bottom 10cm of the mineral soil profile of the Berg River riparian zone along a gradient of *Eucalyptus camaldulensis* invasion from uninvaded, light, moderate and heavy. Species with an asterisk are alien.

## Chapter 5: Effects of *Eucalyptus camaldulensis* invasion on soil physico-chemical properties in riparian zones

A version of this chapter was submitted to the journal *Plant and Soil*.

Reference: Tererai, F., Gaertner, M., Jacobs S.M., Richardson, D.M. 2012. Effects of *Eucalyptus camaldulensis* invasion on soil physico-chemical properties in riparian zones. *Plant and Soil* (submitted).

### Abstract

**Background and aims** Many invasive alien plants alter soil-nutrient regimes of invaded ecosystems, affecting long-term management and restoration. We assessed the effects of *Eucalyptus camaldulensis* invasions over 50 years on soil physical and chemical properties of riparian zones in the Western Cape Province, South Africa.

**Methods** Soil samples were collected beneath the canopy of uninvaded and a gradient of invaded sites, viz. light, moderate and heavy in all seasons. We quantified soil moisture, temperature, litter, primary textural components, concentrations of soil macro (C, N, P and K) and micro (Mn, Zn, Cu and Fe) nutrients, and pH. Available N ( $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N) and P; as well as exchangeable Ca and Mg were also assessed.

**Results** Soil pH levels were significantly lower in invaded sites than in uninvaded sites in all seasons. Litter cover and thickness increased significantly with invasion intensity. Soil moisture decreased consistently with invasion intensity. Total macro, micro and available nutrients did not vary significantly along the invasion gradient ( $p > 0.05$ ), but exchangeable cation content was significantly higher in uninvaded than in invaded sites, especially in winter and spring.

**Conclusion** Sites invaded by *E. camaldulensis* had higher litter build-up than non-invaded sites, but this appears to have little effect on soil-nutrient regimes. Consequently, unlike some other invasive tree species that cause substantial long-lasting changes to nutrient cycling regimes, it appears that restoration following removal of invasive stands of *E. camaldulensis* will not require interventions to return soil to pre-invasion conditions.

**Key words:** Biological invasions • Invasive alien species • Mediterranean climate • Soil available N • Soil cations • Soil N content

## 5.1 Introduction

Many invasive alien plants drive changes in native community composition, structure and diversity (Alvarez and Cushman, 2002; Gaertner et al., 2009; Gooden et al., 2009; Levine et al., 2003; Pyšek and Pyšek, 1995; Vilà et al., 2011). These changes have caused alterations of ecosystem functions such as cycling of water (Le Maitre et al., 2002), nutrients (Aweto and Moleele, 2005; Bernhard-Reversat, 1988; Corbin and D'Antonio, 2004) and disturbance regimes such as fire (Brooks et al., 2004; Tickner et al., 2001). Invasive alien species also alter litter quantity and quality, soil biological community composition, total nutrient stocks, and nutrient fluxes, particularly nitrogen (N) (Corbin and D'Antonio, 2004; Ehrenfeld, 2003; Jeddi et al., 2009). Plant species respond differently to changes in nutrient availability (Mulligan and Sands, 1988), hence changes to nutrient availability influence the diversity of native plant communities (Berendse, 1998; Castro-Díez et al., 2011; Lindsay and French 2005). Consequently, ecosystem ecologists and restoration practitioners have become increasingly interested in understanding the potential effects of invasive plant species on soil processes (Corbin and D'Antonio, 2004).

There are various mechanisms whereby invasive alien plants can alter the nutrient cycle in invaded ecosystems. They may alter the nutrient cycle directly by modifying the quality and quantity of the litter entering the soil, or indirectly through the activity of roots and the creation of microclimates below their canopy (Castro-Díez et al., 2011; Richardson et al., 2007; Yelenik et al., 2007). Invasive plants differ in their capacity to modify soil properties depending on how traits such as growth rate, litter chemistry and other functional properties differ from those of native species (Corbin and D'Antonio, 2004; Jeddi et al., 2009). This in turn affects the structure and composition of soil biological communities (Castro-Díez et al., 2011). Soil macro-detrivores and microbial decomposers mediate the litter decomposition process and release of nutrients into the soil for plant uptake. Litter of some exotic species, for instance *Eucalyptus* species, may inhibit soil microbial activity, resulting in nutrient impoverished soils, especially N (Castro-Díez et al., 2011). Some invasive alien plant species may act as net consumers of nutrients as they are slow and inefficient in recycling the nutrients back to the soil compared to native species (Aweto and Moleele, 2005). On the other hand, there are many examples where invasive species enhance available nutrients in soils [see Ehrenfeld (2003) for a recent review]. Invasive alien plants alter soil-nutrient regimes by initially changing the patterns of dominance of species and plant functional types within a community (Ehrenfeld, 2003). The legacy effects of invasive species may persist long after the invader has been removed (Corbin and D'Antonio, 2004; Marchante et al., 2009).

Site characteristics also influence the nature and magnitude of the effects that an invader may have on soil physical and chemical properties (Dassonville et al., 2008). Plant invasions in terrestrial and riparian ecosystems often have different effects on nutrient regimes, because of the differences in their dominant physical and biogeochemical processes such as denitrification. Riparian zones are much more dynamic, with active and frequent fluvial erosion and depositional processes (Naiman and Decamps, 1997). They can effectively act as traps or sinks of incoming nutrients, especially N and particulate phosphorus (P) (Naiman and Decamps, 1997). They are also generally more susceptible to invasion by alien plants than are terrestrial ecosystems because of natural and anthropogenic disturbance (Planty-Tabacchi et al., 1996; Richardson et al., 2007). Riparian zones are consequently more vulnerable to modification of soil-nutrient regimes induced by invasive alien species. Many riparian forests are heavily invaded by alien plant species, and yet most studies investigating the effects of invasive species on soil physical and chemical properties have been done in terrestrial ecosystems.

*Eucalyptus camaldulensis* favours areas of deposition along watercourses both in its native range and in other parts of the world where it has become a successful invader (Rejmánek and Richardson, 2011; Vilà et al., 2011). This species is known for its fast growth rate (Turner and Lambert, 2008) and its ability to establish well in nutrient poor soils (Mulligan and Sands, 1988). In South Africa, *E. camaldulensis* is one of five eucalypt species identified as invasive (Richardson and Rejmánek, 2011). It was introduced to South Africa more than two centuries ago, and is now widespread in riparian zones of the Western Cape and Mpumalanga provinces (Forsyth et al., 2004). While the invasiveness of *E. camaldulensis* and many of its ecosystem (compared to community) level effects have been acknowledged (Forsyth et al., 2004), the effects of this major invasive species on physical and chemical properties of soils are poorly understood. A review by Vilà et al., (2011) revealed that in general changes in nutrient cycling are subtle such that they are only detected after major impacts on plant species and communities would have occurred. Many invasive alien plants tend to speed up litter decomposition and increase nutrient pools for plant uptake (Ehrenfeld, 2003), in particular N content (Follstad Shah et al., 2009; Lake and Leishman, 2004; Witkowski, 1991). However, some *Eucalyptus* species have been reported to produce nutrient-poor litter which is recalcitrant to decomposition, thus resulting in little or no effect on soil-nutrient pools (O'Connell, 1988). A study of *E. camaldulensis* in a plantation in a semi-arid climate revealed that this species immobilizes nutrients faster than it can recycle them back to the soil compared with the native tree species *Acacia karroo* (Aweto and Moleele, 2005). Most of the studies that have reported elevated C and N in the soil are for N-fixing species (mostly *Acacia*) growing on nutrient poor soils (Gaertner et al., 2011; Witkowski, 1991; Yelenik et al., 2004). Elevated soil nutrients have also been reported in

vegetation assemblages of *Eucalyptus* species, especially when mixed with *Acacia* species (Bauhus et al., 2000; Gaertner et al., 2011; Laclau et al., 2005). These results suggest that the effects of invasive species on soil-nutrient regimes are context dependent, and are mediated by functional properties of the alien plant (e.g., N-fixing ability and growth rate) and properties of the invaded ecosystem (e.g., soil properties and climate) (Castro-Díez et al., 2011; Dassonville et al., 2008; Le Maitre et al., 2011).

Most studies on effects of invasive plant species on soil properties lack any comparison with native species or communities and therefore shed no light on whether soil properties have been altered by invasion (Ehrenfeld, 2003). Most of those that do, employ an observational approach, comparing invaded and uninvaded sites, which does not unravel cause from effect. This paper aims to determine whether there are any changes in soil physicochemical properties with invasion by *E. camaldulensis* in riparian zones of the Western Cape, South Africa, by comparing soil properties along an invasion-intensity gradient from uninvaded to lightly, moderately and heavily invaded sites. Two main research questions are addressed: (1) whether *E. camaldulensis* invasion changes soil physicochemical properties and 2) whether these changes are influenced by the invasion-intensity gradient?

## 5.2 Materials and methods

### 5.2.1 Study site

The Berg River is located north-east of Cape Town in the Western Cape Province of South Africa (Fig. 3.1). The study was conducted within the riparian zone of the Berg River's main stem in the upper catchment, between the towns of Hermon and Franschoek - a distance of 92 km. The study area was chosen because it is a good example of long-established invasions (c. 50 years) of *Eucalyptus camaldulensis* (Geldenhuys, 2008), where any observed differences in soil properties between sites could reasonably be attributed to the influence of the invasive tree. The study area has a mediterranean-type climate with warm dry summers and cool wet winters. The average rainfall across the Berg river catchment is about 550 mm and the average temperature minima and maxima are 11°C and 22°C respectively. Altitude ranges from 247 m at Franschoek to 66m at Hermon. The Berg is a perennial river with high flows and frequent flooding in winter (May to September).

The geology of the study catchment area is dominated by sandstone and quartzites of the Cape Supergroup which have typically nutrient-poor lithologies (Cotter, 2000). Quartzites are associated with sandy soils (Lewis and Illgner, 1998). The riparian zone is characterised by deep greyish alluvial soils formed from river sediment deposits. The whole river stretch has been invaded by alien trees, mainly *E. camaldulensis*, but was interspaced

with individuals of *Acacia mearnsii* and *Populus* spp. (poplars) in some locations. Dominant native woody riparian vegetation includes trees and shrubs of *Diospyros glabra*, *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, and *Searsia angustifolia* which now mainly occur in small pockets or isolated individuals among *E. camaldulensis*. About 65% of the Berg river catchment is under agriculture, mainly vineyards, fruit orchards and wheat fields (Geldenhuys, 2008). Other major agents of human-caused disturbance are clearing or harvesting of *E. camaldulensis* and *A. mearnsii*, while natural disturbance results from flooding, erosion and deposition. Fire seldom penetrates the riparian zone in the study area.

### **5.2.2 Study design**

Study sites were established along a continuum of invasion and were grouped in four “invasion condition classes”, each with four replicates: “uninvaded” (0% – 24% cover of *E. camaldulensis*), “light” (25% – 49% cover), “moderate” (50% – 74%), and “heavy” ( $\geq 75\%$  canopy cover). Most of the invaded sites were predominantly *Eucalyptus* except in a few unavoidable cases where isolated individuals of *Acacia mearnsii*, an invasive tree native to Australia, occurred. We are dealing with a heavily invaded riparian system surrounded by agricultural lands and two of the “uninvaded” sites had a few individuals of *E. camaldulensis* – no suitable sites were totally free of this species. Many studies have found that “natural” (i.e., non-invaded and non-degraded) reference sites in riparian ecosystems are extremely rare or simply do not exist (Butcher et al., 2009; Prins et al., 2005; Richardson et al., 2007; Rosgen, 1994). Previous work in different parts of the world has shown that major impacts of invasive trees, including effects on soil properties, are generally only realized when the invader becomes abundant or dominant (Catford & Vesk et al., 2012, Hejda and Pyšek, 2006), so the presence of a few *E. camaldulensis* trees in our “uninvaded” sites was not a major problem. Care was taken to make sure that plots cover a range of conditions (various soil types, slopes) and vegetation types (such as grassland, shrub, and forest) in which *E. camaldulensis* has achieved dominance. Proximity of invaded and uninvaded sites ensures that sites have similar conditions with reasonable level of confidence, so these were prioritized where they occurred. The sites were randomly and longitudinally located on both sides of the river (Fig. 3.1). Each site measured 10 m along the river and 20 m perpendicular to the river.

