Secondary invasion after clearing invasive *Acacia saligna* in the South African fynbos

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ABSTRACT

It is often assumed that clearing invasive alien species will lead to the dissipation of their negative impacts and recovery of native plant diversity. However, this is often not the case because clearing of primary invasive alien species can lead to secondary invasion by non-target species. We investigated the effects of vegetation type and application of fire during management of biomass after clearing invasive acacias on secondary invasion in the South African fynbos. Furthermore, we determined how these effects change with years after clearing. We sampled vegetation in lowland and mountain fynbos cleared of invasive *Acacia saligna* using the "fell, stack and burn" method. During burning of the stacked slash, the area at the centre of the stack experiences a high severity fire while the area at the edge experiences a low severity fire. After fire, burn scars remain in place of the stacked slash. We sampled in and outside of 80 burn scars over three years after clearing. Overall, we set out to (1) identify species that are secondary invaders; (2) determine whether secondary invader richness and cover differ between where there were high and low severity fires and no fires, and how these differences change with years after clearing; and (3) determine whether secondary invader richness and cover differ in and between lowland and mountain fynbos, and how these differences change with years after clearing. We identified 32 secondary invader species. Mean secondary invader richness was lower where there were high severity fires (2.75) compared to where there were low severity fires (3.28) and no fires (3.24). Mean secondary invader proportion cover was lower where there were no fires (0.14) compared to where there were high severity fires (0.19) and low severity fires (0.2). Three years after clearing, secondary invader richness and cover had not changed or was now higher than in the first year, while secondary invader richness was similar between lowland and mountain fynbos. Secondary invader cover was similar between lowland and mountain fynbos up to two years after clearing but was 58% lower in lowland fynbos in the third year. Fire application after clearing invasive acacias can have positive (i.e. reduction of *Acacia* soil seed banks by triggering mass germination) and negative (i.e. favors the dominance of secondary invaders) effects. As a result, slash should be spread throughout the restoration site instead of being stacked and then burnt to reduce *Acacia* soil seed banks. To avoid the establishment of a second generation of invasive acacias, the seedlings that germinate can be controlled through manual weeding, mowing and herbicide application. Due to the persistence and abundance of secondary invaders up to three years after clearing at levels similar to or higher than in the first year, we conclude that practicing restoration ecologists must manage these species to ensure successful restoration of native plant diversity.

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1. Introduction

The human-mediated movement of species from their native ranges to new areas across the world has resulted in most ecosystems being invaded by multiple species (Hobbs et al., 2006). Invasive alien species often have significant negative impacts on recipient native plant diversity, ecosystem function and services, and these impacts differ in direction and magnitude among various levels of ecological complexity (Musil and Midgley, 1990; Musil, 1993; Pejchar and Mooney, 2009; Vilà et al., 2011). Furthermore, the financial cost of invasive species to recipient ecosystems across the globe is staggering (van Wilgen et al., 2001; Pimentel et al., 2005; Vilà et al., 2010). A significant amount of that cost is allocated to clearing alien species from invaded ecosystems (Hulme, 2006).

It is often assumed that manually clearing invasive species will lead to the dissipation of their negative impacts and the recovery of native

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plant diversity (Wittenberg and Cock, 2005; Grove et al., 2015). This school of thought originates from agriculture where the reduction of a pest often leads to an increase in desirable species (Pearson and Ortega, 2009). However, in complex ecosystems beyond agricultural systems this is often not the case, since invasive species can leave long-lasting legacy effects – i.e. measurable changes to biological, chemical, or physical conditions (Corbin and D'Antonio, 2012). These legacy effects often interact and create barriers that hinder the restoration of desirable native ecosystems in previously invaded areas (Nsikani et al., 2018). Instead of facilitating the recovery of native plant diversity, clearing of target invasive species (hereafter "primary invaders") can lead to secondary invasion – i.e. an increase in the abundance of non-target alien species (Pearson et al., 2016). A global meta-analysis of 60 cases from 38 studies conducted by Pearson et al. (2016) found that a decrease in primary invaders due to clearing often leads to secondary invasion, with only a slight recovery in native plant diversity.

Secondary invaders can proliferate in previously invaded areas because clearing primary invaders often creates a "space" for their recruitment from soil seed banks accumulated prior to primary invasion and/ or from seeds that migrated from surrounding areas by reducing competition (Grubb, 1977; González-Muñoz et al., 2012; Gioria et al., 2014; Pearson et al., 2016). Clearing primary invaders often also increases the availability of resources, such as nitrogen from soil legacy effects (i.e. often in the case of nitrogen fixing primary invaders) and light, which facilitates their growth (Loo et al., 2009; Nsikani et al., 2017). Disturbance often influences resource availability by increasing or decreasing it, depending on the disturbance factor and its severity (Davis et al., 2000). For example, eutrophication can lead to elevated nitrogen availability while severe fire can reduce it through volatilization (Davis et al., 2000; Marchante et al., 2009). Secondary invaders are adept at exploiting disturbances, particularly those that lead to increased resource availability (Pearson et al., 2016). Overall, primary invader suppression is often the most important factor that drives secondary invasion (Pearson et al., 2016).

