



Eucalyptus invasions in riparian forests: Effects on native vegetation community diversity, stand structure and composition

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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 canopy cover. We found that species richness, diversity and structural attributes (e.g. height, relative cover and mean basal area) of native species decreased consistently along the invasion gradient. However, evenness did not change significantly with increasing *Eucalyptus* invasion. Invasion by *E. camaldulensis* 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. This research offers a baseline from which further experimental work can be conducted to determine the mechanisms responsible for changes attributed to *Eucalyptus* invasion.

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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 ecosystem parameters (Hejda and Pyšek, 2006).

Riparian zones, the fringes of rivers or streams, form the interface between aquatic and terrestrial ecosystems and are often characterized 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 ecosystem 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). Furthermore, riparian zones are often associated with anthropogenic activity and disturbance which promotes proliferation of invasive species and subsequent ecosystem changes (Hejda and Pyšek, 2006; Jäger et al., 2007; Meek et al., 2010).

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 (although see Tickner et al., 2001; Mason et al., 2007; 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

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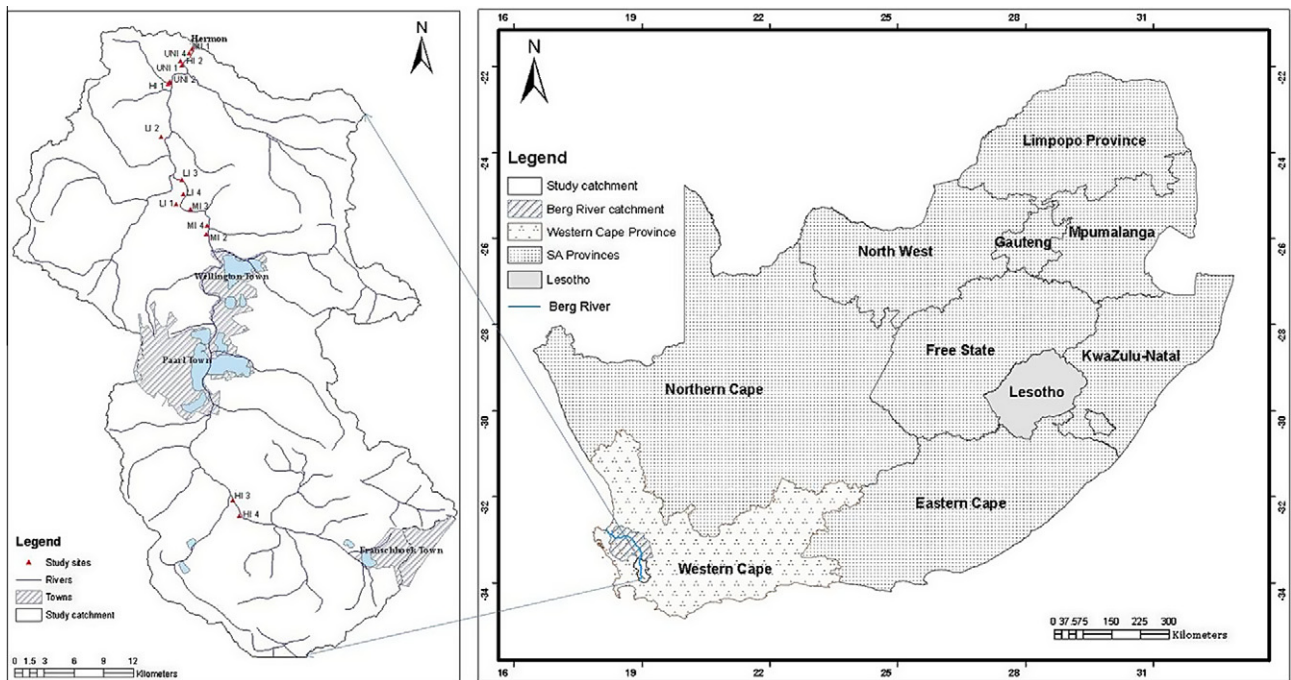


Fig. 1. Distribution of study sites (IND – Indigenous/uninvaded; LI – Light invasion; MI – Moderate invasion; HI – Heavy invasion) along the Berg River stretch between the towns of Hermon and Franschoek; Western Cape, South Africa.

planted alien species (Evans, 1992; Doughty, 2000; Tynelä, 2001; Rejmánek and Richardson, 2011). *E. 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). 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. Specifically we examined changes in diversity, structure and composition of riparian resident communities. We used a gradient sampling comparative approach and compared it to observational approaches used in previous studies. The results of our study are envisaged to inform land managers and policy makers about the effects of invasion on native vegetation community and guide future research.

2. Materials and methods

2.1. Study area

The Berg River is located north-east of Cape Town in the Western Cape Province of South Africa. It is approximately 294 km long

from source to mouth, with a catchment area of 7715 km². 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. 1). The study area was chosen because it is a good example of old invasions (c. 50 years) (Geldenhuis, 2008) in which impact can be reasonably assessed and associated with *E. camaldulensis* invasion with relatively high levels of confidence (Ruwanza et al., 2013).

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. Altitude ranges from 247 m at Franschoek to 66 m at Hermon. The Berg is a perennial river with high flows and frequent flooding in winter (May to September).

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). Soil physico-chemical properties were similar across sites under different levels of invasion (Tererai, unpubl. data). 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 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*.

