

Resilience of Invaded Riparian Landscapes: The Potential Role of Soil-Stored Seed Banks

Farai Tererai · Mirijam Gaertner · Shayne M. Jacobs · David M. Richardson

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Abstract We investigated the potential role of soil-stored seed banks in driving vegetation recovery under varying intensities of invasion by the alien tree *Eucalyptus camaldulensis* along the Berg River in South Africa's Western Cape Province. We asked: How do richness, diversity, and composition of soil-stored seed banks vary with invasion intensity? What is the difference between the seed banks and above-ground vegetation with respect to species richness, diversity, composition, and structure? To what extent do soil-stored seed banks provide reliable sources for restoring native plant communities? Through a seedling-emergence approach, we compared seedling density, richness, and diversity in plots under varying *Eucalyptus* cover. Seed bank characteristics were also compared with those of the above-ground vegetation. Except in terms of diversity and density, the richness and composition of native species

varied significantly among invasion conditions. Despite the paucity of native tree and shrub species in the seed bank, it was more diverse than extant vegetation. Some species occurred exclusively either in the seed bank or in the above-ground vegetation. Although this ecosystem has been degraded by several agents, including *Eucalyptus* invasion, soil-stored seed banks still offer modest potential for driving regeneration of native plant communities, but secondary invasions need to be managed carefully. Remnant populations of native plants in the above-ground vegetation remaining after *E. camaldulensis* clearing provide a more promising propagule source for rapid regeneration. Further work is needed to elucidate possible effects of invasion on successional pathways following *E. camaldulensis* removal and the effects of hydrochory on seed bank dynamics.

Keywords Biological invasions · Ecosystem resilience · *Eucalyptus camaldulensis* · Restoration · Secondary invasions · Seed recruitment

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Introduction

Riparian zones are river and stream margins and often characterized by a distinct flora that differs in diversity, structure, and function from that in adjacent terrestrial ecosystems (Naiman and Décamps 1997; Poff et al. 2011). The flora of riparian zones provides important functions (e.g., riverbank stabilization) and services (e.g., flood attenuation) (Hood and Naiman 2000; Hooper et al. 2005). These functions and services are threatened by ecosystem degradation in many parts of the world (Baattrup-Pedersen et al. 2012), often eroding ecosystem resilience. Resilience, the ability (Wali 1999), or time taken (Mitchell et al. 2000) for an ecosystem to recover to some acceptable structural or functional reference level is often inextricably linked to disturbance (Richardson et al. 2007). The agents of ecosystem degradation in riparian zones are both natural (dynamic hydrology, climate change) and anthropogenic (agricultural activities and water abstraction) (Naiman et al. 1993; Kauffman et al. 1995; Décamps et al. 2004; Bottollier-Curtet et al. 2013). The inherent disturbances of riparian zones create opportunities for recruitment of invasive alien plants (IAPs) (Holmes et al. 2005; Poff et al. 2011; Sîrbu et al. 2012), and these may further threaten ecosystem integrity (Gaertner et al. 2009; Vilà et al. 2011). Besides high human population density, urbanization and agriculture (Underwood et al. 2009), one of the most commonly reported threats to plant diversity in the Mediterranean-type ecosystems, are plant invasions (Richardson et al. 1989; Vitousek et al. 1996; Levine et al. 2003; Pyšek and Richardson 2010; Vilà et al. 2011). Ecological restoration presents opportunities to restore degraded riparian habitats by breaking the cycle of degradation in plant community diversity and ecosystem function (Brudvig 2011). However, since ecosystem degradation is a compound effect of various perturbation agents, teasing out the effects of a single agent such as invasion is difficult, and this complicates restoration efforts (Gaertner et al. 2011; Poff et al. 2011).

Many studies have compared invaded and uninvaded sites to evaluate the effects of plant invasions on standing vegetation (Levine et al. 2003; Gaertner et al. 2009; Vilà et al. 2011; Gioria et al. 2014). However, the above-ground vegetation forms only a part of the overall plant diversity (Margalef 2002). Soil-stored seed banks, a key component of ecosystem resilience, play a significant role in restoration (Holmes and Richardson 1999; Williams et al. 2008; Gioria et al. 2012; Heelemann et al. 2013) yet are also threatened by the agents of degradation in riparian zones (Poff et al. 2011). Thus, there is need for a better understanding of the potential role that soil-stored seed banks could play in restoration of riparian habitats (Landenberger and McGraw 2004; Gioria et al. 2014).

In many degraded ecosystems worldwide where invasive alien plants are one of the agents of disturbance, “clearing” is a widely applied management action (Manchester and Bullock 2000; Beater et al. 2008; Shafroth and Briggs 2008; Flory and Clay 2009). However, simply removing the stressor often fails to stimulate the recovery of native species or to restore the functionality of degraded ecosystems (Galatowitsch and Richardson 2005; Le Maitre et al. 2011; Gaertner et al. 2012). After removal of invasive alien plants, native species may regenerate from remnant native species that co-existed with the invader, from the seed bank and through propagules dispersed from surrounding vegetation and external sources (Bakker et al. 1996; Landenberger and McGraw 2004; French et al. 2011). There are several factors that could account for recruitment limitation after clearing of invasive species. In densely invaded habitats, including riparian zones, which are often associated with suppressed native vegetation, post-clearing recovery relies on soil-stored seeds (Musil and De Witt 1990; Williams et al. 2008; Marchante et al. 2011; Li et al. 2012). However, some native species may have transient or short-lived seed banks (Thompson and Grime 1979; Thompson et al. 1997) or may not form any seed bank (Richardson et al. 2007; Fourie 2008; Vosse et al. 2008). Invasive trees often form almost complete monocultures, thereby disrupting inputs to the soil-stored seed bank by native species; over time, this leads to the attrition of previously deposited native seed stores (Gioria et al. 2012, 2014). Native plants that occur in heavily invaded ecosystems die prematurely or produce few or no seeds (del Moral and Muller 1970; Holmes and Cowling 1997; Levine et al. 2003; Vilà and Gimeno 2007). This often translates into a depauperate seed bank which limits recruitment (Gioria and Osborne 2009; French et al. 2011).

The management action needed for degraded riparian habitats depends on the suite of agents of disturbance and type and extent of damage (Poff et al. 2011). While invasion is part of the disturbance, recovery or restoration of resident plant communities may partly depend on the invader and the invaded habitat (Gaertner et al. 2012; Gioria et al. 2012). Riparian zones in the Western Cape of South Africa are severely degraded by invasive trees such as *Eucalyptus camaldulensis* Dehnh. (Forsyth et al. 2004; Tererai et al. 2013). We investigated regeneration potential from soil-stored seed banks on degraded sites in these riparian ecosystems under different invasion conditions (uninvaded, lightly, moderately, and heavily invaded) and posed the following questions: (1) Is the richness, diversity, and composition of the soil-stored seed banks affected by invasion intensity?; (2) Is there a difference in species richness, diversity, composition, and structure between the seed bank and above-ground vegetation across invasion conditions?; (3) Does the soil-stored seed bank provide

varying potential for regeneration of composition and structure of native plant community across invasion conditions? We evaluated the results to determine guidelines for managing degraded riparian habitats.

