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Sriramamurthy, RT, Bhalla, RS and Sankaran, M orcid.org/0000-0002-1661-6542 (2020) Fire differentially affects mortality and seedling regeneration of three woody invaders in forest–grassland mosaics of the southern Western Ghats, India. Biological Invasions, 22. pp. 1623-1634. ISSN 1387-3547

https://doi.org/10.1007/s10530-020-02207-7

Fire differentially affects mortality and seedling regeneration of three woody invaders in forest-grassland mosaics of the southern Western Ghats, India

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ABSTRACT

Invasion by exotic woody species is a major concern in grasslands worldwide. Woody invasions pose a particularly serious threat to forest-grassland mosaics globally, but the factors influencing the success of woody species in these systems, including the role of disturbances such as fire, are not well understood. In this study, we evaluated the role of fire in influencing mortality and regeneration success of three globally widespread woody invasives, *Acacia mearnsii* (black wattle), *Cytisus scoparius* (scotch broom) and *Ulex europaeus* (gorse) in the montane forest-grassland mosaics of the Nilgiri Biosphere Reserve in the Western Ghats biodiversity hotspot, India. Our results indicate that mortality and regeneration responses to fire are species-specific. Fire-induced adult mortality was highest in scotch broom and lowest in gorse, and high, but variable in wattle. Burning greatly increased the abundance of gorse and wattle seedlings, but only marginally increased scotch broom seedling abundance. Fire effects on invasive seedling densities were most pronounced at the edges of invasive patches. Overall, our results indicate that fires are likely to differentially affect invasion patterns of these three species, with fire potentially encouraging invasion by gorse and wattle and discouraging invasion by scotch broom.

Keywords: Invasion, fire, *Acacia mearnsii*, *Cytisus scoparius*, *Ulex europaeus*, shola-grasslands.

Introduction

Tropical grasslands harbor rich endemic biodiversity and provide critical ecosystem services to dependent human communities (Bond & Parr, 2010; Murphy et al. 2016). However, they are being increasingly threatened by a range of factors including rapid conversion to croplands and plantations, changing climates, invasion by exotic species and alterations of fire regimes (Bond & Parr 2010; Parr et al. 2014; Lehmann & Parr 2016; Ratnam et al. 2016, Thekaekara et al., 2017, Joshi, Sankaran & Ratnam 2018, Sankaran 2019). In the last few decades, several exotic woody plant species have been introduced for their commercial value in temperate and tropical grasslands around the world, including the South American pampas and paramo (Dias et al., 2013; Harden, et al., 2013), the fynbos of South Africa (Bennett, 2014; Rundel, Dickie, & Richardson, 2014), the forest-grassland mosaics of Southern Asia (Otsamo, 2002; Joshi, Sankaran, & Ratnam, 2018) and the grasslands of Australia and New Zealand (Ledgard, 2001; Fahey & Watson, 2019). Many of these species have now become invasive, posing significant threats to grasslands worldwide (Higgins, Richardson, & Cowling, 1996; Rouget, et al., 2002).

Besides invasions by exotic woody species, the anthropogenic alteration of fire regimes is another major factor threatening the ecological integrity of grasslands worldwide (Bond & Keeley, 2005; Bond, Woodward, & Midgley, 2005; Bowman, Boggs, & Prior, 2008; Bond & Parr, 2010; Archibald, 2016). Fires are common occurrences in many temperate and tropical grasslands and savannas (Bond & Keeley, 2005), and have been an intrinsic part of these ecosystems for the last 50,000 years or more (Andersen et al. 1998; Van Wilgen, Biggs, & Potgieter, 1998). However, the extent to which changes in fire regimes influence invasion success in different grasslands worldwide remains unclear. Fires can reduce above ground biomass, release plants from resource limitation by increasing nutrient availability, increase light availability by opening up canopies and release soil seed banks from dormancy, thereby initiating new successional pathways that potentially facilitate invasion (D'Antonio & Vitousek, 1992; Blair, 1997; Sankaran, et al. 2005; DiTomaso, et al. 2006). On the other hand, fires of high intensity can render seeds un-viable while also causing high adult mortality among woody invasives thereby suppressing invasions (Pieterse & Boucher, 1997; Stokes, et al., 2004; Pausas, Moreira & Corcobado, 2012). Because fires are often used as a management tool in grasslands to stimulate grass growth for herbivores and suppress native woody plant biomass (Emery & Gross, 2005; Zouhar, K.., 2008; Hamman et al., 2011), understanding whether fires facilitate or retard invasion by exotic species is critical to managing invasive species in grasslands.

Fire effects on woody invasion in grasslands have thus far been studied mostly in temperate grasslands (Grace, et al. 2000; Mandle et al. 2011) but these relationships are relatively poorly understood in tropical grassland systems. In this study, we investigated the effects of fire on woody invasion in montane forest-grassland mosaics (locally known as shola-grassland mosaics) of the upper elevations of the Nilgiri Biosphere Reserve in the southern Western Ghats, India. These mosaics are characterized by vast expanses of C4 tussock grasses on the slopes, interspersed with stunted tropical evergreen forest patches in the valleys, with clear abrupt transitions between the two (Fig 1a, left panel). During the Colonial era, i.e., 1800s to mid-1900s, several exotic woody plants were introduced in the grasslands of this shola-grassland ecosystem with the intent of increasing woody biomass for utilitarian or for ornamental purposes (Joshi, Sankaran, & Ratnam, 2018), of which three have become major invasive in the landscape – Black wattle

(*Acacia mearnsii*), Scotch broom (*Cytisus scoparius*) and Gorse (*Ulex europaeus*). Archival records show that black wattle (*Acacia mearnsii*) was introduced in the grasslands over a century ago, in 1861, for fuel wood and to extract tannins from the bark for the leather industry (Ranganathan, 1938; Joshi, Sankaran & Ratnam, 2018). Scotch broom was introduced more recently, in 1924, for ornamental and fencing purposes (Srinivasan, et al., 2012; Joshi, Sankaran & Ratnam, 2018). The time of gorse introduction remains unclear, but like scotch broom, it too was introduced for ornamental purposes, for its bright yellow-coloured flowers. All three invasives form mono-dominant stands that support significantly reduced native biodiversity (Fig 1, Fig 2, Srinivasan 2012; Sriramamurthy, 2018), with sharp boundaries between them and the grassland. These invasions have also altered vegetation structure in the landscape, from abrupt woody-grassy biome transitions to a more homogeneously woody biome (Fig 1b, right panel), with the woody invasives covering much of the slopes that were previously predominantly native grasslands , and as a result, have massively reduced the expanse of the grasslands.

Figure 1. a) Images of uninvaded shola-grassland (left panel) with sloping grasslands with forests only in the valleys and b) of invaded shola grasslands (right panel) with large tracts of grasslands on the slope covered by the introduced exotics. Left panel image from Prasenjeet Yadav.