Secondary invaders may also benefit from the post-clearing environment more than native species because of (1) provenance effects – i.e. introduction filters that select for disturbance-adapted traits or release from natural enemies (Buckley and Catford, 2016); (2) the clearing method applied – e.g. use of broadleaf herbicides during clearing can favor the proliferation of secondary invader grasses while suppressing native monocots or dicots (Skurski et al., 2013); and/or (3) anthropogenic activities – e.g. eutrophication can increase nitrogen availability and favor the excessive growth of secondary invaders (Pearson et al., 2016).

Australian acacias have become global invaders since being introduced for a range of ornamental, commercial and subsistence uses (Griffin et al., 2011; Wilson et al., 2011). Approximately 70 Australian *Acacia* species have been introduced to South Africa and at least 14 of these are currently invasive (Richardson et al., 2011). Within South Africa, the fynbos biome is the greatest casualty of Australian *Acacia* invasions and the most studied (van Wilgen et al., 2011). The "fell, stack and burn" method – i.e. fell primary invaders, stack the slash and allow it to dry before burning it, has been widely applied to reduce the cover of acacias (Holmes et al., 2000; van Wilgen et al., 2012; Ruwanza et al., 2013). During burning of the stacked slash, the area at the centre of the stack experiences a high severity fire while the area at the edge experiences a low severity fire (Ruwanza et al., 2013). Previous studies have shown that severe fires after alien clearing alter soil physico-chemical properties such as pH, electrical conductivity and available phosphorus, and induce soil water repellency (Scott et al, 1998; Ruwanza et al., 2013; Maubane, 2016). These changes can reduce native seed germination and seedling survival, and ultimately have negative consequences on recovery of desired native ecosystems (Scott et al., 1998; Ruwanza et al., 2013; Maubane, 2016). After fire, burn scars remain in place of the stacked slash and are visible for over three years after a burn (personal observation).

There have been significant advances in understanding vegetation dynamics after clearing invasive acacias in the fynbos (Holmes and Cowling, 1997; Galatowitsch and Richardson, 2005; Reinecke et al., 2008; Blanchard and Holmes, 2008; Gaertner et al., 2012). However, given the importance of native plant diversity recovery, research focus has understandably been skewed towards native species dynamics, despite a range of secondary invaders being observed in previously invaded areas (Yelenik et al., 2004; Nsikani et al., 2017). Thus, the current knowledge gaps are at least threefold: (1) there has been little work done to identify which species are secondary invaders after clearing invasive acacias in the fynbos. (2) There is little knowledge on the effect of the treatment-related disturbance factor, fire – i.e. no fire, low and high severity, on the extent of secondary invasion after clearing invasive acacias, and whether this changes with years after clearing. (3) There is no knowledge on the effect of fynbos type – i.e. lowland and mountain, on the extent of secondary invasion after clearing invasive acacias, and whether this changes with years after clearing.

We used *Acacia saligna* (Labill.) H.L Wendl. (Fabaceae) invasions in the South African fynbos as case study to address these issues. We addressed the following questions: (1) which species are secondary invaders after clearing invasive *A. saligna*? (2) Does the species richness and cover of secondary invaders after clearing invasive *A. saligna* differ between areas that experienced low and high severity fires and no fires, and do these differences change with years after clearing? (3) Does the species richness and cover of secondary invaders after clearing invasive *A. saligna* differ in and between lowland and mountain fynbos, and do these differences change with years after clearing?

2. Materials and methods

2.1. Study sites

The study was conducted in two fynbos vegetation types, namely lowland Cape Flats Sand Fynbos (CFSF) and Mountain Sandstone Fynbos (MSF), in the Western Cape Province, South Africa (Rebelo et al., 2006). A Mediterranean-type climate with hot dry summers and cool wet winters is characteristic of both fynbos types (Rebelo et al., 2006). Native vegetation is made up of evergreen shrublands characterized by a mixture of proteoid and ericoid shrubs, and restioid (aphyllous graminoid) growth forms (Rebelo et al., 2006).

We selected Blaauwberg Nature Reserve (33°46′5.16″S; 18°27′10.08″E) to study CFSF, and Glencairn (34°09′24.7″S; 18°24′30.1″E) for MSF. Cape Flats Sand Fynbos soil is generally made up of quaternary sand while MSF soil comprises of colluvial sandy loam (Holmes, 2002). Blaauwberg Nature Reserve received a mean annual rainfall of 266 mm during our study period – i.e. 2014 to 2016 (Jacques Kuyler, Blaauwberg Nature Reserve, personal communication), while Glencairn received 775 mm (http://www.csag.uct.ac.za/current-seasons-rainfall-in-cape-town/, 2018). *Acacia saligna* invasions are common both in the mountains and in the lowlands. Blaauwberg Nature Reserve was invaded by *A. saligna* while most of Glencairn was invaded by *A. saligna* and to a lesser extent by *Acacia cyclops* A.Cunn. ex G.Don (Fabaceae) and *Hakea drupacea* (C.F. Gaertn.) Roem. & Schult. (Proteaceae). Prior to clearing *A. saligna*, both study sites had been invaded for longer than 20 years (75–100% cover). Both study sites were cleared of *A. saligna* and burnt in July 2013 and had been left to recover naturally.

