Alison Midgley

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Biological Sciences
Thesis

Plant Community Patterns and Diversity in sites impacted by Eucalyptus Camuldulensis Dehnh.:

Insights from the Berg River, Western Cape

Abstract:

Alien *Eucalyptus* and *Acacia* species are amongst the most prolific invaders of the Berg River catchment, in the Western Cape. This study assessed the effects of invasive species and the potential for passive successional restoration in a heavily invaded riparian site (>80% aerial cover), a cleared riparian site and a pristine reference site. Three plots were demarcated per site, and transects were taken perpendicular to the river on the lower, middle and upper bank. Three 2m^2 quadrats were intensively sampled per transect. Species diversity and community composition of indigenous and alien species were compared by measuring herbaceous, shrub and tree cover. Soil conditions, such as texture, salinity, acidity and moisture, were also compared. Distinctly different plant communities were found in each site, although cleared and invaded sites were more similar to each other. Cleared sites showed >45% cover by invasive successional species and grasses atypical of natural succession patterns. It was proposed that restoration constraints (e.g. method of clearance, intensity of prior invasion, land-use) were encouraging alien re-colonisation. However, there was evidence that the overall the trajectory of successional was favourable for indigenous trees and species. It was suggested that active re-vegetation of indigenous tree species, and adherence to correct clearance methods would aid site restoration.

Introduction

One of the principal threats to biodiversity worldwide has been the introduction of alien species (Ruwanza et al. 2013, Van Wilgen et al. 2007). Riparian vegetation (the biotic communities on the shores of streams and lakes), is particularly susceptible to invasion due to its highly interconnected structure and its potential for human exploitation (Blanchard et al. 2008, Meek et al. 2010). In South Africa, riparian zones and river beds within the fynbos biome are amongst the most damaged, and are often colonised by notorious Australian invasive species (Ruwanza et al. 2013).

Riparian vegetation provides a number of vital ecosystem services on which many people rely, particularly in developing countries (Meek et al. 2010). It stabilises riverbanks, reduces erosion, attenuates floodwaters and aids in groundwater recharge (Meek et al. 2010; Sieben & Reinecke, 2008). It also provides refuge for wildlife and routes for migration and seed propagation (Naiman & Decamps, 1997). Indeed, almost all ecosystem services are ultimately controlled by the composition of riparian vegetation (Naiman & Decamps 1997).

Alien modification of the Berg River

The Berg River, in the Western Cape of South Africa, is one area where riparian vegetation has undergone severe catchment modification by alien species and anthropogenic activity (Geldenhuys, 2010, RHP, 2004). Studies have shown that human interference may be directly responsible for the creation of ideal conditions for proliferation, spread and growth of alien species (Richardson et al. 2007; Holmes et al. 2008; Van Wilgen et al. 2007). The Berg River and its tributaries have been so extensively altered from their natural state that pristine sites are extremely rare. Damming in the upper reaches has altered flow regimes, while agriculture, industry and catchment modification in the lower reaches have altered water quality and habitat integrity (RHP, 2004). In 2004, the River Health Programme classified the Berg River as severely to moderately invaded, naming leading offenders as *Eucalyptus camaldulensis Dehnh*. and *Acacia mearnsii De Wild.* (Ruwanza et al. 2013).

In the Berg River the most abundant invader is *E. camaldulensis Dehnh.* and its hybrids, as well as *Acacia* species. This species forms dense canopies and litter cover, suppressing understory vegetation and exposing banks to erosion and sedimentation (Reinecke et al. 2008, Ruwanza et al. 2013). *E. camaldulensis Dehnh*. tissue and litter has also been shown to have allelopathic properties that inhibit understory vegetation (del Moral & Muller. 1970, Ruwanza et al. 2013). *Eucalyptus* species have also been recorded to increase soil moisture repellency and decrease water availability for irrigation and indigenous species (Shakesby et al. 1993 as cited by Leighton et al. 2004; Galantowitsch and Richardson, 2005). These factors collectively reduce the abundance and biodiversity of indigenous riparian species, threatening natural ecosystem functioning and compromising the delivery of ecosystem services (Reinecke et al. 2008; Levine et al. 2003; Forsyth et al. 2004).

Consequentially, the Berg River has been the focus of several alien clearance operations. In 2006, an invasive alien removal plan was suggested to promote the rehabilitation and restoration of riparian vegetation at several sites along the middle Berg River, between Wellington (Grensplaas) and Hermon Bridge, in the Wynlands District of the Western Cape (Refer to Fig. 1). An experimental design was recommended, which would manipulate invader plant stands to assist in succession of indigenous species. Different methods of removal would thus be assessed on different small scale plots. Previously, private contractors had been used for clearance, although this was costly and abandoned timber debris risked blocking the main river, aggravating floods (Geldenhuys, 2010).

In February 2010, various sites around the main river were cleared by Foresters, the vegetation management company, under the Landcare Program of the Department for Agriculture and Land Affairs (Geldenhuys, 2010). The principal aims of the Landcare Program were to mitigate the impacts of erosion and land degradation through vegetation and biological control, such as removing alien species (King et al. 2003). Although the total clearance of alien vegetation was not an official goal, all large invasive species and their debris were removed from the river banks to improve the river flow and minimise flood damage to agricultural land (Foresters Vegetation Management, 2010).

While there are several approaches to the clearance of alien species, Foresters followed the strategy adopted in large part by the national Working for Water Program (WfW). The clearance methods are based on the assumption that ecosystems are self-reparable and that physical alien removal will restore ecosystem functioning through natural succession (Holmes et al. 2008; Ruwanza et al. 2013). Follow-up treatments include the temporary removal of regenerating aliens, although there is usually no active intervention to aid indigenous regrowth (Reinecke et al. 2009). Whilst this has been successful for control of alien species on a catchment-scale, there has been some debate as to whether passive, successional methods of restoration are effective for sites that have been severely invaded for long periods of time (Holmes et al. 2008).

Previous studies on the success of alien removal programs have shown mixed results. Bellingham et al. (2005, as cited by Beater et al. 2008) and Galantowitsch & Richardson (2005) noted that cleared sites are quickly recolonized by alien successional species, which thereafter alter the conditions for seedling recruitment and growth. Invasive *Eucalyptus* and *Acacia* species often reduce vegetative ground cover, and thus it has been observed that clearance programs without re-vegetation strategies may even exacerbate bank erosion and sedimentation (Sieben & Reinecke, 2008). Furthermore, both Van Wilgen et al. (2012) and Holmes et al. (2008) expressed concern about the dearth of follow-up studies on the effects of clearance programs.

Currently, the extent to which indigenous vegetation recovers after clearance projects is not well understood (Reinecke et al. 2008). It has been suggested that recovery is dependent on degree of damage and the loss of ecosystem resilience during stand invasion (Suding & Hobbs, 2009). Numerous recent studies have questioned whether abiotic and biotic constraints may be determining factors in the success of passive, successional stand recovery (Holmes et al. 2008; Suding & Hobbs, 2009; Ruwanza et al. 2013; Reid et al. 2009; Reinecke et al. 2009).

Active revegetation has been suggested as an alternative means of approach to sites that are no longer capable of self-repair, to prevent reinvasion (Van Wilgen et al. 2012 ; Holmes et al. 2008 ; Ruwanza et al. 2013). Active revegetation requires additional restoration activities after the removal of the invader, such as reseeding or replanting of native vegetation (Holmes et al. 2005). There is much concern for the best method of restoration given the high cost of alien removal, both financially and in terms of human effort; WfW records estimate the total cost of alien removal to be 3.2 billion rand since 1995 (Van Wilgen et al. 2012).

Research Objectives and Aims

The aim of this dissertation was to investigate the impacts of alien species on riparian communities along the Berg River catchment, and how clearance programs faired in achieving restoration goals. The focus was to compare the riparian vegetation of heavily invaded local-scale sites, (>80% aerial cover the past few decades), against that of sites cleared as recently as 3 years ago. A reference site further upriver, where modification was less severe, would be used as a measure of desired diversity and community composition.

Succession in riparian communities is a function of both the self-induced influences of plant communities (autogenic factors) and external, environmentally determined factors (allogenic factors), (Tansley, 1935). The study therefore also included measurements of surrounding environmental variables (such as soil factors, altitude and land-use) on species diversity, community composition and alien invasion.

The primary objectives of the study were to:

a) Examine how *E. camaldulensis Dehnh.* impacted species diversity, community composition and edaphic factors within sites.

b) Assess the potential for indigenous ecosystem recovery in the cleared site, and evaluate potential restoration constraints.

It was expected that the passive successional model would not be very effective in aiding the recolonisation of indigenous species. Invaded stands would show the least diversity and the heaviest invasion of alien species, while cleared stands would show the most diversity of pioneer alien species. Soil EC and acidity was also expected to be higher in invaded stands, where nitrogen fixing and leaf litter are heaviest. Soil moisture would be lower in invaded stands, less so in cleared stands.

The potential for successful restoration of cleared sites in Hermon can be better assessed from insights gained by this dissertation and recommendations can be made for future clearance projects.

Materials and Methods

Study Area and Site Background

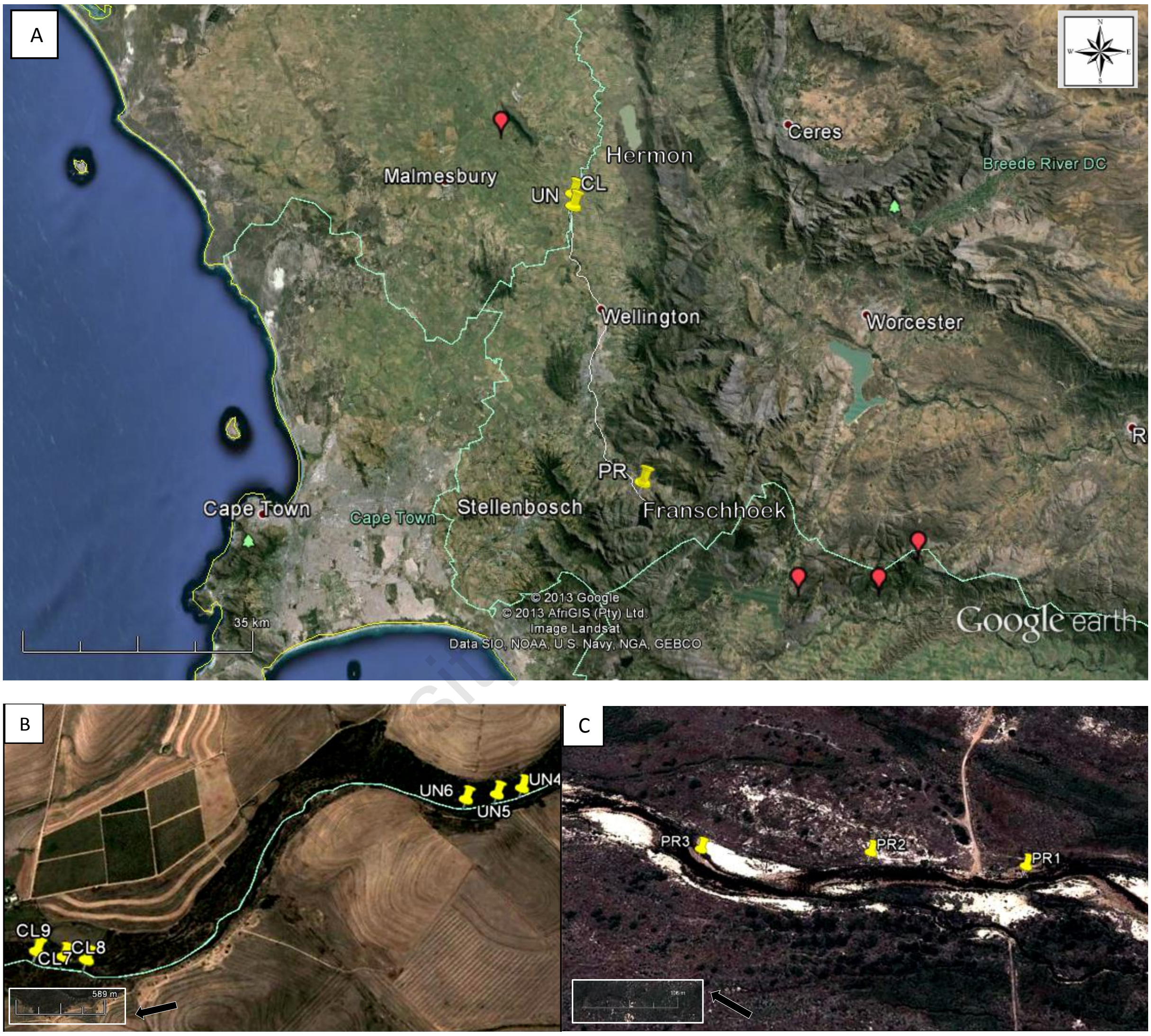

FIGURE 1: A: Location of the Berg River catchment from the upper foothills of the Drakenstein mountains, by Franshhoek, to the lower foothills, by Hermon, Western Cape. The study sites are labelled: PR (Pristine), UN (Uncleared), CL (Cleared). B: The three plots chosen in cleared (CL: 7, 8, 9) and uncleared (UN: 4, 5, 6) sites in the farm of Botmansdrift, Hermon. C: Three plots chosen within the pristine, reference sites (PR: 1, 2, 3). Source: Google maps, Digitalglobe 2013. April 2013.