### **5.2.3 Sampling and data collection**

Soil samples were collected once every season (summer, autumn, winter and spring). Each 10 m x 20 m site was stratified according to observed variation in soil characteristics. Three 5m x 5 m wooden quadrats were randomly placed, one in each stratum. A total of five soil

cores were collected beneath surface debris and litter as in Castro-Díez et al. (2011), using a 5 cm diameter x 20 cm deep auger and bulked into one 500g sample from each of the three quadrats (n = 48 per season). We avoided collecting samples close to *E. camaldulensis* in the "uninvaded" sites. Aliquots meant for analysis of available N were immediately placed on ice and transported to the lab for analysis to prevent nutrient transformation, especially N due to microbial activity. The remaining soil samples were dried at ambient temperature and then passed through a 2 mm sieve; and aliquots for the various analyses sent to a local commercial laboratory for analysis.

#### **5.2.4 Physical properties**

Soil particle size analysis was performed by the hydrometer method. Soil particle fractions (clay, sand, and silt) were quantified on a single occasion as this is an important control over several riparian processes, including C and N mineralization and denitrification. A 5g soil sample was mixed with a 0.01-M  $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$  solution (25 mL) to form a 1:5 ratio, and the pH of the supernatant was measured with a pH meter (after Lindsay and French, 2005).

Soil temperature was measured throughout the year (2011) using data loggers (Higrochron Hi-Res i-buttons), at one hour intervals (n = 8174). Each site had three randomly sited i-buttons (within a depth of 10cm in the soil) that were programmed to take measurements at exactly the same time so that the site soil temperature was taken as the average of three for each season. Volumetric soil moisture measurements were conducted seasonally (summer, autumn, winter and spring; n = 80 measurements per season) using a soil moisture meter (HydroScene® Soil Water Measurement System). Five soil moisture readings were taken randomly in the 200 m<sup>2</sup> sites, with care being taken to cover all soil types. Litter cover and thickness were estimated below the plant canopies in uninvaded and invaded sites. Litter aerial cover was visually estimated to the nearest 5%, while depth (average of five measurements – cm per plot) was the measured thickness of the litter layer from the surface to the mineral soil.

#### **5.2.5 Laboratory analysis of soil chemical properties**

Organic C was assessed by Walkley Black acid digestion method as described in Nelson and Sommers (1996). Total (N) was analysed using a LECO Analyser (CNS 2000™) with a thermal conductivity detector. Mineral N was extracted by adding 100ml KCl 2 N to 5g of soil and shaking the mix for 2hrs on a reciprocating shaker. Available N ( $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N) was analysed with an Automated Wet Chemistry Analyser within 48hours of collection. Plant available P was determined by using ICP OES after Bray II extraction. Trace elements were assessed by ICP EDTA extraction method (Trace) and Boron (B) by ICP hot water extraction method. Soil exchangeable bases were assessed by ammonium acetate extraction.

### **5.2.6 Statistical analysis**

Soil physical properties and chemical properties were compared across the invasion gradient using a one-way ANOVA (invasion factor) for normally distributed data and Kruskal-Wallis ANOVA for non-normal data, followed by pairwise comparison where ANOVA results were significant. Pairwise comparisons of uninvaded and invaded plots (light, moderate and heavy) were performed by student t-tests (normal data) and Mann Whitney U-test (non-normal data). Normality test were performed using Kolmogorov-Smirnov. All statistical analyses were performed with Statistica 10.

## **5.3 Results**

### **5.3.1 Particle size and litter**

Soils from all sites were made up of more than 85% sand. None of the particle sizes varied significantly along the invasion gradient (Kruskal-Wallis ANOVA,  $p < 0.05$ ). Pairwise comparisons however revealed significant differences in mean proportions of clay and sand content of soils between uninvaded and, lightly and moderately invaded sites (Fig. 5.1a).

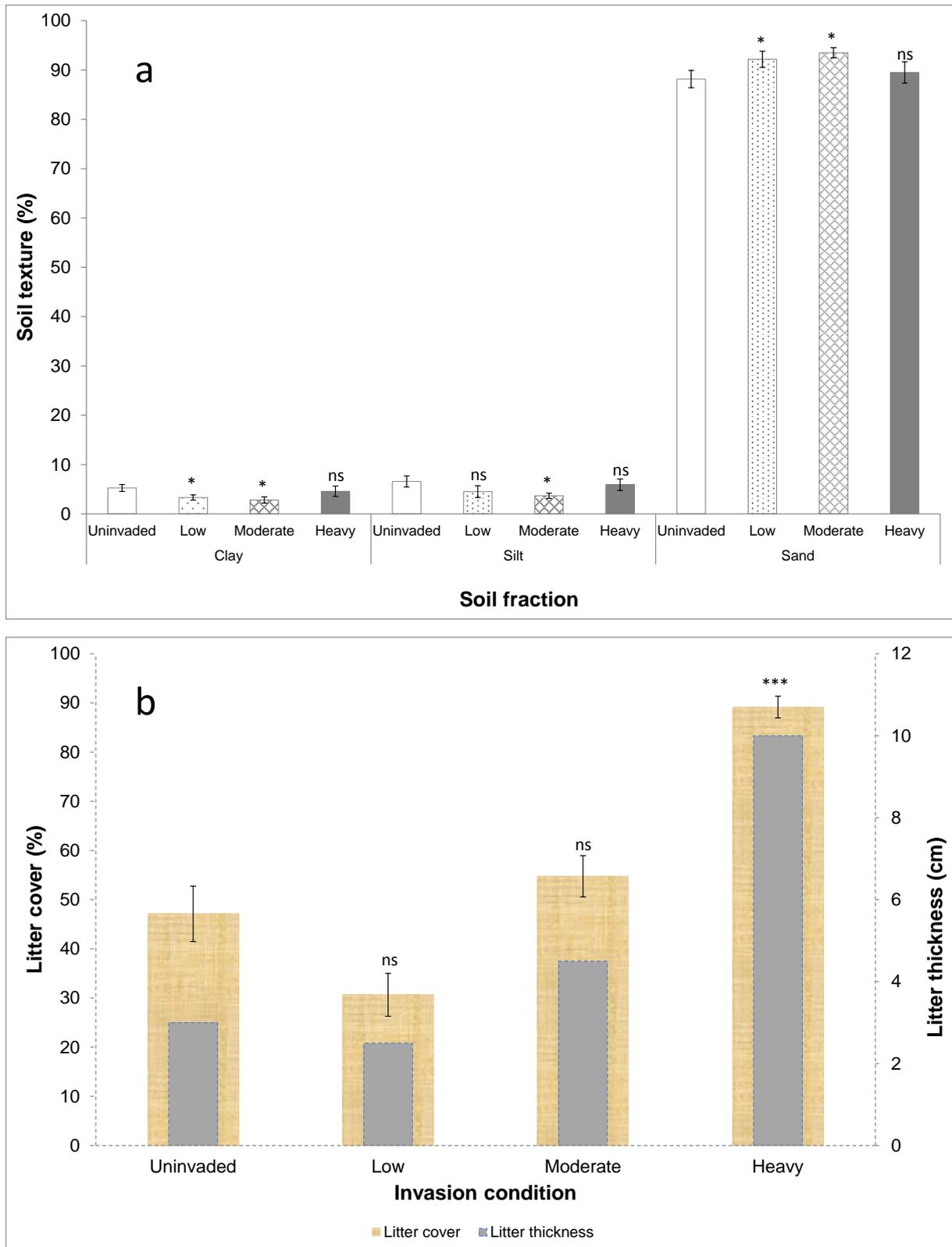


Fig. 5.1. a) Soil texture and b) litter cover and thickness of lightly, moderately and heavily invaded sites compared to unininvaded reference sites along the Berg River in Western Cape Province of South Africa. Significant differences between unininvaded and, lightly, moderately and heavily invaded sites were tested by the non-parametric Mann Whitney U test, since all data were not normally distributed. The measure of variance is the standard error. Significance level: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ ; ns – not significant

There were no significant differences in mean proportions of sand, silt and clay between uninvaded and heavily invaded sites (Fig. 5.1a). Heavily invaded sites had significantly higher litter cover and thickness (Fig. 5.1b). While there is no significant difference between litter cover of uninvaded and moderately invaded sites, the mean depth of litter was greater in the latter.

### 5.3.2 Soil moisture, temperature and pH

In all seasons except autumn, soil moisture content varied significantly along the invasion gradient (Kruskal-Wallis ANOVA,  $p < 0.05$ ). Pairwise comparisons, however revealed that for summer, only uninvaded and lightly invasion sites differed significantly ( $p = 0.001$  - Fig. 5.2a). For winter and spring, uninvaded sites showed significantly higher moisture levels than invaded sites ( $p < 0.05$  - Fig. 5.2a).

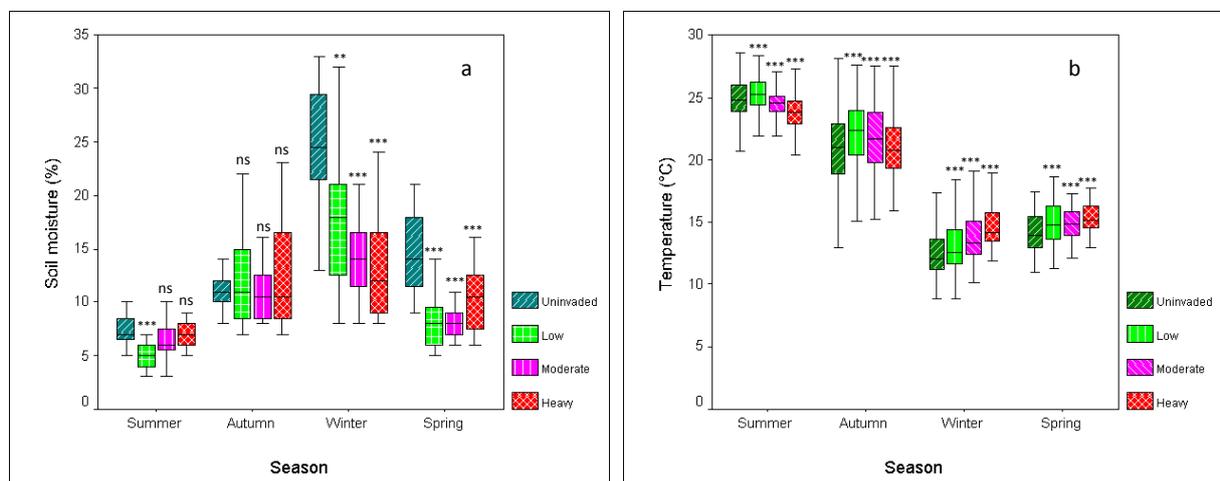


Fig. 5.2. a) Soil moisture and b) soil temperature of lightly, moderately and heavily invaded sites compared to uninvaded reference sites through all seasons along the Berg River in Western Cape Province of South Africa. Significant differences between uninvaded and, lightly, moderately and heavily invaded sites tested by the non-parametric Mann Whitney U test for soil moisture and student t-test for temperature depending on normality. Significance level: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ ; ns – not significant

Soil temperature varied significantly along the invasion gradient through all the seasons (Kruskal-Wallis ANOVA,  $p < 0.05$ ). Pairwise comparisons revealed that the soil temperature of uninvaded compared to invaded sites (light, moderate and heavy) significantly differed (student t-test,  $p < 0.05$ ). Winter and spring seasons showed a consistent increase in temperature along the invasion gradient (Fig. 5.2b).