2.2. Study design

We selected parts of Blaauwberg Nature Reserve and Glencairn where *A. saligna* was cleared using the "fell, stack and burn" method. In September 2014, we randomly selected 40 burn scars in each study

site. Each burn scar was approximately 5 × 3 m in size. From the centre of each burn scar we ran a transect in a south-east direction to the edge and outside of the burn scar. A permanent plot (1 × 1 m) was set up perpendicular to the transect at the centre (high severity fire), edge (low severity fire) and outside of the burn scar (no fire; Fig. 1). Plots at the edge and outside of the burn scars were separated by the same distance as plots at the centre and edge of the burn scar (Fig. 1). In each plot we recorded all species that were present, classified them according to status (i.e. primary invader, secondary invader or native species; South African National Biodiversity Institute, 2016) and estimated their percentage cover. Furthermore, we estimated the percentage cover of bare ground and litter within the plot. Subsequent samplings were done in September of 2015 and 2016. Plant nomenclature follows South African National Biodiversity Institute (2016).

2.3. Statistical analyses

All statistical analyses were done in R version 3.5.1 (R Development Core Team, 2018). We first converted the percentage cover of secondary invader species to proportions. Residual and Q-Q plots were utilized to examine data normality. We fitted generalized linear mixed models (GLMMs) using *glmmADMB* package (Skaug et al., 2013). We determined the effect of fynbos type (i.e. lowland and mountain), fire (i.e. no fires, low and high severity) and their interactions with years after clearing, on species richness (i.e. Poisson error distribution and log link function) and proportional cover of secondary invaders (i.e. Beta error distribution and logit link function). We included "plot" as a random effect to account for variability between plots. We compared the different models via dredging, an automated procedure implemented by the *MuMIn* package, to identify variables that best explain the variability in species richness and proportion cover of secondary invaders (Barton, 2018). Models were compared using information theoretic (I-T) model procedures based on Akaike's information criterion (AIC; Burnham et al., 2011). The best-fitting model was chosen using the second order AIC value, AICc. The model with the lowest AICc value was chosen as the best-fitting model as it had the smallest information loss, even if it did not include all the explanatory variables and their interactions with years after clearing. For each response variable, only one model remained after model selection. Here we report the results of these best-fitting models. Significant mean differences were separated with Tukey's HSD test using the *emmeans* package (Lenth, 2018).
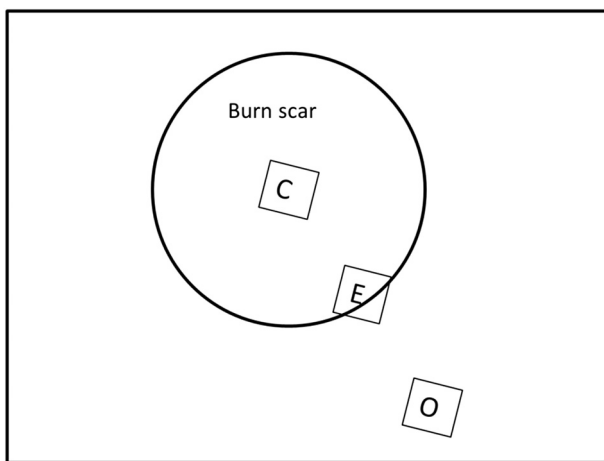

Fig. 1. Schematic diagram of the sampling protocol, showing the spatial arrangement of plots (1 × 1 m) used to sample the centre (C; high severity fires), edge (E; low severity fires) and outside of the burn scar (O; no fire). E and O were separated by the same distance as C and E.

3. Results

3.1. Secondary invader species after clearing invasive A. saligna in the fynbos

We documented 32 secondary invader species in areas cleared of invasive *A. saligna* (Appendix 1). These species were grasses (22%), herbs (72%) and shrubs (6%; Appendix 1). We found that 50% of the secondary invader species occurred in both fynbos types while 9% were only found in lowland fynbos and 41% were only found in mountain fynbos (Appendix 1). From the secondary invader species we identified, 91% occurred in areas that experienced high severity fires, 91% were found where there were low severity fires, and 88% were found where there were no fires (Appendix 1). In the first year after clearing, 78% of the secondary invader species were present while 72% occurred in the second year after clearing, and 84% in the third year after clearing (Appendix 1).

3.2. Effect of fire application after clearing invasive A. saligna in the fynbos on secondary invader richness and cover, and changes thereof with years after clearing

Secondary invader richness was significantly lower where there were high severity fires (2.75) compared to where there were low severity fires (3.28; p < .001; 95% confidence interval = 0.08-0.30; Fig. 2) and no fires (3.24; p = .001; 95% confidence interval = 0.07-0.29; Fig. 2). However, secondary invader richness was similar between where there were low severity fires and no fires (p = .85; 95% confidence interval = −0.12 to 0.09; Fig. 2). Secondary invader cover was significantly lower where there were no fires (0.14) compared to where there were high severity fires (0.19; p = .01; 95% confidence interval = −0.38 to −0.07; Fig. 2) and low severity fires (0.2; p < .001; 95% confidence interval = −0.50 to −0.19; Fig. 2). However, secondary invader cover was similar between where there were high severity fires and low severity fires (p = .13; 95% confidence interval = −0.04 to 0.27; Fig. 2). Secondary invader richness and cover did not change with years after clearing as the "fire severity" and "years after clearing" interaction was not selected in any best-fitting model.