Materials and Methods

Study Site

Our study was conducted on a 92-km stretch of the main stem of the Berg River, in the upper catchment, between the towns of Hermon and Franschhoek, north-east of Cape Town in South Africa's Western Cape province (Fig. 1). The area has a Mediterranean-type climate with warm dry summers and cool wet winters with an annual average rainfall of about 550 mm (Tereraï et al. 2013). The average annual temperature minima and maxima are 11 and 22 °C, respectively. The whole river stretch has been invaded by alien trees, mainly *E. camaldulensis* for c. 50 years, but was interspaced with individuals of *Acacia*

mearnsii De Wild. and *Populus* spp. (poplars) in some locations (Tereraï et al. 2013). The eucalypts are self-sown escapees from original planting sites where they were grown for different purposes including timber, fuelwood, and shelterbelts (Tereraï 2012). Dominant native woody riparian vegetation includes trees and shrubs of *Diospyros glabra* (L.) De Winter, *Kiggelaria africana* L., *Olea europaea* subsp. *africana* (Mill.) P.S. Green, *Podocarpus elongatus* (Aiton) L'Herit. ex Pers, and *Searsia angustifolia* (L.) F.A. Barkley which are now mainly confined to small pockets or isolated individuals within stands of *E. camaldulensis* (Ruwanza et al. 2013; Tereraï et al. 2013).

The Berg River riparian ecosystem is under different kinds of natural and anthropogenic pressures. As a perennial river, it experiences frequent flooding in winter every year (Tereraï et al. 2013). The hydrological regime is influenced by water abstraction for irrigated agriculture which constitutes about 65 % of the catchment (Geldenhuis 2008). Agricultural activities adjacent to the river can alter river sediment regime (Richardson et al. 2007 and

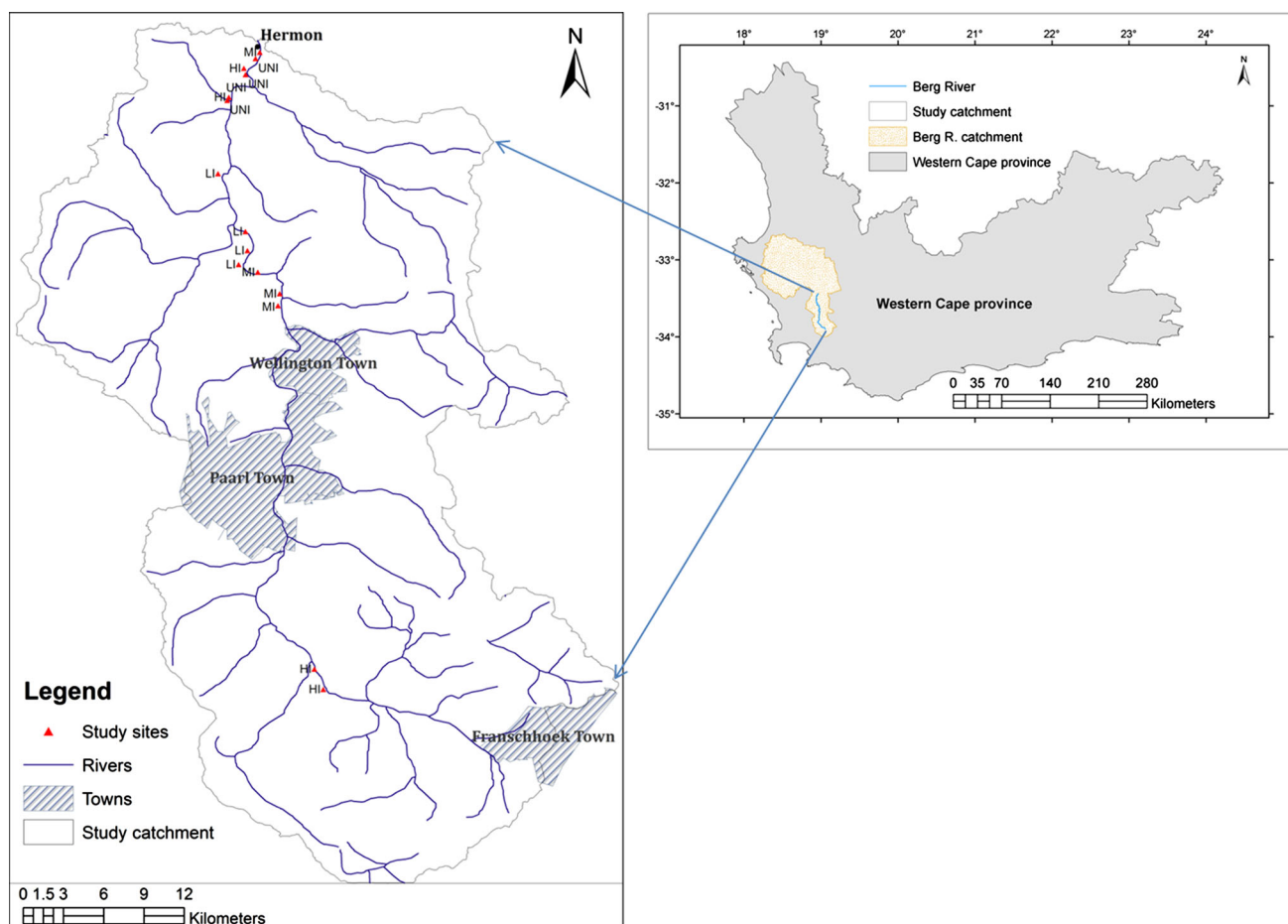
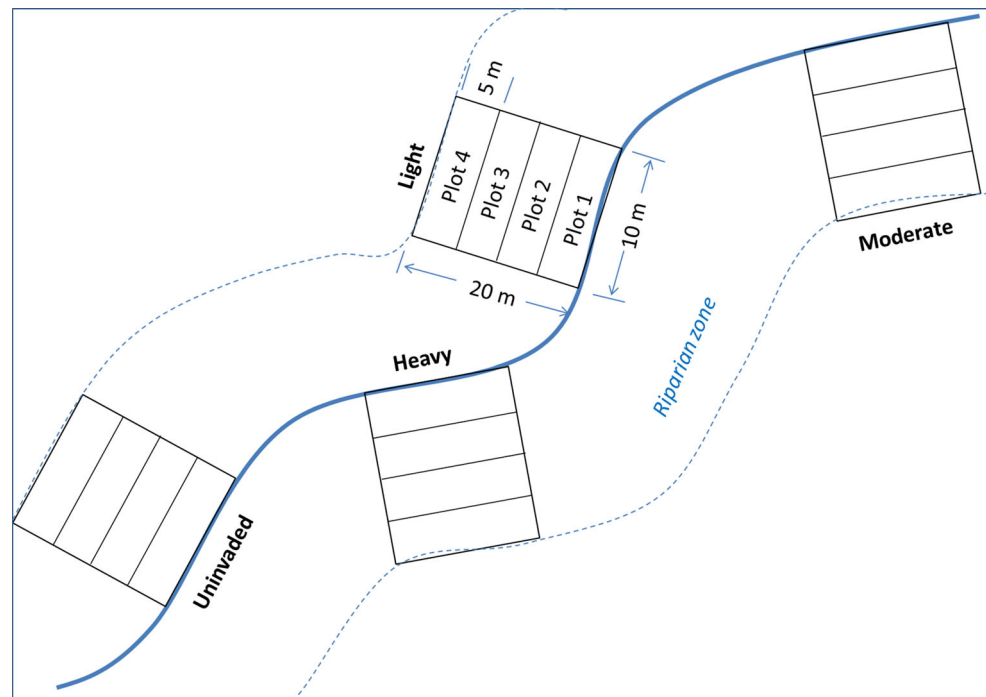