Soils in the study area were generally acidic with a pH of less than 5. pH only varied significantly along the invasion gradient in summer and winter (Kruskal-Wallis ANOVA,  $p < 0.05$ ). Generally, acidity seemed to increase with dryness in all the seasons along the

invasion gradient except for moderately invaded sites (Fig. 5.3). Uninvaded sites were relatively less acidic compared to invaded sites (Fig. 5.3).

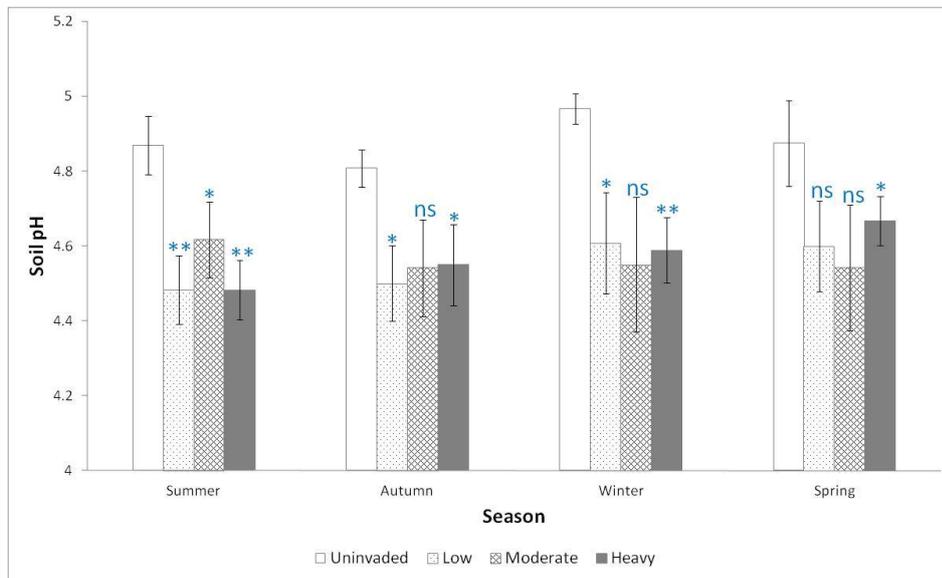


Fig. 5.3. Soil pH of lightly, moderately and heavily invaded sites compared to uninvaded reference sites through all seasons along the Berg River in Western Cape Province of South Africa. Significant differences between uninvaded and, lightly, moderately and heavily invaded sites tested by the non-parametric Mann Whitney U test, since all data were not normally distributed. The measure of variance is the standard error. Significance level: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ ; ns – not significant

### 5.3.3 Total nutrient concentrations

Total organic C did not vary significantly along the invasion gradient for all seasons except spring (Kruskal-Wallis ANOVA,  $p > 0.05$ ). Soils of uninvaded sites generally had higher C content than heavily invaded sites albeit not significant (Table 5.1). Total N concentration did not vary significantly along the invasion gradient in all seasons (Kruskal-Wallis ANOVA,  $p > 0.05$ ), although uninvaded sites exhibited higher soil N content than heavily invaded sites (Table 5.1). Total P did not vary significantly along the invasion gradient (Kruskal-Wallis ANOVA,  $p > 0.05$ ) in all seasons. Pairwise comparisons did not reveal any significant differences between uninvaded, and lightly, moderately and heavily invaded sites, but there was a consistent decline in soil P concentrations in all seasons along the invasion gradient (Table 5.1). Exchangeable potassium (K) was generally lower in summer and autumn, as compared to winter and spring. Summer and spring did not show any significant variation in total potassium along the invasion gradient (Kruskal-Wallis ANOVA,  $p > 0.05$ ). However in all seasons except spring, uninvaded sites exhibited higher K content which decreased along the invasion gradient (Table 5.1). The C/N ratios ranged between 8 and 13 (Table 5.1) and did not vary significantly (Kruskal-Wallis ANOVA,  $p > 0.05$ ), neither did they show any clear tendencies along the invasion gradient.

Table 5.1. Soil macro and micro nutrient properties of the riparian study sites on an invasion gradient and through all seasons along the Berg River of Western Cape, South Africa. Data represent the mean±standard error of all samples. Significance levels: \* p≤0.05; \*\* p≤0.01; and \*\*\* p≤0.001; ns – not significant.

Season	Invasion condition	C (%)	Macro nutrients			C:N	Micro nutrients				
			N (%)	P (mg/kg)	K (mg/kg)		Mn (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Fe (mg/kg)	B (mg/kg)
Summer	Uninvaded	1.94±0.26	0.17±0.02	252.45±31.81	88.80±16.57	12.27±0.38	79.76±13.29	6.94±0.93	1.45±0.15	200.15±9.08	0.39±0.08
	Light	1.79±0.27ns	0.16±0.02ns	260.40±30.31ns	67.67±14.88ns	12.15±0.53ns	27.40±4.72***	6.00±0.21ns	0.86±0.17ns	147.86±19.38*	0.17±0.02**
	Moderate	1.40±0.30ns	0.11±0.02ns	218.35±37.21ns	50.08±10.21*	12.47±1.12ns	34.84±7.69**	10.03±2.17ns	1.48±0.29ns	207.07±37.48ns	0.27±0.05ns
	Heavy	1.87±0.17ns	0.14±0.01ns	204.31±33.88ns	63.00±14.99ns	12.31±0.80ns	65.55±12.02ns	4.85±1.11ns	1.24±0.35ns	218.74±29.57ns	0.25±0.04ns
Autumn	Uninvaded	1.96±0.35	0.14±0.02	205.53±38.67	51.30±6.48	12.08±0.54	62.20±8.69	6.96±1.32	1.66±0.32	183.80±21.85	0.16±0.01
	Light	1.86±0.21ns	0.15±0.02ns	190.21±17.16ns	49.18±6.05ns	11.67±0.54ns	96.34±30.63ns	5.65±0.37ns	0.88±0.01*	158.11±8.15ns	0.29±0.060ns
	Moderate	1.80±0.28ns	0.16±0.02ns	199.38±23.06ns	52.17±8.45ns	11.08±1.04ns	37.73±4.93**	7.86±1.35ns	1.19±0.16ns	178.61±22.59ns	0.20±0.03ns
	Heavy	1.74±0.20ns	0.14±0.02ns	182.66±40.85ns	57.70±12.17ns	12.75±0.89ns	64.81±20.90ns	6.66±1.95ns	1.41±0.38ns	221.60±28.17ns	0.21±0.01ns
Winter	Uninvaded	1.74±0.24	0.17±0.01	227.09±18.40	130.30±14.41	9.72±0.64	58.15±7.47	6.03±0.84	1.21±0.11	227.13±26.10	0.35±0.04
	Light	1.85±0.22ns	0.18±0.02ns	217.34±28.15ns	109.70±18.34ns	10.08±0.63	45.59±5.35ns	6.15±1.17ns	0.84±0.17ns	151.95±15.73*	0.30±0.04ns
	Moderate	1.67±0.21ns	0.17±0.01ns	199.63±21.70ns	94.55±6.41**	9.32±0.76	43.01±7.92ns	7.43±1.36ns	1.07±0.19ns	181.08±25.34ns	0.32±0.05ns
	Heavy	1.55±0.15ns	0.16±0.01ns	171.67±21.35ns	88.27±9.64*	9.23±0.52	52.55±16.06ns	4.39±1.08ns	1.10±0.32ns	232.61±29.88ns	0.19±0.02*
Spring	Uninvaded	2.13±0.14	0.18±0.02	245.86±31.47	119.92±13.39	12.43±0.70	101.55±13.97	9.77±1.37	1.88±0.26	328.82±18.89	0.39±0.03
	Light	2.04±0.21ns	0.18±0.02ns	213.58±26.66ns	77.89±12.46*	11.59±0.80ns	47.59±7.34**	6.19±0.50*	0.88±0.14*	219.24±13.36***	0.29±0.04ns
	Moderate	1.26±0.20**	0.16±0.02ns	196.55±39.50ns	85.36±11.17ns	8.46±0.84***	34.07±6.06***	6.38±1.55ns	1.29±0.29ns	267.64±55.13ns	0.33±0.06ns
	Heavy	1.84±0.22	0.15±0.02ns	183.39±35.98ns	75.73±10.68*	12.55±0.75ns	78.39±21.36ns	6.03±1.37ns	1.44±0.36ns	307.45±37.52ns	0.29±0.05ns

### 5.3.4 Available nutrients

Total available N consistently decreased from summer through autumn and winter to spring. However, within each season there were no significant differences between uninvaded and invaded (light, moderate and heavy) sites ( $p > 0.05$  - Fig. 5.4a). Splitting total available N into nitrate ( $\text{NO}_3^-$ -N) and ammonium ( $\text{NH}_4^+$ -N) showed that there is more of the former in summer and vice versa in autumn (Fig. 5.4b and c).

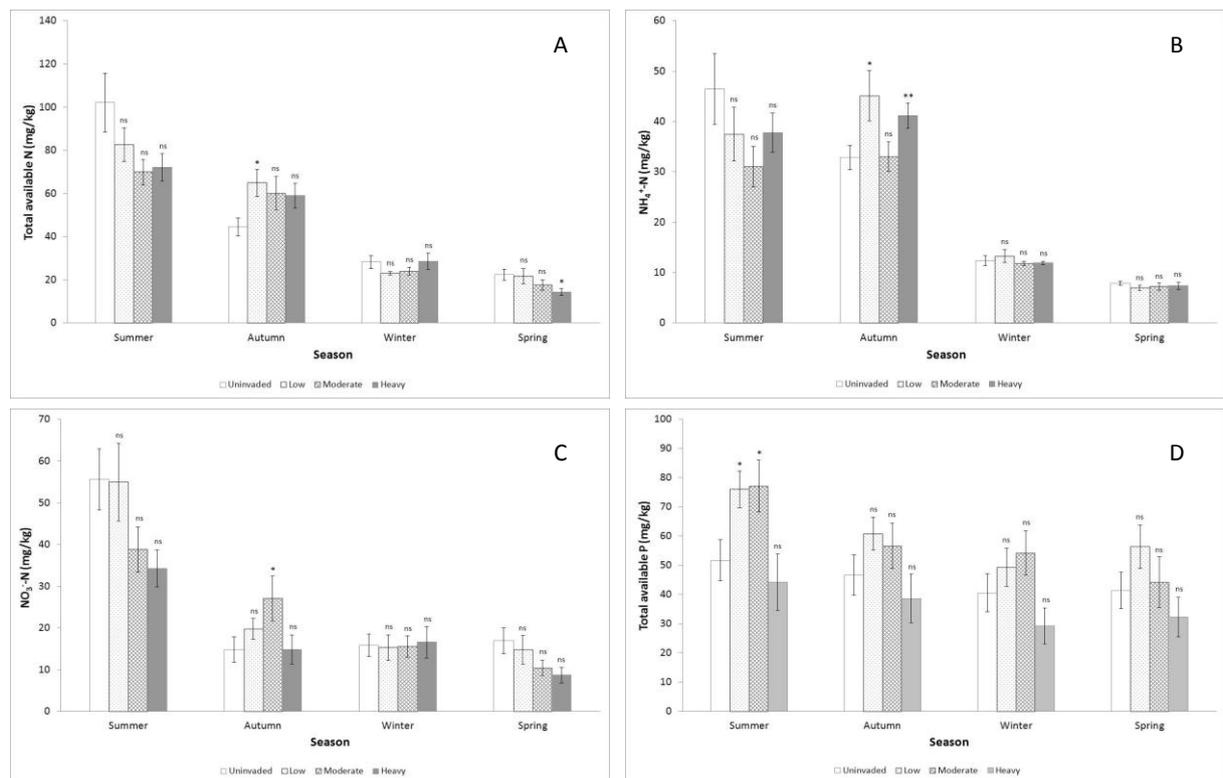


Fig. 5.4. a) Total available N; b)  $\text{NH}_4^+$ -N; c)  $\text{NO}_3^-$ -N and d) total available P of lightly, moderately and heavily invaded sites compared to uninvaded reference sites through all seasons along the Berg River in Western Cape Province of South Africa. Significant differences between uninvaded and, lightly, moderately and heavily invaded sites tested by the non-parametric Mann Whitney U test, since all data were not normally distributed. The measure of variance is the standard error. Significance level: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ ; ns – not significant

Pairwise comparisons revealed no significant differences in total available N,  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N between uninvaded and all invaded plots along the invasion gradient ( $p > 0.05$ ) in any season.  $\text{NO}_3^-$ -N exhibited consistent decreases along the invasion gradient in summer and spring, though not significant. Available  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N were much higher in summer and autumn as compared to winter and spring (Fig. 5.4b and c). Available P did not show any significant variation in any season except in summer (Kruskal-Wallis ANOVA,  $p > 0.05$ ). However, lightly and moderately invaded sites consistently exhibited higher mean values of available P though only significantly in summer (Fig. 5.4d).

