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Secondary invaders in riparian habitats can remain up to 10 years after invasive alien *Eucalyptus* tree clearing

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A B S T R A C T

After the clearing of invasive alien plants, non-target alien species often move in. This is known as secondary invasion and these alien species can suppress native plant species' recovery. This is a global problem that has only recently received attention in South Africa. But whether secondary invaders in riparian areas have similar effects than those in more terrestrial areas is largely unknown globally and in South Africa. Therefore, here we ask which species and growth forms are associated with secondary invasion in riparian areas in the Fynbos biome, and secondly whether secondary invader species richness changes over time post clearing. We found 13 secondary invader species in a riparian area after clearing of alien invasive *Eucalyptus* trees. In the first year after clearing, there were only annuals, but thereafter it was a mix of annuals and perennials (shrubs, herbs, and graminoids). Secondary invader richness did not significantly differ with time after clearing, persisting even up to 10 years. In this riparian area, secondary invader species richness was much lower than that for non-riparian Fynbos areas. From this preliminary study we highlight the need for more research in understanding how secondary invaders influence restoration efforts and native species recovery in riparian systems.

1. Introduction

Riparian habitats are some of the most invaded systems globally (Richardson et al., 2007). Since they act as channels transporting propagules from catchment areas to lowlands, riparian habitats are highly susceptible to alien plant invasions (Naiman and Décamps, 1997; Esler et al., 2008; Geerts and Adedoja, 2021), whether in urban or agricultural settings (Geerts et al., 2016, 2017). Particularly, alien trees are often associated with disturbance – either through natural or man-made processes (Afonso et al., 2020) – whereafter ecosystem services and function are altered by these alien trees (Richardson et al., 2007; Esler et al., 2008; Geerts, 2011; Adedoja et al., 2021; Erckie et al., 2022). To mitigate these impacts, ecological restoration is often required (Richardson et al., 2007). However, actively restoring riparian areas is typically a complicated and expensive process (Zavaleta et al., 2001; Gaertner et al., 2012a). Therefore, restoration is usually a passive process with the only active intervention being the removal of the invasive alien trees, whereafter the ecosystem is left to recover naturally from the soil-stored seed bank and via seed dispersal from adjacent native vegetation (Impson et al., 2013; Roberts and Gilliam, 2014).

Monitoring and evaluation after invasive alien tree clearing is important to assess the success of passive restoration, and to determine whether further interventions are necessary (Holmes et al., 2020). However, most studies evaluating ecosystem recovery after clearing invasive alien trees are short term (i.e. less than 3 years), and focus on the vegetation (e.g.; Ruwanza et al., 2013; Kerr and Ruwanza, 2016; Fill et al., 2018), or medium term (i.e. about 6 years; Galatowitsch and Richardson, 2005) but longer term studies (> 10 years) or those that quantify the recovery of other taxa are becoming more common (e.g. Golet et al., 2008; Heleno et al., 2010; Magoba and Samways 2010; Shanahan et al., 2011; Atkinson et al., 2015; Maoela et al., 2016; Ndou and Ruwanza, 2016; Hale and Swearer, 2017). It is often assumed that native biodiversity recovery will follow the removal of invasive alien trees from ecosystems (Blanchard and Holmes 2008). However, the removal of invasive alien trees often does not translate to full or even partial recovery of native biodiversity (Zavaleta et al., 2001; Pearson et al., 2016; Mangachena and Geerts, 2017;Mangachena and Geerts, 2019). Potential reasons for this include depleted native soil seed banks (Le Maitre et al., 2011), persistent soil legacy effects (Corbin and

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D'Antonio, 2012), re-invasion (Richardson and Kluge, 2008), and/or secondary invasion (Pearson et al., 2016; Nsikani et al., 2018, 2020).

The removal of dominant invasive alien trees may lead to secondary invasion – i.e., the proliferation of non-target alien species following efforts to suppress dominant target invaders (Pearson et al., 2016; Nsikani et al., 2020). The issue of secondary invasion as a hindrance to the re-establishment of native species is increasingly receiving attention globally (e.g. Symstad, 2004; Skurski et al., 2013; Pearson et al., 2016; Nsikani et al., 2018, 2019, 2020). Quantifying secondary invader species richness and growth forms is important to understand the extent of the problem and guide management activities (Nsikani et al., 2020). However, research on secondary invasion has predominantly taken place in purely terrestrial ecosystems (Pearson et al., 2016), particularly in South Africa (Nsikani et al., 2019, 2020). Other ecosystems such as riparian habitats remain underexplored (Nsikani et al., 2020). Therefore, here we explore the nature and persistence of secondary invasion after clearing invasive alien *Eucalyptus camaldulensis* trees from a riparian habitat in the South African fynbos. *Eucalyptus camaldulensis* modifies riparian areas by outcompeting native species, as it has allelopathic effects and changes the water cycle (reviewed in Hirsch et al., 2020).