Fig. 1 Distribution of study sites (UNI uninvasion, LI light invasion, MI moderate invasion, HI heavy invasion) along the Berg River between the towns of Hermon and Franschhoek; Western Cape, South Africa

Fig. 2 Sketch of study design showing the orientation of sites and plots along the Berg River, Western Cape, South Africa. Each site measured 10 m along the river and 20 m perpendicular to the river. Each site was then divided into 10 × 5 m plots for data collection and analysis purposes. The location and order of the different invasion conditions and their replicates were random depending on where suitable sites were found. The dotted lines marking the riparian zone only show the average width at any site along the river, not the full extent



references therein). The Berg River Dam which was constructed in 2007 also regulates the hydrological regime.

Study Design

We studied soil-stored seed banks and above-ground vegetation changes in four categories of invasion (hereafter referred to as “invasion conditions”), each with three replicates ($n = 12$ sites): “uninvaded—UNI” (0–24 %), “light—LI” (25–49 %), “moderate—MI” (50–74 %), and “heavy—HI” (≥ 75 % cover of *E. camaldulensis*). Of all agents of disturbance in the Berg River (including invasion, agricultural activities, water abstraction, and flooding), we selected the factor “invasion” to categorize sites because it clearly differentiated sites. Sites measured 10 m along the river and spanned 20 m of the riparian zone, with plots in 5-m widths perpendicular to the river (Fig. 2). The sites were randomly located on both sides of the river. For each invasion category, we sampled the same conditions (soil types and vegetation types—grass patches, shrub and forest in which *E. camaldulensis* achieved dominance) to ensure the plots were comparable. A few individuals of *E. camaldulensis* occurred in two of the “uninvaded” sites as we could find no sites that were totally free of this species. “Pristine” reference sites, completely free of alien species, are extremely rare or simply do not exist in most ecosystems, including riparian habitats (Rosgen 1994; Richardson et al. 2007; Sieben and Reinecke 2008; Brewer and Menzel 2008). The above-ground vegetation was investigated in a separate study (Tererai et al. 2013), and only a subset of

these data were used for the comparison of the seed bank with the above-ground vegetation in the present study.

Data Collection

Soil samples were collected from uninvaded, lightly, moderately, and heavily invaded plots. Sampling was done late summer (February, 2011), a time we observed seed rain of majority of the plants in order to capture both the long buried and recently dispersed components of the seed bank (Walck et al. 2005; Vilà and Gimeno 2007; Fisher et al. 2008). Soil-stored seed bank sampling was deliberately conducted on the same sites and plots as the above-ground vegetation study (Tererai et al. 2013). This allowed a comparison to be made between characteristics of the soil-stored seed banks and above-ground vegetation. At each site, we sampled four—5 m × 10 m plots (Fig. 2). Three four-square meter sub-plots were located in each plot, making sure that similar conditions (see Sect. 2.2) were sampled. Five soil cores (5-cm diameter × 10-cm depth) were randomly extracted. The five cores from each sub-plot were bulked to constitute a sample ($n = 3$ samples per plot, translating into 144 samples for the 12 sites). Sample bulking was done to reduce variability due to seed clustering or irregular distribution in the soil (Fisher et al. 2008). Detailed data collection methods for the above-ground vegetation are described in Tererai et al. 2013 but in short, individual and species counts and growth forms (graminoids, forbs, shrubs, and trees) were recorded. Plants were identified to species level using field identification

books (Bromilow 2010), and a few were sent to a local herbarium—Compton Herbarium at the National Botanical Institute, Kirstenbosch, Cape Town, South Africa.

Seedling-Emergence Assessment Experiment

A seedling-emergence approach was used to estimate species richness and abundance per unit area (Thompson and Grime 1979). We selected the seedling-emergence approach over other methods because of its ability to assess seed availability, viability, and succession (Gioria et al. 2014). The experiment was set up in March, 2011 in a greenhouse with a transparent roof and walls of agro-shade netting material to enable simulation of diurnal temperatures. The soil was passed through a 10-mm mesh to remove large stones, roots, and litter (Vilà and Gimeno 2007). The soils were placed in trays (300 × 270 mm²) lined with hessian material to prevent seed and soil from washing out. The trays were given a smoke treatment in February to simulate a late summer fire, before the experiment was set up early March. The treatment was conducted by burning native plants in a drum and the smoke pumped into the tent containing the trays. The treatment has been shown to significantly enhance germination response in a variety of Western Cape plant taxa (Holmes and Cowling 1997; Holmes 2002). Five control trays, containing sterilized soil, were included, just in case any external seeds found their way in. The trays were regularly watered and rotated throughout the duration of the experiment. Seedling emergence was recorded every fortnight for nine months. For species that could not be identified immediately, duplicates were removed, and the species were grown until identifiable or until they flowered. Plants that had not flowered at the end of the experiment were compared with field herbarium specimens and identified to species level.

Analysis

Seedlings from the soil-stored seed bank were categorized into natives and aliens. The number of seedlings per tray was converted to density (number of seedlings per square meter) and compared according to invasion condition. Species richness (S) and Shannon-Wiener's diversity index (H') were used to measure seed bank community characteristics. To test for significant differences in species richness, diversity, and seedling density per tray in each invasion condition, we used two-way ANOVA since the data were normally distributed (using Kolmogorov–Smirnov test). While ANOVA results were significant, differences between pairs of invasion conditions were evaluated with Tukey's HSD unequal n test. To determine differences in soil-stored seed bank composition among uninvaded,

lightly, moderately, and heavily invaded sites, we adapted the statistical protocol of Gioria and Osborne (2009): i. PERMANOVA was performed to evaluate differences among invasion conditions; ii. Similarity percentages (SIMPER) were used to identify the species contributing the most to the observed differences; and iii. Analysis of similarity (ANOSIM) was used to measure the degree of species similarity among different invasion conditions within the seed bank. The data were first square root transformed before computing a resemblance matrix on which PERMANOVA, SIMPER, and ANOSIM analyses were based, using the Bray Curtis dissimilarity measure. In all analyses of variance, “invasion” was the fixed factor (four levels, each with three replicates—uninvaded, light, moderate, and heavy), and “site” was the random factor. The main response variable was seedling abundance of the following: i. “all” species, ii. “native” species, and iii. “alien” species. Univariate statistics were computed using Statistica v 10 (Statsoft Inc 2010; <http://www.statsoft.com>), while Multivariate statistics were computed in Primer v 6 and its add-on package, PERMANOVA + (PRIMER-E Ltd, Plymouth, UK).