Traditionally, these grasslands were periodically burned by the indigenous pastoralist Toda community in order to stimulate fresh grass growth for their cattle (Srinivasan 2012; Srinivasan, et al., 2012; Srinivasan, Bhatia, & Shenoy, 2015; personal communication with Toda elders). However, fires have been actively suppressed for the last 30-40 years since the region was declared ‘protected’ by the government (Hiremath & Sundaram, 2013; Das, et al. 2015). At present, detailed information on fire return intervals for the study site are unavailable. Nevertheless, wildfires do periodically occur in the region (Srinivasan 2012), but their impacts on the invasion process at out study site remains unclear. There is evidence for seeds of all three invasive species being released from dormancy by scarification of seed coat by fire, amongst other means (Bossard & Rejmanek, 1994; Pieterse & Boucher, 1997; Anderson & Anderson, 2010; Srinivasan et al. 2012). Previous work also suggests that wattle and gorse are capable of rapidly resprouting from underground root stocks following fire (Rolston & Talbot 1980; Pieterse & Boucher 1997; Richardson & Kluge 2008; Anderson & Anderson 2010), while scotch broom does not appear to be as adept at resprouting following fires (Wyse, Perry & Curran 2018). Severe fires can, nevertheless, result in significant adult mortality, particularly in young dense stands (Pieterse & Boucher 1997; Richardson & Kluge, 2008).

Here, we leveraged a fire that occurred in February 2017 as a natural experiment to investigate fire effects on invasive species and evaluate the potential for fire as a management tool for controlling invasive species in the region. Specifically, we asked: 1) What is the effect of the fire on adult mortality and post-fire regeneration and how do these vary between the different invasive species? 2) What is the effect of fire on seedling recruitment from the soil seed bank and how does this differ across the three species, and along topographic gradients? 3) How does fire affect expansion of the invasives by promoting or discouraging seedling recruitment at the edges of patches, and how does this vary between the three species?

Figure 2. Images of patches of each of the three invasives and the distinct boundaries they share with the grassland – a gorse patch on the top left panel, a large patch of scotch broom in the bottom left panel and a black wattle patch in the right panel.

Methods

Study site and species

The study was conducted in the Avalanche and Korakundah ranges of the Kundah Reserve Forest of the Nilgiri Biosphere Reserve in the southern Western Ghats, India (Fig 3). Elevation here ranges between 1900 and 2400m. The region receives an average annual rainfall of ~2000 mm, primarily from the South-West Monsoon during the months of June-August. Temperatures in the region vary between -5 ºC and 29 ºC. Frost occurs during the months of December, January and February.

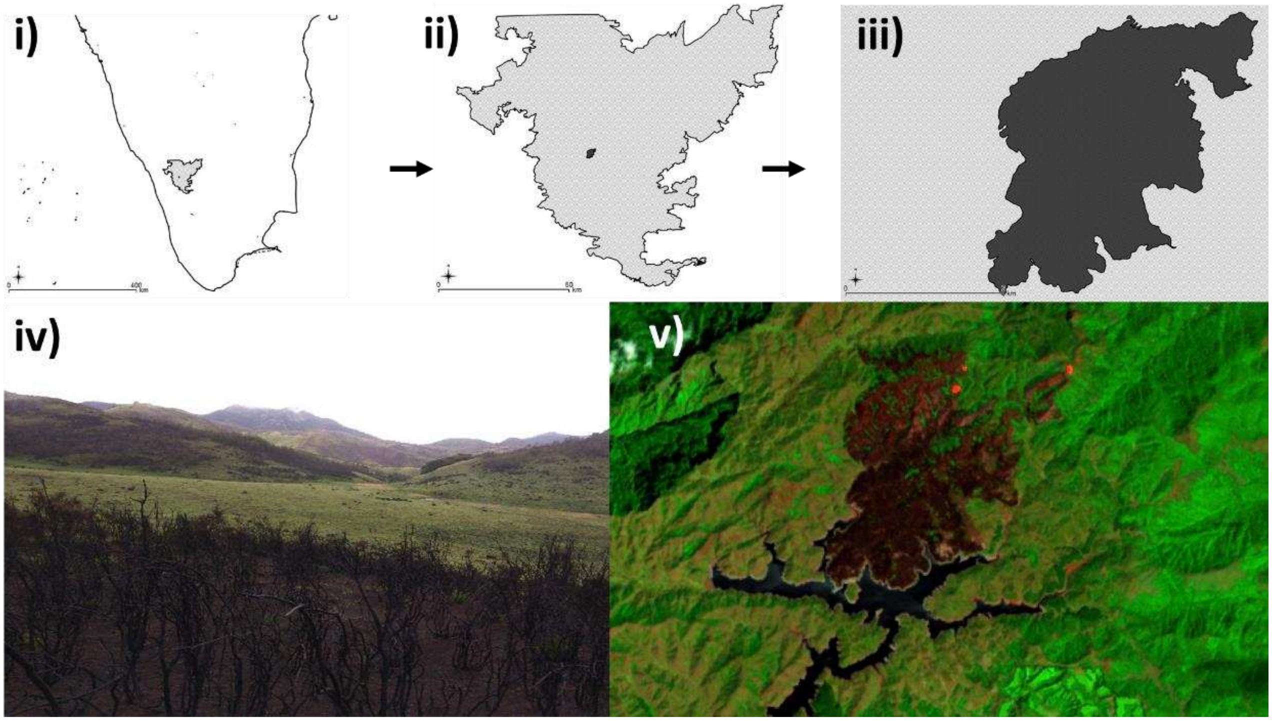

Figure 3. i) A map of peninsular India showing the location of Nilgiri Biosphere Reserve in the Southern Western Ghats, ii) A map of the Nilgiri Biosphere Reserve showing the location of the fire that burned 6.5 km^2 of the reserve in February 2017 in the Avalanche-Korakundah reserve forest areas, iii) Complete fire boundary and adjacent unburnt areas sampled as control sites, iv) A photograph of the burnt site soon after the burn, v) A satellite image of the burnt area while the fire was still burning (red pixels in the top corner of the burn boundary) (base map source: ESRI).

The vegetation in the upper elevations of the Nilgiris is dominated by montane forest-grassland mosaics (Caner, et al., 2000). Paleo-ecological evidence indicates that these systems are at least 40000 years old, relics of the Pleistocene era, pre-dating human settlements in the landscape (Sukumar et. al, 1993, Caner et al., 2003; Caner et al. 2007). However, large tracts of grassland have now been colonized by the three woody invasives. Black wattle is a tree, while the other two are shrubs, all three leguminous perennials belonging to the Fabaceae family (Brown & Ko, 1997;

Leary, et al. 2006, Muir & Vamosi, 2015). Black wattle grows, on average up to 10m in height, and scotch broom and gorse grow about 3m in height (MacCarter & Gaynor, 1980; Brown & Ko, 1997; Rees & Paynter, 1997).