Specifically, we ask (1) which plant species are secondary invaders after clearing alien trees – specifically Eucalyptus – in riparian areas, (2) does secondary invader species richness differ between seasons, and (3) does secondary invader species richness decrease over time? We hypothesize that – similar to purely terrestrial ecosystems – secondary invader species will mostly comprise annual graminoids and herbs (Nsikani et al. 2019), and that this will not differ between seasons. Furthermore, we hypothesize that in passively restored areas, secondary invader richness will remain at levels similar to, or higher than the first year after clearing (Nsikani et al. 2019).

2. Methods

2.1. Study site

The study was conducted in the Fynbos biome of South Africa, along the Berg River, between the towns of Wellington and Hermon (Table S1). The Berg River is 294 km from source to mouth with a catchment area of 7715 km^2 (de Villiers, 2007). Native vegetation – outside riparian areas – is classified as West Coast Renosterveld vegetation type (Mucina and Rutherford, 2006). The climate is Mediterranean with average daily temperature ranging from 8 to 30 °C (Mucina and Rutherford, 2006), and minimum and maximum annual temperatures range between 11 °C and 22 °C respectively (Mucina and Rutherford, 2006). Mean annual precipitation is 550 mm, with June being the wettest month and February being the driest and hottest month (Mucina and Rutherford, 2006).

Invasion by the dominant alien, *Eucalyptus camaldulensis,* dates back approximately 60 years in this area (for a full review on *Eucalyptus camaldulensis* in South Africa, see Hirsch et al., 2020). There is no clear historical information about when the species was introduced, but it is now the dominant tree species in long stretches of the Berg River (Geldenhuys and Bezuidenhout, 2008; Ruwanza et al., 2014). The Berg River vegetation is driven by periodic flooding and consists of herbaceous-shrubby vegetation (approximate average height of 1 m) interspersed by scrub forest (approximate average height of 2.3 m). The pristine state of the vegetation is largely unknown but the *E. camaldulensis,* and to a lesser extent *Acacia mearnsii,* invasions has led to an increase in species richness of native shade-tolerant riparian plant species (Tererai et al., 2013). Study sites were located within a mosaic of agricultural land and were largely surrounded by a monoculture of a specific crop. Therefore, only prevailing land-use at each site was scored (Table S1). Distances between study sites varied from 250 m to 3.5 km (Fig. S1).

2.2. Vegetation surveys

A total of 6 sites along the Berg River were sampled to determine the nature and persistence of secondary invasion post clearing of *E. camaldulensis* and *A. mearnsii*. Clearing was done by Working for Water (WfW) through manual felling of trees (van Wilgen and Wannenburgh, 2016), and no burning was applied. The canopy cover of *E. camaldulensis* in these sites exceeded 55% (mostly more than 85%), with the remainder largely made up of the alien invasive *A. mearnsii*. Sampled sites were cleared in 2005 (two sites), 2007 (two sites), 2008 (one site) and in 2014 (one site). Clearing was done between January and March of each year, and vegetation surveys were conducted between May and November 2014 (i.e. one in winter and one in spring, for a total of 12 surveys). Due to slight differences in the exact timing of sampling and clearing (i.e., in months) in each year, we rounded up the number of years after clearing. For example, nine years and ten months after clearing (clearing conducted in 2005 and sampling conducted in 2014) was rounded up to ten years.

The point intercept method – for 30 m line transects – was used, dropping a vegetation height pole every 2 m along these transects. All plants that touched the vegetation pole or had their canopy directly above the pole, were identified and recorded. When individuals of a particular tree or shrub species were present at multiple points along a transect, it was scored multiple times for percentage cover. Bare ground is not included in the analyses since it made up only 6.5% of the total hit points and this was largely the same across sites. All species were classified according to status (i.e. indigenous, primary invader, or secondary invader (Table 1; South African National Biodiversity Institute, 2016; Mangachena and Geerts 2017, J. R. 2019). Plant species were assigned to the following growth forms based on the classification by Goldblatt and Manning (2000): trees, shrubs, forbs, geophytes (perennial plants that are propagated by buds on underground bulbs, tubers or corms), graminoids (grasses, sedges and restioids – reed-like plants that belong to the Restionaceae) and vines (creeping and climbing plants).