The Berg River rises in the Franschhoek and Drakenstein mountains and flows northward, into St. Helena Bay on the west coast, as shown in Figure 1A (River Health Program (RHP), 2004). It is approximately 294 km long, with a catchment area of 7715km^2. Rainfall peaks from June to August, thus increasing peak river flow and flooding during this time (Ruwanza et al. 2013).

Sandstone fynbos and renosterveld should be the dominant vegetation type in the upper and middle regions, respectively (Table 1). However, both vegetation and channel structure have been severely modified by agriculture, abatement projects and industry (RHP, 2004).

The Berg River catchment has been invaded by *Eucalyptus camaldulensis Dehnh.* for about 50 years, according to satellite image observations (Tererai, 2012 as cited by Ruwanza et al. 2013).

Table 1: Site-specific physiological characteristics of plots on the Berg River (RHP, 2004, Clark & Ractliffe, 2007)

River site	Upper foothills of the Drakenstein Mountains	Lower foothills of the Drakenstein Mountains	
Site	Pristine Site	Uncleared Site	Cleared Site
GeoRef Plot 1 (S, E) (upstream)	33.89991, 19.05317 (±4)	33.56687, 18.93599(±6)	33.48866, 18.93510 (±4)
GeoRef Plot 2 (S, E)	33.89869,19.05230 (±6)	33.50587, 18.93601(±4)	33.48795,18.93559 (±5)
GeoRef Plot 3 (S, E) (downstream)	33.89696,19.051543(±4)	33.50473,18.93647(±7)	33.48704,18.93631 (±4)
Mean annual precipitation (mm/yr)	1412	817	817
Elevation (m. above sea level)	204	83	79
River channel characteristics:	Fan-type braiding, divergent drainage, pool-riffle morphology (Clark & Ractliffe, 2007), heavily cobbled	Open, topography. Cultivated slopes, sinuous channel, pool-riffle morphology (Clark & Ractliffe, 2007) Gradient reduction, increased channel width, course braids.	
Geology	Quartzites and sandstones (Cape Supergroup)	Cape Granite Suite	
Natural vegetation	Sandstone fynbos	Renosterveld	

Scoping and selection of sites on the Berg River

In April 2013, Landcare manager, Mr. Francis Steyn, and private timber contractors, Mr. Sam Lovett and Mr. Philip Holzhausen provided an overview of plot treatments within the Hermon area, Berg River. The private farm of Botmansdrift, Hermon, was selected as it contained both invaded and cleared areas within 1.5 kilometres of one another, which would reduce the variability of sites expected down the river gradient. Permission was granted to conduct the study by land owner, Mr. Carel Visser (See: Acknowledgements).

An unmodified reference area was located in the upper Berg River, approximately two kilometres downstream from the Berg River dam, Franschoek. The site was subjectively classified as pristine based evidence of adult climax species, such as *Prionium serratum* (L.f.) Drège and *Kiggelaria africana* L., which were in flowering season and were identified using portable online resources. It was also upstream from intensive urbanised, industrial or agricultural areas, which should limit anthropogenic stress on the area. The pristine site was chosen with the understanding that the Berg River and its tributaries have all been invaded and modified to some extent (RHP, 2004).

The cleared site was chosen based on degree of invasive clearance, (>99% of alien species cleared) and minimum distance from invaded plots (±150 meters). Clearing had commenced 3 years prior. Invasive trees were felled by hand, the timber and debris removed, stacked, dried and burned, on-site. This was determined to be the most cost-effective way to dispose of the tree debris. Herbicide had been applied to tree stumps to prevent re-sprouting, and special removal methods had been put in place to reduce damage to the soil, native vegetation and banks (Foresters Vegetation Management, 2010).

The uncleared site was chosen based on duration of unhampered invasion (>10years) and the severity of invasive canopy cover (>80%). Vegetation dominance is often established by uppermost canopy cover and thus *E. camaldulensis Dehnh.* was established as the dominant invasive species, despite prolific understory invasion of acacia species. The intensity of invasion of *E. camaldulensis Dehnh.* was determined by measuring diameter at breast height (trunk diameter, at 1.37 m from the ground; Wilson, 2007) and calculating total basal area (m^2/ha), as well as percentage canopy cover.

Field research took place at the end of the growing season in autumn (April) and again in early spring (August), 2013, to compare differences in species composition under different precipitation and inundation conditions.

Method for data capture

A stratified sampling method using belt transects was applied to riparian vegetation communities at chosen sites (Kent, 2011; Sieben & Reinecke 2007; Sieben 2003). Riparian vegetation can be divided into several well-defined longitudinal zones, from the wet bank (at the river's fringes), to the dry bank, at the edge of terrestrial vegetation (Fig. 2). Vegetation patterns can be described in terms of several gradients: the longitudinal gradient describes changes along the river length (from headwaters to the mouth), the lateral gradient describes the pattern change from river edge to the top of the bank, and the geographic gradient describes the climatic and topographical changes across the entire catchment range (refer to Fig.1 and Table 1) (Sieben, 2003). Lateral gradients in particular, lead to lateral zonation of riparian vegetation, and is primarily directed by variations in flood duration and intensity (Sieben & Reinecke, 2007; Naiman & Decamps, 1997; Boucher, 2002 in Clark & Ractliffe, 2007).

The strip transect method is useful to sample each lateral vegetation zone, while being adaptable to the varying physiologies of the plots (Bibby et al. 1992, cited by Krebs, 1999).

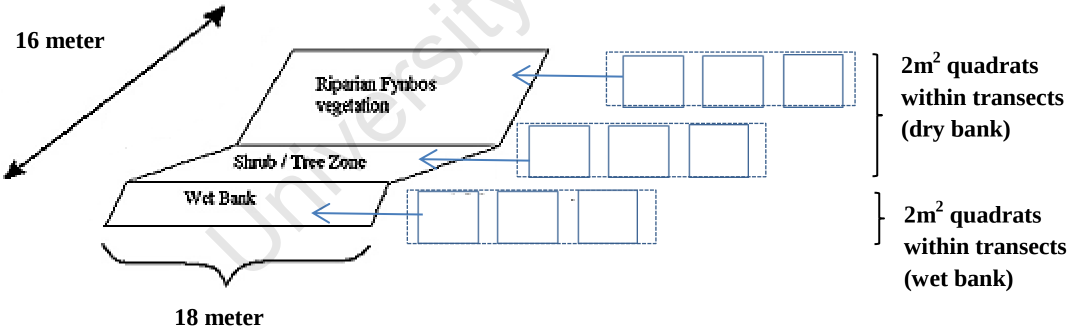

FIGURE 1: Single plot within a site showing lateral zonation of riparian vegetation on the wet bank (river's edge) and dry bank (shrub and fynbos zone) where three 2x2m quadrats (right) have been placed within three transects (Sieben & Reinecke, 2007). [Image not to scale].

Within each site (cleared, uncleared, or pristine) three plots were selected. The selection of plots that were comparable and representative of the plant community was critical (Braun-Blanquet, 1932). An effort was made to locate sites that were comparable in terms of geology, zonation and distance from agricultural or terrestrial vegetation, where possible. Plot locations were geo-referenced (Table 1), and were approximately 50 - 70 meters from one another depending on size and accessibility. Plot size was 18×16 m from wet to dry bank, and three strip transects were taken perpendicular to the direction of stream flow, running 5 meters apart, on the lower (wet bank), middle and upper bank (dry bank) (Fig. 2). Each of the three transects contained three non-overlapping $2m^2$ quadrats, at 6 meter intervals, for intensive sampling.

Species cover was estimated per intensive quadrat and species were categorised into size classes. “Cover” was defined as the percentage of ground surface obscured by the vertical projection of all above-ground plant species, after Peet et al. (1998). Within intensive quadrats, herbaceous cover (<2 meters in height) and shrub cover (< 5 meters in height) was estimated, while large vascular plant cover (>5 meters) was estimated over the entire plot area (as they did not overlap with intensive quadrats). Woody species greater than 5 meters were classified as trees unless the species had clear, physiognomic tree characteristics and was between 3-5 meters. Species height categorisation was based on the methods of Peet et al. (1998). Additional measurements included litter cover of invasive species.

Vegetation analysis

Plant specimens were collected in the field, and preserved in sealed bags in the 4°C fridge, until being sorted. They were then pressed and dried. Samples were identified to species level (where possible) and their origins (native or alien) were completed in the Bolus Herbarium at the University of Cape Town (see acknowledgements), or using *Problem Plants of South Africa* (Bromilow, 2010) and *Easy Identification of some African Wetland Plants* (Van Ginkel et al. 2011). Naturalised species were considered alien. A full list of the identified species can be seen in the Appendix 1. Several samples were sterile (lacking flowers and fruits) or were present as juvenile sprouts, and thus identification to species level was not possible.

Soil collection

Soil properties selected for the study included moisture content, electrical conductivity (EC), soil acidity (pH) and texture (clay, silt or sand percentage), which were measured to give insight into overall site condition. Texture analysis was a useful measurement in understanding soil structure and hydraulic properties, while electrical conductivity has been shown to be correlated with soil nutrients (Miller & Curtin, 2006).

A standard hand-held auger was used to collect 250 grams of soil from a depth of 10 cm, which was taken from the centre of each intensively sampled quadrat. Three additional samples were taken per plot, ±50 meters inland, to provide a control.

Soils were air-dried for a week in the soil laboratory at the University of Cape Town, as a standardisation procedure. They were then sifted through a 2 mm sieve and subsampled for moisture analysis, texture analysis, electrical conductivity (EC) and acidity (pH).

Soil Laboratory Analysis

Soil moisture was calculated using the Standard method outlined by the Australian Department of Sustainable resources (*Soil Survey Standards, Test Method*. 1990). The procedure was repeated to verify the results of certain outlier samples. Soil texture was calculated using the Standard Hydrometer method of Particle-size analysis (see: Gee and Bauder, 1979).

Soil electro-conductivity and pH were measured using an electrical conductivity meter and pH meter respectively. For such measurements soil was diluted with deionised water at a ratio of 1:2, before being placed on a shaking machine for 30 minutes. Samples were left to stand for 20 minutes, then shaken and measured. While increasing dilution of soil samples has been suggested to lead to EC overestimation, this is still a standard procedure in laboratories and low levels of dilution should not cause significant alterations (Reitemeier, 1946). The EC meter was calibrated in 84µS/cm solution at room temperature (25°C). Both meters were regularly calibrated for precaution. To prevent contamination, probes were rinsed with deionised water before calibration, after calibration, and between samples (Electrical Conductivity Information Sheet, n.d.).

Statistical Analysis

Vegetation data

Patterns of diversity amongst herbaceous and shrub communities were assessed using the Statistical software PRIMER-E (Plymouth Routines in Multivariate Ecological Research) ver. 6. The data for species coverage in both April and August were root transformed to normalize data and reduce the weight of abundant species (Osborne, 2002; Field et al. 1982).