All three species are also recognized as invasives in many other parts of the world including Canada, South America, South Africa, New Zealand, Hawaii and North America (MacCarter & Gaynor, 1980; Bossard & Rejmanek, 1994; Pieterse & Boucher, 1997; Davies, et al., 2005; Leary, et al. 2006; Anderson & Anderson, 2010; Paynter et al. 2010; Burrows, Cieraad, & Head, 2015). Their invasion success can be attributed to their shared traits of high propagule production rates, nitrogen fixing ability and small seed size (Rees & Paynter 1997; Peterson & Prasad, 1998; Paynter et al. 2003; Colautti, Grigorovich, & MacIsaac, 2006; Prévosto, et al. 2006; Zouhar, K., 2008; Magda, et al., 2009; Drake, 2011; Hamman, et al. 2011; Magesan, Wang, & Clinton, 2012; Boudiaf et al. 2013; Muir & Vamosi, 2015). Seeds of all three species remain dormant, but viable in the soil seedbank, for many years (MacCarter & Gaynor, 1980; Brown & Ko, 1997; Srinivasan et al. 2012).

These three invasive species typically colonize grasslands by expanding radially from existing patches and displacing native species (Brown & Ko, 1997; Watt et al., 2003; Brooks, D'antonio & Richardson, 2004; Mandle et al. 2011; Srinivasan et al., 2012). All three species tend to form mono-dominant patches (Fig 2) with significantly reduced native biodiversity in the understory, comprising largely of shade-tolerant and weedy native plants (Srinivasan, 2012; pers. obs).

Data collection methods

We studied fire effects on the survival and regeneration of the three invasive species following a wildfire that burned the area in the last week of February, 2017. The fire lasted for three days and burnt an area of 6.3 km^2. We surveyed burned and adjacent unburned control sites nine to fourteen months after the fire (November, 2017 to April, 2018), following to monsoons, to allow for seedling recruitment, which typically occurs during the monsoon, and also allow sufficient time for adults to coppice, so as to better distinguish between actual death (top kill and no coppicing) from only top-kill (death of the above ground biomass followed by coppicing). We quantified fire effects on adult mortality, and seedling abundance patterns in uninvaded grassland, within invasive patches, and at different distances from patch edges for each invasive species. Although we do not have detailed fire histories for the study area, the specific sites chosen for our study had not been burned for at least the last six years (Joshi et al., 2019, pers comm.).

Adult mortality and regeneration from coppicing

Fire effects on adult mortality and regeneration via coppicing were quantified in ten equally sized patches for each of the three invasive species in the burnt areas. Within each patch, the total number of individuals, number of dead individuals and the number of coppicing individuals were counted within a belt transect of length 10m and width 3m. These counts were made only in burnt patches, as initial observations revealed that adult mortality and coppicing were both negligible in unburnt areas, and mortality from other factors such as drying were comparable across the burnt and unburnt areas.

Seedling abundance in grassland

In both burnt and unburnt grassland, data on the number and percentage cover of seedlings of each of the three invasive species were collected in 230 1×1m^2 plots. To ensure unbiased coverage of all grassland areas, sampling plots were selected based on a uniform-random sampling approach. Both control and burnt areas were divided into 46 grids of area 14 hectares each, within which one 30×30m^2 plot was randomly chosen for sampling. Within each 30×30m^2 plot, seedling abundances were quantified in four 1×1m^2 plots at the four corners, and in one in the center. Data were also collected on the abundance of invasive adults within a 7m radius of each 1×1m^2 plot. Values of topographical variables such as slope and aspect were obtained from ASTER DEM imagery (image courtesy of the U.S. Geological Survey).

Seedling abundance at different distances from the edge of a patch

Since all three invasives have been reported to expand into the grassland radially outwards from patch edges, invasive seedling abundances at different distances from the edge of the patches were compared between burnt and unburnt areas to investigate if fire accelerates seedling invasion into grasslands. The main mode of seed dispersal for all three species is by explosion of seed pods, and most seeds fall within 3-7m of an individual (Brown & Ko, 1997; Prévosto, Robert, & Coquillard, 2004; Leary et al., 2006). In both burnt and unburnt areas, twenty patches of each of the three invasive species were opportunistically sampled where there was a discernible patch edge shared with uninvaded grassland. Within each patch, percentage cover of invasive seedlings and adults were quantified in ten 1×1 m^2 plots within a 10m x 1m belt transect laid perpendicular to the edge of the patch. The transect began 3m within the patch, and ended 7m outside the patch edge.

Statistical analysis

Descriptive statistics were used for presenting adult mortality and coppicing data (mean, with 95% Confidence Intervals). Since seedling abundances in grasslands were zero-inflated, fire effects on seedling abundance patterns were analyzed using zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) models (Martin et al., 2005). The analysis was carried out within a generalized linear mixed effects model framework, with fire treatment, invasive adult abundance, slope and aspect as the fixed effects, and the identity of the 30×30m^2 plot as the random effect to account for non-independence of the five 1×1m^2 plots nested within each 30×30m^2 plot. Since slope values are known to affect fire intensities, we included an interaction term of slope and fire treatment in the model. Further, since the presence of adult invasives in the neighborhood can increase soil seed banks, whose germination can be stimulated by fires, we also included an interaction term between burning and adult invasive abundance in the neighborhood in our model. Finally, fire effects on seedling abundances at different distances from invasive patch edges were analyzed using piecewise linear regressions, with the breakpoint set at the edge of the patch and burn treatment and distance from edge as predictors. To facilitate comparison of the relative effects of different predictors on our response variables, the estimates for each predictor were centered and scaled around the mean for all our analyses. The values reported here are the centered and scaled values. All analyses were carried out using R (version 3.5.0, R core team, 2018, accessed on 1/02/2019).

Results

Fire effects on adult mortality and regeneration from coppicing

Fire caused high levels of mortality in scotch broom (94 ± 12%) and black wattle adults (87.8 ± 17%; Fig 4). However, gorse adult mortality was much lower (18 ± 9%). This was primarily because rates of coppicing following burning were very high in gorse (81.5 ± 15%) and negligible for both scotch broom (2.2 ± 10%) and black wattle (2.19 ± 15%; Fig 4).