2.3. Data analyses

To determine the effects of year after clearing (1, 7, 8, and 10 years), and season (winter and spring) on secondary invader richness (the response variable), Generalized Linear Mixed Models – with Poisson error distribution and log link function – were fitted using the *glmmTMB* package (Magnusson et al., 2020). We included "site" and "hit point" as nested random effects to account for variability between sampled sites and hit points. Generalized Linear Mixed Models are the best tool for analysing non-normal data that involve random effects (Bolker et al., 2008). Statistical analyses were done in R version 4.0.3 (R Development Core Team, 2020).

3. Results

A total of 13 secondary invader species were recorded across all sites after clearing invasive alien *Eucalyptus* and *A. mearnsii* trees. In the first year after clearing, 6 of the 13 secondary invader species were present, while 5 occurred in the site cleared seven years ago and, and 9 in the eight and tenth year after clearing (Table 1). Species such as *Lolium multiflorum* (Fig. 1a) persisted over time and was present at all sites, whilst species such as *Echium plantagineum* was only present – but abundant – at one site (Fig. 1b).

In the first year after clearing, all secondary invader species (6) were annuals. After seven, eight and ten years after clearing there was a mix of annuals and perennials, with a third of the species being perennials (Table 1). In the first year after clearing, there were 5 graminoids and 2 herbs as secondary invaders (Table 1). In the tenth year after clearing there were 4 shrubs, 3 herbs and 6 graminoids species (Table 1). The seeds of the secondary invader species are

Table 1
Secondary invader species present after clearing of *Eucalyptus camaldulensis* along the Berg River in the fynbos biome of South Africa.

Species	Life form	Growth form	Seed dispersal mechanism	Prevalence (% of hit points)	1 year after clearing		7 years after clearing		8 years after clearing		10 years after clearing	
					Winter	Spring	Winter	Spring	Winter	Spring	Winter	Spring
Avena fatua	Annual	Graminoid	Animals, farm equipment	9	X	✓	X	X	✓	✓	X	✓
Bromus catharticus	Annual	Graminoid	Wind, birds, small mammals, farm equipment	12	X	✓	X	✓	X	✓	✓	✓
Bromus diandrus	Annual	Graminoid	Water, soil movement, animals	1	X	X	X	X	X	X	X	✓
Echium plantagineum	Annual	Herb	Water, animals	1	X	X	X	X	X	✓	X	X
Hypochaeris radicata	Perennial	Herb	Wind, birds	1	X	X	X	X	X	X	✓	X
Lactuca serriola	Annual	Herb	Wind	5	✓	✓	✓	✓	✓	✓	X	X
Lolium multiflorum	Annual	Graminoid	Birds, small mammals, humans	35	X	✓	✓	✓	✓	✓	✓	✓
Pennisetum clandestinum	Perennial	Graminoid	Soil movement, animals	3	X	X	✓	✓	X	✓	X	X
Rubus cuneifolius	Perennial	Shrub	Birds, small mammals	2	X	X	X	X	X	X	✓	✓
Rumex crispus	Annual	Herb	Wind, water, mammals, birds	5	X	✓	X	X	X	X	X	✓
Solanum pseudocapsicum	Perennial	Shrub	Birds	10	X	X	✓	✓	✓	✓	✓	✓
Sonchus asper	Annual	Herb	Wind, water	1	X	X	X	X	✓	X	X	X
Sonchus oleraceus	Annual	Herb	Wind, birds	5	X	✓	X	X	✓	✓	✓	X