### 5.3.5 Micro nutrients and exchangeable ions

None of the micro nutrients [Manganese (Mn), Zinc (Zn), Copper (Cu), Iron (Fe) and B] varied significantly across invasion conditions (Kruskal-Wallis ANOVA,  $p > 0.05$ ). Mn, Cu, and Fe were consistently higher in uninvaded and heavily invaded compared to light and moderate invasion conditions in all seasons (Table 5.1). Zn and B did not show any detectable trends (Table 5.1). There was significant variation in  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  along the invasion gradient in winter and spring (Kruskal-Wallis ANOVA,  $H_{3,48} = 14$ ,  $p = 0.003$ ;  $7.07$ ,  $p = 0.07$ ) and (Kruskal-Wallis ANOVA,  $H_{3,48} = 20.73$ ,  $p < 0.001$ ;  $10.36$ ,  $p = 0.02$ ) respectively. Exchangeable Ca and Mg were generally higher in uninvaded sites and declined along the invasion gradient in all seasons (Fig 5.5a and b).

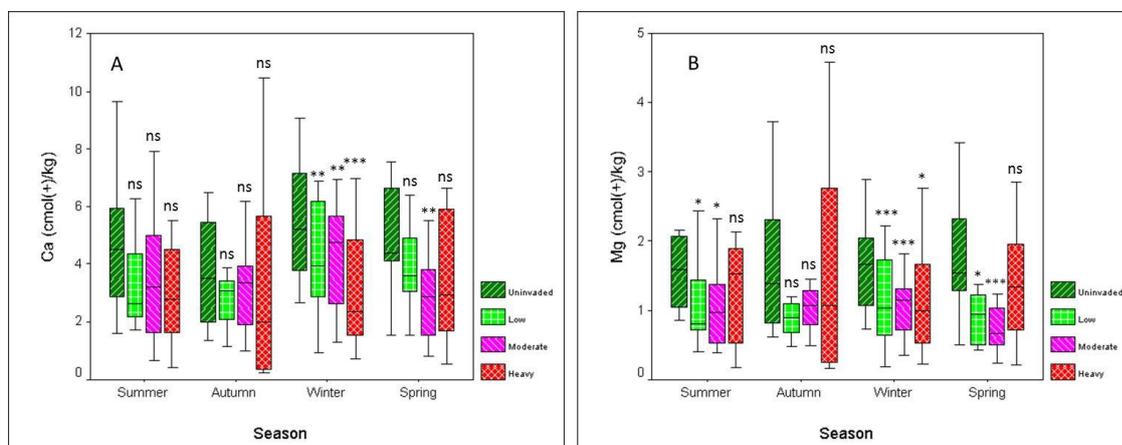


Fig. 5.5. a) Exchangeable Ca and b) exchangeable Mg of lightly, moderately and heavily invaded sites compared to uninvaded reference sites through all seasons along the Berg River in Western Cape Province of South Africa. Significant differences between uninvaded and, lightly, moderately and heavily invaded sites tested by the non-parametric Mann Whitney U test, since all data were not normally distributed. Significance level: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ ; ns – not significant

## 5.4 Discussion

Soils in the study area are from quartzite and sandstone parent materials that are often associated with sandy soils (Cotter, 2000) which are of poor nutrient retention capacity because of insufficient colloidal material (Aweto and Moleele, 2005; del Moral and Muller, 1970; Hazlett et al., 2005). The study area is dominated by well drained sandy soils therefore any clay deposits migrate to deeper layers through illuviation, thereby reducing cation exchange capacity in the rhizosphere of most plants especially native species which often have shallow rooting depths. Vegetation of uninvaded and heavily invaded sites appears to filter sediments in the same way as they had similar proportions of sand, silt and clay. This may be because vegetation at both sets of sites is composed of trees with big stems and little undergrowth (F. Tererai, unpubl. data), and this may partially explain the lack

of significant differences in most soil characteristics measured in this study. Aweto and Moleele (2005) found that an *E. camaldulensis* plantation had higher clay content than a native site in their study of the effects of eucalypts on alluvial soils in Botswana; this is not consistent with our findings. This difference may be explained by the fact that their study was in a terrestrial ecosystem where there are less active hydraulic erosional and depositional processes than in riparian zones where our study was conducted. High clay content often coincides with high C and N (Hazlett et al., 2005), but that was not the case in our study.

Litter cover and thickness tended to increase with increasing cover of *E. camaldulensis*, while soil C tended to decrease. Previous studies have shown that most invasive plant species have a high net primary production (Liao et al., 2008; Lindsay and French, 2005; Vilà et al., 2011), resulting in higher plant biomass compared to native species (Ehrenfeld, 2003). Litter mass may not necessarily be higher (Ehrenfeld, 2003), though in most cases it has different tissue chemistries (Corbin and D'Antonio, 2004, Richardson et al., 2007) and decomposition rates than native species (Ehrenfeld et al., 2001; Vilà et al., 2011). For some *Eucalyptus* species (e.g. *E. camaldulensis*, *E. europphylla* and *E. grandis*), it was found that often litter decomposes at slower rates (Bernhard-Reversat, 1988; Bernhard-Reversat, 1996), probably because of the presence of secondary metabolites (Castro-Díez et al., 2011). This is supported by the fact that uninvaded sites generally had higher C content, though not significantly, yet they had significantly less litter cover and thickness. *Eucalyptus* litter has been reported to be allelopathic (del Moral and Muller, 1970; Khan et al., 2008) and these chemicals may affect decomposition rates, an important regulator of ecosystem productivity (O'Connell, 1988). This may in turn alter the composition of microbial communities (Bernhard-Reversat, 1988), thereby impacting on nutrient mineralization, especially the N cycle. del Moral and Muller (1970) indicated that soil microflora beneath *Eucalyptus* canopy can ameliorate the toxicity of terpenes and phenolics, but this is only through the action of biota that would have adapted to using these toxins, meaning that soil microbial composition will have changed (Ndaw et al., 2009), with possible negative influence on decomposition patterns. *Eucalyptus* litter build-up and its chemical composition may prevent C concentrations in soil to increase, despite higher biomass production and litterfall.

Soil moisture and temperature are very important controls of most soil processes including organic matter mineralization (Adams and Attiwill, 1986; Aweto and Moleele, 2005; O'Connell, 1988). In summer, uninvaded sites had significantly higher moisture compared to lightly invaded sites, and this could be explained by higher insolation in the latter owing to a sparse plant canopy. Uninvaded sites had significantly higher soil moisture in winter and spring (i.e. the rainy seasons) and soil moisture consistently decreased along the invasion gradient, which is the opposite of the results of del Moral and Muller (1970) in the study of a

terrestrial stand of *E. camaldulensis* in California. It would have been expected that heavily invaded sites with thick litter layer would have higher soil moisture content due to the mulching effect (del Moral and Muller, 1970), but eucalypts are known to be able to access water from multiple sources, that is river water during the dry season, ground water during dry season when the rivers have dried up, and soil water during the rainy season (Engel et al., 2005). It is possible that soil moisture in the upper soil layers is depleted faster due to high consumption by *Eucalyptus* (Dye et al., 2004; Dye and Versfeld, 2007; Le Maitre et al., 2002) which has dense roots near the surface (del Moral and Muller, 1970). This may deprive other plant species of moisture, especially those that access water in the upper soil layers; this is likely one reason for the reduced species richness of plants in stands of *E. camaldulensis* in the study area (F. Tererai, unpubl. data). Soil temperatures increased with an increase in *Eucalyptus* cover in winter and spring, when we expected them to decrease. This may be explained by microclimates (Lindsay and French, 2005) that are created by aerial shading and the thick litter layer of *E. camaldulensis*, especially in the absence of fire (O'Connell, 1988). The resulting temperature and moisture conditions may be unfavourable for soil microbial communities on which a lot of native plant species rely.

Consistent with previous studies (Aweto and Moleele, 2005; Berendse, 1998), there is evidence that soil pH is also altered by invasion. Invaded sites had more acidic soils than uninvaded sites; this may be because *E. camaldulensis* takes up or immobilizes nutrients, especially  $\text{Ca}^{2+}$ . A study of Australian *Acacia* species invading the fynbos biome in South Africa showed that these species actually increase soil pH (Musil and Midgley, 1990) as opposed to the reduction effect of *Eucalyptus*. Naudé (2012) however reported lower pH (though not significant) in *Acacia* invaded riparian sites of Mediterranean South Africa. Such effects are likely to be highly site specific (Dassonville et al., 2008). Lower pH beneath *Eucalyptus* has been associated with accumulation of recalcitrant litter (O'Connell, 1988) compared to *Acacia* litter which tends to decompose faster (Marchante et al., 2008; Musil and Midgley, 1990). Low pH levels may limit the growth and activity of decomposing soil microorganisms as soil biological activity is higher in basic than in acidic soil (Castro-Díez et al., 2011) resulting in relatively low macro nutrient concentrations compared to uninvaded sites. Below a pH of 5.5 Mn and aluminium (Al) availability increases to levels that may be unsuitable for plant growth (Berendse, 1998), and soluble P tends to form insoluble compounds with Al and Fe in acidic soils, which are inaccessible to native plants.

In general, uninvaded sites had slightly higher total C, N, P and K concentrations compared to lightly, moderately and heavily invasion sites, though the differences were not significant. Truscott et al. (2008) found similar results in a study of *Mimulus guttatus* invasion of riparian zones in Scotland. This may be explained by a relatively higher pH in uninvaded

sites which favours mineralization. The differences may not have been significant because of possible nutrient leaching in sandy soils (Witkowski, 1991). It may also be that *Eucalyptus* litter takes too long to decompose and gets washed away by flood pulses before nutrients are released hence does not increase C, N and other nutrient pools. These results also concur with those of Aweto and Moleele (2005) who found no significant differences in C and P in a comparative study of soils from an *E. camaldulensis* plantation and an adjoining native savanna woodland. Castro-Díez et al. (2011) also found no evidence to support the hypothesis that the litter of alien species changed soil properties more than native litter in their experimental study in a riparian forest in Spain.

N pools were not significantly different between uninvaded and the gradient of invaded sites, agreeing with the findings of reviews by Ehrenfeld (2003) and Liao et al., (2008) which reported no elevated N especially for non-N-fixing invaders. Despite higher clay content in uninvaded and heavily invaded sites, soil organic C content was similar. Total N, P and K concentrations generally declined, though not statistically significantly, with invasion for all seasons except autumn. A possible reason for these trends is that *E. camaldulensis* litter is of poor nutrient quality (Bernhard-Reversat, 1988), or it has low decomposition rates (Bernhard-Reversat, 1996), or that *Eucalyptus* takes up and immobilizes more nutrients than native plant species. Uninvaded and heavily invaded sites appear to affect total N concentration in a similar way. The soil C/N ratio of all invasion conditions through all seasons did not vary significantly. What is apparent is that the C/N ratios are generally low and this may be attributed to relatively low C, or immobilization of N during decay which is common in mediterranean-type climate ecosystems (Witkowski, 1991). Low C/N ratio causes release of soil N for use by soil microbes, which are normally more competitive than plants, hence plant growth may be suspended contributing to a possible reduction in native plant diversity in invaded sites. The decrease in total organic C with increasing *Eucalyptus* cover could be a consequence of the recalcitrant *Eucalyptus* litter taking long to break down, so the prime supply of C is limited.