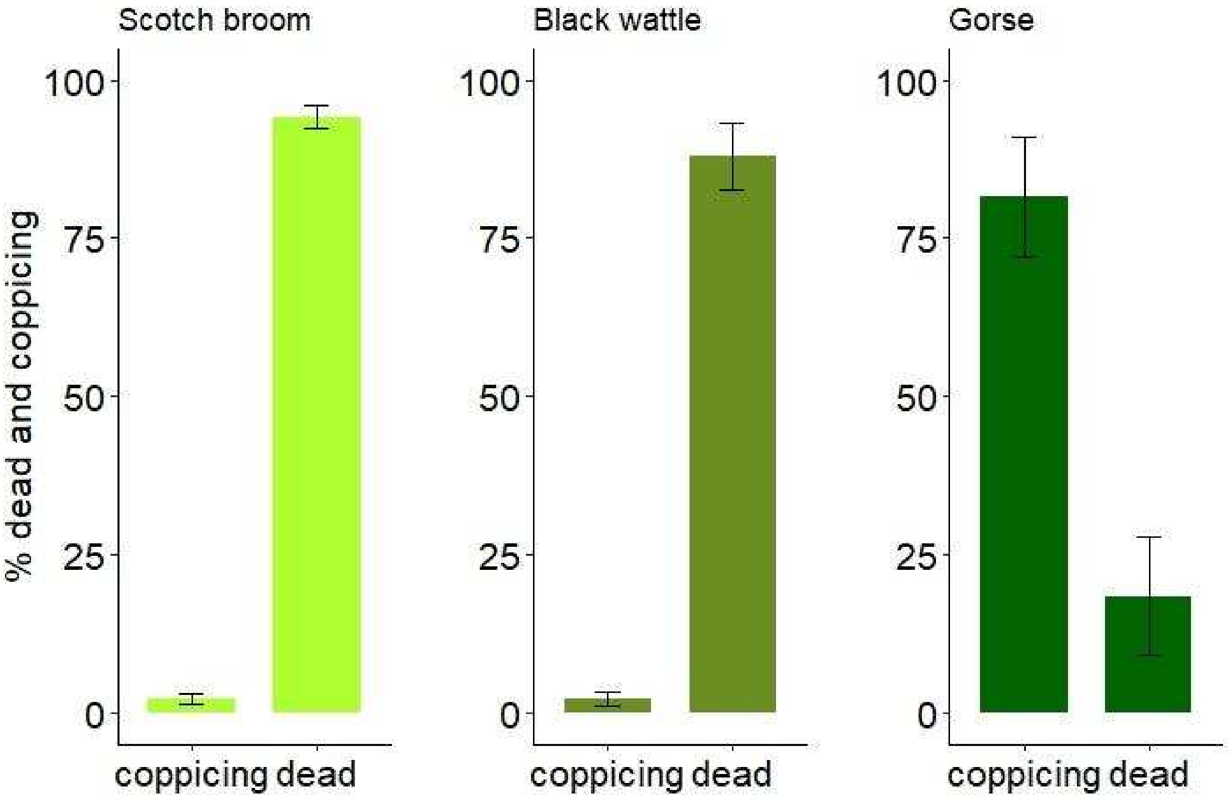

Figure 4. Percentage adult mortality (mean ± 95% CI) and percent regeneration through coppicing following burning for the three study species ($p < .001$ for both adult mortality and coppicing, number of sample patches = 10).

Effects of fire on invasive seedling abundance in grassland

Burning and the presence of invasive adults in the neighborhood were the strongest predictors of invasive seedling abundance in grasslands. In general, unburnt grasslands had very few invasive seedlings. Burning increased invasive seedling abundance, but the magnitude of the effect differed between species. Fire effects on seedling abundances were more pronounced for scotch broom seedlings (model effect size estimate ± se estimate: 3.16 ± 0.85) than black wattle (3.05 ± 1.56), and was highly variable in the case of gorse (3.15 ± 3.02). Fire effects on seedling abundance were additionally contingent on the number of adult invasives in the neighbourhood (see Table 1;

significant fire x adult abundance interaction). In general, seedling abundance following burning increased with increasing adult abundance in the neighborhood for all three invasives, with the magnitude of this effect being particularly pronounced for wattle, less so for gorse and marginal and non-significant for scotch broom (Table 1). The effects of topographical variables were much lower than the burning treatment and invasive adult abundance, except for gorse seedling abundance which tended to be higher in more north-facing areas.

Table 1. Model estimates of effect sizes for different predictors of invasive seedling abundance (number of seedlings) in grassland for the three invasives. Values reported here represent the inverse log-transformed estimates from zero-inflated Poisson models and zero inflated negative binomial distributions' models of invasive seedling abundances as a function of the different predictors. These are centred and scaled estimates, and so effect sizes are comparable across predictors.

Predictors	$e^\wedge{}^{\text{Model estimate}} \pm e^\wedge{}^{\text{Std. error estimate}}$ Effect sizes of each predictor (* - $p < 0.05$)		
	Scotch broom	Black wattle	Gorse
Intercept	0.49 ± 0.11 *	0.12 ± 1.66 *	0.0004 ± 0.001 *
Fire treatment	3.16 ± 0.85 *	3.05 ± 1.56 *	3.15 ± 3.02
Number of conspecific adults in the vicinity	2.52 ± 0.45 *	3.86 ± 1.29 *	6.18 ± 3.66 *
Slope	0.97 ± 0.22	0.5 ± 1.49	0.83 ± 0.81
Aspect	1.08 ± 0.15	1.86 ± 1.26 *	4.61 ± 3.57 *
Fire treatment × slope	0.54 ± 0.18	1.47 ± 1.69	0.83 ± 0.87
Fire treatment × Conspecific adult abundance	2.35 ± 0.88 *	21.99 ± 2.81 *	0.38 ± 0.26

Fire effects on invasive seedling abundance at different distances from patch edges

Seedling densities were typically highest within patches, and declined with increasing distance away from the edge of the patch, except for black wattle where seedling abundances tended to be low both inside and outside patches (Fig 5). In general, burning increased seedling densities, although once again effects differed between species (fig 5). Burning increased seeding abundances more strongly for gorse (7.72 ± .44, $p < 0.05$, i.e model effect size estimate ± se estimate), when compared to black wattle (2.91 ± .22, $p < 0.05$) or scotch broom (.62 ± .12, $p < 0.05$). Burning increased invasive seedling abundances at all distances from the patch edge for all three species, with this effect being most pronounced for gorse and lowest for scotch broom.