A hierarchical cluster analysis was performed to identify similarities in major plant communities from within unordered samples of ground and shrub cover. Tree species greater than 5 meters were not included in Diversity Indices. This is because trees, shrubs, and herbaceous species fulfil different ecological niches, and it was not advised to compare species across such levels (Legendre & Legendre, 2012). Furthermore natural and cleared vegetation was unlikely to have trees greater than 3 meters in height (Holmes et al. 2006). A SIMPROF (Similarity Percentage) test was included to test for evidence of plant community structure and outliers. This was then overlaid onto an MDS (Non-metric multi-dimensional scaling) plot.

Species richness, evenness and abundance between sites were compared by calculating the Shannon-Weiner and Simpson Diversity indices. While species richness (number of species) is a simple, quantitative measure of diversity, it neither takes into account abundance nor evenness of distribution (Heip et al. 1998, Peet 1975). The Shannon Index (H') considers both species richness and the even distribution of species over the entire sample area. The Simpson Index accounts for individual abundance of species per transect, allowing a measure of dominance. Both indices are widely-used across ecological studies and are thus widely comparable (Heip et al. 1998). Below is the Shannon-Weiner Diversity Model as computed by PRIMER:

(H') = - $\sum_{i=1}^{s} \boldsymbol{Pi}.\log\ (\boldsymbol{Pi})$ **where log is to the base e.**

Where $\boldsymbol{Pi}$ is the relative abundance of the $\boldsymbol{i}$th species, and **s** is the number of species. This Shannon-Weiner index is based on the assumption that individuals are randomly sampled from an infinitely large population, and that all species are represented in the population. (Nsor et al. 2008). Values typically lie from 1.5 (least diversity) to 3.5 (highest diversity), with few exceptions exceeding 4.5 (Kent and Coker, 1992).

Thereafter, the Simpson's Index (1-lambda) was computed to account for the proportion of each species per transect:

$$\textbf{(1-lambda)} = \sum[\boldsymbol{Ni}\ (\boldsymbol{Ni} - \mathbf{1})]/[\boldsymbol{N} \times (\boldsymbol{N} - \mathbf{1})]$$

Where ***Ni*** indicates density or number of the ***i***th species, and ***N*** is the total number of individuals in the community. Simpson's Diversity Index computes diversity on a scale of 0 to 1, with a value closer to 1 indicating that several species are similarly abundant throughout the community, while a lower value is indicative of fewer species of dominant abundance (Boothe et al. 2010). These indices were run for all transects, as well as for alien species diversity and native species diversity.

Analysis of Similarities: Soil and vegetation

Multivariate statistics were used on both soil and vegetation data. A two-way Analysis of Similarities (ANOSIM) was done separately for herbaceous cover and shrub cover. Both vegetation and soil data were not normally distributed, although assumptions of homogeneity of variances and normal distribution are not required for the validity of the ANOSIM. Data was root transformed and used to generate a S17 Bray-Curtis similarity matrix. This is not only useful to scale down highly variable data, but also to generate a similarity coefficient that is invariant to changes in scale (Field et al. 1982). Thus, a nested ANOSIM could be used for both soil variables with different scales, and on highly variable vegetation abundance data.

Soil analysis

The results of this test were compared to a nested ANOVA (Analysis of variance) done in R Studio to determine significant differences between sites. The data was log transformed (to the base "e") so as to comply with the nested ANOVA's assumption of normal distribution of data and homogeneity of residuals. Log transformations have the effect of scaling down highly variable data scores so that the data is not skewed (Field & McFarlane, 1967 as cited by Field et al. 1982). Mean values were compared for soil electrical conductivity, pH and moisture content across sites.

Vegetation community structure

The ANOSIM tested the null hypothesis that sites, plots and transects did not differ from each other spatially or temporally (between seasons). The percentage contribution of each species to the similarity of transects was investigated through a one-way SIMPER analysis, using Bray-Curtis dissimilarity. Percentage contribution is based on the ubiquity of certain species at different riparian zones of the river bank. Species that were not major contributors were excluded due to sheer number, thus the resulting percentage contributions of species does not total 100%.

Only plants samples in the 2 m^2 subplots were subject to these analyses, although herbaceous and understory cover, including small trees (<5 m) was included.

Correlation Analysis

The strength of the relationship between environmental variables and plot invasion was assessed through a non-parametric correlation analysis. Soil pH, acidity and moisture were correlated with tree-level plot invasion and litter coverage on ground-level, using the Spearman's Rank Order Correlation, in Statistica ver. 8. The Spearman's Rank Order test does not assume normality, homoscedasticity or linearity (McDonald, 2009), but it does assume independence of ordinal data (Dusick, 2012). Data was ordered and independence was justified based on the 5 meter distance between samples within sites, and the 50+ meter distance between sites (Roalsø, 2012).

Results:

1. *Characteristics of herbaceous and tree cover in Riparian vegetation*

The percentage vegetation cover, which was calculated for the April month, differed substantially between sites (pristine, cleared and invaded). Pristine sites had a minimum vegetation cover of 83% per module, cleared plots had >90% minimum cover per module, and invaded plots had 44% minimum vegetation cover per module.

The total number of recorded species overall was 120, 47 of which were identified as alien species, and 52 of which were identified as native (Appendix 1). Twenty-one were unidentifiable to species level.

Northern-hemispheric herbaceous alien species were most common, particularly those from the families Poaceae and Asteraceae. Alien grasses comprised 25% of the identified species, with many species originating from East Africa (*Eragrostis tef., Pennisetum clandestinum)* and Eurasia (*Bromus diandrus* and *Lolium multiflorum*). Alien Asteraceae comprised 17% of alien species. Asteraceae were often site-specific, with European natives such as *Taraxacum officinale* being commonly found in pristine plots, and American native species such as *Actium minus* predominantly found in downstream sites. American and Australian invasives were particularly common. Amongst indigenous samples, the most common families were Asteraceae (27%), and the graminoid families Restionaceae (8%) Cyperaceae (12%) and Poaceae (12%).

In invaded sites, tree canopy cover (measured over the entire plot of 288 m^2) exceeded 80% in the upper canopy (predominantly *E. camaldulensis*) and 45% in the lower canopy (predominantly *A. mearnsii). Acacia saligna* and what appeared to be a hybrid variation of *E. camaldulensis* (*Eucalyptus* 2) was also found in the understory.

Estimated *E. camaldulensis* stand invasion varied marginally per plot. Plot four had a total basal area per hectare of 118 m^2/ha; plot five had 88 m^2/ha and plot six had 107 m^2/ha stand invasion.

In cleared plots, however, *Eucalyptus 2* and *A. longifolia* only covered 6% of the plot area. In pristine sites juvenile and small *A. longifolia* (<1m) species covered 3% over all plots, as did a species of *Myrtaceae metrosideros* (4% overall).

However, there was a distinct absence of indigenous species above 5 meters in all sites, although small *Brabejum stellatifolium* were found in pristine plots and *Kiggelaria africana* in cleared plots.

1.1. Identifying plant communities: Cluster Analysis and Analysis of Similarity (ANOSIM)

Three different plant communities were identified using hierarchical cluster analysis (HCA) (Fig. 3.2), MDS analysis (Fig. 3.1) and two-way the nested ANOSIM. The plots showed that cleared, uncleared and pristine sites had characteristic herbaceous and shrub (<5 m) species that were significantly different to one another (π=3.41, p<0.1%). The percentage similarity between plant community clusters over time (season) and space (site) is shown at the 2%, 7% and 10% (Fig. 3.1).

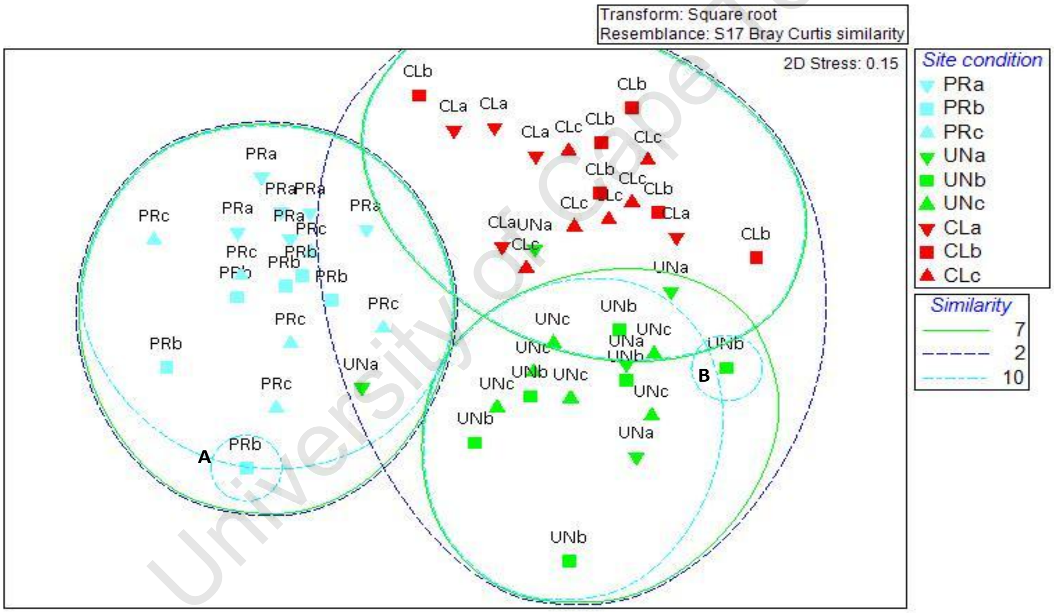

FIGURE 3.1: MDS plot showing clustering of similar plant communities. Samples have with a resemblance of 2%, 7% and 10% are represented, as calculated by the SIMPROF test. Sample origin is indicated by PR (pristine plots), UN (uncleared plots), and CL (cleared plots). Transects in all stands are differentiated by the letters: a (lower bank), b (middle bank), and c (upper bank). Outliers that are more than 90% dissimilar are shown in A and B.

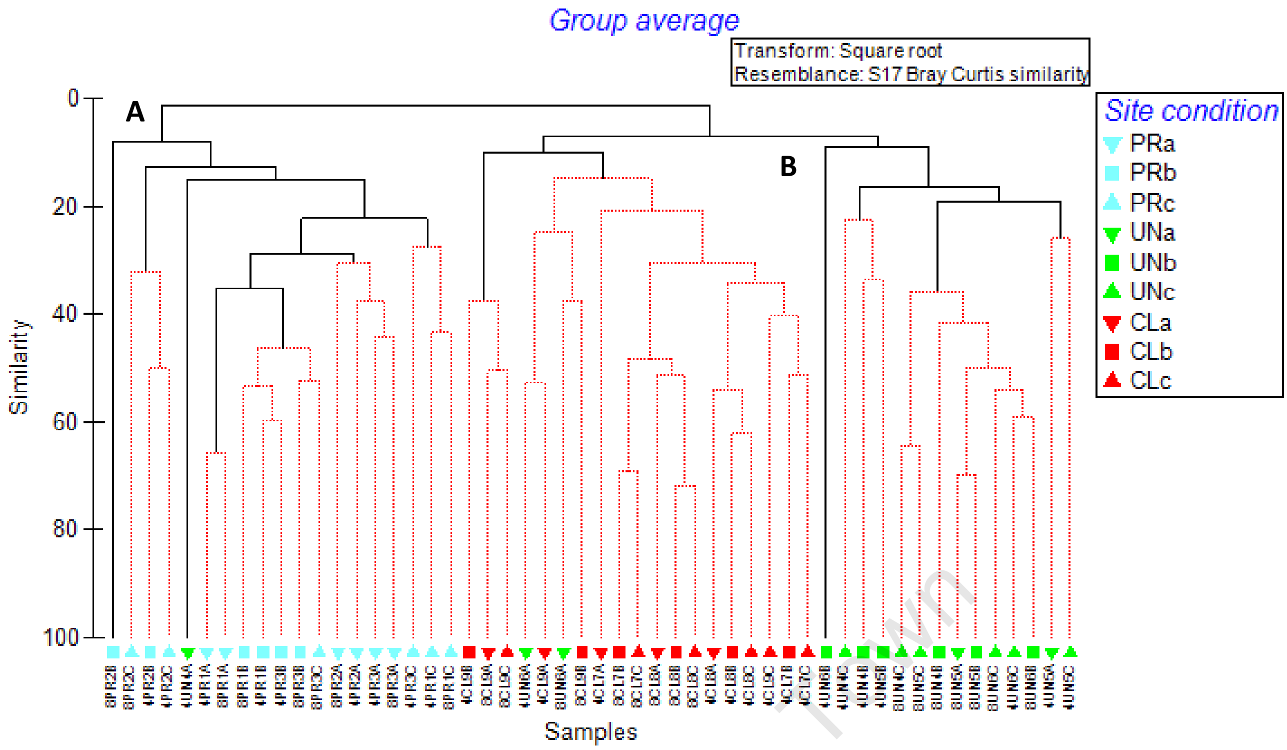

FIGURE 3.2: SIMPROF clustering showing the similarity percentage of three separate plant communities in April and August. Pristine sites (PR) are blue, uncleared sites (UN) are green), cleared sites (CL) are red. Lower bank transects (a), middle banks (b) and upper banks (c) are identified as in the legend. Outliers that are over 90% dissimilar from other sits are shown in A and B. Significantly different sites (p<5%) are shown by black lines, while red lines indicate samples are not differentiable (Clark & Gorley, 2006).