Total available N appears to decrease with an increase in *Eucalyptus* cover, and also as moisture decreases in spring and summer. Bernhard-Reversat (1988) also found that N mineralization decreased with dryness.  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N occur in more or less similar quantities in all seasons except in autumn where conditions seem to favour more ammonification than nitrification. This suggests that the system is not accumulating any  $\text{NO}_3^-$ -N, which is highly susceptible to leaching. There only seems to be an accumulation of  $\text{NH}_4^+$ -N in autumn (reasons of which are not clear) which significantly goes down in winter and summer as conditions conducive for N mineralization deteriorate. The decline in total available N in spring and summer along the invasion gradient, which is largely explained by

$\text{NO}_3^-$ -N suggests eucalypts are competitive consumers of N, more so than native species. Fast growing plant species like *Eucalyptus* have been reported to consume large volumes of water owing to high transpiration rates (Malik and Sharma, 1990; Scott et al., 2004) and in the process bring nutrients to their root zone, resulting in high nutrient uptake (Naiman and Decamps, 1997) at the expense of native species.

Total available P showed a similar trend, but only when comparing uninvaded and heavily invaded sites. The transitional invasion conditions (i.e. light and moderate) consistently had higher plant available P levels. This may be because the newly invaded sites may have favourable conditions for P mineralization, especially relatively higher insolation to the ground owing to less aerial plant cover. Similar work by Naudé (2012) in the riparian zones of Western Cape invaded by mainly *Acacia mearnsii* showed elevated available N and enhanced P mineralization which is typical of N-fixing invaders.

The decrease of total available N in winter and spring coincides with the beginning of the rainy season and time of highest concentration of *Eucalyptus* litter terpenes and phenolics on the soil surface. Litter abscission of *Eucalyptus* is at maximum in summer and during this period the terpenes in litter are volatilized and phenolics are accumulating on the soil surface (del Moral and Muller, 1970). By the beginning of the rainy season (winter), the abundant unleached litter then releases phenolic acid and the terpenes are washed in to the soil. The high concentration of toxins is likely to reduce N mineralization at the beginning of the rainy season, as the soil microbial activity gets affected by the toxins (Castro-Díez et al., 2011). The antibiotic effect of litter toxins is however not quite clear in literature (Castro-Díez et al., 2011; Corbin and D'Antonio, 2004). This finding differs from that of Bernhard-Reversat (1988) who found high N mineralization in a terrestrial *Eucalyptus* stand at the beginning of the rainy season, and decreased towards spring in Australia. They attributed the decrease in spring to the depressing effect of herbaceous growth on N mineralization, but this explanation does not apply in our study because there was no undergrowth beneath heavily invaded sites. However, as the moisture season progresses, the allelopathic substances get degraded (del Moral and Muller, 1970). The decrease in available total N also coincides with a period where  $\text{NO}_3^-$ -N gets leached by the rain down the sandy soil layer (Adams and Attiwill, 1986, Bernhard-Reversat, 1996).

The micronutrients, Mn, Zn, Cu, Fe and B showed no clear trends in all the seasons. Mn, Cu, and Zn appeared to be generally lower in the transitional invasion conditions. This pattern follows that in soil pH, which is consistent with soil pH being a key control of micronutrients (Aweto and Moleele, 2005; Castro-Díez et al., 2011). While there are no significant differences in macro and micronutrients, uninvaded sites generally have a higher

capacity to hold nutrients as evidenced by a relatively higher cation exchange content compared to all invasion conditions. Uninvaded and heavily invaded sites have been found to have relatively higher quantities of clay in this study and we would not expect differences in nutrient holding capacity. However, exchangeable nutrient cation content decreased with increasing invasion suggesting that *E. camaldulensis* immobilizes nutrients more than it can recycle them back into the soil (Adams and Attiwill, 1986; Aweto and Moleele, 2005) especially in winter and partially spring; seasons which coincide with low temperatures, high moisture, and high concentration of *Eucalyptus* litter toxins in the soil. These conditions may reduce productivity of native species, especially in the long term.

Lack of significant changes in nutrient concentrations underneath eucalypts compared to uninvaded sites could be attributed to other factors such as well-drained sandy soils which cause nutrient leaching (Lindsay and French, 2005). The layers to which the nutrients are leached may be beyond the rhizosphere of most native species. Another explanation could be that as eucalypts mine for nutrients, they displace cations from mineral soil to the humus, especially  $\text{NO}_3^-$ -N, and the occasional flooding associated with riparian zones washes away the nutrients (Lindsay and French, 2005; Naiman and Decamps, 1997). *Eucalyptus* may be mining nutrients and not recycling them for several reasons including litter of poor nutrient quality and litter with low decomposition rates (Castro-Díez et al., 2011; Ehrenfeld, 2003; Lindsay and French, 2005). The fact that there are generally higher soil nutrients in uninvaded sites may suggest that *E. camaldulensis* immobilizes soil nutrients faster (Adams and Attiwill, 1986) and that *E. camaldulensis* assemblages are less efficient in nutrient cycling than native plant species (Aweto and Moleele, 2005).

## 5.5 Implications for management and restoration

Contrary to the oft-cited generalization that invasive alien plants elevate soil nutrients, we found no evidence to support this notion for *E. camaldulensis* invasions in riparian zones of the Western Cape, South Africa. Our results show that nutrient dynamics in vegetation assemblages dominated by species that produce secondary metabolites in a riparian zone are complex, involving the interplay of numerous factors. However, total macronutrients are generally lower in invaded areas when compared to uninvaded sites though not statistically significantly. Since the soils in the study area are generally of poor nutrient content, a small decrease in nutrient levels may have significant effects on native plant communities. This may mean that *E. camaldulensis* is more competitive in nutrient uptake than native species, contributing to failure of most native species to establish beneath the canopy. Because large quantities of nutrients in riparian zones, especially C are locked up in woody plant biomass,

complete removal will result in nutrient loss (Hazlett et al., 2005; Ellis and Graley, 1983; Turner and Lambert, 2008). Therefore we suggest that reducing the abundance of *E. camaldulensis* in riparian zones is more appropriate in order to curb the drain of soil nutrients.

It is also possible that *E. camaldulensis* is capable of altering the rates of nutrient cycling, but that nutrient release and uptake may balance out, resulting in no detectable change in soil-nutrient levels (Corbin and D'Antonio, 2004). However, after removal, temporal nutrient enrichment may occur if postclearing conditions continue to favour soil biological activity. This may tip the competitive balance in favour of other nonnative species, especially alien annual herbs that were found to be abundant in the seed bank (F. Tererai, unpubl. data). Esler et al. (2008) warned that secondary invasions following management actions in riparian zones may shift the problem from dealing with one tree species invader to a dense cocktail of alien herbs. Multiple controlled burns may help control the secondary invasions and this has been proven to also reduce soil N in California, in the removal of *Cytisus scoparius* and *Genista monspessulana* compared to mechanical removal or a single fire (Corbin and D'Antonio, 2004). However this depends on what invader you are dealing with, in this case this may actually stimulate secondary invasions of *Acacia mearnsii*. While it is not yet clear how persistent the effects of exotic species on soil processes are and how these impacts affect restoration (Corbin and D'Antonio, 2004), we suggest close monitoring postclearing nutrient dynamics as these may impair establishment of native shrubs, especially at the seedling stage (Lindsay and French, 2005).

The findings of this study show that *E. camaldulensis* alters soil physical properties but not nutrient concentrations in riparian zones. This differentiates it from other common invasive alien tree species in riparian zones of the Western Cape such as *Acacia mearnsii* which affect both soil physical and chemical properties, including nutrient concentrations (Naudé, 2012). Additional research is needed to examine the legacy effects of *E. camaldulensis* invasions. Work is also needed to investigate the vertical distribution of nutrients, along the lines of the work of Schilling et al. (2009), to establish whether indeed *Eucalyptus* litter produces more nutrients than native species and if so, whether they are leached or absorbed by the eucalypts themselves. The understanding of these processes may help in the restoration and long-term management of riparian ecosystems.

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## Chapter 6: Conclusions and recommendations

### 6.1 *Eucalyptus camaldulensis* as an invader of riparian zones

Invasion and restoration ecologists worldwide are concerned about the threats that biological invasions pose to ecosystem composition and function (Le Maitre et al., 2002; Werner et al., 2010). However, there is often a poor understanding of the potential effects that specific invasive species have on certain habitats (Eviner and Chapin III, 2003). This has presented challenges for appropriate management and restoration strategies. The rationale of my PhD study was to gain an understanding of how self-sown stands of invasive tree species affect riparian ecosystems. The purpose was to examine changes in riparian geomorphology, above-ground vegetation, soil-stored seed banks and soil characteristics associated with the widespread invasion of a large tree species (*E. camaldulensis*), and to determine the implications for management and restoration. The study successfully addressed these aims, and also served to expose other aspects where further research is needed. While many studies investigate the impacts of invasive species on certain ecosystem components (e.g. soil properties [see Ehrenfeld (2003) for a review] and plant community composition [see Gaertner et al. (2009) for a review]) my study is unique in that it addresses effects of invaders on several different components of the native ecosystem at the same time. Furthermore, my research is the first to investigate the potential effects of self-sown stands of *Eucalyptus* in riparian habitats. The results presented in this thesis will serve to inform management of invasive alien trees, restoration of degraded riparian ecosystems, and have identified some priorities for future research. I hope that the recommendations can also be applied outside South Africa. In this chapter I will consolidate and integrate the findings from the four components of this study: the geomorphology, above-ground vegetation, soil-stored seed banks and soil physical and chemical properties to derive implications for management of *E. camaldulensis* and restoration of degraded riparian ecosystems.

In common with other studies on *Eucalyptus*, though not in riparian habitats, my PhD project established that invasion of *E. camaldulensis* is associated with several changes in riparian ecosystems, but there were also some surprises (Fig. 6.1).

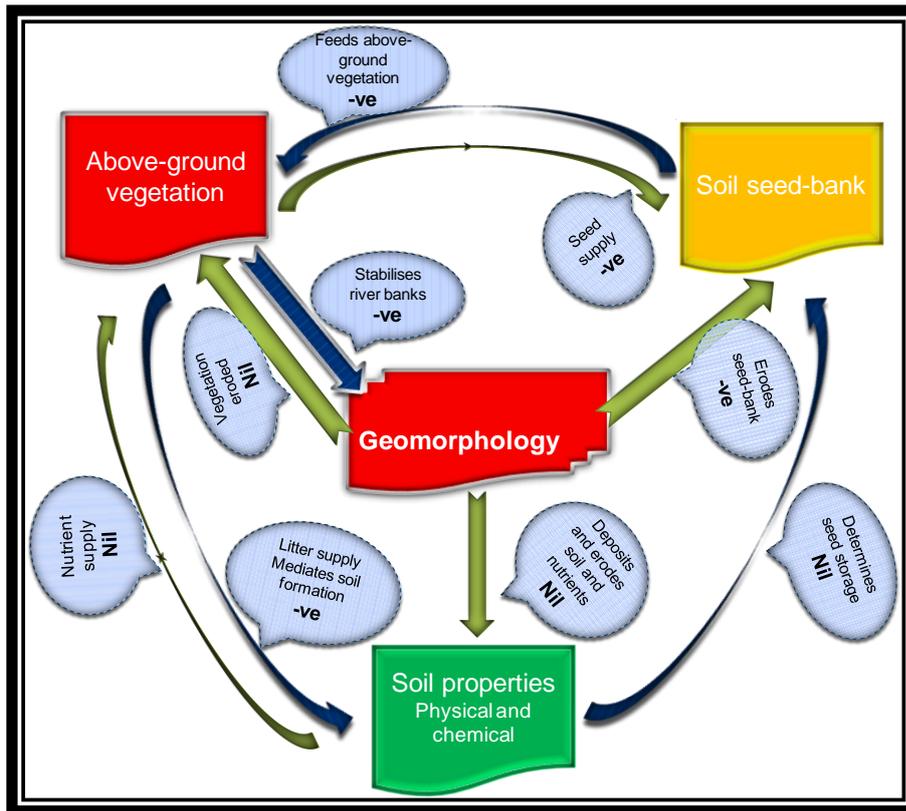


Fig. 6.1. Summary of the key findings of this PhD thesis and a conceptual framework of the effects of *Eucalyptus camaldulensis* invasion in a riparian ecosystem. Tabs with red background show ecosystem components in which over 50 years of invasion has had a negative effect; green - no significant effects have been detected and orange - both negative and positive effects have been detected, but due to changes in other ecosystem components, significant negative effects can be expected in future.