To evaluate the degree of similarity in species composition between plots within the soil-stored seed bank and above-ground vegetation in each invasion condition, we computed the Sørensen's index calculated as follows: $S = 2C/(A + B)$, where A (seed bank) and B (the above-ground vegetation) are the numbers of species in each invasion condition, and C is the number of species common in both (Henderson 2003). The relative frequency of species in each growth form (graminoids, forbs, shrubs, and trees) in the above-ground vegetation and seed bank was computed as a number of species in each growth form as a percentage of maximum possible number of species in all growth forms. Significant differences between either native and alien species or the above-ground vegetation and seed bank within the same invasion condition were tested using Mann–Whitney U test after testing for normality with the Kolmogorov–Smirnov test.

Results

A total of 60 (50 genera and 30 families) and 47 (43 genera and 32 families) plant species were recorded in the soil-stored seed bank and above-ground vegetation, respectively. Of the seed bank species, 33 % were native (mainly shrubs, forbs and graminoids) compared to 40 % in the above-ground vegetation (of which 40 % were trees and shrubs). A total of 36 (13 native and 23 alien) species occurred in both the seed bank and above-ground vegetation. A total of 24 (7 native and 17 alien taxa) species occurred in the soil-stored seed bank only and 11 (6 native

Table 1 ANOVA of the density of seedlings in soil samples collected from uninvaded, lightly, moderately, and heavily invaded sites along the Berg River, Western Cape South Africa

Source of variation	df	Native species		Alien species		<i>Eucalyptus</i>	
		MS	p	MS	p	MS	p
Invasion	3	136,919.70	0.17	2,636,167.29	0.000	99.31	0.20
Site	2	84,273.03	1.10	163,977.49	0.38	32.99	0.59
Invasion × site	6	205,176.34	2.68	1,230,598.81	0.000	201.68	0.01

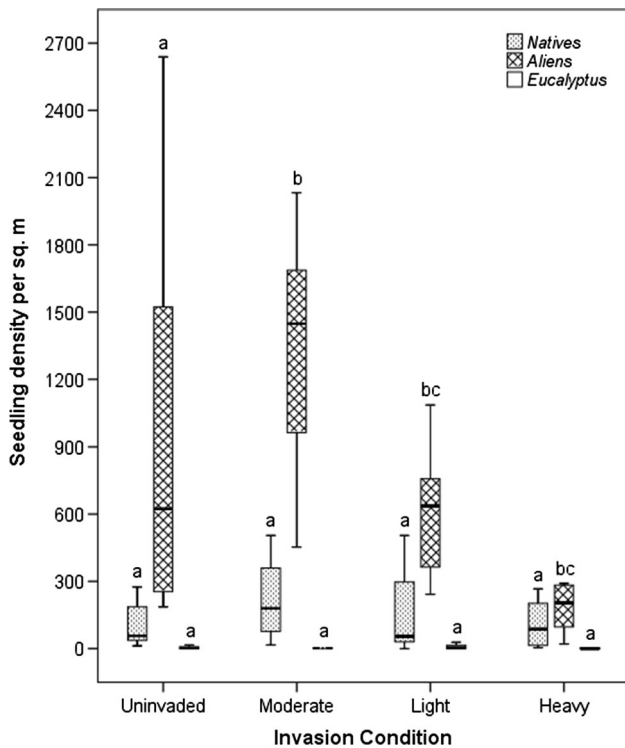


Fig. 3 Density (number of seedlings m^{-2}) of seedlings (native species, alien species, and *Eucalyptus camaldulensis*) in the soil samples collected from uninvaded, lightly, moderately, and heavily invaded sites along the Berg River of the Western Cape, South Africa. The whiskers of each bar represent the non-outlier range, the bar represents the 25th to the 75th percentile, and horizontal line within the bar represents the mean. Superscripts (a, b and c) show results of Tukey HSD post hoc comparisons between all pairs of invasion conditions

and 5 alien taxa) species occurred in the above-ground vegetation only. More than half of the alien species in both the soil-stored seed bank and above-ground vegetation were forbs. There were no significant differences in species composition and diversity within replicates of each invasion condition.

Seed Bank Density, Richness and Diversity

There was no significant difference in the density of seedlings (m^{-2}) of native species [130 (UNI), 344 (LI), 165 (MI), and 110 (HI)] and *E. camaldulensis* [4 (UNI), 6 (LI),

8 (MI), and 2 (HI)] between sites and invasion conditions (Table 1; Fig. 3). However, the interaction of invasion x site was significant for *E. camaldulensis* seedlings, although these occurred in very small numbers in the seed bank. Density of all alien seedlings [894 (UNI), 1428 (LI), 607 (MI), and 328 (HI)] differed significantly among invasion conditions and in the interaction invasion x site but not between sites (Table 1, Fig. 3). Pairwise comparisons showed no significant differences in native and *E. camaldulensis* seedling density between all pairs of invasion conditions (Fig. 3). However, alien species density differed significantly between pairs of invasion conditions; mean density of seedlings was the highest in lightly invaded sites. *Acacia mearnsii* recorded the highest seedling density of 40 (UNI), 804 (LI), 222 (MI), and 925 (HI) seedlings per m^2 .

The richness of native and alien species differed significantly among invasion conditions, and there was a significant interaction of invasion x site but not among sites (Table 2; Fig. 4a). The diversity of alien species differed significantly among invasion conditions, and there was a significant interaction of invasion x site but not among sites (Table 2; Fig. 4b). However, the diversity of natives did not differ among invasion conditions. The richness and diversity of native species were significantly lower than that of alien species in all invasion conditions (Fig. 4a, b). Pairwise comparisons showed that lightly and moderately invaded sites had significantly higher native and alien species richness (Fig. 4a). The diversity of native and alien species was largely similar between all pairs of invasion conditions, except moderately and heavily invaded sites for alien species that exhibited significant differences (Fig. 4b).