This indicates that, at 2% similarity, two separate plant communities could be determined (the pristine site at Franschoek versus cleared and uncleared sites (π=3.41, p<0.1%)) and at 7% similarity, three different plant communities could be identified: uncleared, cleared and pristine (93%, π=2.41, p<0.1%). This result was corroborated in the two-way nested ANOSIM, which showed differences at site-level (R=0.9, p<0.4%), if not any seasonal differences (R=- 0.259, p<70%).

Several outliers were identified, which are approximately 10% similar to the other sites (Fig. 3.1, Fig. 3.2). These outliers were statistically different enough as to be almost excluded from the entire sample set and are shown at A (pristine site, plot 4, similarity: 8%, π=3.32, p<0.1%), and at B (uncleared site, plot 6, similarity: 9%, π=3.05, p<1.4%), (Fig. 3.2 and 3.1). These were due to the absence of species characteristic of the site, as opposed to the presence of rare species.

Certain outliers that were not significantly differentiable (p>5%) are also shown in Fig. 3.2 as they do not cluster in the groupings expected from their site origins (cleared, uncleared or pristine). These were largely comprised of lower transects from the invaded sites (plot 4, transect a (for April) and plot 6, transect a (for April and August)). These sites were isolated due to inundation, litter cover or an absence of vegetative cover.

The Analysis of Similarities (ANOSIM) included a list of pairwise comparisons between plots, which are included in Appendix 2. Grouping was considered non-random if global test statistic R was significantly different from the random model and the p-value 10% or less. R-values generally fall within the range of -1 and +1. A value of 0 generally confirms the null hypothesis, and negative values indicate greater dissimilarity among replicates within transects, than among plots (Chapman & Underwood, 1999). It was confirmed that most differences were between the sites at Hermon (cleared and uncleared) and the pristine site at Franschoek (R=1, p<10%) as opposed to between sites at Hermon (R=0.7, p<10%). Differences between transect zonation within a plot (middle, lower and upper banks) within plots was not significant (R=0.3, p<1.9%).

1.2. Quantifying Species Diversity: Shannon-Weiner and Simpson Indices

The diversity and evenness of spread of species in the pristine site were estimated by the Shannon-Weiner and Simpson Indices (Table 2). In pristine sites Shannon-Weiner values were between 2.4 and 2.5, and Simpson values were greater than 0.91. Given that Shannon-Weiner values (H') usually lie between 1.5 and 3.4, and Simpson values (1- λ) are usually from 0 to 1, these values reflect a moderately high diversity of species, whose abundances are well distributed over the sample area (Molles 1999, cited by Nsor et al. 2008; Kent and Coker, 1992; Boothe et al. 2010).

In comparison, invaded sites showed poor diversity and evenness of spread, (H' = 1.28 to 1.96), as well as greater evidence of dominant species (1- λ = 0.75 to 0.86). Cleared plots showed a similar pattern, with somewhat higher diversity (H" =1.86 -1.93) and slightly fewer dominant species (1- λ = 0.83-0.84).

Both cleared and pristine sites show increases in diversity and spread of abundance up the river bank, while uncleared plots showed most diversity at the lower banks (1.2<H'>1.96, 0.75<1- λ >0.86) with particularly low values on the middle bank.

Table 2 showing descriptive statistics of the Shannon-Weiner (H') and Simpson (1-lambda) Diversity Indices. Means are shown across Pristine (PR), uncleared (UN) and cleared (CL) stands for lower (A), middle (B) and upper (C) transects on the Berg River

Site	**Mean (H')**	**Mean (1-lambda)**	**Std. error** (H')	**Std. dev.** (H')	**Std. dev.** (1-lambda)	**Std. error** (1-lambda)
PRA	2.42	0.91	0.07	0.17	0.02	0.01
PRB	2.47	0.92	0.11	0.27	0.02	0.01
PRC	2.50	0.92	0.10	0.25	0.02	0.01
UNA	1.96	0.86	0.07	0.15	0.05	0.02
UNB	1.28	0.75	0.15	0.38	0.09	0.04
UNC	1.62	0.78	0.17	0.43	0.12	0.05
CLA	1.86	0.83	0.18	0.41	0.09	0.04
CLB	1.85	0.84	0.09	0.21	0.04	0.02
CLC	1.93	0.83	0.08	0.25	0.06	0.03

The representation of alien and native species richness and abundance at herbaceous and shrub level was investigated Shannon-Weiner and Simpson Indices (Fig. 4). Native species diversity is concentrated in pristine plots (Fig. 4A: H'= 1.8), as is the distribution of abundance (Fig. 4B: 1- λ=0.84), as opposed to uncleared sites which are prominently dominant in fewer, alien species (H'=0.89, 1- λ=0.55). In cleared plots, alien diversity and abundance seems to be higher than natives (H'=1.3 and H=1.0 respectively). However, there is substantial overlap of error for alien and native diversity in cleared and uncleared sites.

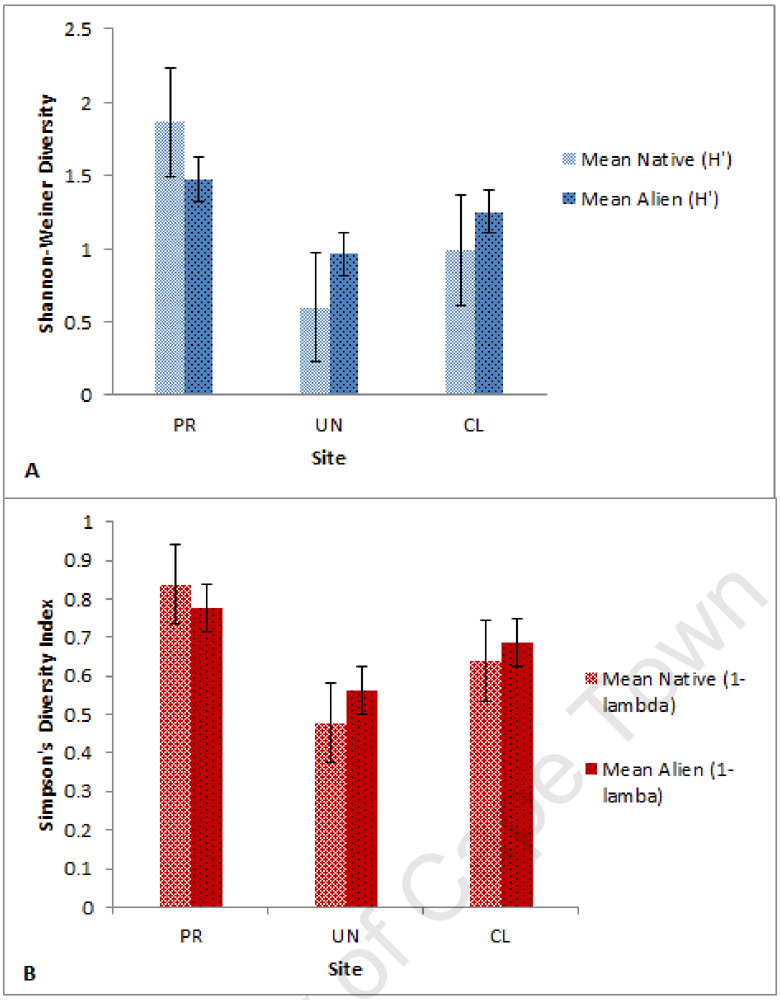

FIGURE 4A: Graphs showing the Shannon-Weiner Index for alien and native species cover. Values usually fall between 1.5 (lowest diversity and evenness of spread) and 3.5 (high diversity and evenness of spread). FIG. 4B: Simpson Diversity Indices for alien and native species cover. Values fall from 0 (dominance of a select few species) and 1 (equal dominance of species). Sample origin is indicated by PR (pristine plots), UN (uncleared plots), and CL (cleared plots). This is taken as an average over all plots (1-9) and transects.

1.3. Plant community composition: SIMPER analysis

Fig. 5 shows the contribution of each species to percentage site similarity. Forty-seven species were found to contribute somewhat to plot similarity, ten of which were recorded in Fig. 5 as they were most ubiquitous (contributing more than 5% to plot similarity). Native graminoids, (such as *Ficinia indica* and *Pentaschistis glandulosa)* were plentiful, particularly the riparian fynbos elements *Calopsis paniculata* (64% in the lower banks, 25% in the middle banks and 5% in upper banks). Native species such as *Prionium serratum* and *Stoebe plumose* were available in smaller distributions and show the high native diversity of the site. However, *Acacia longifolia* and certain alien grasses (*Paspalum urvellei* and *Briza minor)* were still well distributed.

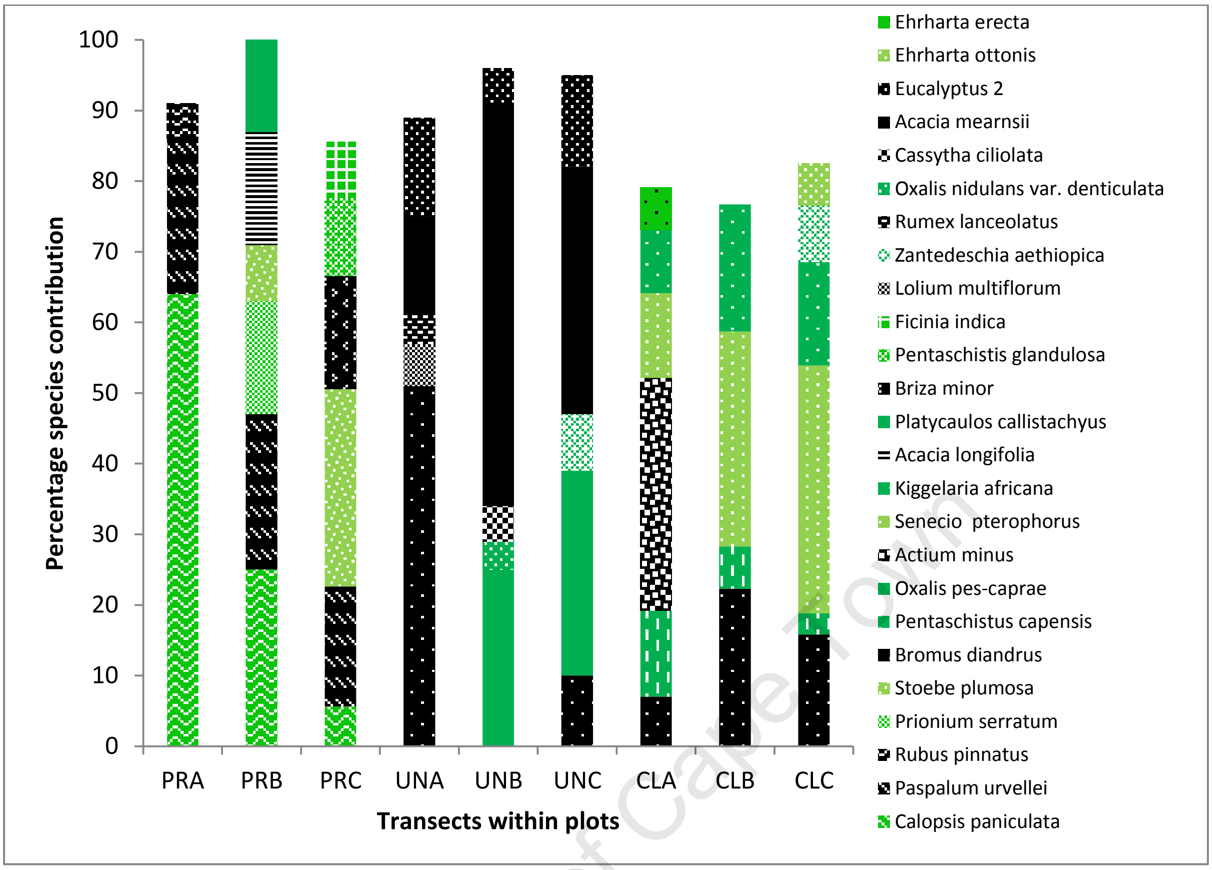

FIGURE 5: The 25 most frequently occurring species across sites: PR (pristine plots), UN (uncleared plots), and CL (cleared plots). Transects along the banks differentiated by: A (lower bank), B (middle bank), and C (upper bank). Different patterns denote different species; black indicates alien species invasive and green indicates indigenous species.

