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## Does soil seed bank diversity limit post-fire regeneration in small, fragmented, long-unburnt remnants of fire adapted vegetation?

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### ABSTRACT

Soil collected from 38 sites on Kangaroo Island in South Australia, containing small remnants of senescent *Eucalyptus cneorifolia*-dominated mallee, was subject *ex situ* to both smoke aerosol and heat treatment to simulate burning. Further soil from a subset of 29 of the sites was left untreated as a control. A total of 113 native plant species and 50 introduced species germinated across all sites. Fifty-three of the native plant species that germinated were absent in the above-ground vegetation, including twelve rare or threatened species, and three species previously unrecorded from Kangaroo Island. Fourteen native species and six introduced species germinated in heat plus smoke treated soil but not in untreated soil from the same sites. Non-metric multidimensional scaling ordination indicated differences in native species composition between sites with a long history of sustained livestock grazing (“grazed” sites) and largely ungrazed sites (“ungrazed” sites). On average, significantly more native species germinated from treated soil sampled from “ungrazed” sites than were found in the standing vegetation, while for “grazed” sites this difference was not significant. This indicates the greater potential for post-fire regeneration of native vegetation from the soil seed bank of ungrazed sites than from that of long grazed sites. Both “ungrazed” and “grazed” sites contained weeds in their soil seed banks, including some species which were stimulated by heat plus smoke. This indicated that competition from weeds is potentially a problem when fire is used as a management tool to regenerate senescent understoreys.

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### 1. Introduction

Increases in fire danger and unplanned fires are a likely consequence of climate warming in several regions of the globe, including southern Australia (Cary, 2002), necessitating an increased management response. Management or prescribed burning is an important and widely-applied tool used in the landscape-scale management of fire-prone ecosystems across the world, and as Penman et al. (2011) point out, management burning is commonly used to achieve two outcomes:— a reduction in fuel loads to mitigate the severity of unplanned wildfires (“fuel-reduction” burning), and a manipulation, protection or restoration of the status and composition of ecosystems (“ecological” burning). As the use of this management tool is likely to increase, it is important that we gain a better understanding of the consequences of management burning on the properties of ecosystems.

While high frequency management burning has been implicated in the decline of a number of plant species (Bradstock et al., 1997; Gill and Bradstock, 1995), the absence of fire can also result in reduced plant species diversity (Keith et al., 2002; Keith and Bradstock, 1994) due to processes such as competitive exclusion (Keith and Bradstock, 1994) and the need for fire for the recruitment of many understorey plant species (Auld and O’Connell, 1991; Keith et al., 2002; Orscheg and Enright, 2011). Management burning may be particularly useful for biodiversity conservation where clearance for agriculture has left scattered small remnants of native vegetation (Gill and Williams, 1996). In such agricultural landscapes, fires may no longer develop because of fire suppression and low fuel loads (Yates et al., 1994; Gill and Williams, 1996; Hobbs, 2003) and consequently plants in small remnants that rely on fire for recruitment may have few opportunities for regeneration (Yates and Ladd, 2005). Small remnants in heavily cleared agricultural landscapes are important since they often contain high concentrations of threatened plant communities (Davies, 1982, 1983, 1999) and plant species (Davies, 1986, 1992; Taylor, 2003). In their recent review of key research questions regarding the use of fire for biodiversity conservation, Driscoll et al. (2010) identified processes influencing the impact of fire regimes on biota as a major area requiring further study, and they

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also identified habitat loss and fragmentation as one of the three most important of such processes.

Effects of fire on vascular flora have been well documented in many forest communities in Australia (review in Gill and Catling (2002) and Vivian et al. (2008)) and elsewhere (e.g., USA; review in Keane et al. (2008)), and, to a lesser extent, in communities dominated by mallees (multi-stemmed *Eucalyptus* trees) in Australia (review in Bradstock and Cohn (2002), Bradstock et al. (2006) and Clarke et al. (2010)). However, fire research in Australia has largely centered on large, relatively unmodified areas of vegetation little affected by vegetation clearance or stock grazing, where large wildfires still occur relatively frequently. In such situations, burning has been found to increase the diversity of understorey plant species (Bradstock and Cohn, 2002) as long as fires are not too frequent. Conversely, there has been relatively little investigation of the effects of fire on small remnants in highly fragmented landscapes, where edge effects and surrounding land uses are important factors (Laurance, 2008). Where intensive, long-term grazing and fire exclusion have resulted in the loss of most plant species from the above-ground vegetation, regeneration of native vegetation communities is largely dependent on the survival of a healthy soil seed bank, and the ability of land managers to stimulate germination from this seed bank.

The current soil seed bank project aimed to establish a baseline set of data on the composition of soil seed banks at sites to be burnt as part of the Eastern Plain Fire Trial (EPFT), a large-scale fire ecology experiment being undertaken by the South Australian Department of Environment, Water and Natural Resources in conjunction with a large number of operational and research partners. The objective of the EPFT is to develop a better understanding of the role of fire for maintaining ecosystem diversity and health. It will involve conducting management burns at a variety of intensities in highly fragmented communities and measuring the *in situ* plant regeneration response.