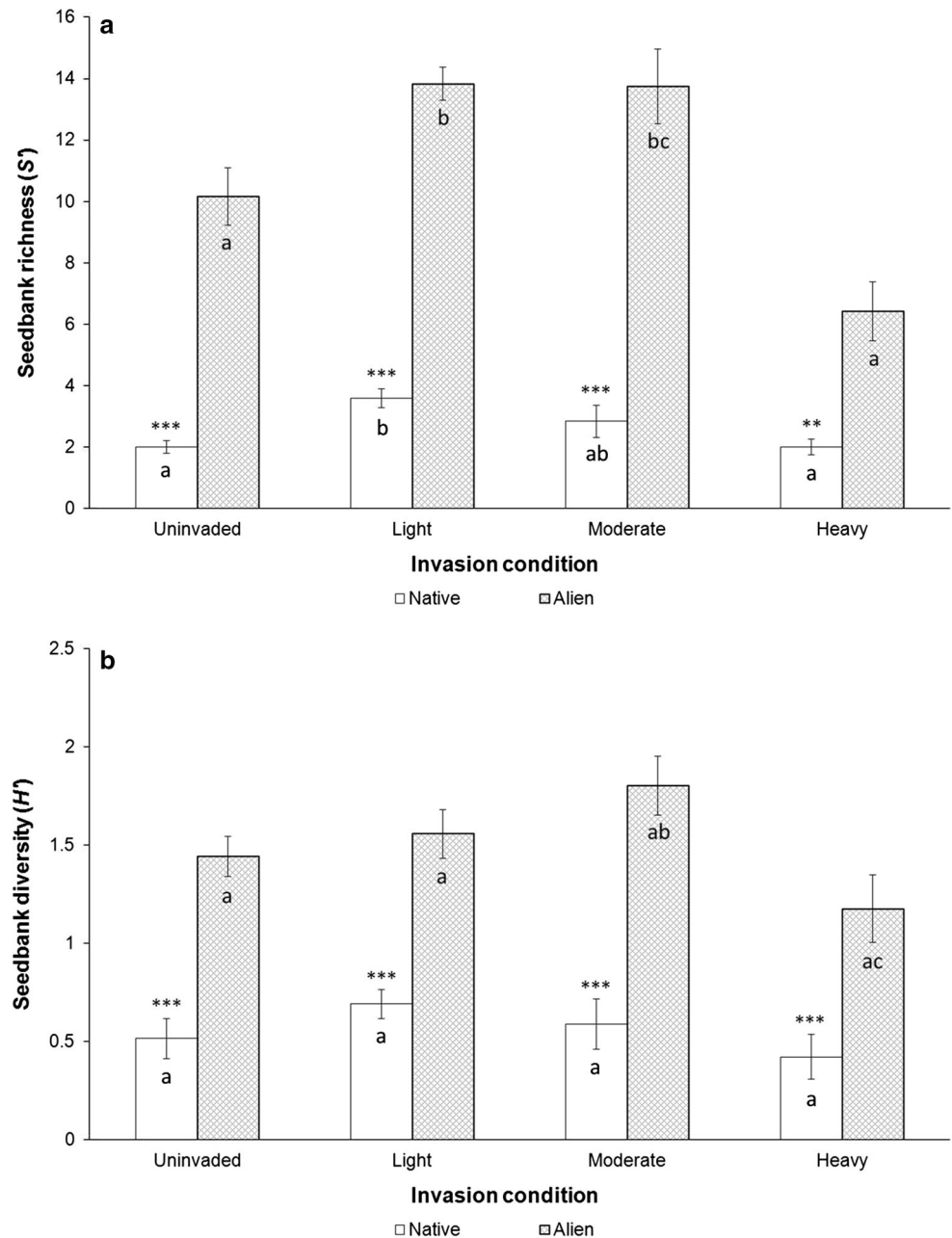
Species Composition of Seed Banks

A PERMANOVA analysis of “all,” “native,” and “alien” seed bank species showed that there were significant differences in species composition among invasion conditions ($F = 6.99, 4.47, \text{ and } 7.19$, respectively). The Monte Carlo test showed significant differences between all possible pairs of invasion conditions ($p < 0.001$). There was a higher similarity (ANOSIM) of alien (42 %, $p < 0.01$) than native (23 %, $p < 0.01$) species among invasion

Table 2 ANOVA of native and alien species richness and diversity in soil samples collected from uninvaded, lightly, moderately, and heavily invaded sites along the Berg River, Western Cape South Africa

Source of variation	df	Native species				Alien species			
		Richness		Diversity		Richness		Diversity	
		MS	<i>p</i>	MS	<i>p</i>	MS	<i>p</i>	MS	<i>p</i>
Invasion	3	6.97	0.002	0.16	0.31	149.14	0.000	0.81	0.004
Site	2	0.58	0.60	0.14	0.33	13.08	0.09	0.30	0.16
Invasion × site	6	3.53	0.01	0.20	0.17	43.31	0.000	0.71	0.001

Fig. 4 Native and alien plant species **a** richness and **b** diversity (mean ± SE) of soil samples collected from uninvaded sites ($n = 12$), lowly ($n = 12$), moderately ($n = 12$), and heavily ($n = 12$) invaded sites along the Berg River, Western Cape, South Africa. Significant differences between all pairs of uninvaded, lowly, moderately, and heavily invaded sites were tested by Tukey HSD (depicted by *a*, *b* and *c*), and significant differences between alien and native richness and diversity in each invasion condition were tested by Mann–Whitney *U* test (depicted by * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$)



conditions. SIMPER results showed that the differences among the various invasion conditions are mainly explained by alien plant species, the major contributors to

these differences being *Solanum retroflexum* Dunal. and *A. mearnsii* (explaining an average of 30 % of detected differences in all invasion conditions except uninvaded sites)

Table 3 ANOVA of the number of growth forms in soil samples collected from uninvaded, lightly, moderately and heavily invaded sites along the Berg River, Western Cape South Africa

Source of variation	df	Vegetation		Seed bank	
		MS	p	MS	p
Invasion	3	5.61	0.01	2.67	0.001
Site	2	0.58	0.61	0.06	0.84
Invasion × site	6	1.36	0.35	1.48	0.003

Fig. 5 a Comparison of number of growth forms (mean ± SE) and **b** relative frequency (%) of species in each growth form in the seed bank and above-ground vegetation of soil samples collected from uninvaded ($n = 12$), lightly ($n = 12$), moderately, ($n = 12$) and heavily ($n = 12$) invaded sites. Significant differences were tested by Turkey HSD and that between seed bank and above-ground vegetation in the same invasion condition (asterisk) were tested by Mann–Whitney U test after testing for normality of data with Kolmogorov–Smirnov