In uncleared plots, nine species were found to be considerable contributors to site community similarity. Five other species were not included as they contributed to less than 5% similarity between pristine plots). Alien grasses, such as *Bromus diandrus* (51%), dominate lower banks, while the native *Oxalis pes-caprae* contributes mostly to the middle and upper bank (25-30% respectively). *Acacia mearnsii* and *Eucalyptus* are dominant woody species, native trees being completely absent.

Cleared plots had twenty species of considerable frequency recorded, eight of which were included in Fig. 5, the rest contributing less than 5% between cleared pltos. Only two major contributors to percentage site similarity were alien (*Actium minus* (28%) in the lower banks and *Bromus diandrus,* throughout). Dominant native species include the *Senecio pterophorus*

, and native grasses such as *Ehrharta ottonis, Ehrharta erecta* and *Pentaschistus capensis.* Importantly, small woody individuals of *Kiggelaria africana,* and sparsely distributed *Salix mucronata* are the first indication of potential indigenous canopy recovery.

2. Physical and Chemical properties of Soil: Two-way Nested ANOSIM

The Nested ANOVA and post-hoc Tukey tests, done in R Studio did not reveal many patterns of soil properties. However the two-way nested ANOSIM in PRIMER showed statistically significant differences between site groups (R=0.6, p<2.5%), although not between plot groups within sites (R=0.12, p<0.1%).

Pairwise comparisons between sites showed that soil properties in the pristine site were most different to those in cleared and uncleared sites (R=0.7, p<10%), but there were no discernible differences between the cleared and uncleared sites (R=-0.04, p<70%). Likewise, pairwise comparisons of internal plot groups could not statistically distinguish cleared plots from invaded plots. The table of pairwise comparisons was included in Appendix 3.

2.1.Chemical Properties of soil: Acidity and Salinity

Fig. 6 was generated from the means of soil moisture percentage, electrical conductivity (EC) and acidity over each transect. Control samples (D), which were taken out of the riparian zone, showed the highest moisture percentage, pH and EC to be in the cleared zone, followed by uncleared plots, with pristine plots showing the lowest EC and moisture and most acidity. This is merely an indicator of soil properties outside of the riparian zone**.**

Overall, the soil acidity ranged from 5.0 (strongly acidic) to 6.5 (slightly acidic), with strongly to moderately acidic soils concentrated in the pristine area (5.0-6.0). Cleared and invaded sites differed marginally, (5.5-6.0 in the invaded site and 5.6-6.5 in the cleared site, although cleared sites seemed slightly more alkaline (Practical Use of Soil Analysis Results, n.d.).

Comparatively, sites ranged from 100 -650 micro Siemens/cm, although at that range salinity was too low across sites to really be comparable. Salinity increased marginally downstream from pristine, to uncleared to the cleared site.

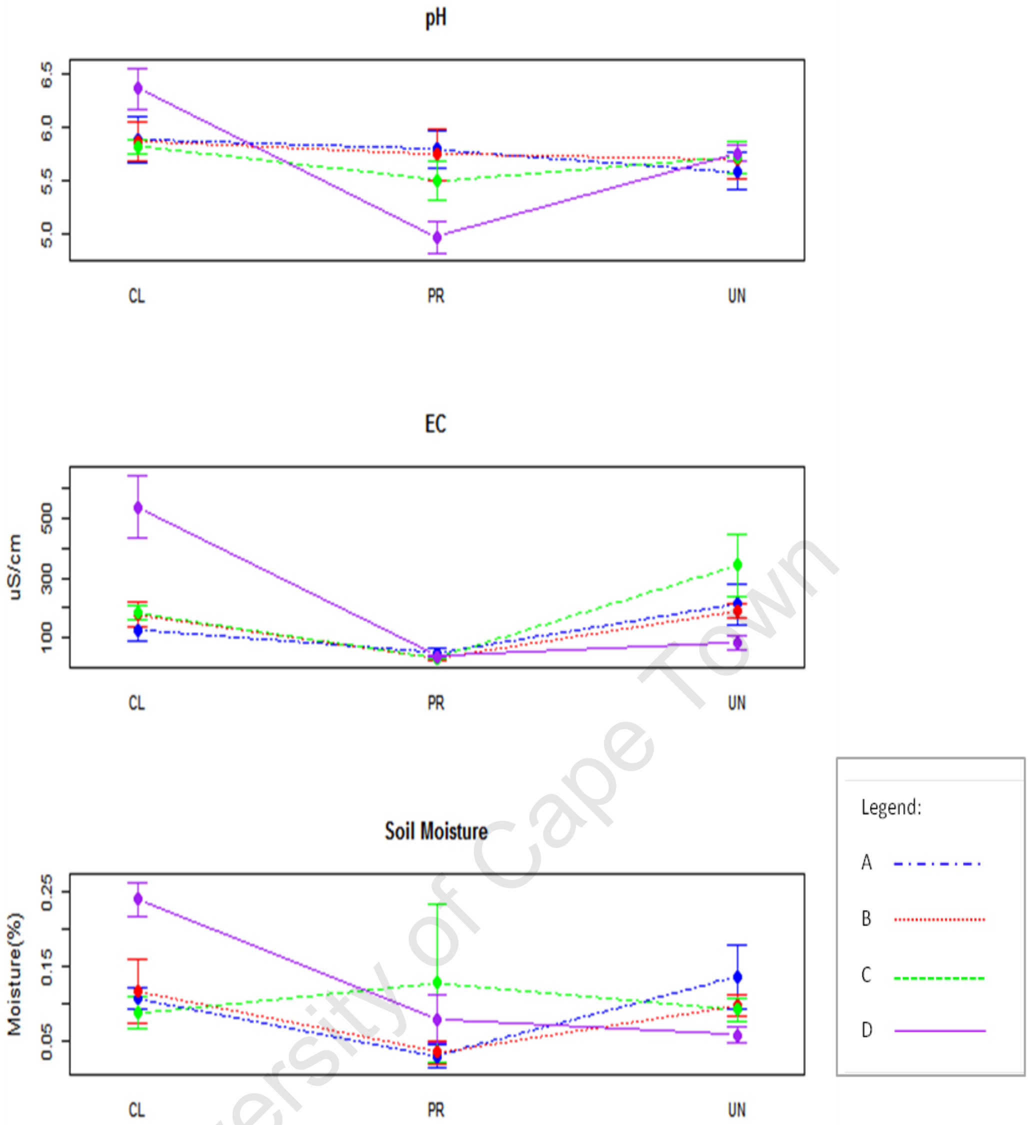

FIGURE 6: The mean values of soil acidity (pH), electrical conductivity (EC) and moisture percentage are presented for transects on the lower, (A), middle (B), and upper bank, (C), as well as in the terrestrial control zone (D). This is measured for PR (pristine plots), UN (uncleared plots), and CL (cleared plots).

2.1. Physical properties of soil: Texture and Moisture

Overall, soils were relatively dry (0.05 – 0.25% moisture), an indication that the ability to retain moisture is lacking, even if the soils were wet on-site. The uncleared and cleared sites showed similar percentage moisture, while the pristine sites showed low moisture, except for the upper bank, which as high variance (<0.05-0.25% moisture).

Soil texture, which is determined by the ratio of soil to silt and clay, was predominantly coarse and sandy in all sites. Mean values per plot were calculated for comparison, with pristine and cleared sites showing greater than 70% sand. Notably, the uncleared site had a smaller percentage of sand and a greater percentage of silt (24%) than either cleared (18%) or pristine sites (6%) (Table 3).

Table 3: Mean percentage of sand, silt and clay in soil samples across sites (PR (pristine plots), UN (uncleared plots), and CL (cleared plots) down the Berg River

Site	*Sand (%)*	*Silt (%)*	*Clay (%)*
PR	*89.7*	*6.3*	*3.9*
UN	*67.5*	*23.8*	*8.7*
CL	*73.1*	*18.5*	*8.5*

2.3. Correlation Statistics

Spearman's Rank Order Correlation investigated possible relationships between the density of litter and invasive tree cover, with soil variables such as EC (electrical-conductivity, µS/cm), acidity (pH) and moisture content (%).

The Spearman's Rank Order Correlation did not reveal any strong correlations between variables. However, a weak correlation existed between soil moisture and tree density (N=108, rs=0.2, p=0.1%), as well as tree cover and EC (N=108, rs=0.4, p<0.0001%). Litter cover and EC were also moderately correlated (N=108, rs=0.3, p<0.02%). These values indicate that one factor increases positively as the other increases. The confidence interval of this test was 95%. The table is included in Appendix 4.

FIGURE 7: Scoping view of the study sites from the lower transects: Pristine site in the headwaters (A), Uncleared site (B), and furthest downstream the Cleared site (C). Photo taken: Alison Midgley, 02/08/2013.

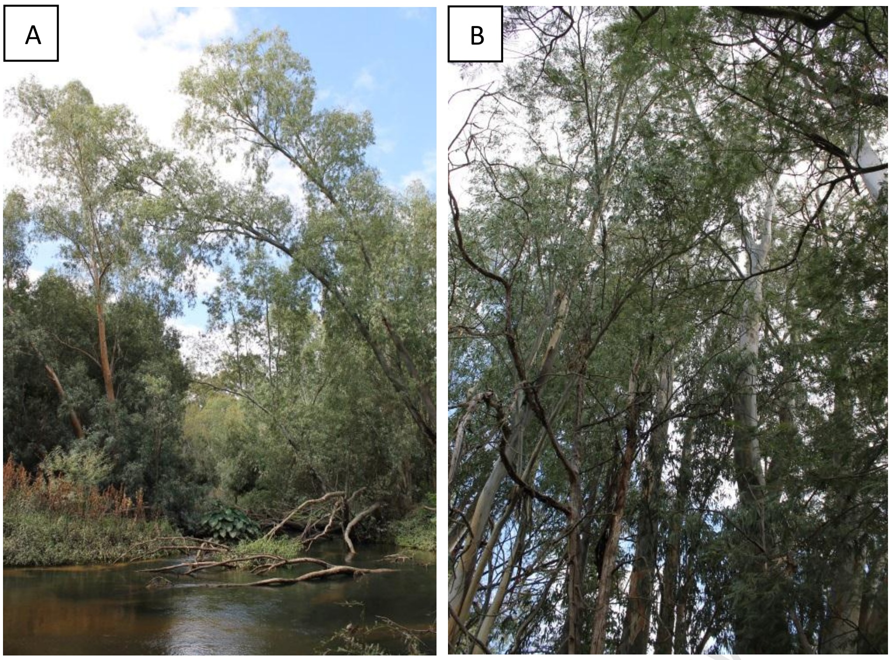

FIGURE 8: Effects of invasive *E. camaldulensis* and *Acacia* species in invaded sites. A: Overhanging trees and fallen branches block the main river and tributaries, increasing flood risks. B: Dense overstory canopy restricts sunlight to the understory.