The study presented here examines the pre-burn composition of the soil seed bank and the above-ground vegetation at each of the EPFT burn sites. It also investigates the response of the soil seed bank to the fire-related cues of heat and smoke in order to make some predictions about the likely response of the plant community to management burning events.

The following four key questions were addressed:-

- (1) Does a diverse and germinable native soil seed bank remain in the small and highly fragmented remnants of senescent mallee vegetation?
- (2) How does the plant species composition of the soil seed bank within small remnants of senescent mallee communities differ from that of the above-ground vegetation?
- (3) How does past, sustained livestock grazing affect the diversity of the germinable soil seed bank?
- (4) To what extent does the application of a simulated burning treatment stimulate the germination of seeds from the seed bank?

While extensive research has been undertaken into the effect of grazing on soil seed banks of rangelands (e.g., Bertiller, 1992; Kinloch and Friedel, 2005; Nichol et al., 2007; Kassahun et al., 2009) and grasslands (e.g., O'Connor and Pickett, 1992; Kratochwil et al., 2002; Márquez et al., 2002) around the world, the effects of grazing on the soil seed bank of small remnants of tree- or mallee-dominated vegetation surrounded by agricultural land is poorly known, despite such management practices being widespread in temperate regions around the world. Therefore, the results of the present study have broad application in the regeneration of small remnants of native vegetation in fragmented landscapes.

## 2. Material and methods

### 2.1. Site location and sampling

Kangaroo Island is Australia's second largest island after Tasmania and is situated off the coast of South Australia. It has a Mediterranean climate, with mean annual rainfall ranging from 500 to 900 mm (Burrows, 1979). The island consists predominantly of plains and plateaux infrequently incised by rivers and streams (Daily et al., 1979). Native vegetation over the majority of the island is dominated by mallees (multi-stemmed *Eucalyptus* trees) and has been extensively cleared for mixed wheat and sheep farming. In north-eastern Kangaroo Island, where the soil is most fertile (cracking clays and alkaline duplex soils; Northcote, 1979), only 16% of the original native vegetation remains following extensive clearance in the 1950s and 1960s (EPFT Working Group, 2008) despite this being one of the driest areas of the island. Remaining areas are mostly small and highly fragmented and have been isolated and not burnt for more than 30 years (Mowling and Barrett, 1981; EPFT Working Group, 2008). The area contains seven nationally threatened plant species (Davies, 1986, 1992, 1996; Bickerton and Davies, 2000; EPFT Working Group, 2008) and two threatened plant communities (*Eucalyptus cneorifolia*–*E. phenax* open-scrub and *Eucalyptus cneorifolia*–*E. rugosa* open-scrub over *Rhagodia candolleana*; Davies and Overton, 1998) which are potentially threatened in the longer term by fire exclusion. These communities are included in the Kangaroo Island Narrow-leaved Mallee (*Eucalyptus cneorifolia*) Eastern Plains Complex, a group of plant communities nominated for listing as nationally threatened ecological community under the Australian Government Environmental Protection and Biodiversity Conservation Act 1999 (Russell, 2009). It is of great conservation interest, therefore, to understand whether management burning can reverse the decline in species richness in these small remnants, as well as provide a management option that can be used for recovery of threatened plant species and communities at a landscape scale on Kangaroo Island and within comparable fragmented vegetation elsewhere.

Understanding soil seed banks is important since they are essential for seedling regeneration following fires and their composition may differ markedly from that of the above-ground vegetation. Data on the composition of both soil seed banks and above-ground vegetation were collected from 38 sites being studied as part of the EPFT (EPFT Working Group, 2008; Taylor, 2011a,b). All of these sites contained small patches (<5 ha) of native vegetation dominated by *Eucalyptus cneorifolia* (Kangaroo Island narrow-leaved mallee). At the time of the soil sampling and vegetation surveys, all sites had been unburnt for at least 20 years, some sites for over 70 years (S. Davidson pers. obs.; R. Davies pers. obs.). Twenty-four of these patches (sites) were isolated remnants in privately owned paddocks and had been accessible to sheep and/or cattle for at least 20 years (referred to as "grazed sites" hereafter). The remaining 14 sites ("ungrazed sites") were on fenced roadsides or quarry reserves, and therefore had not been exposed to prolonged periods of livestock grazing.

In each site, all plant species present in the above-ground vegetation were recorded from three 20 × 20 m<sup>2</sup> plots. This sampling was undertaken both in autumn (early March 2009) and spring (late September 2009) to cover a greater range of flowering times for different species, and results were combined for each site.

Soil sampling was undertaken in early March 2009. Twenty 1 × 1 m<sup>2</sup> quadrats were spaced at 2 m intervals around the perimeter of each above-ground vegetation sampling plot. Two 150 ml cores of soil (covering 30 cm<sup>2</sup> each) were extracted from within each of these quadrats. Only the top 5 cm of soil was collected since previous research (Auld and Denham, 2006; Auld and

O'Connell, 1991; Fisher et al., 2009; Wills and Read, 2007) has found that the majority of the soil seed bank lies above that depth. The forty samples from each treatment plot were then bulked and mixed, resulting in 6 l of soil per plot.