3.3. Effect of fynbos type on secondary invader richness and cover after clearing invasive A. saligna, and changes thereof with years after clearing

There was a significant interaction between the effects of fynbos type and years after clearing on secondary invader richness between: (1) the first and second year after clearing (p = .03; 95% confidence interval = −0.49 to −0.03; Fig. 3); and (2) the second and third years after clearing (p = .002; 95% confidence interval = 0.12 to 0.52; Fig. 3). In lowland fynbos, secondary invader richness significantly increased by 64% in the second year after clearing but did not change significantly thereafter (Fig. 3). In mountain fynbos, secondary invader richness did not significantly change in all years after clearing (Fig. 3). Secondary invader richness did not significantly differ between lowland and mountain fynbos in all years after clearing (Fig. 3).

There was a significant interaction between the effects of fynbos type and years after clearing on secondary invader cover between: (1) the first and second year after clearing (p < .001; 95% confidence interval = −1.16 to −0.51; Fig. 3); (2) the first and third year after clearing (p < .001; 95% confidence interval = 0.30 to 0.97; Fig. 3); and (3) the second and third year after clearing (p < .001; 95% confidence interval = 1.17 to 1.76; Fig. 3). In lowland fynbos, secondary invader cover significantly increased by 388% in the second year after clearing but significantly decreased by 65% in the third year to a level similar to that in the first year (Fig. 3). In mountain fynbos, secondary invader cover significantly increased by 90% in the second year after clearing but did not significantly change in the third year (Fig. 3). Furthermore, secondary invader cover did not significantly differ between lowland
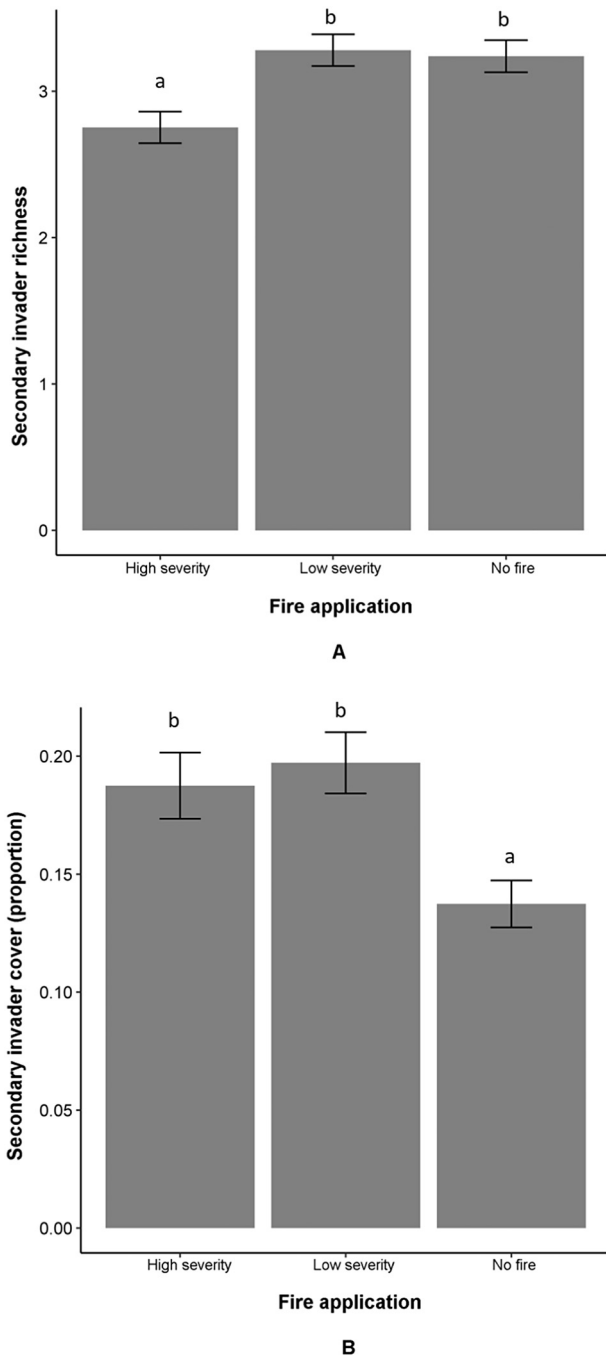
Fig. 2. Secondary invader richness (A) and cover (B) where there were high and low severity fires and no fires after clearing invasive *A. saligna* in the fynbos. Mean values of secondary invader richness or cover with the same letter are not significantly different. Error bars represent ± SE.

and mountain fynbos in the first two years after clearing but was significantly lower by 58% in lowland fynbos compared to mountain fynbos in the third year (Fig. 3).

4. Discussion

4.1. Secondary invader species after clearing invasive A. saligna in the fynbos

The number of secondary invader species documented in our study is significantly larger than those recorded by previous studies after clearing *A. saligna* invasions (Yelenik et al., 2004) and areas invaded

by multiple species in the fynbos (Reinecke et al., 2008; Ruwanza et al., 2013). This is likely because we sampled two types of fynbos over a three-year period and therefore were able to capture variation associated with vegetation type and multi-year vegetation monitoring.