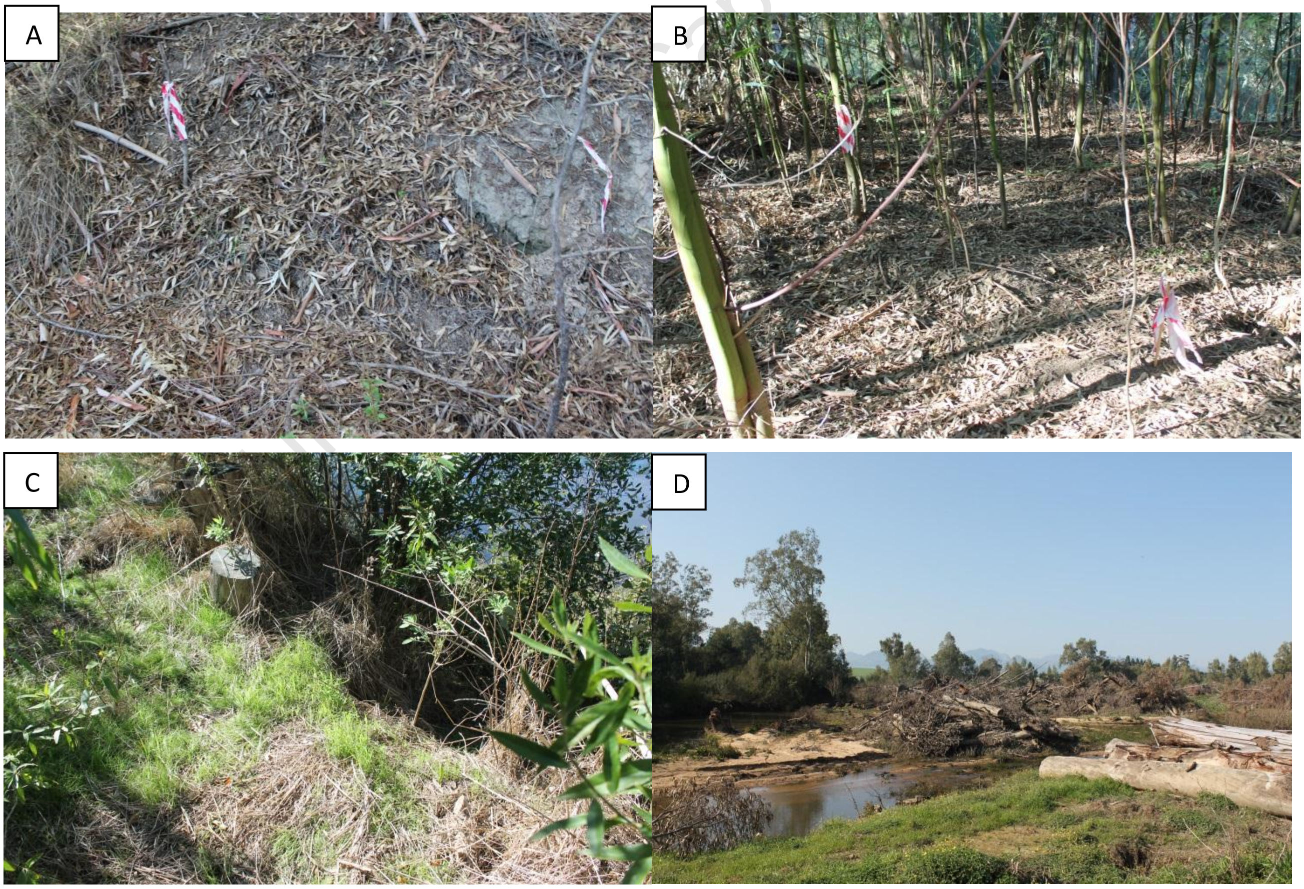

FIGURE 9: Site-specific impacts affecting native vegetation cover. A: Evidence of bank erosion, loss of vegetation cover and litter inundation under *E. camaldulensis* canopies in the invaded site (Plot 6, middle bank transect). B: Dense litter and seed cover below densely invaded *E. camaldulensis* plots (Plot 5, upper bank). C: Evidence of sheer slope erosion where *E. camaldulensis* had been cleared 4 years prior (Plot 8, lower bank transect). D: Mechanisms of clearance in cleared area: *E. camaldulensis* is felled, stacked and burned on-site. Photo: Alison Midgley, 24/04/13.

Discussion:

Allogenic effects and Autogenic effects on community composition

Distinctly different herbaceous plant communities were shown to exist for each site (cleared, invaded and pristine) in this study. Cleared plots more closely resembled invaded plots (similarity 7%, R=0.7, p<10%) than pristine plots (similarity 1.5%, R=1, p<10%). The primary difference in plant communities was the level of invasion by woody alien species (*Eucalyptus* and *Acacia*) and the degree of species richness. Species diversity tended to decline with altitude, as alien stand invasion increased. Invaded plots were relatively depauperate, dominated by few, alien species in the upper canopy and herbaceous layer. Cleared sites were more diverse, with twenty species contributing to site similarity, although only eight of these were dominant. Alien species also contributed substantially to vegetation cover (>45%). Reference plots were extremely diverse, with forty-seven species contributing to site similarity, only ten of which were dominant. This is contrary to expectations based on the principals of succession, which suggests that post-clearance, successional stages should show greater species diversity than stable, climax stages (Kent, 2011).

However, uninvaded reference sites were approximately 127 meters higher than invaded and cleared sites. Sites are also influenced by the dynamics of the greater catchment and terrestrial landscape. In the Western Cape, multiple environmental gradients act along the river reaches, changing conditions for riparian species. Geographical gradients, for example, coincide with changes in geology, precipitation and topography, and change soil type and exposure to fire on a local scale (Sieben, 2003). Longitudinal gradients (changes along the river reaches) are closely linked to the geographical gradient, and mostly determine erosion and sedimentation (Sieben, 2003). Lateral gradients (the changes up the river bank) affect fluctuations in fluvial processes, hydrological power and inundation frequency, altering channel flow and site moisture levels (Sieben, 2003).

Thus, while plant communities determine many properties of riparian ecosystems, environmental gradients, in turn, heavily influence the patterns of plant communities. However, the underlying feedback processes between invasive species and hydro-geomorphological processes have not been well investigated (Richardson et al. 2007). This is likely due to the complexity of separating the impacts of alien species from environmental variables (Richardson et al. 2007; Nsor, 2012). For example, while life history traits of species and the ability to recover under different post-disturbance conditions often determine the success of establishment, specific microsites defined by soil moisture, temperature fluctuations, light conditions etc. are often required before seeds will germinate (Richardson et al. 2007). In the following section, the effects of gradient versus invasive tree density on site condition will be discussed in terms of the soil analysis results.

Allogenic and Autogenic effects on soil properties

The results of the soil analysis revealed certain patterns in site condition that were not initially noticeable. It was expected that *E. camaldulensis* would reduce soil moisture content, through soil water repellency and consumption (Galatowitsch & Richardson, 2005). However, pristine sites had the lowest moisture content (mostly <0.05%), particularly in the lower banks. This may be because, where floodplain sediments are course and permeable, fluctuations in groundwater and soil moisture are directly associated with river water levels (Mackenzie et al. 1999 as cited by Richardson et al. 2007). The upper banks were highly variable, possibly because the river was heavily braided and inundation levels fluctuated considerably. The downstream soils were similar in moisture content, due to heavier water loads downstream and the flattening of floodplains down river. This means that soil moisture was more an indicator of gradient changes than alien impacts, although results indicate that moisture levels are not necessarily limiting.

Soil salinity (EC), on the other hand, was correlated with tree density ($N=108$, $r_s=0.4$, $p<0.0001\%$), and litter ($N=108$, $r_s=0.3$, $p<0.02\%$), which may indicate soil enrichment by nitrogen-fixing *acacias* or organic leaf matter (Yelenik et al. 2004; Levine et al. 2003). EC is known to be strongly correlated with soil nutrients (e.g. calcium, magnesium, potassium, sulphuric acid), including nitrate. Nitrate provides a direct measurement of plant limiting nutrients, and can be an indicator of fertilisers or nitrogen-fixing invasive species (Patriquin et al. 1993). High EC levels have also been linked to soil acidification in several studies (Patriquin et al. 1993; Bobbink et al. 1998). This explains the high soil acidity in invaded soils (5.5 -6.0).

Acidic soils that are relatively rich in nutrients may also be attributed to land-use. Nutrient-rich runoff from surrounding anthropogenic activities has been found to benefit competitive alien species (Milton, 2004; Meek et al. 2010; Nsor, 2012). Meek et al. (2009) showed that very few native species have managed to survive in riparian zones adjacent to agricultural land, although the reason is not clear. This is important as both the cleared and uncleared sites were located on farmland.

In the following sections of this study, the trends revealed within the invaded sites will be discussed, with particular reference to the impacts of *E. camaldulensis* invasion on site condition, and site-specific allogenic factors influencing riparian vegetation.

The effects of E. camaldulensis and invasive species on site condition

E.camuldulensis and *A. mearnsii* are known to disrupt the natural ecosystem functioning of riparian vegetation by altering soil properties, channel morphology and ground cover (Reinecke et al. 2008, Levine et al. 2003). The affects that these changes have in determining species composition tend to change up the lateral profile of the bank (from the lower wet bank, to the middle and upper dry bank), (Richardson et al. 2007). For example, in this study, the lower bank had higher exposure to sedimentation and inundation from upstream erosion and river blockage by fallen branches (Fig. 8A), whilst the middle bank was heavily eroded by *Eucalyptus* root systems (Fig. 7B). Even in cleared sites, the bank slopes remained steeply eroded three years post-clearance (Fig. 9C).

The upper bank was less affected by fluctuating moisture levels (moisture decreased up the bank slope), but was more affected by leaf litter and canopy cover, (Fig. 8B, 9A and 9B), limiting colonising species to shade tolerant, robust varieties. This may have directly decreased the survival rate and establishment of certain plant propagules (Holmes et al. 2006). Indeed, species diversity was particularly low in the middle banks (H': 1.28), where erosion was heaviest, and where canopy and litter cover was high. The loss of vegetation cover was great enough for several of the understory quadrats to be considered outliers in the cluster analysis (Fig. 3.1, 3.2), and the few species recorded within the litter zone were predominantly small, weedy (<10cm) herbaceous annuals.

The dominant herbaceous species here were the native geopyte *Oxalis pes-caprae*. *Oxalis pes-caprae* is a known to be a pernicious invader of cultivated land and disturbed areas worldwide (Tu, 2003). It is highly tolerant of variable climates and is quick to re-colonise disturbed areas, even after herbicide application (Vila et al. 2006, Tu, 2003). The lower banks (H': 1.96) were dominated by competitive, alien annual grasses, like the aggregate species *Bromus diandrus* and *Lolium multiflorum.* These are characteristic of moisture-rich, disturbed or cultivated land, and are problematic for crops and livestock as they carry diseases and parasites that can be lethal (Cape Nature, n.d.). The river corridor may be a means of dispersal for these species, as they were located predominantly in the lower banks.

As an aside, it must be added that the SIMPER analysis, (which identified the most frequently occurring species in plots), does not compare or account for the percentage of vegetation cover per plot. Thus, in areas with large tracts of bare ground and limited vegetation cover, species diversity may have been exaggerated by the presence of a few, rare, often juvenile species (e.g. *Lolium multiflorum*, *Rumex lanceolatus).*

Nevertheless, Moral & Muller (1970) also found that only tolerant species of *Lolium multiflorum*, *Bromus* spp. and *Trifolium* spp., were able to thrive under *E. camaldulensis* stands in California. They also found that seedlings very seldom germinated or reached maturity. While Moral & Muller (1970) attributed this to allelopathy in leaf litter, this is unlikely to be the predominant inhibitor in this study for two reasons: Firstly, *E. camaldulensis* was shown to not to inhibit herbaceous species on sandy soils in the study by Moral & Muller (1970). However, the sites along the Berg River were highly sandy (>65%), as shown in the texture analysis (Table 3). Secondly, allelochemicals do not completely inhibit understory growth without other limiting factors (e.g. soil nutrients and moisture), (Moral & Muller, 1970, Nsor et al. 2012). But in this study, invaded areas showed the highest electrical conductivity of the sites (100 soil- 480 µS/cm), the highest overall acidity (pH of 5.4-5.8) and a relatively high moisture percentage (0.07-0.17%). Thus, it is more likely that the factors inhibiting seedlings are the competitive exclusion of light and the smothering of seedlings by leaf litter.