The geomorphological environment provides a physical template in which above-ground vegetation, soil-stored seed bank and soil components exist and any changes in geomorphology may influence the state of the other components (Rowntree, 1991). Evidence of riverbank stabilization and steepening, narrowing of the channel, riverbed incision was detected in the riparian environment. Steepening of the river banks for instance, reduces the capacity of riverbanks to store seeds, to support woody vegetation, and to act as a seed bed for recruitment (Rowntree, 1991). *Eucalyptus camaldulensis* invasion was associated with decreases in native plant species richness and diversity. This decrease in native plant species diversity is envisaged to translate to a reduction in the diversity of native soil-stored seed banks, and eventually to a depletion of the native soil-stored seed bank in the long term. Surprisingly, more than 50 years of *Eucalyptus* invasion has not yet resulted in a depauperate soil-stored seed bank in this riparian ecosystem. An important finding is that besides *Eucalyptus*, *Acacia mearnsii* occurred in very small numbers in above-ground vegetation, but in large number in the soil-stored seed bank (F. Tererai, unpubl. data). This

shows that despite small numbers in above-ground vegetation, which may be due to shading by eucalypts, the *Acacia mearnsii* seed in the soil is likely to pose a threat of secondary invasions after clearing of *Eucalyptus* (Esler et al., 2008; French et al., 2011). Soil physical and chemical properties did not exhibit any significant changes associated with *Eucalyptus* invasion. This is despite changes in litter composition and quality due to changes in species composition, especially replacement of a multi-species ecosystem with a mono-specific *Eucalyptus* assemblage. Even though no significant changes could be detected in some components of the riparian ecosystem, there is potential that these may become significant with time.

## 6.2 Novelty of my research

This research sheds light on the potential effects that invasive alien trees are likely to have in small but very important landscape elements – riparian zones. My PhD is the first to examine the effects of self-sown invasive *E. camaldulensis* in a riparian ecosystem in order to inform management and restoration. Previous literature mostly studied ecosystem-level effects (e.g. high water consumption, changes in fire regimes) of eucalypts, and comparatively fewer studies examined community-level effects (e.g. suppression of native species). The findings of the study constitute two major contributions to the literature on invasion and restoration ecology.

First, I studied a combination of ecosystem and community-level effects, and explored their interactions as well as implications of changes in one to the other. This helped to provide a holistic picture of the effects of *E. camaldulensis* and to inform long term and sustainable management and restoration. Management and restoration perspectives based on isolated components of the riparian habitat are of limited value (Gregory et al., 1991; Busch and Smith, 1995; Eviner and Chapin III, 2003). For instance, if one had only studied above-ground vegetation, results would have understated the real threat of imminent secondary invasions, which is apparent only from a study of the soil-stored seed bank. A multidimensional study of this nature helps to reduce uncertainty over causation, that is, studying several key aspects of an ecosystem eliminates some factors, thus narrowing down to only those for which significant associations with invasion are detected.

Second, invasion ecologists have faced methodological limitations in studying the effects of invasive plants, especially large tree species. Traditionally, studies on the effects of invasive plants on native species used a binary comparative approach of invaded and uninvaded sites. This approach has been criticised for its failure to separate causes and

effects of invasion. I applied an observational comparative approach with gradient sampling, that is, I compared uninvaded sites and a continuum of invaded sites based on aerial cover of the invader. This approach enabled the detection of trends in changes in the riparian zone in line with varying invasion densities. This method increased our confidence of the association of detected changes in the riparian ecosystem to invasion.

I used photogrammetry and GIS, techniques that have not been widely used to detect geomorphological changes associated with invasive alien trees. The results show that there is potential in the application of these techniques.

### **6.3 Implications for management and restoration**

The goal of controlling invasion should be the restoration of ecosystem function as opposed to the ideal, but often untenable, aim of restoring a degraded ecosystem to its pre-invasion state. The aim of controlling *Eucalyptus* invasion is to reduce its influence and maintain the riparian zone at levels where the natural disturbances determine its state.

The findings of all four components suggest the need for management of *E. camaldulensis* invasions at the Berg River. Reducing the density, rather than total clearing at the beginning appears to be the most appropriate intervention. This is considering that total clearing may destabilise riverbanks and promote proliferation of invasive alien plants. Selected native shrub species co-exist with *Eucalyptus* and a reduction in density of the later will enable recovery of these remnant native species post-clearing. I also assume that native species will resume seed production that has been observed to be suppressed (F. Tererai, unpubl. data). A reduction in density of eucalypts, as opposed to total clearing will also ensure recovery of above-ground vegetation without significant destabilisation of the river channel.

The results of the above-ground vegetation and seed bank studies revealed that secondary invasions are an imminent threat after clearing of *E. camaldulensis*. It is possible that the invasion problem may just change form, from the problem of dealing with individual trees to a cocktail of alien herbs (Esler et al., 2008) or other invasive tree species, probably *Acacia mearnsii*. I propose that a reduction of density rather than total clearing which exposes the ground to new conditions (e.g. immediate full insolation) may reduce the aggressiveness of opportunist alien herb and tree species that are present in the seed bank. It is also important to devise methods to deal with secondary invasions as they may suppress native plant species recovery, especially through seed recruitment. Possible

methods to use would be hand-pulling of seedling or spraying, but the latter appears more practical.

It is important to note that even for those aspects that did not exhibit significant changes, there is no room for complacency. The riparian zone is a dynamic complex of interrelated systems and a change in one may trigger a chain reaction. The fact that no significant changes have been detected in soil-nutrient content may simply mean that not enough time has elapsed for such changes to manifest, or that there are confounding factors. Continuous monitoring of the various aspects of the ecosystem is therefore imperative.

#### **6.4 Challenges**

Some challenges were encountered during my project. The main one was the clearing of some of the study sites before data collection was completed. The collection of temperature, moisture and soil samples was disrupted by these clearing operations in the Berg River. Two solutions were adopted: 1) Two of the heavily invaded sites that were cleared were replaced with similar sites within a distance of 100 m; and 2) An arrangement was made with WfW, the authority responsible for the clearing, and the contractors to make sure that study sites were not disturbed. Another challenge, closely related to clearing, was the loss of some of the moisture and temperature data loggers. Fortunately I had at least three at any one site, so there was no total loss of data at any site.

Other challenges were methodological. In contrast to the other literature on the effects on invasive alien trees in riparian habitats, I studied a relatively small perennial river that is densely invaded such that terrain modeling for the purposes of reconstructing historical changes was difficult. The current results of the geomorphology component are only indicative of change, but quantification was not possible for some channel parameters such as historical channel depth. This requires long-term field measurements and monitoring of the same sites on which cross sectional surveys have been conducted in this study.

Finally, I must caution that although the approach yielded satisfactory results, and improves our scientific basis for decision making, it is not a panacea as one can still not be absolute about causation. Another methodology-related challenge is that effects of invasion are not confined to human life span such that often times an ecologist is faced with a situation where they may need to know the history of invasion and changes in an ecosystem

in order to appropriately design management and restoration strategies, as well as predicting future trends.

### **6.5 Priorities for future research**

In the geomorphology component, there is need for continuous monitoring of channel morphological properties through field measurements. Monitoring will help with quantifying changes in channel morphology, compared to attempting to reconstruct the history, which is often difficult and time consuming. Further research work is needed to determine whether riparian vegetation is only responding to changes and interacting with channel morphology, or is driving the change. Agriculture emerged as one of the key controls of riparian zone dynamics and there is need for further research to establish the actual contribution of agricultural activities in shaping river morphometry.

The gradient comparative approach yielded satisfactory results for the above-ground vegetation and soil studies. However, because of the uncertainties associated with assigning causation, some ecologists have proposed experimental approaches, involving either removal or introduction (Hejda and Pyšek, 2006; Hulme and Bremner, 2006; Truscott et al., 2008). However, this approach is difficult for studies of large tree invaders because of the high costs of clearing, the unethical nature of introductions especially in sensitive ecosystems such as riparian zones, or the long time it takes for native plant communities to respond after clearing. For this study system, opportunities for an experimental clearing approach exists as some of the heavily invaded sites used in this study have already been cleared or are targeted for clearing in the near future (Ruwanza et al., 2012). Further experimental work is needed to determine the mechanisms responsible for changes associated with *Eucalyptus* invasion.

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**SUPPLEMENTARY MATERIAL:****Appendix 3.1.**

Species composition in plots along the invasion gradient from “uninvaded”, “lowly”, “moderately” and “heavily” invaded plots along the Berg River, Western Cape, South Africa. Mean relative species covers are shown (n = 30 uninvaded plots; 19 lowly invaded plots; 25 moderately invaded plots; and 25 heavily invaded plots). Only species with at least 1% mean cover in one treatment are shown. Aliens are indicated by (\*)

Species	Species code	Family	Growth form	Uninvaded	Low	Moderate	Heavy
<i>Acacia mearnsii</i> *	AcacMear	Fabaceae	Tree	-	8.1	4.1	13.5
<i>Diospyros glabra</i>	DiosGlab	Ebenaceae	Shrub	2.6	1.4	5.2	8.1
<i>Eucalyptus camaldulensis</i> *	EucaCama	Myrtaceae	Tree	1.8	6.8	11.6	23.0
<i>Kiggelaria africana</i>	KiggAfri	Kiggelariaceae	Tree	7.9	6.8	7.6	8.1
<i>Oxalis purpurea</i>	OxalPurp	Oxalidaceae	Geophyte	1.3	-	-	1.4
<i>Searsia angustifolia</i>	RhusAngu	Anacardiaceae	Small Tree	3.5	2.7	2.9	5.4
<i>Rubus fruticosus</i> *	RubuFrut	Rosaceae	Shrub	2.2	-	2.3	4.1
<i>Solanum pseudocapsicum</i> *	SolaPseu	Solanaceae	Forb	3.5	-	-	1.4
<i>Zantedeschia aethiopica</i>	ZantAeth	Araceae	Geophyte	11.8	2.7	8.1	10.8
<i>Bromus catharticus</i> *	BromCart	Poaceae	Grass	3.5	5.9	4.1	1.4
<i>Cissampelos capensis</i>	CissCape	Menispermaceae	Vine	5.3	-	4.1	1.4
<i>Cynodon dactylon</i> *	CynoDact	Poaceae	Grass	-	1.4	1.2	1.4
<i>Melianthus major</i>	MeliMajo	Meliantaceae	Shrub	2.2	0.9	-	1.4
<i>Oxalis pes-caprae</i>	OxalPes-	Oxalidaceae	Geophyte	3.1	-	1.2	1.4
<i>Asparagus africanus</i>	AspeAfri	Asperagaceae	Shrub	2.6	1.8	3.5	-
<i>Isolepis antarctica</i>	IsopAnta	Cyperaceae	Grass	-	-	-	-
<i>Lactuca serriola</i> *	LactSeri	Asteraceae	Forb	-	5.9	3.5	-
<i>Chenopodium ambrosioides</i> *	ChenAlbu	Chenopodiaceae	Shrub	2.6	1.8	2.3	-
<i>Podocarpus elongatus</i>	PodoElon	Podocarpaceae	Tree	6.6	-	1.7	-
<i>Rumex crispus</i> *	RumeCris	Polygonaceae	Forb	4.4	3.6	2.9	-
<i>Stellaria media</i> *	StelMedi	Caryophyllaceae	Forb	1.8	-	3.5	-
<i>Xanthium strumarium</i> *	XantStru	Asteraceae	Forb	1.8	1.4	-	-
<i>Persicaria lapathifolia</i> *	PersLapa	Polygonaceae	Forb	-	-	1.7	1.4
<i>Sonchus oleraceus</i> *	SoncOler	Asteraceae	Forb	2.2	1.4	1.7	-
<i>Halleria lucida</i>	HallLuci	Scrophlariaceae	Small Tree	-	1.8	1.7	-
<i>Cyperus rotunda</i>	CypeRotu	Poaceae	Grass	-	0.5	-	-
<i>Fumaria muralis</i> *	FumaMura	Fumariaceae	Forb	1.3	5.0	1.2	-
<i>Solanum nigrum</i> *	SolaNigr	Solanaceae	Forb	2.2	5.4	1.2	1.4
<i>Taraxacum officinale</i> *	TaraOffi	Asteraceae	Forb	-	-	-	4.1
<i>Senecio halimifolius</i>	SeneHali	Asteraceae	Shrub	-	1.4	-	1.4
<i>Melasphaerula</i>	MelaRamo	Iridaceae	Geophyte	3.5	-	-	-