4.2. Effect of fire after clearing invasive A. saligna in the fynbos on secondary invader richness and cover, and changes thereof with years after clearing

Secondary invader richness was lower where there were high severity fires compared to where there were low severity fires and no fires, which had similar secondary invader richness. This is most likely due to differential recruitment of species from the seed bank (or after dispersal) as a result of the differing fire severities and no fire application. Seed banks of most species are generally found in the uppermost 3–5 cm (Holmes, 2002; Fourie, 2008) with many small seeds unable to germinate from lower down the soil profile (Bond et al., 1999). During burning of stacks near soil surface temperatures can reach 81 °C in moist soil while in dry soil they can reach 330 °C (Behenna et al., 2008). Therefore, soil seed banks of secondary invaders were likely destroyed by the high severity fires while those that experienced low severity fires were able to survive and recruit. Indeed, germination rates are improved by the lower heat if seeds are fire cued (Korb et al., 2004; Behenna et al., 2008; Ruwanza et al., 2013; Halpern et al., 2014). Secondary invaders where there were no fires germinate without the inconvenience of having their soil stored seeds destroyed by high severity fires. We suspect that secondary invader richness did not significantly change with years after clearing because a few new species managed to find their way to our study sites while some species were lost each year, possibly as a result of competition (Grubb, 1977).

Severe fires can have significant negative effects on soil structure and microbial communities (Neary et al., 1999; Korb et al., 2004; Cilliers et al., 2005) with negative consequences on the germination of some species (Korb et al., 2004; Ruwanza et al., 2013; Cilliers et al., 2004). For example, high severity fires can lead to soil water repellency – i.e. reduced water infiltration, which can then reduce seed germination as a result of lowered water availability to the seeds (Scott et al, 1998; Ruwanza et al., 2013).

In contrast to secondary invader richness, secondary invader cover was lower where there were no fires compared to where there were high and low severity fires, which had similar secondary invader cover. This may be a result of elevated nitrogen levels resulting from burning the large amounts of stacked biomass. Dominance of secondary invaders is facilitated by elevated nitrogen availability (Vitousek and Walker, 1989; Le Maitre et al., 2011; Nsikani et al., 2017), and burning of stacks can elevate nitrogen availability – i.e. both NH_4^+ and NO_3^- levels (Korb et al., 2004; Fornwalt and Rhoades, 2011). For example, after burning stacks in British Columbia, soil nitrate levels were 19 times higher in burnt areas compared to unburned areas (DeSandoli et al., 2016). We accept that some available nitrogen may be lost through volatilization during the burning of stacks (Riggan et al., 1994; Marchante et al., 2009), and with time through leaching, particularly NO_3^- (Dunn et al., 1979). Despite losses in available nitrogen, it is possible that higher than normal levels persist up to three years after clearing (Nsikani et al., 2017), thereby leading to a lack of change in secondary invader cover with years after clearing.

4.3. Effect of fynbos type on secondary invader richness and cover after clearing invasive A. saligna, and changes thereof with years after clearing