Post clearance restoration and regeneration in cleared sites

Natural riparian vegetation along the Berg River should comprise of broad-leaved woody scrubs, perennial shrubs and small trees (Reinecke et al. 2008). Graminoids (Poaceae, Cyperaceae and Juncaceae) and forbs should dominate the understory, with regular recruitment of woody and perennial species (Reinecke et al. 2008). Small, indigenous trees (3-10 meters) and fynbos elements (Restionaceae and Ericaceae) may be present (Reinecke et al. 2008).

A relatively long time frame is expected for ecosystem recovery experiments. However, studies have shown that seedlings from dominant indigenous guilds usually emerge within the first few years following clearing (Reinecke et al. 2007; Vosse et al. 2008). It is thus possible to assess the likely trajectory of indigenous recovery within two years from initial clearance.

In this experiment, alien and native species diversity was very similar (maximum H':1.4-1.5 respectively), although the dominant species seemed to be native Asteraceae (*Senecio pterophorus*) and, most notably, indigenous woody species of *Kiggelaria africana*. Often, post-clearance plots have been show to lack indigenous woody species, both above-ground and in soil seed banks. Cleared sites also showed evidence of small, sparsely distributed *Salix mucronata* individuals.

However, there was an absence of functionally important woody species including: *Brabejum stellatifolium, Metrosideros angustifolia, Morella serrate.* Vosse et al. 2008 also found a dearth of indigenous woody species in post-clearance sites, which they believed inhibited the potential for stand recovery. Such indigenous trees usually form low, closed canopies that are relatively resistant to wind and animal-dispersed alien seeds by fauna (such as *Briza, Lolium, Acacia and Bromus),* (Reinecke et al. 2008). The invasion of native vegetation by *E. erecta* was also found to be inhibited by seed covering structures (McIntyre & Ladiges, 1985).

Interestingly, annual and perennial grasses were also dominant across cleared plots. However, in natural riparian vegetation, grasses (native or alien) should only form a minor part of post-disturbance successional communities, (Reinecke et al. 2008). Annual Mediterranean grasses, such as *Bromus diandrus* and *Digitaria debilis,* were dominant across plots. *Digitaria debilis,* like *B. diandrus,* is a known weedy invasive in many parts of the world (Verloove, 2008). Indigenous perennial grasses (such as *Pentaschistis capensis* and *Ehrharta* species) were also pervasive, although these species are known pioneers of moist, disturbed habitats (McIntyre & Ladiges, 1985; Fish & Victor, 2010).

Reasons for the invasion of annual and perennial grasses that are atypical of natural vegetation may indicate that external variables, such as habitat disturbance from land-use, may be promoting grass spread. However, invasive pioneering grasses have also been shown to spread following the clearance of *Acacia* species (Yelenik et al. 2004). *Acacia* species increase the rates of soil mineralisation, making nitrogen available to competitive, tolerant species both before and after clearance (Yelenik et al. 2004, Levine et al. 2003, Milton, 2004). Milton (2004) found that the alien grasses, such as *Bromus diandrus* grow, even grow better under sites that have been invaded by alien *Acacia,* due to nutrient-enrichment from organic matter and litter deposition. Similar trends were recorded in European heathlands that had been exposed to nitrogen deposition from atmospheric pollution (Bobbink et al. 1998).

The results of the soil analysis indicate that soil salinity was, indeed, higher in terrestrial (D) samples of the cleared sites downhill from agricultural land (Maximum EC: 550 μS/cm). However, soils in the cleared sites were moderately acidic and had low overall salinity (EC: 100-200μS/cm), compared to the highly acidic and nutrient poor soil typical of fynbos sandstone, of the pristine site (pH<5.8, EC<100 μS/cm).

It is thus possible that the invasion of alien grasses is more a factor of dispersal of alien propagules from invaded sites upstream, or from disturbed, cultivated land. However, the results of the study indicate that the trajectory of succession may be in favour of indigenous colonisation, if follow up treatments prevent reinvasion by *Acacia* and *Eucalypt*. Potential constraints of the sites that may inhibit this trajectory towards recovery of will be discussed in the following section.

Restoration constraints of the study

One of the principal targets of clearance projects is ecosystem repair of alien-invaded riparian zones. "Ecosystem repair" has been defined by Holmes et al. (2008) as actions to overcome environmental limitations of an ecosystem to improve functional integrity or biodiversity. However, the damage and severity of invasion, the complexity of interactions between site-specific biotic and abiotic factors (e.g. land use, erosion), and the methods of clearance may compromise the ability of the site to self-repair (Holmes et al. 2008). For example, Galatowitsch & Richardson, (2005) showed that the traditional "fell and burn" techniques (which were used for clearance in this study, see: Fig. 9D) may be potentially damaging to native vegetation. Alien slash fires from on-site burning have been shown to eliminate soil-stored seed banks, due to the high soil temperatures (Holmes et al. 2000). This can change species composition to favour wind-dispersed pioneer species and prohibit or restrict the recovery of indigenous vegetation, compared to "fell and remove" or active revegetation methods (Holmes et al. 2000). Alien grass invasion may also represent a restoration constraint, as grass species are known to reduce woody seedling survival (Reinecke et al. 2008).

Furthermore, restoration is often constrained by the initial site invasion intensity. For example, Galatowitsch & Richardson, (2005) showed that sites that were originally less densely invaded were more likely to shift from small-stature species to closed canopies of large, indigenous species. In this experiment, the cleared plots were originally severely invaded (>80% aerial cover), decreasing the likelihood that indigenous woody species will recolonize without aid.

While passive succession has been shown to be highly successful in rehabilitating invaded sites elsewhere in the Berg River, (Ruwanza et al. 2012; Nsor, 2012; Galatowitsch & Richardson, 2005), active re-vegetation of woody species has been suggested in the case of in the case of long-standing, invaded stands, where the catchment has undergone modification through erosion and sedimentation (Galatowitsch & Richardson, 2005; Holmes et al. 2006). Indigenous trees are relatively resistant to disturbance and are considered good options for re-vegetation efforts (Meek et al. 2010; Galatowitsch & Richardson, 2005). However, they are often require closed canopies for establishment, are slow growing and have high juvenile mortality rates in post-clearance sites (Galatowitsch & Richardson, 2005). Thus, the planting of absent woody species (e.g. *Brabejum stellatifolium*, *Metrosideros angustifolia*, *Kiggelaria africana)* in place of sowing seeds, has been suggested as a better catalyst for site recovery (Reinecke et al. 2007).

Clearing methods are also encouraged to include off-site burning to reduce site damage as are consistent, post-cleareance treatments. (Holmes et al. 2000). However, it is understood that to reduce costs, post-clearance is often left to local land-owners after one or two post-clearance treatments, which means that upkeep is largely dependent on the owners own initiative.

Study constraints

Several constraints compromised the comparability of the pristine, cleared and invaded sites in this experiment. Firstly, the sampling period took place April and August 2013, whereas the usual flowering time for species in this area was September to January (Meek et al. 2010). Thus, 15 samples were not able to be identified to species level, as sample plants were sterile (without flowers/fruits), and many species were in ear. Furthermore, this study comprised a natural experiment using active clearance sites, as opposed to a controlled field experiment. Thus, the interpretation of the results is somewhat limited by the comparability of the sites and their site histories.

The function of the reference site should also be called to attention. Uninvaded sites along the Berg River are extremely rare and species composition in the lower reaches is significantly different to that of the upper reaches (RHP, 2004). Additionally, even if an ideal reference site was available, it is possible that ecosystem change in invaded sites is already irreversibly damaged (Holmes et al. 2008). For this reason it has been argued that it is better to re-establish important ecosystem services and mitigate the negative effects of site invasion rather than attempt to restore the species composition of reference plots (Holmes et al. 2008).

The reference site was, however, useful in establishing a comparable land-mark for species diversity, and allowed the identification of some native species that have survived under less severe land use change and invasion (e.g. *Brabejum stellatifolium, Kiggelaria africana* and *Prionium serrata).*

The time frame and size of the study area are also relatively small, especially considering that species composition is continually changing in riparian zones (Richardson et al. 2007). The focus on a single case-study may seem to compromise the generality of the results, but given the dynamism and patchiness of riverine systems, a smaller-scale study was able to provide some detail into the relationships between environmental and species condition. As the study only investigated a small area of the Berg River, it would be interesting to collect data from nearby catchments where *Eucalyptus* has been cleared and compare primary successional species.

The intention of investigating soil properties, land-use and altitude was to gain insight into the conditions which promote or inhibit growth of particular species, although the experiment did not attempt to investigate chemical and microbial aspects of the soil and litter. It would be interesting to do a follow-up study to investigate these variables, potentially including a bioassay to test for allelopathic chemicals or a soil water repellency test.

Conclusion

This study provided a snapshot in time of the impacts of alien invasion on local-scale plots along the Berg River. Invaded stands showed clear evidence of long-term damage, including altered soil condition (heightened nutrients from litter or nitrogen-fixing acacias), bank erosion, loss of diversity and loss of overall vegetation cover. The patterns of erosion in invaded sites were present in cleared sites, three years post-clearance.

The cleared site had a high proportion of atypical grass invasion, although it did show signs of recovery of indigenous woody vegetation (particularly *Kiggelaria africana*), which is interesting as they are often absent from soil seed banks (Reinecke et al. 2008). The care taken to reduce bank and native vegetation damage during clearance (Foresters Vegetation

Management) as well as adherence to follow-up clearance has aided the trajectory of the stand towards restoration, although on-site burning may have slowed progress.

The extent to which indigenous communities recover and resist further invasion is imperative to the success of the clearance projects on the Berg River. Planting indigenous woody species (e.g. *Brabejum stellatifolium*, *Metrosideros angustifolia*, and *Kiggelaria africana*,) may restore over-story canopies that promote natural ecosystem function, and prevent further invasion in future years.

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Appendix 1

Table of specimens identified to species level, where possible, in the sites along the Berg River in 2013

Species number	Family	*Genus*	*Species*	First Published by:	Native Origin
1	Asteraceae	*Arctium*	*minus*	Bernh.	America
2	Poaceae	*Eragrostis*	*tef.*	(Zucc.) Trotter	East Africa
3	Poaceae	*Pennisetum*	*clandestinum*	(Hochst. ex Chiov.)	East Africa
4	Poaceae	*Paspalum*	*distichum*	L.	Asia
5	Oxalidaceae	*Oxalis*	*pes-caprae*	L.	South Africa
6	Chenopodiaceae	*Chenopodium*	*ambrosioides*	L.	Americas
7	Polygonaceae	*Rumex*	*crispus*	L.	Eurasia
8	Solanaceae	*Solanum*	*nigrum*	L.	Eurasia
9	Ateraceae	*Cotula*	*anthemoides*	L.	South Africa
10	Poeaceae	*Ehrharta*	*ottonis*	Kunth. ex. Nees.	South Africa
11	Asteraceae	*Senecio*	*pterophorus*	D.C.	South Africa
12	Poaceae	*Ehrharta*	*erecta*	Lam	South Africa
13	Commelinaceae	*Commelina*	*africana*	Linn.	Southern Africa
14	Cyperaceae	*Cyperus*	*fastigiatus*	Rottb.	South Africa
15	Poeaceae	*Echinochloa*	*crus-galli*	L.	Asia
16	Solanaceae	*Solanum*	*africanum (americanum)*	Mill. (Mill.)	S. America
17	Solanaceae	*Solanum*	*burbankii*	Bitter.	S. America
18	Apocynaaceae	*Araujia*	*sericifera*	Brot.	S. America
19	Chenopodiaceae	*Chenopodium*	*album*	L.	Worldwide