<i>ramosa</i>							
<i>Cheilanthes capensis</i> *	CheiCape	Sinopteridaceae	Fern	1.3	-	-	-
<i>Maytenus Oleoides</i>	MaytOleo	Celastraceae	Tree	4.8	-	-	-
<i>Olea europaea</i> ssp. <i>Africana</i>	OleaEuro	Oleaceae	Tree	3.5	1.8	2.9	2.7
<i>Tradescantia flumensis</i> *	TradFlum	Commelinaceae	Forb	-	2.7	4.1	1.4
<i>Picris echioides</i> *	PicrEchi	Asteraceae	Forb	-	-	-	-
<i>Sonchus asper</i> *	SoncAspe	Asteraceae	Forb	-	3.6	-	1.4
<i>Solanum mauritianum</i> *	SolaMaur	Solanaceae	Tree	-	-	-	1.4
<i>Briza minor</i> *	BrizMino	Poaceae	Grass	-	1.4	-	-
<i>Echium plantagineum</i> *	EchiPlan	Boraginaceae	Forb	-	1.4	-	-
<i>Erodium moschatum</i> *	ErodMosc	Geraniaceae	Forb	-	2.3	-	-
<i>Bromus diandrus</i> *	BromDian	Poaceae	Grass	-	3.2	-	-
<i>Phytolacca octandra</i> *	PhytOcta	Phytolaccaceae	Shrub	-	3.6	1.2	-
<i>Arundo donax</i> *	ArunDona	Poaceae	Reed	-	-	1.2	-
<i>Panicum maximum</i>	PaniMaxi	Poaceae	Grass	-	-	1.7	-
<i>Tropaelium majus</i> *	TropMaju	Tropaeolaceae	Forb	-	-	2.3	-
<i>Araujia sericifera</i> *	ArauSeri	Apocynaceae	Vine	-	-	1.7	-
<i>Oxalis capensis</i>	OxalCape	Oxalidaceae	Geophyte	-	-	1.7	-
<i>Leonotis leonurus</i>	LeonLeon	Lamiaceae	Shrub	-	-	-	1.4

**Appendix 3.2.**

Results of similarity percentages analysis (SIMPER) summarizing the species contributing significantly to observed differences uninvaded (n=30); lowly (n=19); moderately (n=25); and heavily (n=25) invaded plots based on species abundance measure from the 10 m x 5 m plots along the Berg River, Western Cape, South Africa. For full species names see appendix A.

*“Uninvaded” Sites**Average similarity: 26.01*

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
ZantAeth	3.58	8.28	0.87	31.84	31.84
PodoCarp	3.31	6.55	0.5	25.17	57
KiggAfri	2.83	4.65	0.5	17.87	74.87
Tree1111	1.72	2.27	0.31	8.74	83.61
OleaEuro	1.11	0.72	0.21	2.76	86.36
RhusAngu	0.63	0.5	0.21	1.93	88.3
GrasGeop	0.74	0.47	0.21	1.82	90.12

*“Lowly” invaded sites**Average similarity: 24.07*

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
AcacMear	2.81	8.57	0.68	35.6	35.6
BromCart	2.11	4.48	0.67	18.59	54.19
KiggAfri	1.8	2.74	0.4	11.38	65.57
RhusAngu	0.95	1.11	0.28	4.63	70.2
RumeCris	0.71	0.89	0.26	3.69	73.9
SolaNigr	0.45	0.89	0.42	3.69	77.58
OleaEuro	1.06	0.85	0.19	3.55	81.14
BromDian	0.49	0.81	0.31	3.37	84.51
ZantAeth	0.83	0.65	0.2	2.71	87.22
LactSeri	0.48	0.59	0.39	2.44	89.66
ErodMosc	0.73	0.57	0.22	2.36	92.01

*“Moderately” invaded sites**Average similarity: 17.47*

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
KiggAfri	2.62	7.48	0.53	42.8	42.8
ZantAeth	1.86	2.67	0.35	15.29	58.09
TradFlum	1.76	2.05	0.22	11.74	69.83
OleaEuro	0.78	0.75	0.18	4.29	74.13
DiosGlab	0.76	0.73	0.34	4.2	78.33
BromCart	1.26	0.73	0.18	4.16	82.49
AspaAfri	0.83	0.62	0.21	3.55	86.04
AcacMear	0.58	0.55	0.21	3.16	89.21
RhusAngu	0.86	0.43	0.13	2.48	91.69

*“Heavily” invaded*

*Average similarity: 18.20*

<b>Species</b>	<b>Av.Abund</b>	<b>Av.Sim</b>	<b>Sim/SD</b>	<b>Contrib%</b>	<b>Cum.%</b>
AcacMear	2.73	10.74	0.57	59	59
KiggAfri	1.64	2.76	0.46	15.17	74.18
ZantAeth	0.59	2.01	0.29	11.04	85.22
FumaMura	1.2	0.74	0.19	4.06	89.28
DiosGlab	0.39	0.53	0.2	2.9	92.18

#### Appendix 4.1.

Plant species and their percentage frequency recorded in the germination greenhouse experiment on soils collected from top 10cm of the mineral soil profile of the Berg River riparian zone along a gradient of *Eucalyptus camaldulensis* invasion from uninvaded, low, moderate and heavy. Species with an asterisk are alien.

Species	Code	family	Growth form	common name	Status	Uninvaded %	Low %	Moderate %	Heavy %
<i>Acacia longifolia</i> *	AcacLong	Fabaceae	Tree	Long-leaved wattle	Alien	0.00	8.33	8.33	5.00
<i>Acacia mearnsii</i> *	AcacMear	Fabaceae	Tree	Black wattle	Alien	37.50	91.67	91.67	90.00
<i>Acacia saligna</i> *	AcacSalig	Fabaceae	Tree	Port Jackson	Alien	0.00	8.33	8.33	0.00
<i>Arctotheca calendula</i>	ArctCale	Asteraceae	Forb	Cape weed	Native	18.75	8.33	8.33	5.00
<i>Briza minor</i> *	BrizMino	Poaceae	Grass	Little quaking grass	Alien	12.50	8.33	8.33	15.00
<i>Bromus catharticus</i> *	BromCart	Poaceae	Grass	Rescuegrass	Alien	50.00	83.33	83.33	25.00
<i>Bromus diandrus</i> *	BromDian	Poaceae	Grass	Rippgut brome	Alien	0.00	41.67	41.67	10.00
<i>Chenopodium album</i> *	ChenAlbu	Amaranthaceae	Forb	White goose foot	Alien	37.50	16.67	16.67	20.00
<i>Chenopodium ambrosioides</i> *	ChenAmbr	Chenopodiaceae	Shrub	Wormseed goosefoot	Alien	100.00	75.00	75.00	65.00
<i>Cirsium vulgare</i> *	CirsVulg	Asteraceae	Forb	Scotch thistle	Alien	0.00	8.33	8.33	0.00
<i>Cissampelos capensis</i>	CissCape	Menispermaceae	Vine	Davidjies	Native	6.25	8.33	8.33	0.00
<i>Conyza bonariensis</i> *	ConyBona	Asteraceae	Forb	Horseweed fleabane	Alien	87.50	83.33	83.33	80.00
<i>Cynodon dactylon</i> *	CynoDact	Poaceae	Grass	Bermuda grass	Alien	0.00	0.00	0.00	10.00
<i>Cyperus rotunda</i>	CypeRotu	Poaceae	Grass	Coco-grass	Native	68.75	83.33	83.33	45.00
<i>Digitaria sanguinalis</i> *	DigiSang	Poaceae	Grass	Crabgrass	Alien	18.75	25.00	25.00	10.00
<i>Diospyros glabra</i>	DiosGlab	Ebenaceae	Shrub	Fynbos Star-apple	Native	0.00	0.00	0.00	5.00
<i>Echium plantagineum</i> *	EchiPlan	Boraginaceae	Forb	Patterson's curse	Alien	12.50	0.00	0.00	5.00
<i>Erodium moschatum</i> *	ErodMosc	Geraniaceae	Forb	Musky heron's bill	Alien	6.25	41.67	41.67	15.00
<i>Erucastrum austroafricanum</i>	ErucAust	Brassicaceae	Forb		Native	0.00	8.33	8.33	25.00
<i>Eucalyptus camaldulensis</i> *	EucaCama	Myrtaceae	Tree	River red gum	Alien	56.25	50.00	50.00	30.00
<i>Euphorbia helioscopia</i> *	EuphHeli	Euphorbiaceae	Forb	Umbrella milkweed	Alien	18.75	16.67	16.67	0.00
<i>Fumaria muralis</i> *	FumaMura	Fumariaceae	Forb	Fumitory	Alien	6.25	75.00	75.00	20.00
<i>Helichrysum asperum</i>	HeliAspe	Asteraceae	Forb		Native	6.25	0.00	0.00	5.00