## 2.2. Fire-related soil treatment and glasshouse germination

Both heat and smoke are important in the regeneration of many south-eastern and south-western Australian plant species. We chose to combine both treatments since several previous studies (e.g., Auld and Denham, 2006; Morris, 2000; Read et al., 2000; Thomas et al., 2003; Tieu et al., 2001) have found synergistic effects on germination from treatment with both heat and smoke. We heated soil containing seed to 80 °C for 60 min since previous experimental studies (Auld and O'Connell, 1991; Kenny, 2000; Morris, 2000) have found that the optimum temperature range to stimulate germination in most species is between 80 and 100 °C, and at least 45 min is required to allow temperatures of 80 °C to penetrate into the center of a soil mass (Williams et al., 2005).

Soil from all plots and sites was subjected to a combined heat plus smoke treatment to simulate fire effects. For each plot, 2.1 l of the bulked and mixed soil was sieved through an 8 mm aperture mesh to remove large pieces of litter, and thoroughly mixed to distribute any seed evenly throughout the sample. The heat plus smoke treatment involved first placing soil in aluminum trays in an oven at 80 °C for 60 min with stirring after 30 min to ensure soil was evenly heated. The soil was then transferred to 30 cm × 36 cm seedling trays lined with 900 ml of washed sterile sand and then subjected to a cool smoke aerosol treatment in a PVC-framed plastic tent as described by Read et al. (2000).

At a subset of 29 sites, a further 2.1 l subsample of the bulked soil from one plot per site was similarly sieved and placed in a tray as a control. These control trays were not subjected to the heat plus smoke treatment. The soil from the remaining nine sites was used in a separate study (Rawson et al., 2012) which examined in more detail the effect of smoke and heat treatments, alone and in combination.

Germination was undertaken in a glasshouse to eliminate other effects which may prevent successful seedling regeneration, such as seedling predation and inadequate rainfall following germination. Trays were randomly positioned in a glasshouse on 2nd April 2009 and allowed to sit for one week following the heat plus smoke treatment before being watered by an automatic sprinkler system. Trays were watered for 5 min every day for the first week to saturate the soil, but this was subsequently reduced to 2 min a day or less, to ensure that the soil remained damp but not waterlogged. Trays were systematically rotated around the glasshouse once a week to reduce position effects. The germination experiment was run for 18 months, with seedlings identified and recorded for each tray on a monthly basis. To reduce competition between seedlings, plants were removed from each tray once sufficiently mature for identification to species level. Species were categorized as either native or introduced species in accordance with Barker et al. (2005, 2010). Although recognizing plant species as 'native' or 'introduced' can be problematic in the absence of palaeoecological data (Willis and Birks, 2006), this categorization is facilitated on Kangaroo Island by the island's recent European settlement (early 19th century), the lack of Aboriginal occupation for over 2000 years previous to this settlement (Lampert, 1979) and the predominance of Australian endemics in the flora.

## 2.3. Analyses

Differences between the composition and species richness of the germinable soil seed bank and above-ground vegetation were investigated using ordination and generalized linear mixed-models,

respectively. Ordinations were derived from matrices of dissimilarities based upon the presence or absence of species. The dissimilarities between the above and below-ground native species composition in the study sites were related to the grazing history of the sites using a non-parametric Mann–Whitney test. Effects of grazing history on germinable species richness were examined using mixed-model analyses in the “lme4” package (Bates and Maechler, 2010) of the R statistical system (R Development Core Team, 2010). In the latter analyses, sites were treated as a random grouping factor and numbers of species germinating in trays) were assumed to follow a Poisson distribution. In these analyses, germination data from treated soil from all 38 sites were used, with data from the three plots from each site being combined before statistical analysis.

Differences in species germination between heat plus smoke treated and untreated (control) soil samples were similarly analyzed using mixed models and the data from the 29 sites for which both control and treatment germination trays were available. However, this analysis used data from one plot per site, since control trays were not set up for the other two plots at each site.

## 3. Results

### 3.1. The nature of the germinable seed bank in fragmented remnants

A total of 113 native and 50 introduced plant species germinated from both the treated soil and control soil, over all 38 sites (Appendix S1). Of these, 104 native and 46 introduced species germinated from heat plus smoke treated soil. In comparison, 112 native and 45 introduced plant species were recorded from the above-ground vegetation at the same sites (Appendix S1).

Of the 166 native species recorded overall, the main lifeform classes were perennial shrub/subshrubs/twiners (45%), perennial forbs (19%), and annual/ephemeral forbs (15%; Table 1). In contrast, 37% of the 67 introduced species were annual/ephemeral grasses and 37% were annual/ephemeral forbs, with perennial shrubs comprising only 7% (Table 1).

A total of twenty species that are rare or threatened at the national, state or regional level (Barker et al., 2005; Willoughby et al., 2001) germinated from the treated and untreated soil (Appendix S1). Two of these taxa, *Olearia macrodisca* and *Spyridium eriocephalum* var. *glabrisepalum*, are listed as threatened under the Australian Government *Environmental Biodiversity and Conservation Act 1999*. Of note was the germination of the nationally endangered daisy *Olearia microdisca* from soil collected from two road reserves and one non-roadside remnant where the species previously was unknown. Only eight of the twenty significant species that germinated from soil were also found in the above-ground vegetation (viz., *Eutaxia diffusa*, *Prostanthera chlorantha*, *Epilobium billardierianum* subsp. *cinereum*, *Grevillea muricata*, *Lagenophora huegelii*, *Eucalyptus phenax* subsp. *compressa*, *Senecio quadridentatus*, *Spyridium eriocephalum* var. *glabrisepalum*; Appendix S1). However, a further four significant taxa were only found in the above-ground vegetation. One of these, *Xanthorrhoea semiplana* subsp. *tateana*, is a serotinous obligate seeder, while another, *Tricoryne tenella*, is able to survive fires as below-ground tubers. The remaining two, *Beyeria subsecta* and *Microlaena stipoides*, are perennials which rely on seed to regenerate following intense fires.