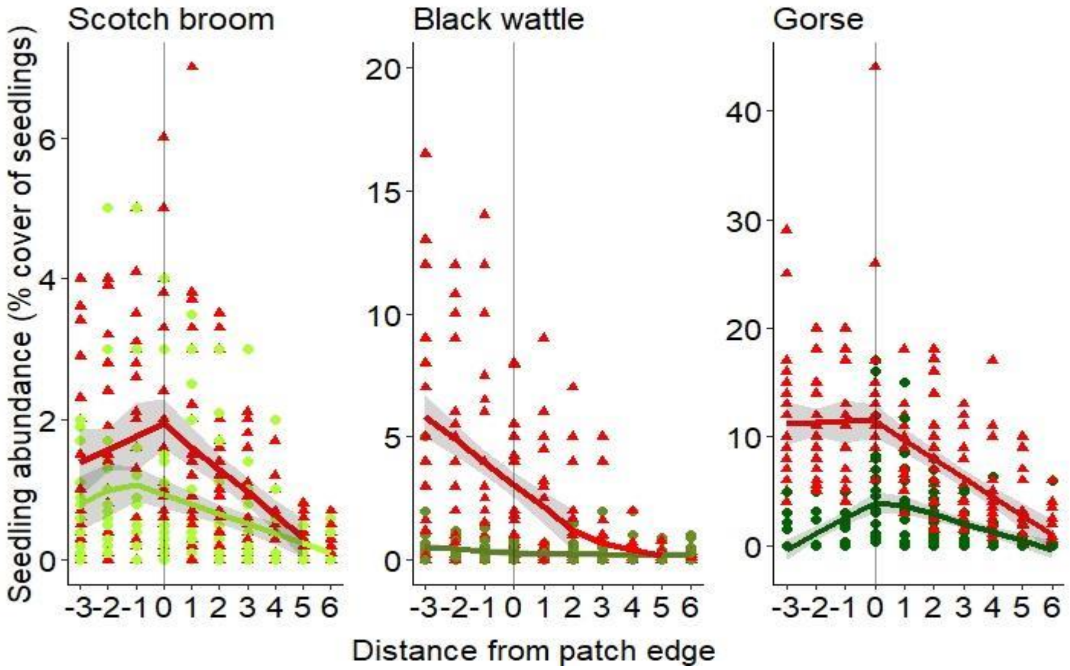

Figure 5. Invasive seedling abundance at different distances from the patch edges, with zero representing the patch edge and negative and positive values represent distances inside and outside patch edges, respectively. Circles represent seedling abundances in control patches and triangles represent seedling abundance in burnt patches. The solid lines and grey ribbons around them are model estimates of the means and standard errors, respectively, from the breakpoint regression model. Note that the y-axes ranges differ between species.

Discussion

Fire affected mortality and regeneration of the three invasives to different extents. While black wattle and scotch broom suffered very high adult mortality following burning, post-fire mortality of gorse adults was low. These differences were primarily driven by differences amongst the three species in the levels of coppicing following fire; almost all burnt gorse individuals coppiced, while there was barely any coppicing in scotch broom and black wattle. Burning increased invasive seedling abundance, both in the grassland and at the edges of invaded patches. Increases in seedling abundance following burning was highest for gorse, somewhat less, but high for black wattle and lowest for scotch broom. Collectively, these results suggest that fires are likely to have differential effects on the invasion trajectories of these three species at our study site.

Grace et al. (2000) provide a general conceptual framework to understand relationships between fire regimes and invasions by characterizing invasive species based on their responses to fire in terms of survival, reproduction and colonization, and their effects on the native community. Within this broad framework, our three study species fall under different classes, differing in their fire-invasion relationships and the extent to which they are likely to be promoted or suppressed by fires. Gorse represents a species that is likely to be promoted by fires, giving it a competitive advantage over the natives. Gorse had very low adult mortality following fire, with almost all individuals coppicing from burnt stumps, and some even flowering within a year following burning. At the same time, germination of gorse was also greatly encouraged by fire. Species such as gorse, that fall under this category, also tend to have fuel altering characteristics that encourage fires (Anderson & Anderson, 2010, Sriramamurthy 2018), allowing for a post-fire competitive advantage through a positive feedback loop with fires. For controlling such a species, fire by itself is thus unlikely to be very effective.

Black wattle and scotch broom in our study area, on the other hand, fall within the type of species whose adults are killed by fires, but whose colonization from the seedbank is encouraged following burning through the release of seeds from dormancy. Both black wattle and scotch broom suffered high adult mortality from fire, accompanied by enhanced germination. For such species, occasional fires can promote invasions while frequent fires can suppress them (Grace et al. 2000; DiTomaso et al. 2006). Scotch broom and black wattle could therefore be potentially controlled through the use of frequent fires, with fire-return intervals less than the time taken by these species to reach reproductive maturity, thereby killing adults, while simultaneously exhausting the soil seedbank. Interestingly, the responses we observed for black wattle in our study is in stark contrast to patterns reported earlier from southern Africa where significant coppicing following burning has been reported for this species, particularly among juvenile trees (26-50mm stem diameter at 20cm height; Pieterse & Boucher 1997). At present, the reasons underlying these differing responses are not clear. Although mortality of black wattle was high in our study, it was also very variable. Immature wattle adults retain more water than mature ones and are less flammable (Brown & Ko, 1997), and many younger individuals within wattle patches hadn’t burned at all in our study, providing a potential explanation for the contrasting responses observed here. Clearly, there is a need for more detailed studies on the response of black wattle to fire in this landscape.

Ultimately, the extent to which fires are likely to promote or retard invasions by these different species in this landscape will depend not just on the frequency of future fires, but also on their intensities. Intense fires can enhance adult mortality and thin out invasive stands, while also suppressing germination by rendering seeds of invasive species unviable. Previous work suggests that the local temperatures that render seeds unviable differs between these species. Scotch broom seeds have been reported to remain viable up to temperatures of ~130ºC, above which most become unviable (Rivas et al. 2006, and Tarrega et al. 1992). Temperatures up to 100ºC have been shown to stimulate germination of black wattle seeds (Sao Jose et al 2019), although temperatures at which seeds of this species become unviable remains unclear. On the other hand, heating up to 150ºC has been shown to increase germination in common gorse and other closely related species (Stokes et al. 2004), with temperatures greater than 150ºC also having negligible impacts of seed viability (Zabkiewicz & Gaskin 1978), suggesting that gorse seeds can survive and germinate at fire intensities that kill scotch broom seeds. Thus, whether fire encourages or discourages colonization from seed by these different species is likely to depend on the intensity of fire within the soil microhabitat of invasive patches. Because woody invasion in grasslands can alter fuel characteristics and fire behaviour (Brooks et al., 2004; Emery & Gross, 2005; Zouhar, 2008; Brooks & Lusk, 2009; LeQuire, 2009; Mandle et al., 2011; van Wilgen, 2015), fire intensities can differ between patches dominated by the three invasives. Indeed, estimates of fire intensities based on remotely sensed proxies for the same fire indicate that fire intensities were much higher in invaded areas than in uninvaded areas, with gorse-dominated areas attaining some of the highest fire intensities (Sriramamurthy, R., 2018), potentially providing gorse with a post-fire advantage over other invasives and native species.