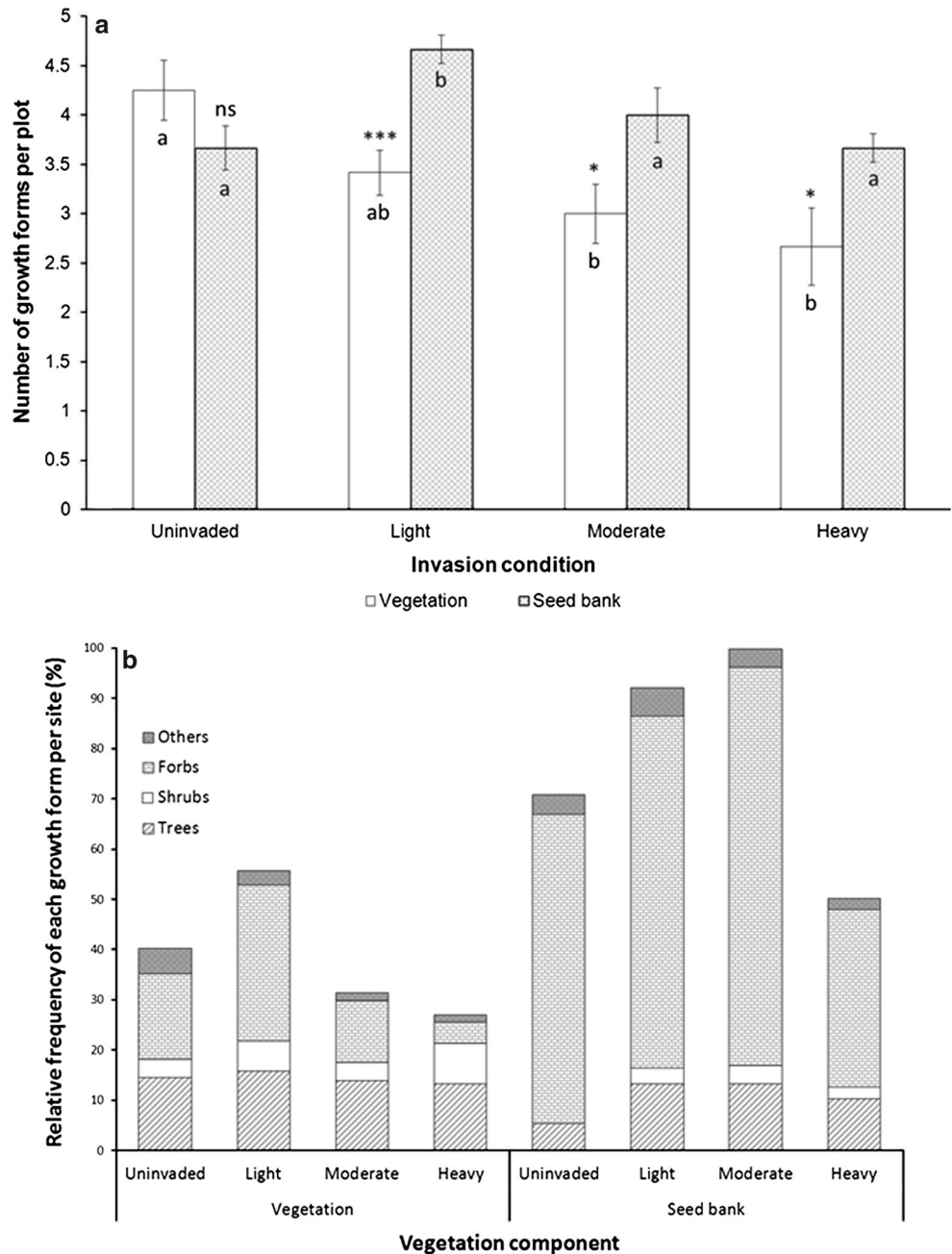


Table 4 Sørensen's community coefficient (S) for comparison between the above-ground vegetation and seed banks of riparian plots sampled in uninvaded sites and at sites with light, moderate and heavy invasions of *Eucalyptus camaldulensis* along the Berg River in Western Cape, South Africa

Invasion condition	Site number	Sørensen's index	Average Sørensen's index
Uninvaded	1	0.206	0.167
	2	0.173	
	3	0.122	
Light	1	0.374	0.367
	2	0.241	
	3	0.486	
Moderate	1	0.161	0.151
	2	0.088	
	3	0.204	
Heavy	1	0.077	0.192
	2	0.231	
	3	0.267	

(see Appendix S3). A few native fynbos species, such as *Stoebe plumosa* (L.) Thunb. (a shrub occurring in all invasion conditions) and *Aspalathus* species (only occurring in uninvaded and heavily invaded sites) were recorded in the seed bank (see Appendix S1). Other native species in the seed bank included *Senecio halimifolius* (forb), *Cyperus rotundus* L. (graminoid), and *Isolepis antarctica* (L.) Roem. & Schult. (sedge).

Seed Bank: Above-Ground Vegetation Comparison

The number of growth forms in the seed bank and above-ground vegetation differed among invasion conditions but not sites (Table 3; Fig. 5). However, the interaction invasion \times site was only significant for seed bank (Table 3; $p < 0.05$). The seed bank exhibited significantly higher average number of growth forms per plot than that of the above-ground vegetation (Fig. 5a). Pairwise comparisons showed a decrease in mean number of growth forms of the above-ground vegetation as *E. camaldulensis* cover increased compared to the seed bank where mean number of growth forms were only significantly higher in lightly invaded sites (Fig. 5a). Generally, the seed bank had a higher frequency of forb species compared to the above-ground vegetation (Fig. 5b). The majority of the forb species were alien. Relatively fewer trees were recorded in the seed bank, and no shrubs were recorded in seed bank under uninvaded sites (Fig. 5b).

There was a generally low correspondence of species between the above-ground vegetation and soil-stored seed bank, with the highest similarity being recorded in lightly invaded sites (Table 4). There was a significantly higher