About 65% of the Berg River catchment is under agriculture (Geldenhuis, 2008). The Berg River hydrological regime is regulated by irrigation flow abstraction for farming and by the Berg River dam which was built in 2007 in its headwaters. These anthropogenic disturbances may have an influence on proliferation of invasive plants (Bacon et al., 1993; Busch and Smith, 1995). Other major agents of human 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.

2.2. Study species

E. camaldulensis Dehn. has one of the widest natural distributions of any Australian tree species. It is a riparian species and occurs 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). *E. 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 19th 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). *E. 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).

2.3. Study design

Study sites were established along a continuum of invasion (hereafter referred to as invasion gradient), and were grouped into four “invasion classes”, each with four replicates ($n = 16$ sites):

“uninvaded” (0–24% cover of *E. camaldulensis*), “light” (25–49% cover), “moderate” (50–74%), and “heavy” ($\geq 75\%$ canopy cover). In this study, “uninvaded” refers to sites that were almost free of eucalypts and were used as control (reference) sites. Two of the uninvaded sites had a few individuals of *E. camaldulensis* as no suitable sites totally free of this species could be found. Studies in several parts of the world 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; Clewell and Rieger, 2008; Prins et al., 2005; Richardson et al., 2007; Brewer and Menzel, 2009). 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). Invaded sites were dominated by *E. camaldulensis*, but there were isolated individuals of *Acacia mearnsii*, an invasive tree native to Australia.

Sites measured 10 m along the river and spanning the whole riparian zone, with plots in 5 m widths perpendicular to the river. The sites were randomly and longitudinally located on both sides of the river. Close proximity of invaded and uninvaded sites ensured that sites had similar ecological conditions. All sites had similar disturbance regime as they were all influenced by the Berg River dam which is located at the headwaters and no major differences in landuse were observable.

2.4. Data collection

To examine plant species composition across a gradient of *E. camaldulensis* invasion, we recorded percentage canopy cover of native and alien species, counts, height (average and maximum), and diameter (basal and breast height) data in 10 m \times 5 m plots from the 16 sites in spring (September and October), 2010. Plant height was estimated using a height rod, canopy cover percentage was estimated visually, and diameter was measured using callipers. We also estimated ground cover in terms of litter, bare soil,

Table 1
Native and alien species Shannon diversity index (H') and evenness (J') based on species abundance (% cover) data in all 10 m \times 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).

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

Significance level:
ns – Not significant.
* $p \leq 0.05$.
** $p \leq 0.01$.
*** $p \leq 0.001$.

Table 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 |
|-----------------------------|------------------|----------|-------------------------------|----------|------------|------------|--------------------|
| | | | 1st axis | 2nd axis | | | |
| Major species | Presence/absence | CCA | 42 | 66.7 | 1.69 | 0 | 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 | 5.33 |

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 *E. camaldulensis* was excluded from this analysis.

and rock material within the same plots. Plot numbers varied from four to nine per site depending on the width of the riparian zone ($n = 99$ plots). 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 of 2011 to capture plants that could have been missed.

2.5. Statistical analysis

All analyses were based on number of plots 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* canopy cover. 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). *E. camaldulensis* canopy cover was correlated with total plant species richness, total diversity and richness and diversity of native species to assess changes associated with the invader at the plot scale.

To evaluate the differences in plant 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 2), either canonical correspondence analysis (CCA) or redundancy analysis (RDA) was used. Gradient lengths greater than four show that data are heterogeneous hence a unimodal model of

species response (CCA) was used. If gradient length was less than three, a linear method (RDA) was used (Lepš and Šmilauer, 2003). 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 and transformed accordingly, and split into: (i) major species (species with at least 1% cover in one invasion class – 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 analyzed 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 canopy 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. Results

3.1. Floristic diversity

3.1.1. 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 (being 56.3% trees and shrubs, 25% geophytes and