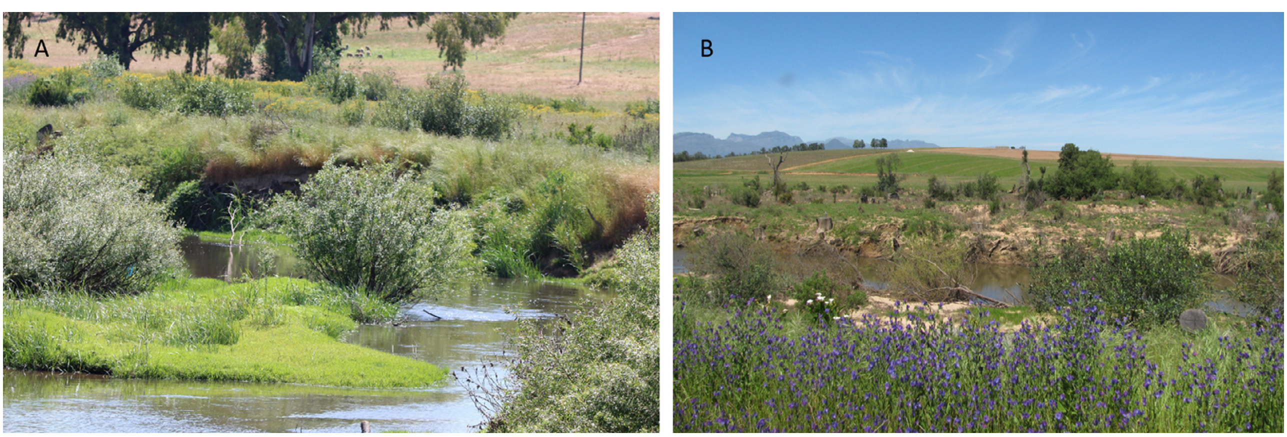

Fig. 1. Riparian areas cleared of alien invasive *Eucalyptus camaldulensis* trees with secondary invaders such as A) *Lolium multiflorum* and B) *Echium plantagineum* in the foreground with cleared areas in the background.

mostly dispersed by wind, water, animals or birds (Table 1). Secondary invader richness did not differ significantly with year after clearing between the first and seventh (p = 0.67; 95% confidence interval = −0.46 to 0.29), eight (p = 0.24; 95% confidence interval = −0.78 to 0.19), and tenth year (p = 0.93; 95% confidence interval = −0.45 to 0.50; Fig. 2a). Similarly, secondary invader richness did not differ significantly with season (p = 0.28; 95% confidence interval = −0.57 to 0.16; Fig. 2b).

4. Discussion

Here we show that secondary invaders in riparian areas can persist up to 10 years after clearing *E. camaldulensis.* This confirms our hypothesis that without active management of secondary invasion, secondary invader richness will remain at similar levels over time. Our hypothesis that secondary invaders will mostly comprise of annual grasses and herbs does hold for all years after clearing, even though some shrubs appear 10 years post clearing. The problem of secondary invaders might be context dependant, with the invasive tree species being removed, the method of removal, surrounding land use and many other variables potentially influencing secondary invasions in riparian areas (Fleishman et al., 2003; Loo et al., 2009). Therefore, understanding secondary invaders in riparian areas is critical to determine when, how and to what extent we should respond to the problems associated with invasive *Eucalyptus*, or invasive trees more generally. Here, we provide one of the first studies on secondary invaders in riparian areas in the Fynbos biome.

Overall, the number of secondary invader species in our study (13 species) is much lower than the more than 30 species found by Nsikani et al. (2019) in non-riparian fynbos habitats, and by Ruwanza et al. (2013) in riparian areas, but slightly higher than the 3–7 species in Reinecke et al. (2008), also from riparian areas. Ruwanza et al. (2013) found mostly alien herbs and graminoids as secondary invaders, but their study only spanned one year. Similar to this study, Reinecke et al. (2008) found mostly grasses as secondary invaders up to four years after clearing. Large variability is expected, since the initial invasive species differ, time period of invasions vary, a controlled burn was conducted in some cases (and then stack burning applied in some cases, whilst not in others) and surrounding land use as a source of propagules will differ. This study was conducted in