Three of the native species that germinated from soil treated with heat plus smoke were new records for Kangaroo Island, i.e. not listed as occurring on Kangaroo Island in the *Census of South Australian Plants* (Barker et al., 2005, 2010). These were all short-lived ephemeral species: the forb *Callitriche sonderi*, the grass *Lachnagrostis robusta* and the sedge *Isolepis congrua*. Of these, *Callitriche sonderi* germinated from the soil seed bank at only one site, a small remnant of vegetation which had a long history of grazing and fire exclusion (over 70 years). This site also contained the *Eucalyptus*

**Table 1**

Numbers of species in each lifeform class recorded (1) only from soil trays (SSB), (2) only from the above-ground vegetation (AG) or (3) from both.

Lifeform classes	Numbers of species (% of all native or introduced species recorded)			
	SSB only	AG only	SSB and AG	All records
<b>Native species</b>	<b>54 (33%)</b>	<b>53 (32%)</b>	<b>59 (36%)</b>	<b>166 (100%)</b>
Trees/mallees	0 (0%)	5 (3%)	2 (1%)	7 (4%)
Perennial shrubs/subshrubs/twiners	18 (11%)	24 (14%)	30 (18%)	72 (45%)
Perennial grasses	3 (2%)	1 (1%)	3 (2%)	7 (4%)
Perennial non-grass graminoids	5 (3%)	2 (1%)	2 (1%)	9 (5%)
Perennial forbs	7 (4%)	14 (8%)	11 (7%)	32 (19%)
Annual/ephemeral grasses	4 (2%)	0 (0%)	0 (0%)	4 (2%)
Annual/ephemeral non-grass graminoids	7 (4%)	1 (1%)	2 (1%)	10 (6%)
Annual/ephemeral forbs	10 (6%)	6 (4%)	9 (5%)	25 (15%)
<b>Introduced species</b>	<b>22 (33%)</b>	<b>17 (25%)</b>	<b>28 (42%)</b>	<b>67 (100%)</b>
Perennial shrubs	0 (0%)	3 (4%)	2 (3%)	5 (7%)
Perennial grasses	1 (1%)	0 (0%)	1 (1%)	2 (3%)
Perennial forbs	3 (4%)	3 (4%)	1 (1%)	7 (10%)
Annual/ephemeral grasses	8 (12%)	6 (9%)	11 (16%)	25 (37%)
Annual/ephemeral graminoids	2 (3%)	0 (0%)	1 (1%)	3 (4%)
Annual/ephemeral forbs	8 (12%)	5 (7%)	12 (18%)	25 (37%)

*cnorifolia*–*Eucalyptus phenax* open-scrub vegetation community which is endemic to Kangaroo Island where it is considered to be threatened (Davies and Overton, 1998; Davies, 1999). *Lachnagrostis robusta* similarly only germinated from soil from one site, while *Isolepis congrua* germinated from soil from a wide range of sites. None of these three species was recorded from the above-ground vegetation.

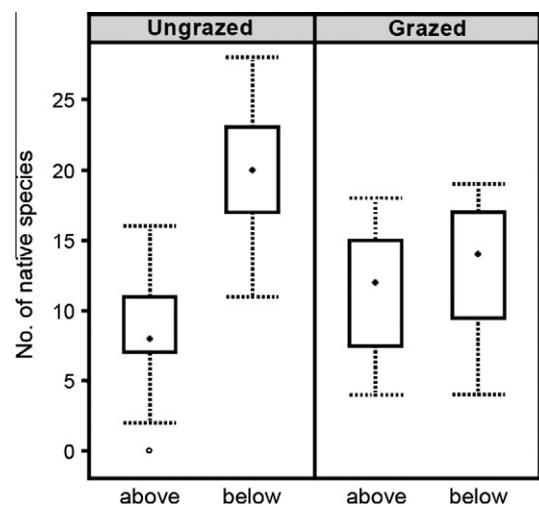
### 3.2. Comparisons of above- and below-ground diversity

Excluding eight specimens for which identification to species level was not possible due to lack of fertile material, 53 native species and 22 introduced species germinated from treated or control soil from at least one site but were not found in the above-ground vegetation at any of the sites (Appendix S1). Of these, 18 native species and nine introduced species germinated at 10% or more of sites (Appendix S1). Conversely, twelve native species and four introduced species occurred relatively frequently (>10% of sites) in the above-ground vegetation but were absent in the germinable soil seed bank (Appendix S1). Despite differences in species composition, relative proportions of species within most lifeform classes did not differ markedly between the above-ground vegetation and the soil seed bank (Table 1). The greatest difference was for annual/ephemeral non-grass graminoids and grasses, with over four times more species occurring in the soil seed bank than in the above-ground vegetation (Table 1).