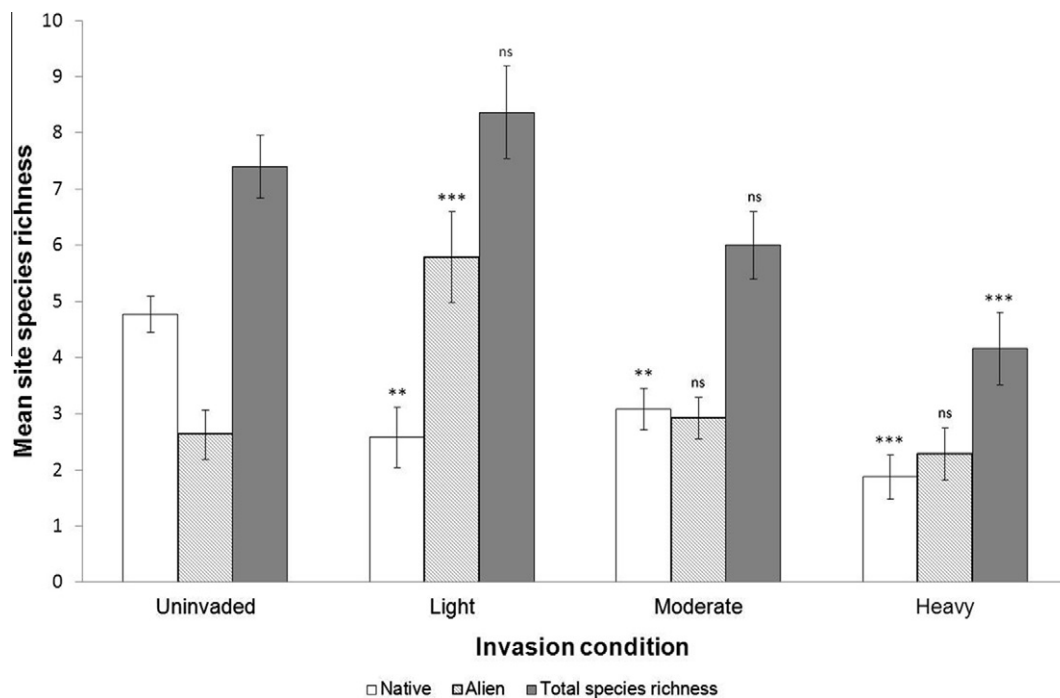


Fig. 2. Native and alien plant species richness (mean \pm SE) of plots in uninvaded ($n = 30$) sites compared to plots in lightly ($n = 19$), moderately ($n = 25$) and heavily ($n = 25$) invaded sites along the Berg River, Western Cape province, South Africa (significant differences between uninvaded and, lightly, moderately and heavily invaded sites were tested by the non-parametric Mann–Whitney U test, since all data were not normally distributed). Significance level $*p < 0.05$; $**p < 0.01$; and $***p < 0.001$, ns – not significant.

6.3% grasses), while 43 were alien plant species (constituting 55.8% forbs, 16.3% grasses, and 11.6% trees and shrubs). The light invasion plots had significantly higher species richness than the high invasion plots ($Z = -3.38$; $df = 55$ $p < 0.001$). Total number of native species recorded in uninvaded (21), lightly (19), moderately (15) and heavily (13) invaded sites decreased consistently. 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 exhibited significant differences in total plant species richness ($Z = -3.38$, $df = 55$, $p < 0.001$) (Fig. 2). There was a significant difference in native species richness among the four invasion conditions (Kruskal–Wallis ANOVA: $H_{3,99} = 27.41$, $p = 0$). Pair-wise comparisons showed that there was a consistent decline in native species richness as invasion of *E. camaldulensis* increased (Fig. 2). There were also significant differences in alien species richness among the four invasion conditions ($H_{3,99} = 15.48$, $p < 0.001$). Pair-wise 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. 2).

3.1.2. 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, species evenness among these plots was similar ($H_{3,99} = 1.83$, $p = 0.61$). While diversity of both native and alien species differed 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 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 1).

3.2. Stand structure

The height of native tree and shrub species consistently decreased with increasing height of *E. camaldulensis* across invasion conditions (Fig. 3a). There were no other alien trees or shrub species in uninvaded sites. Height of other alien tree and shrub species (including *A. mearnsii*) among lightly, moderately and heavily invaded sites was similar (Fig. 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. 3b). Plant species density per hectare was similar for either native species, *E. camaldulensis* or other alien tree and shrub species (Fig. 3c).

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 ($p > 0.05$)