<i>Isolepis antarctica</i>	IsopAnta	Cyperaceae	Grass	Sedge	Native	75.00	58.33	58.33	90.00
<i>Kiggelaria africana</i>	KiggAfri	Kiggelariaceae	Tree	Wild peach	Native	12.50	0.00	0.00	10.00
<i>Lactuca serriola</i> *	LactSeri	Asteraceae	Forb	Prickly lettuce	Alien	93.75	75.00	75.00	65.00
<i>Leonotis leonurus</i>	LeonLeon	Lamiaceae	Shrub	Wild dagga	Native	0.00	16.67	16.67	10.00
<i>Lolium multiflorum</i> *	LoliMult	Poaceae	Grass	Italian ryegrass	Alien	56.25	33.33	33.33	40.00
<i>Malva parviflora</i> *	MalvParv	Malvaceae	Forb	Small mallow	Alien	18.75	0.00	0.00	5.00
<i>Medicago polymorpha</i> *	MediPoly	Fabaceae	Forb	bur clover	Alien	12.50	0.00	0.00	0.00
<i>Melaspheerula ramosa</i>	MelaRamo	Iridaceae	Geophyte	Fairy-Bells	Native	18.75	8.33	8.33	0.00
<i>Melianthus major</i>	MeliMajo	Meliantaceae	Shrub	Honey bush	Native	0.00	16.67	16.67	0.00
<i>Olea europaea ssp. Africana</i>	OleaEuro	Oleaceae	Tree	Wild olive	Native	12.50	0.00	0.00	0.00
<i>Oxalis pers-caprae</i>	OxalPesc	Oxalidaceae	Geophyte	Cape sorrel	Native	6.25	50.00	50.00	20.00
<i>Oxalis purpurea</i>	OxalPurp	Oxalidaceae	Geophyte	Purple woodsorrel	Native	12.50	25.00	25.00	0.00
<i>Oxalis species</i>	OxalSpec	Oxalidaceae	Geophyte		Native	6.25	8.33	8.33	0.00
<i>Persicaria lapathifolia</i> *	PersLapa	Polygonaceae	Forb	Spotted knotweed	Alien	6.25	33.33	33.33	5.00
<i>Phytolacca octandra</i> *	PhytOcta	Phytolaccaceae	Shrub	Forest inkberry	Alien	6.25	91.67	91.67	20.00
<i>Picris echioides</i> *	PicrEchi	Asteraceae	Forb	Oxtongue	Alien	50.00	50.00	50.00	25.00
<i>Poa annua</i> *	PoaAnnua	Poaceae	Grass	Annual meadow grass	Alien	12.50	8.33	8.33	20.00
<i>Podocarpus elongatus</i>	PodoElon	Podocarpaceae	Tree	Yellow wood	Native	12.50	8.33	8.33	0.00
<i>Rumex crispus</i> *	RumeCris	Polygonaceae	Forb	Curly dock	Native	93.75	83.33	83.33	55.00
<i>Selago canescens</i>	SelaCane	Scrophulariaceae	Shrub	Bitter bush	Native	0.00	8.33	8.33	0.00
<i>Senecio halimifolius</i>	SeneHali	Asteraceae	Shrub		Native	12.50	66.67	66.67	60.00
<i>Sesbania punicea</i> *	SesbPune	Fabaceae	Shrub	Red sesbania	Alien	6.25	0.00	0.00	0.00
<i>Sida cordifolia</i> *	SidaCord	Malvaceae	Forb	Heart-leaf sida	Alien	0.00	0.00	0.00	0.00
<i>Solanum mauritianum</i> *	SolaMaur	Solanaceae	Tree	Bugweed	Alien	0.00	8.33	8.33	0.00
<i>Solanum nigrum</i> *	SolaNigr	Solanaceae	Forb	Black nightshade	Alien	87.50	91.67	91.67	75.00
<i>Solanum pseudocapsicum</i> *	SolaPseu	Solanaceae	Forb	Jerusalem Cherry	Alien	25.00	0.00	0.00	0.00
<i>Solanum retroflexum</i> *	SolaRetr	Solanaceae	Forb	Wonderberry	Alien	100.00	100.00	100.00	85.00
<i>Sonchus asper</i> *	SoncAspe	Asteraceae	Forb	Sharp-fringed Sow	Alien	25.00	41.67	41.67	15.00

				Thistle					
<i>Sonchus oleraceus</i> *	SoncOler	Asteraceae	Forb	Sow thistle	Alien	68.75	66.67	66.67	65.00
<i>Stellaria media</i> *	StelMedi	Caryophyllaceae	Forb	Chickweed	Alien	75.00	50.00	50.00	30.00
<i>Stoebe plumosa</i>	StoePlum	Asteraceae	Shrub	'khoi'-kooigoed	Native	12.50	8.33	8.33	15.00
<i>Taraxacum officinale</i> *	TaraOffi	Asteraceae	Forb	Common dandelion	Alien	12.50	0.00	0.00	25.00
<i>Trifolium repens</i> *	TrifRepe	Fabaceae	Forb	White clover	Alien	25.00	0.00	0.00	0.00
<i>Tropaelium majus</i> *	TropMaju	Tropaeolaceae	Forb	Nasturtium	Alien	0.00	0.00	0.00	0.00
<i>Verbiana bonarensis</i> *	VerbBona	Verbenaceae	Forb	Purple top	Alien	31.25	16.67	16.67	20.00
<i>Xanthium strumarium</i> *	XantStru	Asteraceae	Forb	Large cocklebur	Alien	37.50	0.00	0.00	15.00
<i>Zantedeschia aethiopica</i>	ZantAeth	Araceae	Geophyte	Arum lily	Native	37.50	25.00	25.00	10.00

#### Appendix 4.2.

Plant species and their percentage frequency recorded in the germination greenhouse experiment on soils collected from bottom 10cm of the mineral soil profile of the Berg River riparian zone along a gradient of *Eucalyptus camaldulensis* invasion from uninvaded, low, moderate and heavy. Species with an asterisk are alien.

Species	Code	family	Growth form	common name	Uninvaded %	Low %	Moderate %	Heavy %
<i>Acacia longifolia</i> *	AcacLong	Fabaceae	Tree	Long-leaved wattle	6.25	0.00	0.00	14.29
<i>Acacia mearnsii</i> *	AcacMear	Fabaceae	Tree	Black wattle	31.25	91.67	75.00	95.24
<i>Acacia saligna</i> *	AcacSalig	Fabaceae	Tree	Port Jackson	0.00	8.33	6.25	4.76
<i>Arctotheca calendula</i>	ArctCale	Asteraceae	Forb	Cape weed	12.50	8.33	31.25	28.57
<i>Aspalathus species</i>	AspeSpec	Fabaceae	Shrub	Cape gorse	6.25	0.00	0.00	4.76
<i>Briza minor</i> *	BrizMino	Poaceae	Grass	Little quaking grass	0.00	33.33	12.50	4.76
<i>Bromus catharticus</i> *	BromCart	Poaceae	Grass	Rescuegrass	37.50	83.33	18.75	28.57
<i>Bromus diandrus</i> *	BromDian	Poaceae	Grass	Ripgut brome	0.00	16.67	0.00	9.52
<i>Cirsium vulgare</i> *	CirsVulg	Asteraceae	Forb	Scotch thistle	6.25	0.00	6.25	4.76
<i>Chenopodium album</i> *	ChenAlbu	Amaranthaceae	Forb	White goose foot	50.00	25.00	37.50	47.62
<i>Chenopodium ambrosioides</i> *	ChenAmbr	Chenopodiaceae	Shrub	Wormseed goosefoot	100.00	100.00	93.75	66.67
<i>Conyza bonariensis</i> *	ConyBona	Asteraceae	Forb	Horseweed fleabane	68.75	41.67	56.25	42.86

<i>Cynodon dactylon</i> *	CynoDact	Poaceae	Grass	Bermuda grass	0.00	8.33	6.25	4.76
<i>Cyperus rotunda</i>	CypeRotu	Poaceae	Grass	Coco-grass	81.25	100.00	93.75	76.19
<i>Digitaria sanguinalis</i> *	DigiSang	Poaceae	Grass	Crabgrass	0.00	25.00	50.00	14.29
<i>Echium plantagineum</i> *	EchiPlan	Boraginaceae	Forb	Patterson's curse	0.00	0.00	12.50	9.52
<i>Erodium moschatum</i> *	ErodMosc	Geraniaceae	Forb	Musky heron's bill	6.25	50.00	18.75	14.29
<i>Erucastrum austroafricanum</i>	ErucAust	Brassicaceae	Forb		0.00	8.33	6.25	19.05
<i>Eucalyptus camaldulensis</i> *	EucaCama	Myrtaceae	Tree	River red gum	6.25	8.33	6.25	23.81
<i>Euphorbia helioscopia</i> *	EuphHeli	Euphorbiaceae	Forb	Umbrella milkweed	6.25	16.67	31.25	4.76
<i>Fumaria muralis</i> *	FumaMura	Fumariaceae	Forb	Fumitory	0.00	91.67	37.50	23.81
<i>Isolepis antarctica</i>	IsopAnta	Cyperaceae	Grass	Sedge	87.50	100.00	100.00	95.24
<i>Kiggelaria africana</i>	KiggAfri	Kiggelariaceae	Tree	Wild peach	6.25	8.33	0.00	9.52
<i>Lactuca serriola</i> *	LactSeri	Asteraceae	Forb	Prickly lettuce	50.00	16.67	25.00	23.81
<i>Leonotis leonurus</i>	LeonLeon	Lamiaceae	Shrub	Wild dagga	0.00	58.33	25.00	9.52
<i>Lolium multiflorum</i> *	LoliMult	Poaceae	Grass	Italian ryegrass	31.25	25.00	31.25	33.33
<i>Malva parviflora</i> *	MalvParv	Malvaceae	Forb	Small mallow	12.50	8.33	0.00	9.52
<i>Medicago polymorpha</i> *	MediPoly	Fabaceae	Forb	bur clover	18.75	16.67	18.75	4.76
<i>Melasmaerula ramosa</i>	MelaRamo	Iridaceae	Geophyte	Fairy-Bells	12.50	8.33	0.00	4.76
<i>Melianthus major</i>	MeliMajo	Meliantaceae	Shrub	Honey bush	0.00	8.33	0.00	4.76
<i>Oxalis pers-caprae</i>	OxalPesc	Oxalidaceae	Geophyte	Cape sorrel	0.00	50.00	18.75	23.81
<i>Oxalis purpurea</i>	OxalPurp	Oxalidaceae	Geophyte	Purple woodsorrel	6.25	41.67	0.00	4.76
<i>Persicaria lapathifolia</i> *	PersLapa	Polygonaceae	Forb	Spotted knotweed	0.00	8.33	12.50	19.05
<i>Phytolacca octandra</i> *	PhytOcta	Phytolaccaceae	Shrub	Forest inkberry	0.00	66.67	25.00	33.33
<i>Picris echioides</i> *	PicrEchi	Asteraceae	Forb	Oxtongue	50.00	25.00	37.50	19.05
<i>Poa annua</i> *	PoaAnnua	Poaceae	Grass	Annual meadow grass	12.50	0.00	6.25	9.52
<i>Rubus fruticosus</i> *	RubuFrut	Rosaceae	Shrub	European blackberry	6.25	8.33	6.25	23.81
<i>Rumex crispus</i> *	RumeCris	Polygonaceae	Forb	Curly dock	87.50	75.00	75.00	71.43
<i>Senecio halimifolius</i>	SeneHali	Asteraceae	Shrub		6.25	66.67	12.50	52.38

<i>Sesbania punicea</i> *	SesbPune	Fabaceae	Shrub	Red sesbania	0.00	0.00	0.00	14.29
<i>Sida cordifolia</i> *	SidaCord	Malvaceae	Forb	Heart-leaf sida	6.25	0.00	18.75	4.76
<i>Solanum nigrum</i> *	SolaNigr	Solanaceae	Forb	Black nightshade	37.50	100.00	75.00	57.14
<i>Solanum pseudocapsicum</i> *	SolaPseu	Solanaceae	Forb	Jerusalem Cherry	25.00	0.00	0.00	4.76
<i>Solanum retroflexum</i> *	SolaRetr	Solanaceae	Forb	Wonderberry	87.50	100.00	87.50	76.19
<i>Sonchus asper</i> *	SoncAspe	Asteraceae	Forb	Sharp-fringed Sow Thistle	0.00	16.67	6.25	9.52
<i>Sonchus oleraceus</i> *	SoncOler	Asteraceae	Forb	Sow thistle	6.25	25.00	25.00	28.57
<i>Stellaria media</i> *	StelMedi	Caryophyllaceae	Forb	Chickweed	75.00	41.67	43.75	28.57
<i>Stoebe plumosa</i>	StoePlum	Asteraceae	Shrub	'khoi'-kooigoed	0.00	8.33	6.25	14.29
<i>Taraxacum officinale</i> *	TaraOffi	Asteraceae	Forb	Common dandelion	6.25	8.33	0.00	4.76
<i>Trifolium repens</i> *	TrifRepe	Fabaceae	Forb	White clover	18.75	0.00	0.00	9.52
<i>Tropaelium majus</i> *	TropMaju	Tropaeolaceae	Forb	Nasturtium	0.00	0.00	12.50	4.76
<i>Verbiana bonarensis</i> *	VerbBona	Verbenaceae	Forb	Purple top	25.00	16.67	31.25	4.76
<i>Xanthium strumarium</i> *	XantStru	Asteraceae	Forb	Large cocklebur	6.25	8.33	6.25	4.76
<i>Zantedeschia aethiopica</i>	ZantAeth	Araceae	Geophyte	Arum lily	31.25	25.00	6.25	14.29