### 3.3. Influence of livestock grazing history on germinable soil seed bank diversity

Across sites, differences between the numbers of native and introduced species germinating from treated soil, compared with numbers recorded from the above-ground vegetation, varied according to the past stock grazing history of the site.

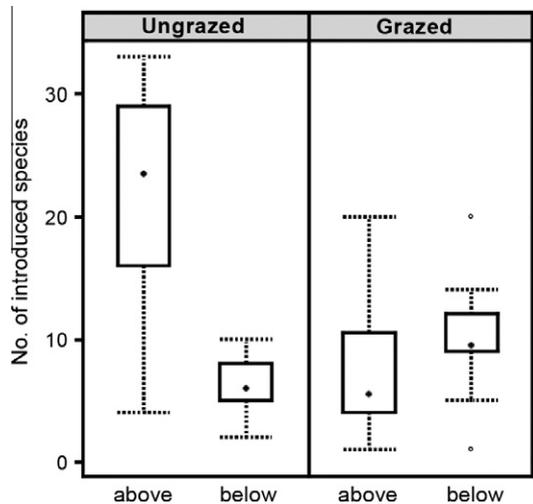
In sites that were long-ungrazed (“ungrazed” sites), an average of 20.1 native species germinated from the heat-and-smoke treated soil samples, whereas an average of 8.3 was found in the above-ground vegetation (Fig. 1). However, in sites which had a long history of livestock grazing (“grazed” sites), the average number of native species germinating from the treated soil samples (12.9) was similar to that recorded from the above-ground vegetation (11.2, see Fig. 1). The relatively greater disparity in “ungrazed” sites was reflected in a highly significant interaction between position (above or below-ground) and grazing history in the mixed-model analysis ( $z = -5.4$ ,  $P < 0.001$ ; Fig. 1).



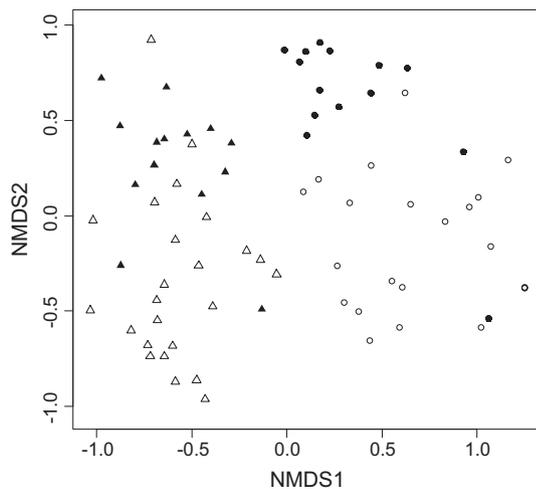
**Fig. 1.** Comparison of above-ground native species richness (“above”) with germinable soil seed bank species richness (heat plus smoke treated soil; “below”), at “ungrazed” sites and “grazed” sites (sites with a long history of sustained grazing).

In contrast, the average number of introduced species per site germinating from treated soil samples in the “ungrazed” sites (6.1) was considerably lower than the average number found in the above-ground vegetation (21.6; Fig. 2). As was the case for the native species, the average number of introduced species germinating from the heat plus smoke treated soil samples in the “grazed” sites (9.8) was higher than that found in the corresponding above-ground vegetation (7.2; Fig. 2) and again, the relative disparity in above-ground and below-ground counts in “grazed” and “ungrazed” sites was reflected in a highly significant interaction in the mixed-model analysis ( $z = 9.91$ ,  $P < 0.001$ ; Fig. 2).

As well as the above differences in species richness values, we also found significant differences in native species composition between “grazed” and “ungrazed” sites. This was found when species presence and absence data from heat plus smoke treated soil from all 38 sites was subjected to non-metric multidimensional scaling (NMDS) ordination analysis. A plot of ordination results (Fig. 3) shows distinct clustering of native species scores depending on whether they were recorded from (1) above-ground vegetation compared with the germinable soil seed bank, and (2) “grazed” compared with “ungrazed” sites.



**Fig. 2.** Comparison of above-ground introduced species richness (“above”) with germinable soil seed bank species richness (heat plus smoke treated soil; “below”), at “ungrazed” sites and “grazed” sites (sites with a long history of sustained grazing).



**Fig. 3.** Results of NMDS ordination analysis of presence and absence data for native species in Kangaroo Island Eastern Plains Fire Trial sites. Comparison of species composition of above-ground vegetation (AG); and heat plus smoke treated soil from the same sites (SSB) in grazed and “ungrazed” sites (○ = grazed AG, ● = “ungrazed” AG, △ = grazed SSB, ▲ = “ungrazed” SSB).

Jaccard dissimilarity coefficients were calculated between the above-ground and below-ground native plant communities in each site using data on species presences and absences. The median dissimilarity between above-ground and below-ground native plant communities was significantly greater in “grazed” sites (0.92) than in “ungrazed” sites (0.80; Mann–Whitney rank sum test,  $Z = -2.10$ ,  $P < 0.04$ ).