Overall, our results indicate that burning at the landscape scale is unlikely to be an effective strategy to control invasives in a complex, multi-species invasion system such as our study site, as it can elicit divergent responses amongst different invasive species. Infrequent large-scale fires, such as the one studied here, can in fact promote expansion of all species. Although the effect of fire on adult mortality varied considerably across the three species in our study, fire increased seedling abundances in all cases, both in the grassland and at the edge of invasive patches, leading to patch expansion in all cases. To be effective as a management tool, burning will therefore need to be targeted at the level of individual patches, with burning regimes tailored to the species in question. Prescribed burning as a restoration tool is likely to be most effective in the case of scotch broom, which had high adult mortality and amongst the lowest post-fire regeneration from seed of the three invasives in this study. Notably, an earlier study on scotch broom-fire relationships in the same region also recognized the potential for fire as a tool for control of this species (Srinivasan 2012; Srinivasan et al. 2012). They similarly reported widespread adult mortality following burning and an initial pulse of recruitment from seed, but no further recruitment for up to 18 months following the fire (Srinivasan et al. 2012), likely a consequence of seedbank depletion following burning. However, community composition of burnt scotch broom patches was still distinct from uninvaded grassland 18 months following burning, and largely comprised of shade-tolerant weedy native species. Their results also indicated that native species diversity in uninvaded grasslands was fairly resilient to fires, recovering to their pre-burn states within a relatively short period of time (Srinivasan 2012). Frequent patch-level prescribed burning may therefore potentially be a tool to control scotch broom in this landscape, killing adults while also simultaneously depleting local seed banks. However, this may need to be supplemented by other management efforts such as re-seeding in order to restore the native community. Importantly, before such management interventions are initiated, there is a critical need for more detailed experimental studies that quantify the effects of more frequent fires on the seed banks of scotch broom and on native plant communities.

Restoration of grasslands invaded by wattle and gorse pose greater challenges. Our results indicate that fires are likely to strongly favor gorse invasion in the landscape, and have spatially variable effects on black wattle invasion. Seedlings of black wattle were very rare in the grassland overall, but burnt grassland areas had greater black wattle seedling abundance than unburnt grassland. Fire stimulated black wattle seed banks to a greater extent inside patches than outside. This is in contrast to earlier studies which have reported patch expansions of as much as 20m from the edge of infestation following fires (Pieterse & Boucher 1997). Whether this is a consequence of a lack of seeds in the seedbank outside patch edges as a result of limited seed dispersal in our study site is unclear. This could also be an effect of the intensity differences between the invasive patches and the grasslands, since the different intensities would have led to differences in the release of seeds from dormancy (Sriramamurthy, 2018). Notably, unburnt black wattle patches had very few seedlings within and outside the patches, suggesting that patch expansion in this species is likely to be relatively slow in the absence of burning.

So far, invasion control and grassland restoration efforts by the park managers in the landscape has predominantly been physical uprooting and mass felling, primarily of black wattle, which appears to have had little to no effect in reducing invasion levels of this species (Unkule, 2017) . The other two invasives are not actively managed. Our study provides valuable data on the species-specific nature of the responses of these invasives to fire, and for evaluating the potential of fire as a tool for controlling invasion and aiding restoration of these grasslands. However, we recognize that in the absence of detailed fire histories of our study sites, disentangling the legacy effects of past fires on observed responses is problematic, highlighting the need for detailed long-term experiments to understand the effects of different fire frequencies and intensities on invasive species responses and seed bank dynamics in our study site. Importantly, there is also an urgent need to simultaneously quantify the responses of native species to both fire and invasion, particularly for gorse and wattle where data are currently lacking for our study site, and for more and better-quality information on fire regimes in the landscape. Such information will be critical for evaluating the role of fire in the invasion process in this system, and for designing effective strategies for the restoration and management of these unique ecosystems.

ACKNOWLEDGEMENTS

This study was funded by grants from Sir Dorabji Tata Trust, Department of Science and Technology, Foundation for Ecological Research, Advocacy and Learning, and the National Centre for Biological Sciences, India. The authors of this study would also like to thank Dr. Jayashree Ratnam, Dr. Atul Joshi, Dr. Ankila Hiremath and Manaswi Raghurama for help in ideation and drafting the manuscript. Constant support from Selva Kumar, Kamal Raj, Susilan and Kumaran from the field team also deserves due credit. We are also very grateful to the two anonymous reviewers who have provided many useful comments on the manuscript.