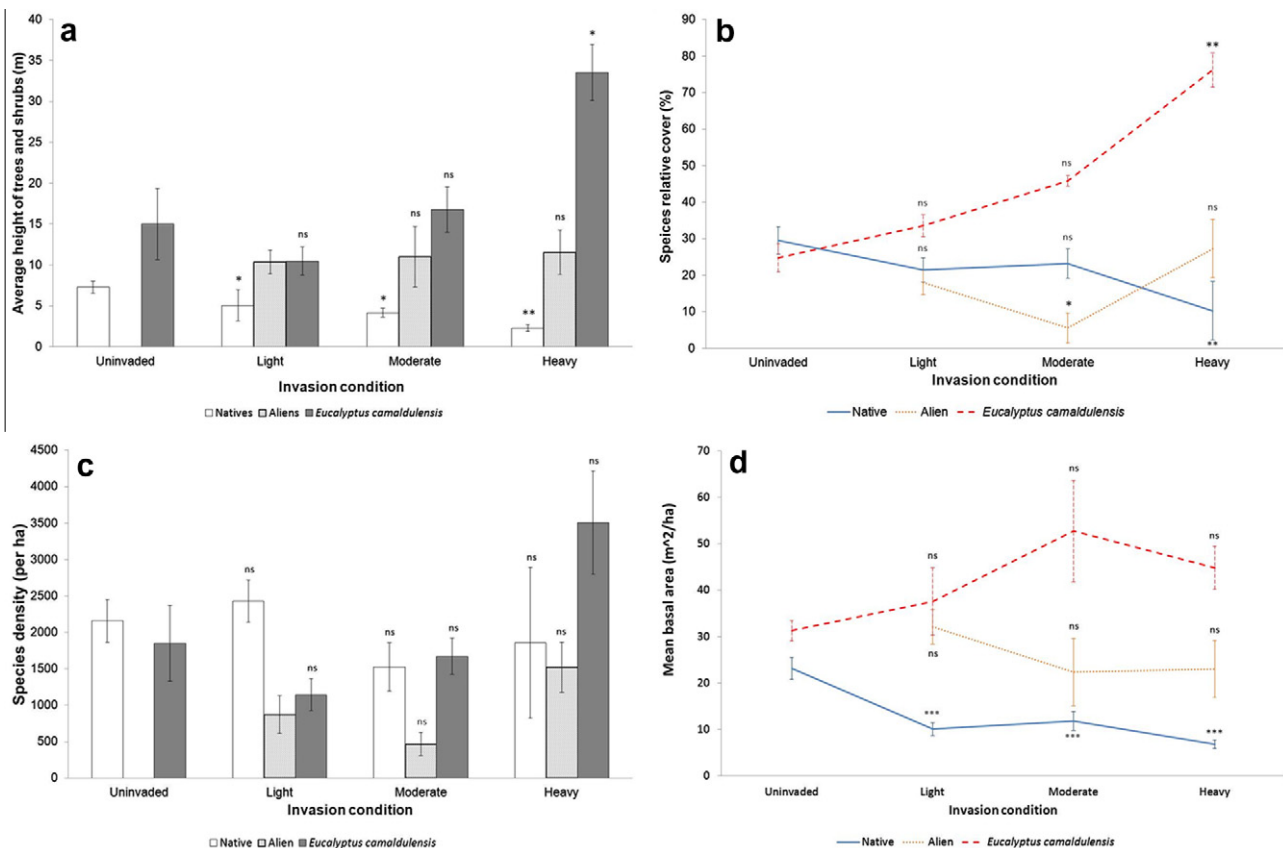


Fig. 3. (a) Mean height of trees and shrubs >1.3 m; (b) Species relative cover (%); (c) Mean density of trees and shrubs >2 m; and (d). Mean basal area (measured at 30 cm above ground and converted to area) of alien and native plants >2 m in height. All pair-wise comparisons are made against the uninvaded (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. Significance level * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$, ns – not significant.

(Fig. 3d) in terms of *E. camaldulensis* basal area. However, basal area of native tree and shrub plant species decreased significantly as basal diameter of eucalypts increased (Fig. 3d) along the invasion gradient ($H_{3,138} = 19.47$, $p < 0.001$).

3.3. Relationship between *E. camaldulensis* and native and alien plant species characteristics

Correlation analysis 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. 4). There was, however, no significant correlation between *E. camaldulensis* density and native plant species density per ha (Spearman $r = -0.21$; $p = 0.12$).

3.4. Floristic composition

E. 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 invasion class) and presence/absence data ($p < 0.001$, Table 2). In the CCA of major species percentage canopy cover, the first axis (λ) 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 2). Differences in plant species composition along the invasion gradient were ascertained by a follow up test - 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 (λ) ex-

plained an average 40%, while the second axis explained a cumulative average of 72.5% of the variation in species data (Table 2). The Monte-Carlo permutation test for the significance of the gradient was statistically significant ($p < 0.05$, Table 2). Most species, especially native, were negatively correlated to high levels of *E. camaldulensis* invasion (Fig. 5a–d). Of the native tree and shrub species, *D. glabra*, *S. angustifolia*, *K. africana* and *P. elongatus* showed some tolerance of *E. camaldulensis* invasion (Fig. 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. 5b).

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 B, Supplementary material. *K. africana* and *Zantedeschia aethiopica* contribute up to 83% to the observed differences in heavily invaded sites, and are common in all the invasion conditions.

4. Discussion

This paper aimed to determine 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 canopy cover. The invasion of *E. camaldulensis* is associated with declines in richness and diversity of riparian plant communities. The structure and composition of native plant communities changed with increasing cover of *E. camaldulensis*.