#### 3.4. Effects of heat and smoke treatment on soil seed bank germination

There were 29 sites for which paired treatment and control trays were available (from a single plot within each site). Of these 29 sites, only six were “ungrazed” and due to this small sample size, and because a companion paper (Rawson et al., 2012) focussed on response to fire-related cues in “ungrazed” sites, further analyses of the effects of burning in this paper are restricted to the 23 “grazed” sites. For these sites, the average number of native species germinating from soil treated with heat plus smoke (6.0)

was not significantly different than that from untreated soil (5.7,  $z = 0.30$ ,  $P = 0.76$ ). Similarly, the mean number of introduced species germinating from treated soil (4.7) was not significantly different than that for control trays (4.0,  $z = 1.2$ ,  $P = 0.23$ ).

Species composition differed between heat plus smoke treated trays and control trays. Of the 79 native species germinating in experimental trays of soil from “grazed” sites, 14 species germinated only in trays treated with heat plus smoke, while 11 species germinated only in control trays. The remaining 54 species (68%) of these native species germinated from both treated and untreated soils. Of the 40 introduced species, six species were only present in heat plus smoke treated trays while eight were only present in control trays.

The responses of individual species to the treatments are presented in Appendix S1. Over all such trays, 71% of species germinated from both treated and untreated soil. While the remaining species only germinated under one treatment, the majority occurred at low frequencies (1–2 trays) and often as single plants, making interpretation of results difficult. Exceptions were *Ixodia achillaeoides* subsp. *alata* and *Pultenaea tenuifolia* which were absent from control trays despite several plants occurring in a number ( $\geq 4$ ) of comparable treatment trays.

## 4. Discussion

### 4.1. Soil seed bank limitations to native regeneration following fire

Previous studies (e.g., Bossuyt et al., 2006) have found that a dominant overstorey in the absence of disturbance can lead to a loss of species from the soil seed bank. While our study indicated such an effect for long-unburnt, heavily-fragmented remnants of *Eucalyptus cneorifolia* dominated mallee communities, it also illustrates the potential value of undertaking regeneration burns in such areas despite some attrition of the soil seed bank through senescence. One hundred and thirteen native species germinated from soil collected from the 38 sites studied, including twenty species which were rare or threatened at the national, state or regional level and three native species not previously recorded from Kangaroo Island (Appendix S1). While a similar number (112) of species were recorded from the above-ground vegetation at these same sites, the species composition of the seed bank and the above-ground vegetation differed, as shown by the ordination analysis (Fig. 3). Forty-eight percent (53) of the species recorded from the soil seed bank were not observed in the above-ground vegetation, including twelve of the rare or threatened species and all three of the new records for Kangaroo Island. This is a greater disparity than those observed in other southern Australian studies. For example, Wills and Read (2002, 2007) found 32% and 25%, respectively, of heathland seed bank species to be absent from the above-ground vegetation, while Hill and French (2003) found a comparable figure of only 15% for a woodland community. Our data indicate both the degree to which *Eucalyptus cneorifolia* suppresses the understorey in the long-term absence of fire and also the longevity of some components of the soil seed bank under mallee. Long-lived soil seed banks have also been found in other eucalypt-dominated communities in temperate Australia (e.g., jarrah forest in Western Australia unburnt for 22 years; Koch et al., 2009). Despite the findings of previous researchers (e.g., Orscheg and Enright, 2011) that obligate seeders that require disturbance to break seed dormancy are particularly vulnerable to long-term fire exclusion, we found a number of such species (e.g., *Eutaxia* spp., *Pultenaea* spp., *Dillwynia hispida*, *Daviesia arenaria*, *Kennedia prostrata*) germinating from long-unburnt sites (20+ years) where these species had disappeared from the above-ground vegetation.

The way which a vegetation community responds to a disturbance event such as fire is dependent on how its component

species: (1) persist during the disturbance event or colonize after the event; and (2) persist and reach maturity post disturbance (Noble and Slatyer, 1980). It is also dependent on the timing of critical life history events of these species. Noble and Slatyer (1980) referred to these attributes as Vital Attributes and used them as basis for classifying species into Species Types according to their response to disturbance. Our findings confirmed the existence of four of the Species Types described in Noble and Slatyer (1980) and Hobbs et al. (1984). We found 53 native species and 22 introduced species which were in the soil seed bank but absent from the above-ground vegetation. Similar to the findings of Hobbs et al. (1984), we found that the majority (98%) of these native species were examples of Type S Species (species with long viability, stored in the soil) while only a small number (2%) were Type D species (had widely dispersed seeds, e.g. *Senecio quadridentatus*, *Lachnagrostis* spp.). In contrast, we found twelve native species which were relatively frequent in the above-ground vegetation ( $\geq 10\%$  sites; Appendix S1) but which germinated neither from the treated nor from the untreated soil. Five of these species were examples of Type V species, viz. species which have plant parts which are capable of surviving fires and recovering by vegetative growth. These consisted of perennial trees (*Eucalyptus* spp.), shrubs (*Melaleuca* spp., *Xanthorrhoea semiplana* subsp. *tateana*) and forbs with perennial tubers (*Drosera* spp., *Pterostylis nana*). A number of the species absent from the soil seed bank were examples of Type C Species (also called serotinous obligate seeders), viz. species having seeds with short viability which survive fires within protective fruits or cones. These included *Petrophile multisepta*, *Xanthorrhoea semiplana* subsp. *tateana* and some *Eucalyptus* and *Melaleuca* species.