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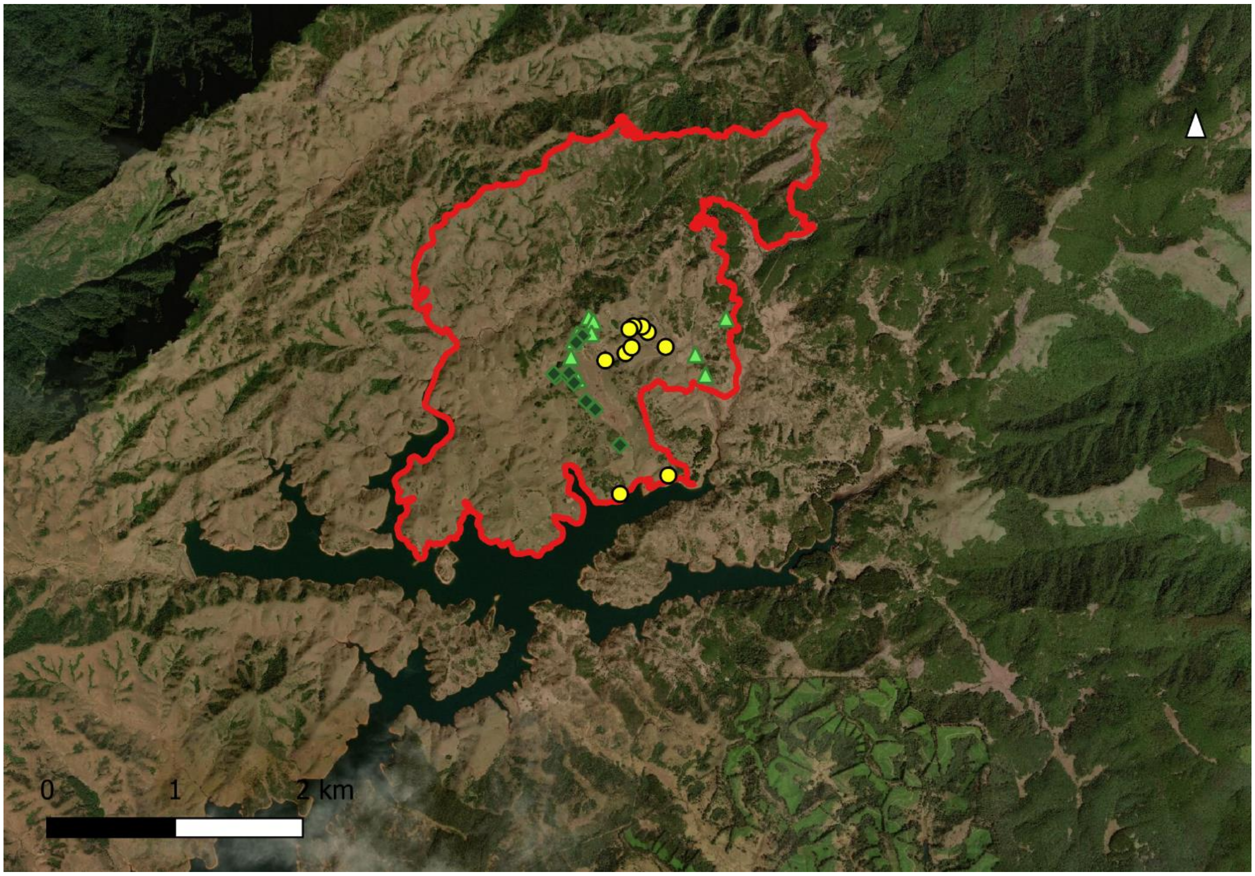
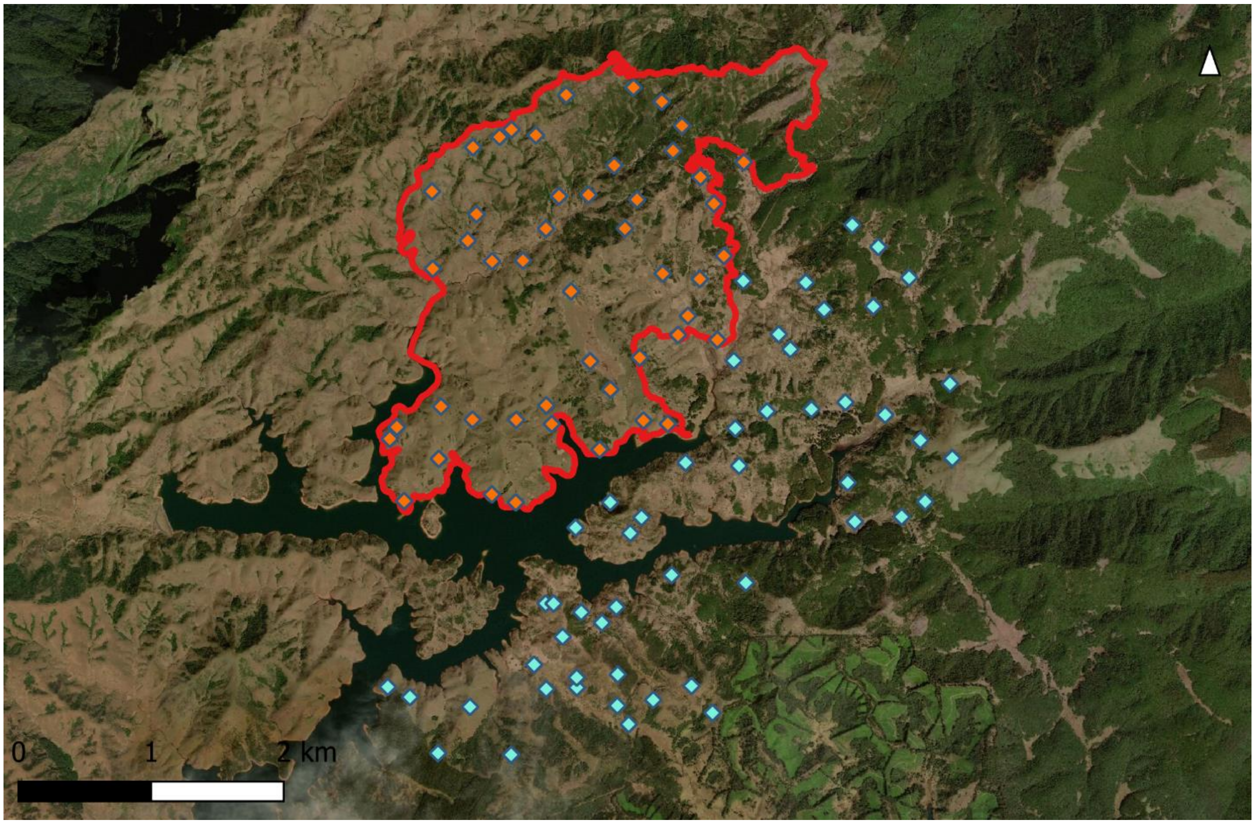
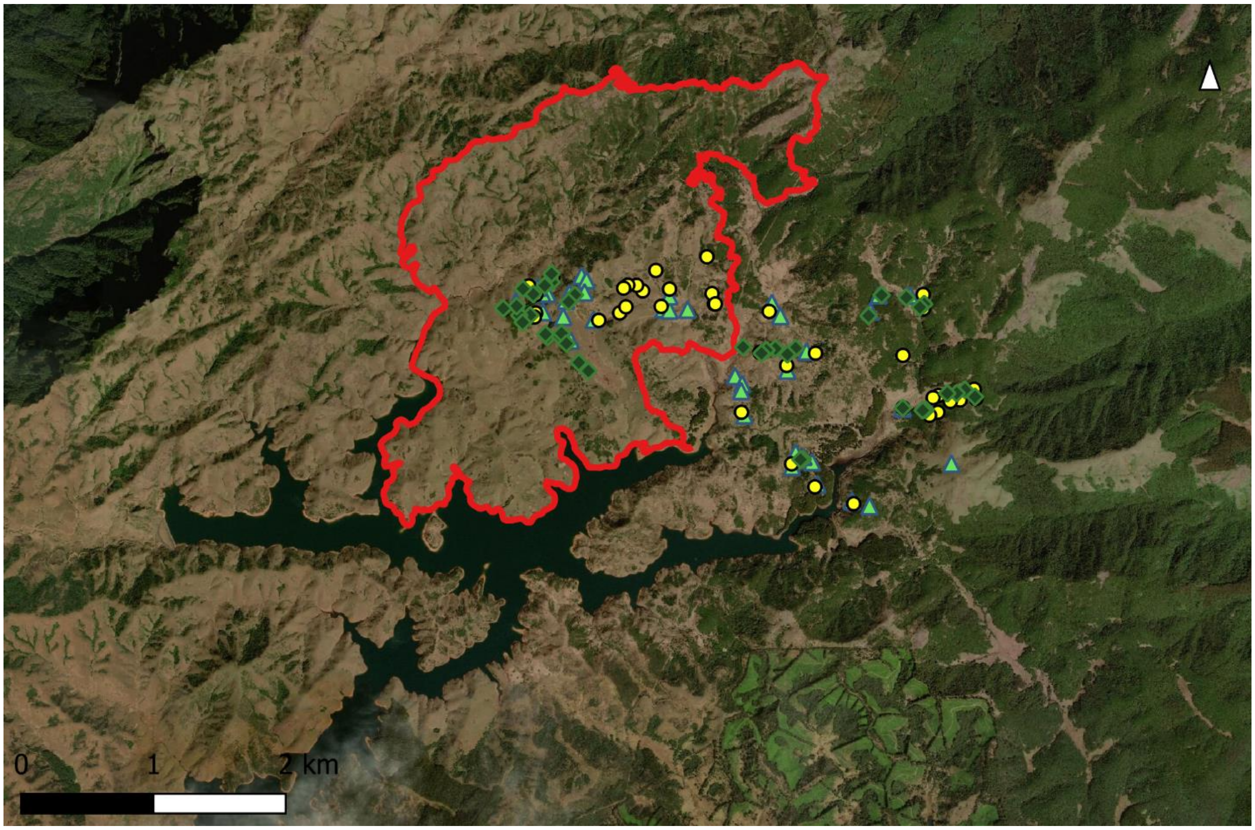
Supplement



S1- Figure 1. Sampling patches for recording post-fire adult mortality and coppicing The area within the red boundary is the burned area, and the coloured shapes are the invasive patches. The bright green triangles are the scotch broom patches, the deep green diamonds are the gorse patches and the yellow circles are wattle patches.