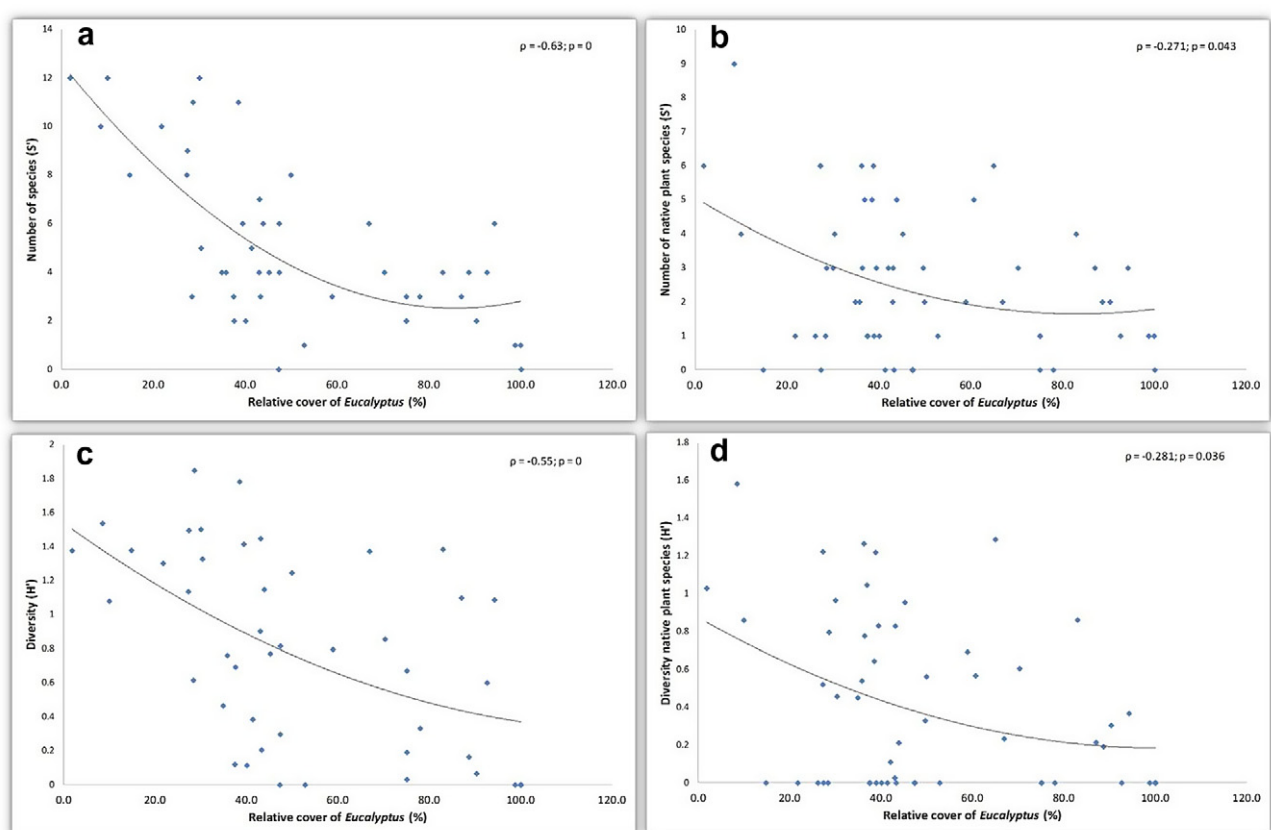


Fig. 4. Relationship between *E. camaldulensis* relative cover and: (a) richness of all plant species; (b) richness of native all plant species; (c) diversity of all plant species (H'); and (d) diversity of native plant species based on species abundance data in all 10 m \times 5 m plots containing *E. camaldulensis* along the Berg River, Western Cape, South Africa.

4.1. Relationships between invasion and floristic diversity and structure

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 area, and percentage canopy cover) were negatively correlated with the same attributes of *E. camaldulensis*. *E. camaldulensis* 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 of 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 species beneath their canopies, and the vegetation in both formed closed canopies. It has been argued that shading could be associated with 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). Our observation supports this argument; *E. camaldulensis* achieves over 75% canopy cover in the riparian zone, and this, coupled with its medium height, limits light penetration to the forest floor, thus limiting undergrowth.

Allelopathy could be another reason for limited undergrowth (or reduced species richness) underneath eucalypts. Allelopathic potential of *Eucalyptus* spp. 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). The allelopathic potential of *Eucalyptus* spp. distinguishes them from other common tree invaders of riparian zones such as *Tamarix* spp. which have been suggested to be non-allelopathic (Lesica and DeLuca, 2004). *Eucalyptus* species are also known for their characteristic thick litter layer (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* spp. have been associated with altering nutrient cycling regimes (del Moral and Muller, 1970; Gaertner et al., 2011). Changes in nutrient cycling may alter species competitive regime, and this often leads to a 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). With on-going succession, competitive native and invasive species outcompete less competitive species which leads to declines in species richness and diversity (as described in the intermediate disturbance hypothesis (Schwilk et al., 1997; Townsend et al., 1997). Our results support this argument. Both invaded and uninvaded sites were dominated by a few competitive tree and shrub species. Invaded sites were dominated by *E. camaldulensis*, while uninvaded sites were dominated by tree and shrub species such as *K. africana*, *P. elongatus*, *O. europaea* subsp. *africana*, *D. glabra*, and *S. angustifolia* (see Appendix B 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.

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 the floristic diversity results. While some native plant species showed tolerance of invasion, they were most present in 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 *E. camaldulensis* stands. However, their growth form was mainly shrubby, as opposed to trees in uninvaded sites. Herbaceous and graminoid species were the most affected, as they disappeared completely in heavily invaded sites. Interestingly, even other alien plants including some taxa of *Acacia*, especially *A. mearnsii*, decreased with increasing abundance of *E. camaldulensis*, 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.

E. 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 supports the findings of 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 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.

E. camaldulensis co-existed with a few isolated individuals of other invasive species such as *Acacia longifolia* and *A. mearnsii*. After *E. camaldulensis*, *A. mearnsii* was second in abundance in all invasion conditions and can be seen as a potential early opportunist successor after *E. camaldulensis* clearing. Furthermore, *A. mearnsii* was particularly dominant in the soil-stored seed bank (Tererai, unpubl. data).

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 risky and unethical (Hejda and Pyšek, 2006), 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