In lowland fynbos, secondary invader richness increased in the second year after clearing but did not significantly change afterwards, while in mountain fynbos, secondary invader richness did not significantly change up to three years after clearing. Furthermore, secondary invader richness was similar between lowland and mountain fynbos up to three years after clearing. We suspect that the increase in secondary invader richness came about as a result of new secondary invader
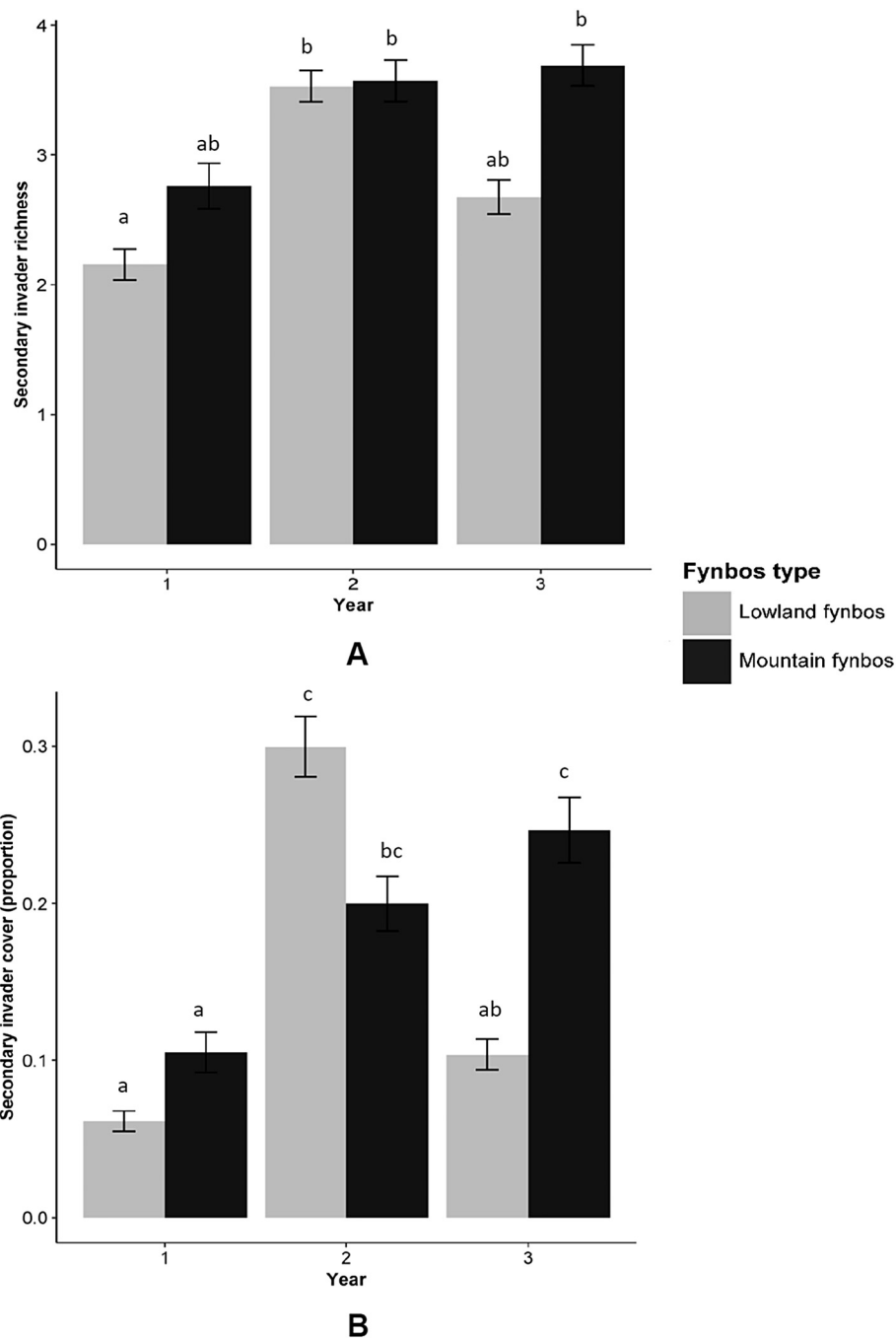
Fig. 3. Secondary invader richness (A) and cover (B) in lowland and mountain fynbos over three years after clearing invasive *A. saligna*. Mean values of secondary invader richness or cover with the same letter are not significantly different. Error bars represent ± SE.

species which had not already established in the previously invaded area but existed in surrounding areas, dispersing into the previously invaded area with or without the aid of humans (Pearson et al., 2016). The lack of significant differences in secondary invader richness between lowland and mountain fynbos suggests that secondary invasion is not habitat-specific, and both fynbos types are vulnerable to and affected by secondary invasion (Pearson et al., 2016).

The increase in secondary invader cover in the second year after clearing in both fynbos types is most likely a result of them growing and increasing their size with time. Our findings support those by Grove et al. (2015) in areas previously invaded by *Cytisus scoparius* in Washington, U.S.A, where secondary invader cover increased with time up to 22 months after clearing. We suspect that the decrease in secondary invader cover observed in lowland fynbos in the third year after

clearing was caused by an increase in native plant diversity recovery. Native species cover in our lowland fynbos study site increased by 81% in the third year after clearing, while the mountain fynbos study site only experienced a 28% increase (M.M. Nsikani, unpublished data). Several studies have suggested that the recovery of native plant diversity can suppress secondary invader dominance through competitive interactions (Reinecke et al., 2008; Sher et al., 2010; Gaertner et al., 2012; Pearson et al., 2016; González et al., 2017). It is worth noting that the establishment of one native species may not be enough to suppress secondary invader dominance, but an assortment of native species may be required. For example, during active restoration of a site invaded by *Pennisetum clandestinum*, one of the secondary invaders documented in our study, sowing native *Leucadendron coniferum* did not suppress its dominance (Gaertner et al., 2012).

5. Conclusions and implications for restoration

Restoration ecologists need to be aware that a range of secondary invaders may be dominant and persistent after clearing invasive acacias. Furthermore, burning stacked slash after clearing invasive acacias could have negative effects as it favors the dominance of secondary invaders. We acknowledge that fire application after clearing invasive acacias could also have positive effects – i.e. reduction of *Acacia* soil seed banks by triggering mass germination through prescribed burning using low-intensity fires (Holmes and Cowling, 1997). As a result, we suggest that slash should be spread throughout the restoration site instead of being stacked and then burnt. To avoid the establishment of a second generation of invasive acacias, the seedlings that germinate can be manually weeded (Fill et al., 2017), mowed (Richardson and Kluge, 2008) or treated with herbicides (Krupek et al., 2016). Management of secondary invasion can then take place afterwards. Secondary invasion is not habitat-specific and can persist up to three years after clearing at levels similar to or higher than in the first year after clearing. Depending on practical considerations, we urge practicing restoration ecologists to manage secondary invasion through actions such as herbicide or graminicide application, grazing, manual weeding, mowing, prescribed burning, soil nitrogen management, soil solarization and weed mats (Nsikani et al., 2018). We acknowledge that some of these management actions, e.g. mowing, herbicide application and grazing, could lead to the loss of recruiting native species. Therefore, we encourage practicing restoration ecologists to consider the unintended consequences of management actions applied during management of secondary invaders after clearing invasive acacias.