S2- Figure 2. Sampling locations for recording seedling abundance in burnt and unburnt (control) areas. The area within the red boundary is the burned area, and the coloured diamonds are the sampling grids in the grassland. The red dots are grids in the burnt sites and the blue dots are grids in the unburnt sites.



S3- Figure 3. Sampling patches for recording seedling abundance at the edges of invasive patches. The red area is the fire boundary, and the coloured shapes are the invasive patches. The bright green triangles are the scotch broom patches, the deep green diamonds are the gorse patches and the yellow circles are wattle patches.

S4- Image 1. Photograph of coppicing gorse stumps and regeneration from the seedlings. The arrow in the foreground points to a seedling of gorse and the arrow in the background points to a newly regenerated gorse individual from a burnt stump.

S5- Table 1. Table with estimates scotch broom (*Cytisus scoparius*) seedling abundance in grassland in burnt and unburnt areas, for the model #S ~ T + A + Sl + As + T×A + T×Sl (Number of scotch broom seedlings ~ treatment + number of scotch broom adults + slope + aspect + treatment×number of scotch broom adults + treatment×Slope). The values reported here are the coefficients (refer Appendix 2. Fig. 1.), from a Zero inflated Poisson model and the calculated mean values of the estimates of slope and intercept along with the inverse log transformed estimates and the standard errors. McFadden's pseudo $R^2 = 0.2257986$.

Measure	Estimate from the ZIP model	Std.Error from the ZIP model	Mean effect on number of seedlings ($e^{\wedge \text{Estimate}}$)	Std. Error ($e^{\wedge \text{Std. Error estimate}}$)	Pr(>|z|) (* - p value below .05)
Intercept	-0.7159	0.2262	0.488752	0.110556	0.0016*
Fire treatment	1.1518	0.2684	3.163883	0.849186	1.80E-05*
Scotch broom adult abundance	0.9226	0.1795	2.515823	0.45159	2.80E-07*
Slope	-0.0285	0.2238	0.971902	0.2175512	0.8988
Aspect	0.0792	0.1418	1.082421	0.153487	0.5768
Fire treatment × slope (interaction term)	-0.6184	0.3294	0.538806	0.177483	0.0605
Fire treatment × scotch broom adult abundance (interaction term)	0.8547	0.3763	2.350669	0.884557	0.0231*

S6- Table 2. Table with estimates black wattle (*Acacia mearnsii*) seedling abundance in grassland in burnt and unburnt areas, for the model #W ~ T + A + T×A (Number of black wattle seedlings ~ treatment + number of black wattle adults + treatment×number of black wattle adults). The values reported here are the coefficients (refer Appendix 2. Fig. 2.), from a Zero inflated Poisson model and the calculated mean values of the estimates of slope and intercept with standard errors from the ZIP (Zero Inflated Poisson model), along with the inverse log transformed estimates and the standard errors. McFadden's pseudo $R^2 = 0.207084$.

Measure	Estimate from the ZIP model	Std.Error from the ZIP model	Mean number of seedlings (e^$^{\text{Estimate}}$)	Std. Error (e^$^{\text{Std. Error estimate}}$)	$\text{Pr}(>\lvert z\rvert)$ (* - p value below .05)
Intercept	-2.1163	0.507	0.1204	1.6603	3.0E-05*
Fire treatment	1.118	0.445	3.0587	1.5604	0.014*
Wattle adult abundance	1.3526	0.259	3.8674	1.2956	1.7E-07*
Slope	-0.6780	0.399	0.5076	1.4903	0.0891
Aspect	0.6255	0.239	1.8691	1.2699	0.0087*
Fire treatment × Slope	0.38626	0.527	1.4714	1.6938	0.4599
Fire treatment × Wattle adult abundance	3.0910	1.036	21.999	2.8179	0.0028*

S7- Table 3. Table with conditionally averaged estimates for gorse (*Ulex europaeus*) seedling abundance in grassland in burnt and unburnt areas, for the top 5 models explaining gorse seedling numbers. The slope and intercept estimates with standard errors from the ZIP (Zero Inflated Poisson model) are reported in the table, along with the inverse log transformed estimates and the standard errors.

Measure	Estimate from the ZIP model	Std.Error from the ZIP model	Mean number of seedlings (e^$^{\text{Estimate}}$)	Std. Error (e^$^{\text{Std. Error estimate}}$)	$\text{Pr}(>\lvert z\rvert)$ (* - p value below .05)
Intercept	-7.7744	2.7889	0.00042036	0.001172	0.00543*
Fire treatment	1.1473	0.9583	3.14967729	3.018336	0.23235
Gorse adult abundance	1.822	0.5917	6.184214519	3.6592	0.00211*
Slope	-0.1878	0.9738	0.828780447	0.807066	0.84747
Aspect	1.5273	0.7749	4.605724563	3.568976	0.04934*
Fire treatment × Slope	-0.1845	1.046	0.83151994	0.86977	0.86038
Fire treatment × Gorse adult abundance	-0.964	0.6918	0.381364373	0.263828	0.16456

S8 - Table 4. Model estimates of seedling abundances at different distances from the edge from a breakpoint regression models. * indicate p values below .05

Predictors	Model estimate of effect sizes		
	Scotch broom	Black wattle	Gorse
Intercept	1.17 ± .26 *	0.17 ± .20	3.97 ± .56 *
Fire treatment	0.62 ± .12 *	2.91 ± .22 *	7.72 ±.44 *
Distance (inside)	0.16 ± .12	-0.21 ± .10 *	1.38 ±.28 *
Distance (outside)	-0.20 ± .17	0.15 ± .17 *	-0.68 ± .42 *
Distance (inside) × Fire Treatment	-0.08 ± .12 *	-0.64 ± .12 *	0.25 ± .31 *
Distance (outside) × Fire Treatment	-0.08 ± .17 *	-0.64 ± .18 *	-1.81 ± .44 *