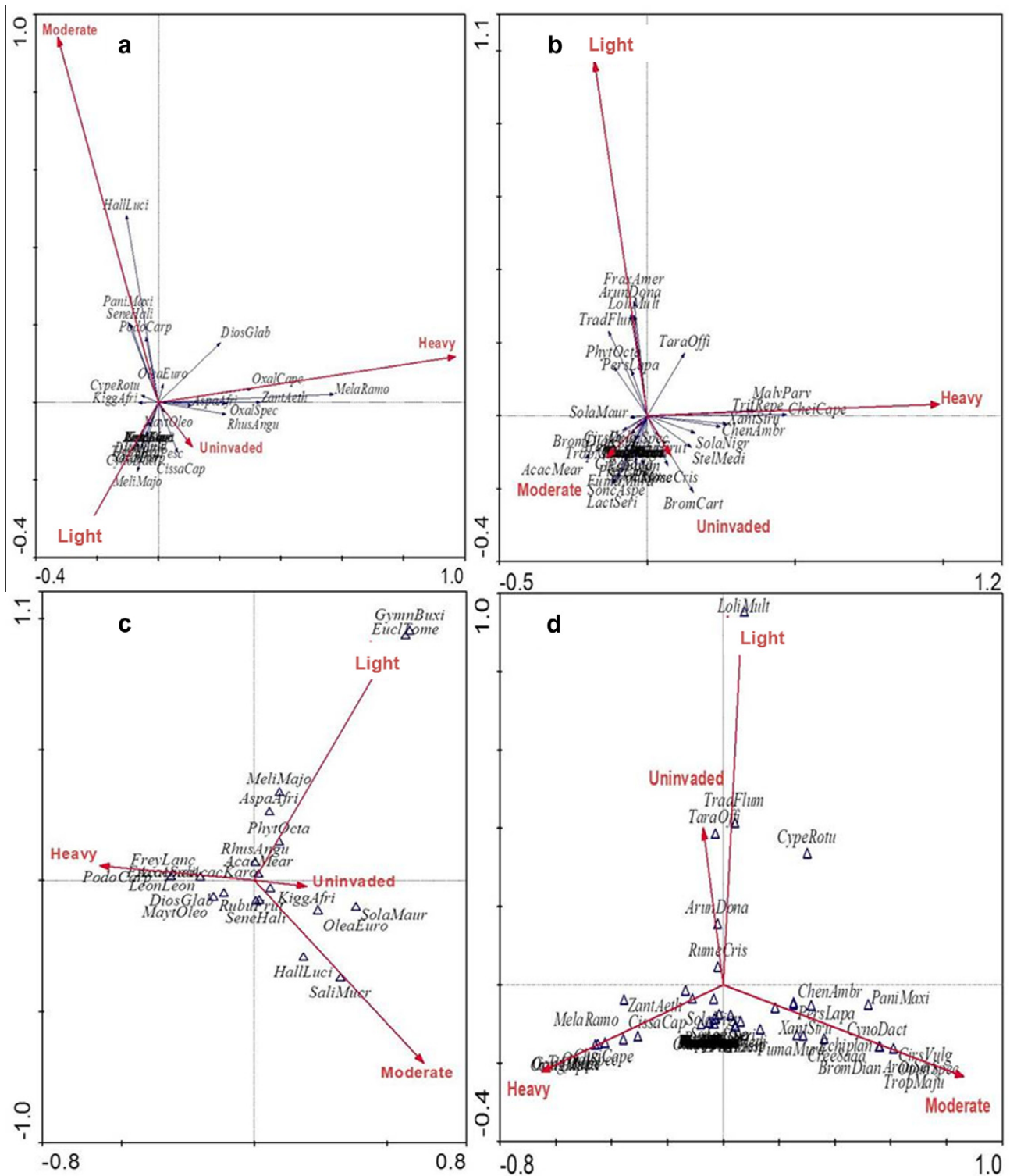


Fig. 5. Canonical correspondence analysis and redundancy analysis ordination diagrams showing the response of (a) native, (b) alien, (c) tree and shrub, and (d) forbs/graminoids/geophytes/vine species to the invasion by *E. camaldulensis* based on species covers. *Eucalyptus camaldulensis* was not included in the Monte-Carlo test, and species names are abbreviated, see Appendix A for full names. Data were split into groups to clarify differences among sites.

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. 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. We also caution that we only studied one river system so results may or may not be consistent with other areas.

5. Implications for management

The results suggest that invasion of *E. camaldulensis* in riparian zones is a major threat for the conservation of native biological diversity in South Africa. As *E. camaldulensis* is an invader in other parts of the world (Booth, 2012) these results could be applicable elsewhere. 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 survive for 500–1000 years (Jacobs, 1955), the continued presence of this species is likely to transform riparian ecosystems. Management of *E. camaldulensis* invasions to reduce the density seems more feasible than the often untenable option of eradication (Ogden and Rejmanek, 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 (Rejmanek and Richardson, 2011; Booth, 2012). 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 *E. camaldulensis* removal relies on the choice of the right combination of methods, and their consistent application over sufficient time (Starfinger et al., 2003).

An experimental removal approach could be adopted 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., 2013). These could serve as experimental removal sites for future studies measuring native vegetation response to *E. camaldulensis* removal. Other specific questions that would be interesting to address are: (1) Is there interspecific facilitation between *A. mearnsii* and *E. camaldulensis* that co-exist at some sites; and (2) Is there a difference between the effects of *E. camaldulensis* and those of dominant native species.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.02.016>.

References

Alvarez, M.E., Cushman, J.H., 2002. Community-level consequences of a plant invasion: effects on three habitats in coastal California. *Ecol. Appl.* 12, 1434–1444.

Bacon, P.E., Stone, C., Binns, D.L., Leslie, D.J., Edwards, D.W., 1993. Relationships between water availability and *Eucalyptus camaldulensis* growth in a riparian forest. *J. Hydrol.* 150, 541–561.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. *For. Ecol. Manage.* 254, 1–15.

Barling, R.D., Moore, I.D., 1994. Role of buffer strips in management of waterway pollution: a review. *Environ. Manage.* 18, 543–558.

Booth, T.H., 2012. Eucalypts and their potential for invasiveness particularly in frost-prone regions. *Int. J. Forest. Res.* 2012, 1–7.

Brewer, J.S., Menzel, T., 2008. A method for evaluating outcomes of restoration when no reference sites exist. *Restor. Ecol.* 17, 4–11.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Di Tomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.

Busch, D.E., Smith, D.S., 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern US. *Ecol. Monogr.* 65, 347–370.

Butcher, P.A., McDonald, M.W., Bell, J.C., 2009. Congruence between environmental parameters, morphology and genetic structure in Australia's most widely distributed eucalypt, *Eucalyptus camaldulensis*. *Tree Genet Genomes* 5, 189–210.