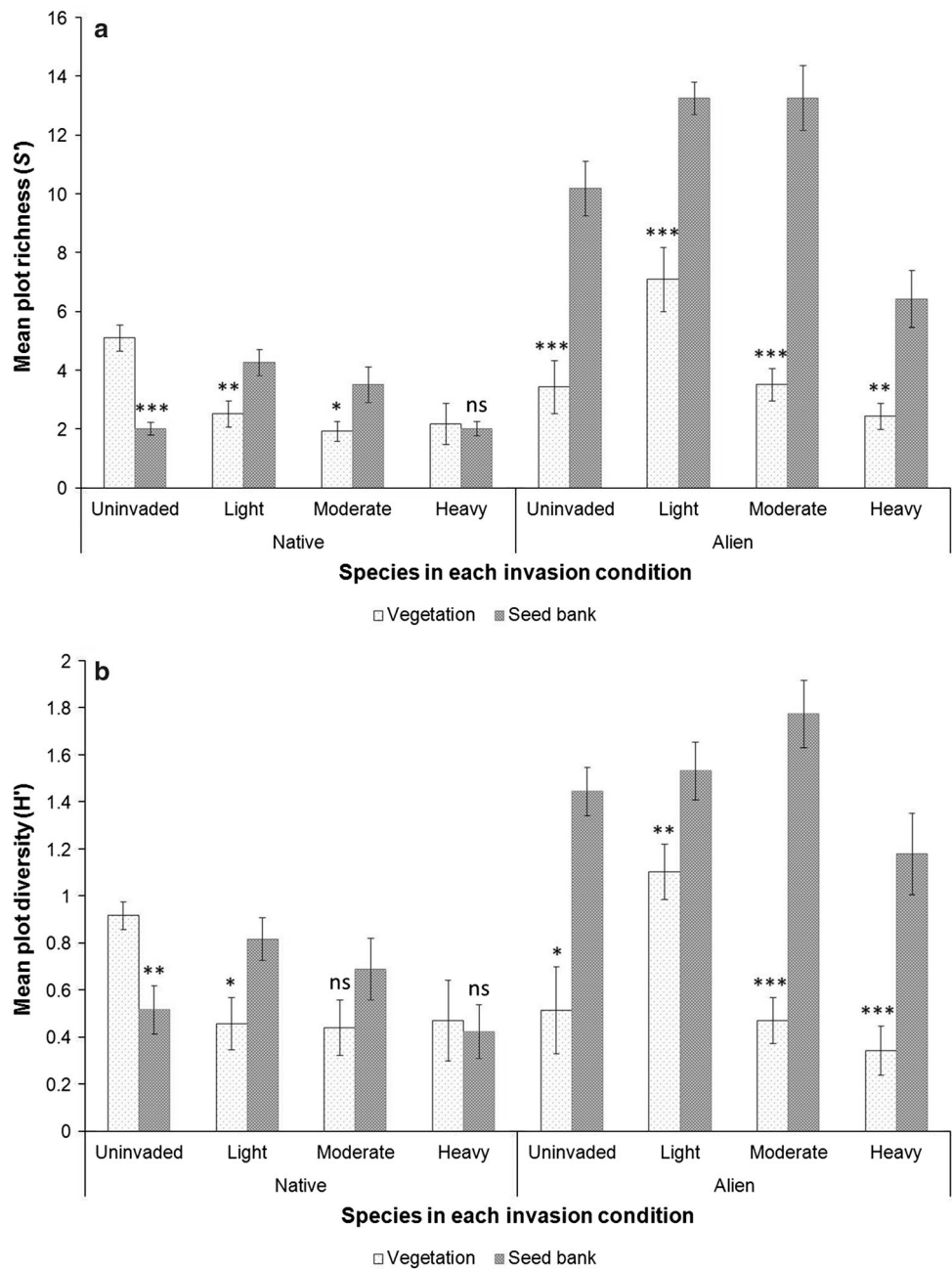
richness and diversity of native species in the above-ground vegetation in uninvaded sites than in the seed bank, and alien species exhibited the exact opposite trend (Fig. 6a, b). Seed bank exhibited generally higher richness and diversity of native species in lightly, moderately, and heavily invaded sites compared to the above-ground vegetation (Fig. 6a). The seed bank also showed significantly higher richness and diversity of alien species in all invasion conditions. PERMANOVA revealed that species composition of both the above-ground vegetation and seed bank varied significantly among invasion conditions. Species similarity between invaded and uninvaded sites was, however, higher in the seed bank (48 %) than in the above-ground vegetation (25 %). Common tree and shrub species such as *Kiggelaria africana*, *Diospyros glabra*, and *Olea europaea* ssp. *africana* were more abundant in the above-ground vegetation than the seed bank. Native tree and shrub species such as *Asparagus africanus* Lam., *Freylinia lanceolata* Saccardo, *Halleria lucida* L., *Maytenus oleoides* (Lam.) Loes., and *Salix mucronata* Thunb. that are known to be able to recruit from seed were not recorded in the seed bank. Conversely, the native shrubs *Ericastrum austroafricanum* Al-Shehbaz & S.I. Warwick, *Selago canescens* E.Mey., *S. plumosa* (L.) Thunb, and *Helichrysum asperum* (Thunb.) Hilliard & B.L.Burt were found in the seed bank but not in the above-ground vegetation.

Discussion

We investigated the resilience of soil-stored seed banks on degraded sites in riparian ecosystems under different invasion conditions (uninvaded, lightly, moderately and heavily invaded). The study was conducted in riparian ecosystems in the Western Cape Province, South Africa. Although this ecosystem has been degraded by several agents, including *Eucalyptus* invasion, soil-stored seed banks still potentially offer a reasonable contribution toward regenerating native plant communities. However, remnant native species are likely to make a more significant contribution to restoration, which should entail the removal of *E. camaldulensis*.

The natural regeneration of vegetation communities after disturbance is believed to lie in the potential contribution of buried native seed populations (Bakker et al. 1996, Thompson et al. 1997; Cui et al. 2013). In our study, native species density and diversity in the soil seed bank did not differ among invasion conditions, and all sites will hence require similar restoration actions. The similarity in density and diversity of native species may in part be explained by the homogenizing effect of flood pulsing that is characteristic of riparian zones (Richter and Stromberg 2005; Vosse et al. 2008; Baattrup-Pedersen et al. 2012).

Fig. 6 The above-ground vegetation and seed bank characteristics **a** mean plot species richness, **b** mean plot diversity recorded in the seed bank experiment and above-ground vegetation study both conducted on 12 sites along the Berg River, Western Cape, South Africa. Significant differences between pairs of uninvaded, lightly, moderately, and heavily invaded sites were tested using the non-parametric Mann–Whitney *U* test, since all data were not normally distributed and are depicted by **p* < 0.05; ***p* < 0.01; and ****p* < 0.001, *ns* not significant



Native species richness varied among invasion conditions which could be explained by comparatively higher number of species in lightly and moderately invaded sites, with relatively open canopy cover (Terera et al. 2013). Soil-stored seed banks occurring in disturbed areas with relatively open vegetation canopy which allows more light penetration to forest floor undergrowth exhibit a high richness and diversity of species, mainly forbs (Luzuriaga et al. 2005).

Our results show that soil-stored seed banks can potentially aid ecosystem restoration. However, restoration activities might be compromised by the low representation

of native and the high representation of alien species in the soil seed bank. Soil-stored seed banks of degraded sites are often characterized by severe depletion of richness and abundance of native (especially woody) species (Galatowitsch and Richardson 2005; Reinecke et al. 2008; Meers et al. 2012) which can be explained by prolonged and frequent disturbances such a flooding and alien species invasions (Esler et al. 2008; Holmes and Cowling 1997; Richardson et al. 2007). Additionally, many *Eucalyptus* species produce allelopathic substances which may constrain the growth and reproduction of understory plants (del Moral and Muller 1970, Zhang et al. 2010). However,