Declaration of Competing Interest

None.

Acknowledgements

Appendix 1. Secondary invaders found where there were high and low severity fires and no fires, up to three years after clearing invasive *A. saligna* in lowland and mountain fynbos. H = high severity fires; L = low severity fires; N = no fires. 1 = species present; − = species absent

Species	1st Year						2nd Year						3rd Year					
	Lowland fynbos			Mountain fynbos			Lowland fynbos			Mountain fynbos			Lowland fynbos			Mountain fynbos		
	H	L	N	H	L	N	H	L	N	H	L	N	H	L	N	H	L	N
Avena fatua	–	–	–	1	1	1	–	1	–	1	1	1	–	1	–	1	1	1
Briza maxima	–	1	1	1	1	1	–	1	1	1	1	1	1	1	1	1	1	1
Bromus diandrus	–	–	–	1	1	1	–	–	–	1	1	1	–	1	1	1	1	1
Cirsium vulgare	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	1	1	1
Conyza bonariensis	–	–	–	1	1	1	–	–	–	–	1	–	–	–	–	–	1	–
Conyza sumatrensis	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	–	–
Echium plantagineum	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erodium moschatum	1	1	1	1	–	1	1	1	1	1	1	1	1	1	–	–	–	–
Euphorbia helioscopia	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	1	1	1
Fumaria muralis	1	1	1	–	–	–	1	1	1	–	–	–	1	1	1	–	–	–
Gamochaeta pensylvanica	1	1	1	–	–	–	1	1	1	–	–	–	1	1	1	–	–	–
Geranium purpureum	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	1	1
Helminthotheca echioides	–	–	–	1	1	1	–	–	–	1	1	1	–	–	–	1	1	1
Hypochaeris radicata	–	–	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lactuca serriola	–	–	–	1	1	1	–	–	–	1	1	1	–	–	–	–	1	1
Lantana camara	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Lolium multiflorum	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	1	1	1
Lolium perenne	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–
Medicago polymorpha	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	1	–
Myoporum tenuifolium	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Pennisetum clandestinum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–
Polypogon monspeliensis	–	–	–	1	1	1	–	–	–	1	1	1	–	–	–	–	–	–
Raphanus raphanistrum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Rapistrum rugosum	1	1	1	1	1	1	–	1	1	1	1	1	–	1	1	1	1	1
Silene gallica	–	–	–	–	–	–	1	1	1	–	1		–	–	–	–	–	–
Sisymbrium orientale	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–
Solanum nigrum	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	1	–
Sonchus asper	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	1	1	1
Sonchus oleraceus	–	–	–	1	1	1	–	–	–	1	1	1	–	–	–	1	1	1
Stellaria media	–	–	–	–	–	–	–	–	–	1	1	1	–	1	–	1	1	1
Taraxacum officinale	1	1	1	–	–	1	1	1	1	1	1	1	1	1	1	1	1	1
Torilis arvensis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	1	–

Appendix 2. R-output of generalized linear mixed models (GLMMs) of the effects of position on the burnt stack, years after clearing, fynbos type and the interaction between fynbos type and years after clearing, on secondary invader cover and richness. Significant differences were separated using Tukey's HSD test

      1.   Secondary invader cover

```
> summary(model16)

Call:
glmmadmb(formula = Proportion ~ as.factor(Year) + Fynbos_type +
    Position + as.factor(Year):Fynbos_type + (1 | Plot), data = mydata,
    family = "beta")


Coefficients:
                                           Estimate Std. Error z value Pr(>|z|)
(Intercept)                                 -2.3762     0.1356  -17.52  < 2e-16 ***
as.factor(Year)2                             1.5218     0.1190   12.79  < 2e-16 ***
as.factor(Year)3                             0.3116     0.1264    2.46  0.01371 *
Fynbos_typeMountain_fynbos                   0.2434     0.1719    1.42  0.15689
Positionedge                                 0.1165     0.0772    1.51  0.13116
Positionoutside                             -0.2258     0.0800   -2.82  0.00477 **
as.factor(Year)2:Fynbos_typeMountain_fynbos -0.8330     0.1648   -5.05  4.3e-07 ***
as.factor(Year)3:Fynbos_typeMountain_fynbos  0.6307     0.1714    3.68  0.00023 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=646, Plot=78
Random effect variance(s):
$`Plot`
            (Intercept)
(Intercept)      0.2414

Beta dispersion parameter: 7.8561 (std. err.: 0.49179)


Log-likelihood: 590.603

> confint(model16)
                                                2.5 %       97.5 %
(Intercept)                                -2.64204951 -2.11035049
as.factor(Year)2                            1.28854469   1.75505531
as.factor(Year)3                            0.06382055   0.55929945
Fynbos_typeMountain_fynbos                 -0.09358701   0.58032701
Positionedge                               -0.03475102   0.26769102
Positionoutside                            -0.38261672  -0.06898328
as.factor(Year)2:Fynbos_typeMountain_fynbos -1.15608046 -0.50991954
as.factor(Year)3:Fynbos_typeMountain_fynbos  0.29466417   0.96673583

> Sum
  Year Fynbos_type       lsmean       SE  df asymp.LCL   asymp.UCL .group
     1 Lowland_fynbos  -2.4126433 0.1405945 Inf -2.782553 -2.0427338  a
     1 Mountain_fynbos -2.1692733 0.2213758 Inf -2.751722 -1.5868251  a
     3 Lowland_fynbos  -2.1010833 0.1796582 Inf -2.573771 -1.6283958  ab
     2 Mountain_fynbos -1.4804733 0.2944141 Inf -2.255088 -0.7058586   bc
     3 Mountain_fynbos -1.2270133 0.2854382 Inf -1.978012 -0.4760145    c
     2 Lowland_fynbos  -0.8908433 0.1725763 Inf -1.344898 -0.4367885    c

Results are averaged over the levels of: Position
Results are given on the logit (not the response) scale.
Confidence level used: 0.95
Conf-level adjustment: sidak method for 6 estimates
Results are given on the log odds ratio (not the response) scale.
P value adjustment: tukey method for comparing a family of 6 estimates
significance level used: alpha = 0.05

> Sum
 Position   lsmean        SE  df asymp.LCL asymp.UCL .group
 outside  -1.902912 0.1869684 Inf -2.349343 -1.456480  a
 centre   -1.677112 0.1678582 Inf -2.077913 -1.276310   b
 edge     -1.560642 0.1834637 Inf -1.998705 -1.122578   b

Results are averaged over the levels of: Year, Fynbos_type
Results are given on the logit (not the response) scale.
Confidence level used: 0.95
Conf-level adjustment: sidak method for 3 estimates

Results are given on the log odds ratio (not the response) scale.
P value adjustment: tukey method for comparing a family of 3 estimates
significance level used: alpha = 0.05
```