Previous research (Gosper et al., 2010) has similarly found serotinous obligate seeders to be poorly represented in the soil seed bank and therefore dependent on the survival of individuals in the above-ground vegetation to enable seedling recruitment after fire. Thus, the absence in the above-ground vegetation of the senescent sites we surveyed of several serotinous obligate seeders (e.g., *Hakea rugosa*, *Melaleuca gibbosa*) recorded as common in healthy *Eucalyptus cneorifolia* dominated communities in previous surveys (Davies, 1996; Davies and Overton, 1998; EPFT Working Group, 2008) is a matter of concern. As also found by previous researchers (e.g., Hill and French, 2003; Read et al., 2000), eucalypts were also poorly represented in the soil seed bank but this is of less concern since these species generally persist in senescent vegetation unless killed by diseases such as *Phytophthora*.

The paucity we found of certain perennial species in the soil seed bank, compared with the seed of annual forbs and grasses, has been observed by a number of previous researchers (e.g., Chaideftou et al., 2009; Clarke and Dorji, 2008; Hill and French, 2003; Pettit and Froend, 2001; Shen et al., 2007). This particularly applies to overstorey species and has been attributed to the short-lived nature of the soil-borne seed of some perennial species (Auld, 1995; Auld et al., 2000) and higher rates of animal predation of seed of overstorey species (Shen et al., 2007). As in our study, some previous research (e.g., Dutoit and Alard, 1995) has found late-succession perennial species to be more often absent in the soil seed bank, compared with early succession short-lived species which rely more on a persistent soil seed bank as part of their opportunistic strategy. However, where perennial species are present in the above-ground vegetation, their absence from soil seed banks does not limit their ability to regenerate after fire since many such species are able to regenerate by re-sprouting (Vivian et al., 2009; Wills and Read, 2007).

#### 4.2. Effect of grazing history on soil seed bank

We found marked differences in the floristic composition of soil seed banks of grazed and ungrazed sites (Fig. 3), as have a number

of previous researchers (e.g., Chaideftou et al., 2009; Cooper, 2006; Kinloch and Friedel, 2005; Márquez et al., 2002; Nichol et al., 2007). This pattern has been attributed by some researchers to the seed banks of some species disappearing or decreasing with grazing (Jutila and Heli, 1998; Kassahun et al., 2009) due to the death of individual plants or reduction in flowering or seeding (Kratochwil et al., 2002). This particularly applies to some species of perennial grasses (Bertiller, 1992; O'Connor and Pickett, 1992). Conversely researchers have also found the soil seed bank of other species to increase with grazing (Bertiller, 1992, 1996; Erkkilä, 1998; Kassahun et al., 2009) in particular disturbance adapted species, such as weeds (Clements et al., 2007) and many annual species (Zhao et al., 2001). Our findings suggested that native species in ungrazed sites had much greater potential to regenerate from the soil seed bank following fire than those in grazed sites, while the reverse was true for weeds. At ungrazed sites, significantly more native species germinated from treated soil samples than were found in the associated above-ground vegetation, while for grazed sites we found no significant differences. Conversely, Marage et al. (2006) found fewer species in the soil seed bank than in the above-ground vegetation of ungrazed forest, but the reverse situation in grazed forest. We also found floristic differences between the soil seed bank and above-ground vegetation (Fig. 3), in both grazed and ungrazed sites as was found by Chaideftou et al. (2009) in European forests. In contrast, researchers of other vegetation communities (e.g., grasslands; Zhan et al., 2007) have found that plant species abundance and composition in the soil seed bank was similar to the corresponding above-ground vegetation regardless of grazing pressure.

Unlike some other vegetation communities (e.g., some grasslands; Jacquemyn et al., 2011) that require grazing disturbance to maintain native species diversity, a long history of grazing may cause irreversible changes to the above-ground and below-ground species composition in senescent mallee vegetation. In such cases, the vegetation is unlikely to return to a formerly diverse state following regeneration burns, and a different type of management intervention, such as the reintroduction of understorey species from similar adjacent areas, may be necessary.

#### 4.3. Effect of heat and smoke on individual species

We found no significant difference between numbers of native species germinating from heat plus smoke treated soil and untreated soil collected from grazed sites. These findings contrast with those of an allied study of ungrazed sites containing the same communities on Kangaroo Island (Rawson et al., 2012) which found significantly more native species germinating from heat plus smoke treated soils compared with untreated soils. Hill and French (2003) and Wills and Read (2007) similarly found significantly higher numbers of native species germinating from heat treated soils collected from ungrazed heathlands and woodlands in south eastern Australia.

Nevertheless, we did find differences in floristic composition and evidence that at least two native species are largely fire dependent for seed germination. These species, the legume *Pultenaea tenuifolia* and the composite *Ixodia achillaeoides* subsp. *alata*, were absent from all control trays, despite germinating in treated trays from seven and nine sites respectively. These finding agree with previous research that has found heat and/or smoke treatment significantly increases germination of *I. achillaeoides* and legumes (Enright et al., 1997), the latter family being particular responsive to heat shock (Bell, 1999). While another twelve native species germinated only in heat plus smoke treated trays, these results must be interpreted with caution since all occurred at low densities and frequencies as did eight native species which germinated only in control trays.