it may simply be that native (especially woody) species never form a large and persistent seed bank in this ecosystem (Greet et al. 2013). A depauperate seed bank lacks resistance to primary and secondary invasions (Gioria et al. 2012). The higher degree of dissimilarity of native species among invasion conditions suggests that native species have been affected more than alien species. This finding concurs with those of Holmes and Cowling (1997), Holmes (2002), and Vosse et al. (2008). The fact that natives are affected more than aliens is not surprising because alien species have life-history traits that predispose them to persist in the face of unpredictable disturbance (Truscott et al. 2006). Most native species in the seed bank were shrubs, forbs, and graminoids, whereas alien species were dominated by trees and forbs. The most widespread alien species were an invasive tree, *A. mearnsii* with seed longevity >50 years (Holmes 1989) (although not in uninvaded sites), and a forb, *S. retroflexum* occurring in all invasion conditions. The dominance of a few alien species in soil-stored seed banks is a common finding in many studies of invasive alien plants in areas with high disturbance regimes (Esler et al. 2008; Reinecke et al. 2008; Gioria et al. 2011, 2014) and poses significant challenges with secondary invasions (Bakker and Wilson 2004; Ruwanza et al. 2013; Gioria et al. 2014). Although *E. camaldulensis* is dominant in the above-ground vegetation especially in moderately and heavily invaded sites, it appeared to have a small seed bank. This may be ascribed to a short-lived seed bank typical of the genus *Eucalyptus* and poor seedling survival under shaded conditions leading to seed bank depletion (Rejmánek and Richardson 2011; Booth 2012; Tereraí et al. 2013). *Eucalyptus*, however, has a high potential to resprout (Nicolle 2006), and this may be a threat to autogenic native vegetation recovery. Appropriate follow-up interventions will be needed to reduce this potential threat.

The soil-stored seed bank is likely to offer a comparatively limited contribution toward native vegetation recovery (agreeing with the findings of Greet et al. 2013) because of the low correspondence between species in the seed bank and above-ground (Holmes and Richardson 1999). This pattern is consistent with reports of low species similarity between the soil-stored seed bank and above-ground vegetation across ecosystems, including wetlands (see Hopfensperger 2007 for a review). The fact that the soil-stored seed bank was more diverse than above-ground vegetation, consistent with the findings of Holmes and Cowling (1997) in the fynbos biome of South Africa, Díaz-Villa et al. (2003) in Mediterranean Spain and French et al. (2011) in Australian coastal dunes, is more of a threat than a merit to restoration because of the dominance of alien species (Esler et al. 2008; Ruwanza et al. 2013). The influence of hydrochory (seed dispersal in water), bringing in seed of species that are not

present in established vegetation (Bakker et al. 1996; Vogt et al. 2006) may explain the generally higher diversity of species in the soil-stored seed bank. The occurrence of native tree and shrub species in small numbers in the soil-stored seed bank may indicate suppressed reproductive capacity of native species (del Moral and Muller 1970; Holmes 2002; Tereraí et al. 2013). However, we do not rule out the possibility that seeds of trees and shrubs dominant in the above-ground vegetation, e.g., *K. africana*, *D. glabra*, and *O. europaea ssp. africana* were actually present in the seed bank, but may require specific germination cues (Holmes and Cowling 1997; Williams et al. 2008) that were absent in the range of conditions that we provided. We also assume that no seeds were lost during sieving because we used a sieve with holes big enough to let the seeds of all native tree and shrub species through.

Natural riparian vegetation recovery can happen in two possible ways. The first pathway is from a diverse native soil-stored seed bank that still exists (although it may not contain all the species in established vegetation), but as discussed earlier, autogenic ecosystem recovery from seed recruitment may be hampered by low native seed densities and the challenge of secondary invasions (French et al. 2011; Gioria et al. 2014). The small numbers of tree and shrub species in the seed banks are of special concern as these have been identified as key species for restoration of riparian vegetation, given their above-ground dominance in uninvaded sites in comparison to other growth forms (Meek et al. 2010; Tereraí et al. 2013). The second and most probable (possibly quicker) pathway is recovery from the above-ground remnant native species that currently co-exist with *E. camaldulensis* and usually remain after clearing. Quick establishment of native tree and shrub canopy is critical in order to suppress micro biophysical conditions created by clearing riparian corridors and may likely favor secondary invasions (Galatowitsch and Richardson 2005). We thus highlight the importance of keeping intact patches of native species which may re-establish and commence seed production and recruitment, in order to reduce the need for active restoration, costs for which are often prohibitive (Reinecke et al. 2008). It may also be necessary to reintroduce some native taxa and growth forms that were not represented in the seed bank (e.g., *P. elongatus* and *M. oleoides*). This will facilitate recovery of a complete mosaic of species for an optimally functional ecosystem (Vosse et al. 2008). A third potential pathway that we did not investigate is the augmentation of the soil-stored bank from external sources, including upstream sites (Galatowitsch and Richardson 2005); this pathway is likely to introduce non-target species as dispersal methods do not differentiate between native and alien seeds.

The challenge with restoring the vegetation of riparian sites is to ensure that propagules of non-target (non-native) species are kept out of cleared sites. The use of machinery

for clearing, which is necessary for large tree invaders such as eucalypts, usually exposes seeds buried deep in the soil and triggers germination of IAPs that have a superior competitive edge to exploit favorable microsites (Baattrup-Pedersen et al. 2012). This necessitates the integration of monitoring and follow-up clearing (possibly hand-pulling and herbicide application) into restoration programs of riparian zones (Esler et al. 2008; Holmes et al. 2008; Flory and Clay 2009). Tererai et al. (2013) suggested a reduction of *E. camaldulensis* density, as opposed to total clearing, to provide a buffer to inhibit the proliferation of alien species that constrain native vegetation recovery (see also Ruwanza et al. 2013). No substantial legacy effects are expected after clearing of *E. camaldulensis* since allelopathic chemicals are readily leached from the soil (May and Ash 1990), and soil physico-chemical properties have not been significantly altered by the presence of the eucalypts (Tererai et al. 2014), and soil–water repellency induced by *E. camaldulensis* in these systems does not persist long after stands are cleared (Ruwanza et al. 2013).

Conclusions

Information gained in this study has important implications for the formulation of improved strategies for enhancing the conservation status of degraded riparian ecosystems invaded by *E. camaldulensis*. Successful restoration programs of degraded ecosystems depend on a comprehensive assessment of the type and extent of degradation, as well as remnant native species and a viable soil-stored seed bank. Several crucial aspects emerge from this study. Firstly, *E. camaldulensis* forms a small short-lived seed bank which makes local eradication achievable. Regular follow-up operations will be crucial since eucalypts resprout (Nicolle 2006; Rejmánek and Richardson 2011). Secondly, the diverse soil-stored seed bank of native species and remaining patches of native species in the above-ground vegetation are both important for driving restoration. Thirdly, the knowledge of the composition of the post-clearing soil-stored seed bank is important for planning to deal with possible germination and establishment of non-target species, especially important invasive species such as *A. mearnsii* which are abundant in the seed bank. Further investigations on temporal seed bank dynamics are needed to improve our understanding of the role of hydrochory which potentially plays an important role of augmenting the soil-stored seed bank from riparian areas upstream.

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