Catford, J.A., Vesk, P.A., Richardson, D.M., Pyšek, P., 2012. Quantifying levels of biological invasion: towards the objective classification of invaded and invisible ecosystems. *Glob. Change Biol.* 18, 44–62.

Clewell, A., Rieger, J.P., 2008. What practitioners need from restoration ecologists. *Restor. Ecol.* 5, 350–354.

Cotter, E., 2000. Depositional setting and cyclic development of the lower part of the Witteberg Group (Mid-to Upper Devonian), Cape Supergroup, Western Cape, South Africa. *S. Afr. J. Geol.* 103, 1–14.

Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Ann. Rev. Ecol. Evol. Syst.* 34, 183–211.

Davis, M., 2003. Biotic globalization: does competition from introduced species threaten biodiversity. *Bioscience* 53, 481–489.

Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Del Tredici, P., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J., Briggs, J.C., 2011. Don't judge species on their origins. *Nature* 474, 153–154.

del Moral, R., Muller, H.C., 1970. The allelopathic effects of *Eucalyptus camaldulensis*. *Am. Midl. Nat.* 83, 254–282.

Doughty, R.W., 2000. *The Eucalyptus: a Natural and Commercial History of the Gum Tree*. Johns Hopkins University press Baltimore, MD, Maryland, USA.

Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6, 503–523.

Evans, J., 1992. *Plantation forestry in the tropics*. Clarendon Press, Oxford, USA.

Forsyth, G.G., Richardson, D.M., Brown, P.J., van Wilgen, B.W., 2004. A rapid assessment of the invasive status of *Eucalyptus* species in two South African provinces. *S. Afr. J. Sci.* 100, 75–77.

Gaertner, M., Den Breeÿen, A., Richardson, D.M., 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geog.* 33, 319–338.

Gaertner, M., Richardson, D.M., Privett, S.D.J., 2011. Effects of alien plants on ecosystem structure and functioning and implications for restoration: insights from three degraded sites in South African fynbos. *Environ. Manage.* 48, 57–69.

Geldenhuys, C.J., 2008. Practical guidelines for the rehabilitation of forest-related streambank vegetation with removal of invader plant stands along the Berg River, Western Cape (Report no. FW-02/08). South Africa.

Gooden, B., French, K., Turner, P.J., Downey, P.O., 2009. Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biol. Conserv.* 142, 2631–2641.

Hejda, M., Pyšek, P., 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol. Conserv.* 132, 143–152.

Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393–403.

Holmes, P., Cowling, R., 1997. The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *J. Appl. Ecol.* 34, 317–332.

Hood, W.G., Naiman, R.J., 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecol.* 148, 105–114.

Hooper, D., Chapin, F., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A., Vandermeer, J., Wardle, D., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.

Hulme, P.E., 2003. Biological invasions: winning the science battles but losing the conservation war. *Oryx* 37, 178–193.

Hulme, P.E., Bremner, E.T., 2006. Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J. Appl. Ecol.* 43, 43–50.

Jacobs, R., 1955. Growth habits of the eucalypts, Forestry and Timber Bureau Canberra.

Jäger, H., Tye, A., Kowarik, I., 2007. Tree invasion in naturally treeless environments: Impacts of quinine (*Cinchona pubescens*) trees on native vegetation in Galápagos. *Biol. Conserv.* 140, 297–307.

Kent, M., Coker, P., 2002. *Vegetation Description and Analysis: a Practical Approach*, second ed. John Wiley & Sons Ltd, Chichester, England.

Khan, M.A., Hussain, I., Khan, E.A., 2008. Allelopathic effects of *Eucalyptus (Eucalyptus camaldulensis* L.) on germination and seedling growth of wheat (*Triticum aestivum* L.). *Pakistan J. Weed Sci. Res.* 14 (1–2), 9–18.