20	Salicaceae	*Populus*	*canescens*	Sm.	Europe
21	Poaceae	*2*			
22	Poaceae	*Ehrharta*	*1*		South Africa
23	Poaceae	*Digitaria*	*debilis*	(Desf.) Willd.	Eurasia
24	Myrtaceae	*Leptospermum*	*laevigatum*	F. Muel	Aus
25	Ateraceae	*Conyza*	*canadensis*	(L.) Conq	Cannada, NA
26	Chenopodiaceae		*1*		
27	Poaceae	*Paspalum*	*urvillei*	Steud	S. America
28	Restionaceae	*Calopsis*	*paniculata*	H. P. Linder	South Africa, hermanus
29	Restionaceae	*Elegia*	*1*		South Africa
30	Amaranthaceae	*Alternanthera*	*pungens*	H.B.K.	S. America
31	Proteaceae	*Brabejum*	*stellatifolium*	L.	South Africa
32	Rosaceae	*Rubus*	*pinnatus*	Lilld.	Northern Hemisphere
33	Cyperaceae	*Ficinia*	*capillifolia*	(Schrad.) C.B. Clarke	South Africa
34	Asteraceae	*1*			Northern Hemisphere
35	Anacardiaceae	*Rhus*	*angustifolia*	L	South Africa
36	Asteraceae	*Taraxacum*	*officinale*	G.H. Weber ex. Wiggers	Europe
37	Poeaceae	*Pennisetum*	*macrourum*	Trin.	South Africa
38	Poeaceae	*4*			
39	Asteraceae	*Stoebe*	*plumosa*	(L.) Thunb.	South Africa
40	Poaceae	*Pentaschistis*	*glandulosa*	(Schrad.) L.	South Africa
41	Poaceae	*Pentaschistis*	*1*		
42	Achariaceae	*Kiggelaria*	*africana*	L.	South Africa
43	Restionaceae	*Restio*	*filiformis*	Poir.	South Africa
44	Restionaceae	*Platycaulos*	*callistachyus*	(Kunth) H. P. Linder	South Africa
45	Asteraceae	*Vellereophyton*	*dealbatum*	Thunb.	South Africa
46	Ericaceae	*Erica*	*1*		
47	Ericaceae	*Erica*	*curviflora*	L.	South Africa
48	Poaceae	*Pentaschistis*	*airoides*	L.	South Africa
49	Poeaceae	*Briza*	*minor*	L.	Northern Hemisphere
50	Asteraceae	*Senecio*	*1*		South Africa
51	Poaceae	*3*			
52	Rosceae	*Cliffortia*	*cymbifolia*	Weim.	South Africa
53	Dennstaedtiaceae	*Pteridium*	*aquilinum*	(Luin) Kuhn	Northern Hemisphere
54	Asteraceae	*Hymenolepis*	*parviflora*	L.	South Africa
55	Restionaceae	*Calopsis*	*1*	H. P. Linder	South Africa
56	Cyperaceae	*Ficinia*	*palleus var. pallas/argyropa*	(Schrad.) Nees.	South Africa
57	Rhamnaceae	*Phylica*	*2*		
58	Cyperaceae	*Isolapis*	*prolifera*	(Rottb.) R. Br.	North America
59A	*Unidentifiable sprouts (<1cm)*				
59B	*Unidentifiable sprouts (<1cm)*				
59E	*Unidentifiable sprouts (<1cm)*				
59F	*Unidentifiable sprouts (<1cm)*				
59G	*Unidentifiable sprouts (<1cm)*				
59H	*Unidentifiable sprouts (<1cm)*				
60	Cyperaceae	*Ficinia*	*indica*	(Lam.) H.Pfeiff.	South Africa
61	Asteraceae	*Chrysanthemoides*	*monilifera*	(L.) Norl	South Africa

62	Oftia	*Africana*	*1*	Bocq.	South Africa
63	Oxalidaceae	*Oxalis*	*nidulans var. denticulata*	E.Z. and (W. Dod) Salter	South Africa
64	Cyperaceae	*Cyperus*	*denudatus*	Linn. F.	South Africa
65	Prioniaceae	*Prioniaceae*	*serratum*	(L.f.) Drège	South Africa
66	Haloragaceae	*Laurembergia*	*repens*	(L.) P.J. Bergius	South Africa
67	Asteraceae	*Taraxacum*	*officinale*	G.H. Weber ex Wiggers	Europe
68	Asteraceae	*Vellereophyton*	*dealbatum*	(Thunb.) Hilliard & Burtt	South Africa
69	Droseraceae	*Drosera*	*capensis*	L. (Linnaeus)	South Africa
70	Lobeliaceae	*1*			South Africa
71	Junaceae	*1*			
72	Rhamnaceae.	*Phylica*	*1*		Europe
73	Asteraceae	*Senecio*	*2*		
74	Asteraceae	*Athanasia*	*trifurcata*	(L.) L.	South Africa
75	Junaceae	*Juncus*	*lomatophyllus*	Spreng.	South Africa
76	Species	*1*			
77	Species	*2*			
78	Species	*3*			
79	Species	*4*			
80	Salicaceae	*Salix*	*mucronata*	Thunb.	South Africa
81	Araceae	*Zantedeschia*	*aethiopica*	(L.) Spreng.	South Africa
82	Lauracaceae	*Cassytha*	*ciliolata*	Nees.	S. America
83	Mesembryanthemaceae	*Carpobrontus*	*edulis*	(L.) L. Bolus	South Africa
84	Juncaceae	*Juncus*	*oxycarpus*	Krasii Mochet	Africa
86	Asteraceae	*Senecio*	*Burchellii*	D.C.	South Africa
87	Ranunculaceae	*Clematis*	*brachiata*	Thunb.	South Africa
88	Polygonaceae	*Rumex*	*lanceolatus*	L.	Eurasia
89	Ateraceae	*Sonchus*	*asper*	(L.) Hill	Europe
90	Poaceae	*Avina*	*sativa*	L.	west africa
91	Poaceae	*1*			
92	Poaceae	*Eragrostis*	*curvula*	(Schrad). Nees	South Africa
93	Asteraceae	*Conzya*	*bonariens*	(L.) Cronq	America
94	Poaceae	*Bromus*	*diandrus*	(Gussonei Paul) Roth.	Europe
95	Iridaceae	*Watsonia*	*zeyheri*	L. Bol.	South Africa
96	Poaceae	*Pentaschistis*	*capensis*	(Nees). Stapf	South Africa
97	Asteraceae	*2*			
98	Poaceae	*Eragrostis*	*curtipedicellata*	Buckley	South Africa
99	Asteraceae	*Athanasia*	*crithmifolia*	(L.) L.	South Africa
100	Cyperaceae	*Cyperus*	*1*	Rottb.	South Africa
101	Polygalaceae	*Muraltia*	*1*	(L.) DC.	South Africa
102	Lycopodiaceae	*Lycopodium*	*cernuum*	L.	Australia
103	Poaceae	*Lolium*	*multiflorum*	Lam.	Europe
104	Asteraceae	*Othonna*	*quinquedentata*	Thunb.	South Africa
105	Asteraceae	*3*			
106	Asteraceae	*Senecio*	*lyratus*	h. f.	South Africa
107	Polygonaceae	*Rumex*	*cordatus*	Poiret	Northern Hemisphere
108	Asteraceae	*Bidens*	*pilosa*	L.	Americas
109	Helminthotheca	*Picris*	*Echioides*	L.	Northern Hemisphere
110	Lamiaceae	*Melissa*	*officinalis*	L.	Europe
111	Fabaceae	*Lessertia*	*frutescens*	(L.) Goldblatt and J.C. Manning	South Africa

112	Apiaceae	*Foeniculum*	*vulgare*	Gaertn.	Europe
113	Myrtaceae	*Eucalyptus*	*camaldulensis*	*Dehnh.*	Australia
114	Myrtaceae	*Eucalyptus*	*2*		Australia
115	Fabaceae	*Acacia*	*longifolia*	(Andr.) Willd.	Australia
116	Myrtaceae	*Metrosideros*	*1*		Australia
117	Fabaceae	*Acacia*	*saligna*	(Labill.) Wendl F.	Australia
118	Fabaceae	*Acacia*	*mearnsii*	De Wild.	Australia

Statistical Analyses in PRIMER:

Identifying plant communities and measuring species richness

Appendix 2

Table 4: Two-way Nested ANOSIM on Vegetation: Pairwise comparisons of species vegetation between stands (1-9), which are nested within sites: Pristine sites (stands 1-3), uncleared sites (stands 4-6), cleared sites (7-9). [PRIMER-E]

```
Pairwise Tests
                R  Significance      Possible        Actual  Number >=
Groups  Statistic       Level %  Permutations  Permutations   Observed
1, 2        0.463            10            10            10          1
1, 3        0.111            30            10            10          3
1, 4        0.185            40            10            10          4
1, 5            1            10            10            10          1
1, 6            1            10            10            10          1
1, 7        0.778            10            10            10          1
1, 8            1            10            10            10          1
1, 9            1            10            10            10          1
2, 3        0.093            40            10            10          4
2, 4         0.37            20            10            10          2
2, 5            1            10            10            10          1
2, 6            1            10            10            10          1
2, 7        0.907            10            10            10          1
2, 8            1            10            10            10          1
2, 9            1            10            10            10          1
3, 4        0.222            40            10            10          4
3, 5            1            10            10            10          1
3, 6            1            10            10            10          1
3, 7        0.778            10            10            10          1
3, 8            1            10            10            10          1
3, 9            1            10            10            10          1
4, 5       -0.259           100            10            10         10
4, 6       -0.185           100            10            10         10
4, 7        0.444            10            10            10          1
4, 8        0.556            10            10            10          1
4, 9        0.444            10            10            10          1
5, 6       -0.037            70            10            10          7
5, 7        0.685            10            10            10          1
5, 8            1            10            10            10          1
5, 9        0.926            10            10            10          1
6, 7        0.185            30            10            10          3
6, 8        0.444            20            10            10          2
6, 9        0.333            30            10            10          3
7, 8        0.204            20            10            10          2
7, 9        0.407            20            10            10          2
8, 9        0.815            10            10            10          1
```

- ***Highlighted variables* should *differ from one another (pristine from cleared and from uncleared).***

Appendix 3:

Table 5: Two-way Nested ANOSIM on Soil data: Pairwise comparisons of soil data between plots (1-9), which are nested within sites: Pristine sites (stands 1-3), uncleared sites (stands 4-6), cleared sites (7-9). [PRIMER-E]

```
Pairwise Tests
               R  Significance      Possible        Actual  Number >=
Groups Statistic       Level %  Permutations  Permutations   Observed
1, 2       0.091           5.6       1352078           999         55
1, 3       0.263           0.2       1352078           999          1
1, 4       0.219           0.6       1352078           999          5
1, 5       0.299           0.2       1352078           999          1
1, 6        0.56           0.1       1352078           999          0
1, 7       0.453           0.1       1352078           999          0
1, 8       0.748           0.1       1352078           999          0
1, 9       0.088           7.3       1352078           999         72
2, 3       0.103           4.5       1352078           999         44
2, 4       0.518           0.1       1352078           999          0
2, 5       0.608           0.1       1352078           999          0
2, 6       0.895           0.1       1352078           999          0
2, 7       0.657           0.1       1352078           999          0
2, 8       0.919           0.1       1352078           999          0
2, 9       0.142           1.5       1352078           999         14
3, 4       0.615           0.1       1352078           999          0
3, 5       0.724           0.1       1352078           999          0
3, 6       0.936           0.1       1352078           999          0
3, 7       0.719           0.1       1352078           999          0
3, 8       0.951           0.1       1352078           999          0
3, 9       0.328           0.1       1352078           999          0
4, 5       -0.06          90.9       1352078           999        908
4, 6       0.176           1.5       1352078           999         14
4, 7       0.002            39       1352078           999        389
4, 8        0.16           1.2       1352078           999         11
4, 9       0.058          13.4       1352078           999        133
5, 6       0.079           9.4       1352078           999         93
5, 7      -0.005          43.9       1352078           999        438
5, 8       0.073          10.6       1352078           999        105
5, 9       0.092            10       1352078           999         99
6, 7       0.198           0.7       1352078           999          6
6, 8       0.231           0.5       1352078           999          4
6, 9       0.342           0.1       1352078           999          0
7, 8      -0.001          41.3       1352078           999        412
7, 9       0.145           3.5       1352078           999         34
8, 9       0.325           0.5       1352078           999          4
```

- ***Highlighted variables should differ from one another (pristine from cleared and from uncleared).***

Appendix 4:

Table 6: Spearman Rank Order Correlation for Soil properties, alien tree invasion and litter cover (red values are significant ($p<0.5$)):

	Valid	Spearman	t(N-2)	p-level
moisture (%) &litter	108	0.130541	1.355604	0.178106
moisture (%) & tree density	108	0.240895	2.555421	0.012024
EC &litter	108	0.295914	3.189464	0.001875
EC & tree density	108	0.388459	4.340288	0.000033
pH &litter	108	-0.021309	-0.219440	0.826729
pH & tree density	108	-0.020559	-0.211716	0.832735