A relatively high proportion (82%) of native species germinated in the absence of heat plus smoke. This proportion is higher than that found in other south-eastern Australian studies, which have found germination rates of between 36% and 50% (Auld and Denham, 2006; Enright et al., 1997; Wills and Read, 2002). The higher percentages in the current study may be due to two factors. Firstly, the sites studied have been undisturbed for several decades so the soil seed bank is likely to be old. Previous research (Morrison et al., 1992) has found reduced levels of dormancy in older seed, this being attributed to factors such as the breakdown over time of impervious seed coats and the leaching of chemicals which inhibit germination (Baskin and Baskin, 1998). Alternatively, the sieving process used to remove litter and break up soil clumps during the current experiment may have resulted in partial scarification of seed coats, facilitating germination.

#### 4.4. Potential for weed invasion following regeneration burns

We recorded 67 introduced plant species from the 38 sites studied either in the soil seed bank or in the above-ground vegetation (Tables 1 and Appendix S1). This was despite sampling being undertaken away from the edges of the native vegetation remnants. As with other studies (e.g., Hill and French, 2003) we found a number of introduced species (five herbs and four grasses and graminoids) not present in the above-ground vegetation but occurring relatively frequently ( $\geq 10\%$  of sites) in the soil seed bank. Increased competition from weeds can be a problem when using fire to manage degraded native vegetation since introduced species can dominate the soil seed bank (Fisher et al., 2009) and the increased nutrient levels and reduced competition from natives after fire can enable weeds to germinate and grow rapidly (Dixon et al., 1988; Hitchmough et al., 1994; Davies, 2000; Fisher et al., 2009). This is particularly the case with small isolated fragments of native vegetation since their high perimeter-area ratios increase the overall impact of edge effects such as “weed rain” and fertilizer drift from surrounding agricultural land (Ewers and Didham, 2006; Lienert, 2004). The present results indicate that competition from weeds is potentially a problem where fire is being used to regenerate senescent understoreys in small remnants of native vegetation.

We found that the relationship between above-ground and soil seed bank introduced species richness differed significantly between “grazed” sites and “ungrazed” sites. Ungrazed sites had on average significantly more introduced species in the above-ground vegetation than grazed sites (Fig. 2). This possibly reflects the closer proximity of ungrazed sites to roads. Previous researchers (e.g., Meunier and Lavoie, 2012) have found that roads function as suitable habitats and corridors for invasive plant species and can contribute significantly to the spread and establishment of weeds into native vegetation. This may explain why we found fewer introduced species in the above-ground vegetation at grazed sites which were mostly located away from roadsides.

We found no significant difference in mean numbers of introduced species germinating from heat plus smoke treated soil compared with control trays despite previous studies finding fire reducing the abundance of some introduced species (e.g., for *Briza maxima*; McMahon, 1991). While our results applied only to grazed sites, similar results were found for comparable ungrazed sites in an allied study (Rawson et al., 2012). However, our results strongly suggest that fire is likely to stimulate germination of some specific weed species. Nine introduced species not found in the long-unburnt above-ground vegetation germinated relatively frequently from heat plus smoke treated soil ( $\geq 10\%$  of sites; Appendix S1). Previous studies (e.g., Lunt, 1990; Prober and Thiele, 1996; Contreas et al., 2011) have found germination of introduced legumes and grasses to be particularly stimulated by burning. The present study found similar effects for introduced legumes in grazed mallee

vegetation. Of the five introduced legumes that were recorded relatively frequently ( $\geq 10\%$  of sites; *Trifolium cernuum*, *T. glomeratum*, *T. subterraneum*, *T. suffocatum*, *T. arvense*), all germinated from heat plus smoke treated soil from a number of sites where they were absent in the above-ground vegetation (Appendix S1). The situation with introduced grasses was more complex. While three of the eight frequently encountered introduced annual grasses (*Aira elegantissima*, *Polypogon maritimus*, *P. monspeliensis*) germinated from heat plus smoke soil from more sites than they occurred in the above-ground vegetation, the reverse situation applied to the other five species (*Ehrharta longiflora*, *Lolium rigidum*, *Poa infirma*, *Vulpia bromoides* and *Lagurus ovatus*; Appendix S1).

#### 4.5. Conclusion

While the present study indicated the value of undertaking management burns to regenerate the native understorey of small, highly-senescent and fragmented remnants of fire adapted vegetation, it also indicates the risk of competition from weeds following burns, especially by introduced species for which germination is stimulated by fire. Our study showed that a large diversity of species, including rare and threatened plants, may survive in the soil seed bank, despite being absent in the above-ground vegetation. However, the persistence of these species in the field following a regeneration burn will likely depend on numerous factors including the season and intensity of the burn, competition with weeds, interactions with herbivores and pollinators, and rainfall. As has been found with other studies (e.g., Roura-Pascual et al., 2009), our finds indicate that weed management needs be a prime consideration when planning regeneration burns. An important consideration is the timing of burns since previous research (Potts and Stephens, 2009) has found that this can have a significant effect on non-native annual grass germination. The influence of these factors on post-fire survival of regenerating native vegetation will be the subject of future papers from this group.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.08.013>.

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