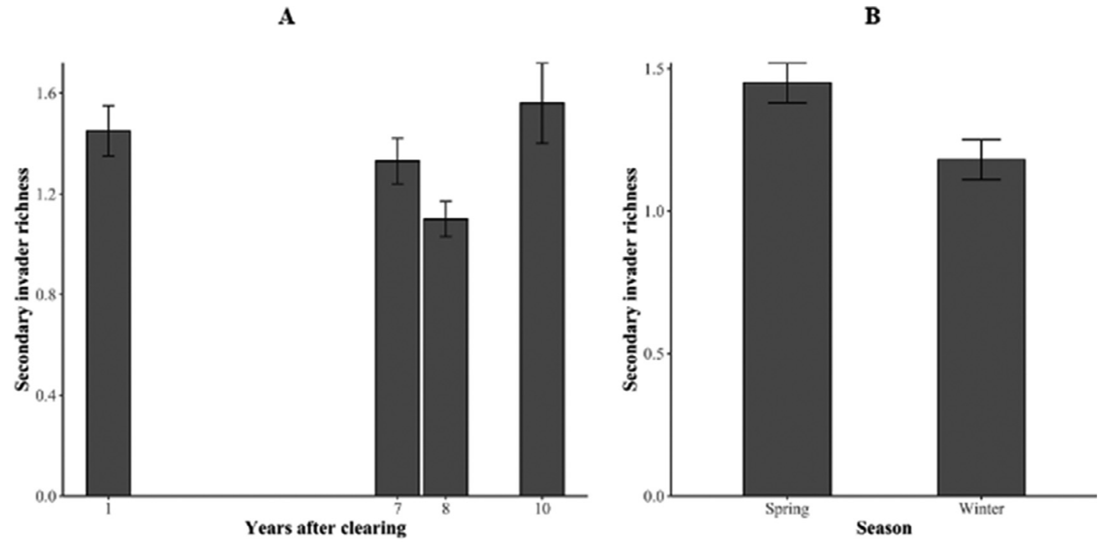

Fig. 2. Secondary invader species richness with a) time since clearing of alien invasive *Eucalyptus camaldulensis* and b) secondary invader species richness differences between winter and spring in a riparian area in the fynbos biome. Error bars represent ±SE.

an agricultural matrix, and a significant propagule pressure of alien weedy species is thus present. However, some species might have germinated from the soil seed bank since it contains many alien herbaceous weedy species (Tererai et al., 2015). In contrast, regular flooding might decrease soil seed banks and create conditions that might limit the establishment of a more diverse community of secondary invaders.

Immediately after clearing, we found no woody secondary invaders, but only herbaceous secondary invaders which persisted up to a decade after clearing. The reason why we mostly have annual graminoids and forbs is probably that their seeds easily spread from surrounding agricultural areas (Table 1). In contrast, Ruwanza et al. (2018) found that although alien herbs and graminoids dominated soon after clearing of *Eucalyptus* trees (Ruwanza et al., 2013), over time, these were replaced by woody invasive alien plants due to the lack of follow-up clearing. However, the high graminoid component after alien tree clearing might differ depending on the alien invasive tree species being cleared. For instance, Reinecke et al. (2008) found that after *Acacia* clearing, alien grasses dominated, whilst after pine clearing, passive restoration resulted in good recovery of riparian vegetation, even though being species poor. This abundance of graminoids as well as herbs has been reported before and might be linked to their faster growth rates and shorter life cycles or soil nutrient enrichment (Yelenik et al., 2004; Balamurungan et al., 2000; Nsikani et al., 2021), increased leaf litter and/or soil micro-nutrient concentrations due to the *Eucalyptus* invasion (Gaertner et al., 2011). These then persist over time through positive feedback loops in so called alternative stable states (Gaertner et al., 2012b; Holmes et al., 2020). Potentially in conjunction with continuous reinvasion from surrounding areas, whilst some species are lost each year, possibly as a result of competition Grubb (1977).

In contrast to nutrient poor terrestrial fynbos areas, riparian zones have relatively fertile soils, which is expected to enhance forest development (Reinecke et al., 2008). This higher availability of nutrients would also be expected to promote the growth of secondary invaders – which are adapted to high resource availability – in riparian areas versus the nutrient poor fynbos, but neither appear to be the case (McLendon and Redene, 1992; Paschke et al., 2000; Perry et al., 2010). This might be due to limited number of sites, and all within one river system. Considering the variable results between studies on secondary invaders, there is scope for creating a list of all secondary invader species in South Africa. This should include riparian and terrestrial habitats and ideally include information on the initial invasive species, length of invasion and environmental factors (such as, whether fire was applied and how and surrounding land use) to allow for predictions of the secondary invader community (Wilson et al., 2020). Our results should be interpreted with caution since we used a space-for-time substitution and the various sites had different land uses, their management and invasion histories may also have differed.

In conclusion, secondary invaders can persist up to 10 years after clearing, and at levels similar to those soon after the removal of alien tree invaders. We focused on species richness and composition and did not consider cover because the expectation is that cover will increase with time since clearing (Grove et al., 2015). Depending on practical considerations, we advise that alien species clearing should be integrated with restoration activities to avoid alien invasive trees just being replaced by more herbaceous alien invasive species (Pearson et al., 2016). Considering that even with active restoration some level of secondary invasion is likely due to persistence of secondary invader seeds in the soil or surrounding areas. Furthermore, the fact that current efforts to remove alien invasive tree species generates suitable habitat that can be invaded by secondary invaders highlights the need for revegetation by seeding native species (Cutting and Hough-Goldstein, 2013). However, we also highlight the need for more research in understanding how secondary invaders influence restoration efforts and native species recovery in riparian areas in South Africa .

Declaration of Competing Interest

The authors declare no conflict of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2021.11.040.

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