2. Secondary invader richness

```
> summary(model16)

Call:
glmmadmb(formula = Richness ~ as.factor(Year) + Fynbos_type +
    Position + as.factor(Year):Fynbos_type + (1 | Plot), data = mydata,
    family = "poisson")


Coefficients:
                                             Estimate Std. Error z value Pr(>|z|)
(Intercept)                                    0.5787     0.0883    6.55  5.6e-11 ***
as.factor(Year)2                               0.5291     0.0858    6.16  7.1e-10 ***
as.factor(Year)3                               0.2463     0.0912    2.70  0.00691 **
Fynbos_typeMountain_fynbos                     0.2595     0.1079    2.40  0.01619 *
Positionedge                                   0.1922     0.0563    3.41  0.00064 ***
Positionoutside                                0.1818     0.0565    3.22  0.00130 **
as.factor(Year)2:Fynbos_typeMountain_fynbos   -0.2595     0.1170   -2.22  0.02655 *
as.factor(Year)3:Fynbos_typeMountain_fynbos    0.0609     0.1208    0.50  0.61407
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=642, Plot=78
Random effect variance(s):
$`Plot`
            (Intercept)
(Intercept)    0.054742
Log-likelihood: -1137.45

> confint(model16)
                                                  2.5 %       97.5 %
(Intercept)                                  0.40564654   0.75171346
as.factor(Year)2                             0.36089473   0.69738527
as.factor(Year)3                             0.06758184   0.42493816

Fynbos_typeMountain_fynbos                   0.04797989   0.47094011
Positionedge                                 0.08184523   0.30265477
Positionoutside                              0.07102736   0.29263264
as.factor(Year)2:Fynbos_typeMountain_fynbos -0.48883579  -0.03020421
as.factor(Year)3:Fynbos_typeMountain_fynbos -0.17587685   0.29772885

> Sum
 Year Fynbos_type        lsmean          SE df asymp.LCL asymp.UCL .group
    1 Lowland_fynbos   0.7033733 0.09092115 Inf 0.4641563 0.9425904  a
    3 Lowland_fynbos   0.9496333 0.12372198 Inf 0.6241161 1.2751506  ab
    1 Mountain_fynbos  0.9628333 0.13887531 Inf 0.5974471 1.3282196  ab
    2 Mountain_fynbos  1.2324533 0.19352497 Inf 0.7232817 1.7416249   b
    2 Lowland_fynbos   1.2325133 0.11964854 Inf 0.9177134 1.5473132   b
    3 Mountain_fynbos  1.2700193 0.18976873 Inf 0.7707305 1.7693081   b

Results are averaged over the levels of: Position
Results are given on the log (not the response) scale.
Confidence level used: 0.95
Conf-level adjustment: sidak method for 6 estimates
P value adjustment: tukey method for comparing a family of 6 estimates
significance level used: alpha = 0.05

> Sum
 Position   lsmean         SE df asymp.LCL asymp.UCL .group
 centre   0.9337777 0.1096014 Inf 0.6720783  1.195477  a
 outside  1.1156077 0.1212057 Inf 0.8262003  1.405015   b
 edge     1.1260277 0.1219549 Inf 0.8348313  1.417224   b

Results are averaged over the levels of: Year, Fynbos_type
Results are given on the log (not the response) scale.
Confidence level used: 0.95
Conf-level adjustment: sidak method for 3 estimates
P value adjustment: tukey method for comparing a family of 3 estimates
significance level used: alpha = 0.05
```

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