- Le Maitre, D.C., Van Wilgen, B.W., Chapman, R.A., McKelly, D.H., 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *J. Appl. Ecol.* 33, 161–172.
- Lepš, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO, Analysis*. Cambridge University Press, New York, USA.
- Lesica, P., DeLuca, T.H., 2004. Is tamarisk allelopathic. *Plant Soil* 267, 357–365.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. Royal Soc. London Ser. B – Biol. Sci.* 270, 775–781.
- Lewis C., Illgner P., 1998. Fluvial conditions during the Holocene as evidenced by alluvial sediments from above Howison's Poort, near Grahamstown, South Africa. *T. Roy. Soc. S. Afr.* 53, 53–67.
- Marchante, H., Marchante, E., Freitas, H., 2003. Invasion of the Portuguese dune ecosystems by the exotic species *Acacia longifolia* (Andrews) Willd.: effects at the community level. In: *Plant Invasions: Ecological Threats and Management Solutions*. Backhuys, Leiden, The Netherlands, pp. 75–85.
- Mason, T., French, K., Russell, K., 2007. Moderate impacts of plant invasion and management regimes in coastal hind dune seed banks. *Biol. Conserv.* 134, 428–439.
- May, F., Ash, J., 1990. An assessment of the allelopathic potential of *Eucalyptus*. *Aust. J. Bot.* 38, 245.
- McDonald, M.W., Brooker, M.I.H., Butcher, P.A., 2009. A taxonomic revision of *Eucalyptus camaldulensis* (Myrtaceae). *Aust. Syst. Bot.* 22, 257–285.
- Meek, C.S., Richardson, D.M., Mucina, L., 2010. A river runs through it: land-use and the composition of vegetation along a riparian corridor in the Cape Floristic Region, South Africa. *Biol. Conserv.* 143, 156–164.
- Mensforth, L.J., Thorburn, P.J., Tyerman, S.D., Walker, G.R., Url, S., Walker, R., 1994. Sources of water used by riparian *Eucalyptus camaldulensis* overlying highly saline groundwater. *Ecology* 100, 21–28.
- Naiman, R.J., Decamps, H., 1997. The ecology of interfaces: riparian zones. *Annu. Rev. Ecol., Evol., Syst.* 28, 621–658.
- Ogden, E.J., Rejmanek, M., 2005. Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: implications for management. *Biol. Conserv.* 125, 427–439.
- Planty-Tabacchi, A.-M., Tabacchi, E., Naiman, R.J., Deferrari, C., Decamps, H., 1996. Invasibility of species-rich communities in riparian zones. *Conserv. Biol.* 10, 598–607.
- Prins, N., Holmes, P.M., Richardson, D.M., 2005. A reference framework for the restoration of riparian vegetation in the Western Cape, South Africa, degraded by invasive Australian Acacias. *S. Afr. J. Bot.* 70, 767–776.
- Pyšek, P., Prach, K., 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to Central Europe. *J. Biogeogr.* 20, 413.
- Pyšek, P., Richardson, D.M., 2010. Invasive species, environmental change and management, and ecosystem health. *Annu. Rev. Environ. Resour.* 35, 25–55.
- Rascher, K.G., Große-Stoltenberg, A., Mágua, C., Meira-Neto, J.A.A., Werner, C., 2011. *Acacia longifolia* invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests. *Biol. Invasions* 13, 1099–1113.
- Rejmanek, M., Richardson, D.M., 2011. *Eucalypts*. In: Simberloff, D., Rejmanek, M. (Eds). *Encyclopedia of invasive introduced species*, pp. 203–209.
- Reynolds, L.V., Cooper, D.J., 2010. Environmental tolerance of an invasive riparian tree and its potential for continued spread in the southwestern US. *J. Veg. Sci.* 21, 733–743.
- Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P., Hobbs, R.J., 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Divers. Distrib.* 13, 126–139.
- Rosgen, D., 1994. A classification of natural rivers. *Catena* 22, 169–199.
- Ruwanza, S., Gaertner, M., Esler, K.J., Richardson, D.M., 2013. Both complete clearing and thinning of invasive trees lead to short-term recovery of native riparian vegetation in the Western Cape, South Africa. *Appl. Veg. Sci.* doi: 10.1111/j.1654-109X.2012.01222.x.
- Sax, D., Gaines, S.D., 2008. Species invasions and extinction: the future of native biodiversity on islands. *PNAS* 105, 11490–11497.
- Schwilk, D., Keeley, J., Bond, W., 1997. The intermediate disturbance hypothesis does not explain fire and diversity patterns in fynbos. *Plant Ecol.* 132, 77–84.
- Scott, D.F., Lesch, W., 1997. Streamflow responses to afforestation with *Eucalyptus grandis* and *Pinus patula* and to felling in the Mokobulaan experimental catchments, South Africa. *J. Hydrol.* 199, 360–377.
- Shafroth, P.B., Briggs, M.K., 2008. Restoration ecology and invasive riparian plants: an introduction to the special section on *Tamarix* spp. in Western North America. *Restor. Ecol.* 16, 94–96.
- Shafroth, P.B., Cleverly, J.R., Dudley, T.L., Taylor, J.P., Van Riper, C., Weeks, E.P., Stuart, J.N., 2005. Control of *Tamarix* in the western United States: implications for water salvage, wildlife use, and riparian restoration. *Environ. Manage.* 35, 231–246.
- Starfinger, U., Kowarik, I., Rode, M., Schepker, H., 2003. From desirable ornamental plant to pest to accepted addition to the flora? – the perception of an alien tree species through the centuries. *Biol. Invasions* 5, 323–335.
- Stromberg, J., Shafroth, P., Hazelton, A., 2012. Legacies of flood reduction on a Dryland river. *River Res. Appl.* 28, 143–159.
- Taylor, C.M., Hastings, A., 2004. Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *J. Appl. Ecol.* 41, 1049–1057.
- Thompson, K., Hodgson, J.G., Rich, T.C.G., 1995. Native and alien invasive plants: more of the same. *Ecography* 18, 390–402.
- Tickner, D.P., Angold, P.G., Angela, M., Mountford, J.O., 2001. Riparian plant invasions: hydrogeomorphological control and ecological impacts. *Progr. Phys. Geogr.* 25, 22–52.
- Townsend, C.R., Scarsbrook, M.R., Dolédec, S., 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnol. Oceanogr.* 42, 938–949.
- Truscott, A.M., Palmer, S.C., Soulsby, C., Westaway, S., Hulme, P.E., 2008. Consequences of invasion by the alien plant *Mimulus guttatus* on the species composition and soil properties of riparian plant communities in Scotland. *Perspect. Plant Ecol. Evol. Syst.* 10, 231–240.
- Tyynelä, T.M., 2001. Species diversity in *Eucalyptus camaldulensis* woodlots and miombo woodland in Northeastern Zimbabwe. *New Forest.* 22, 239–257.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. *Am. Sci.* 84, 468–478.
- Witkowski, E.T.F., 1991. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. *J. Appl. Ecol.* 28, 1–15.
- Yelenik, S., Stock, W., Richardson, D.M., 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restor. Ecol.* 12, 44–51.