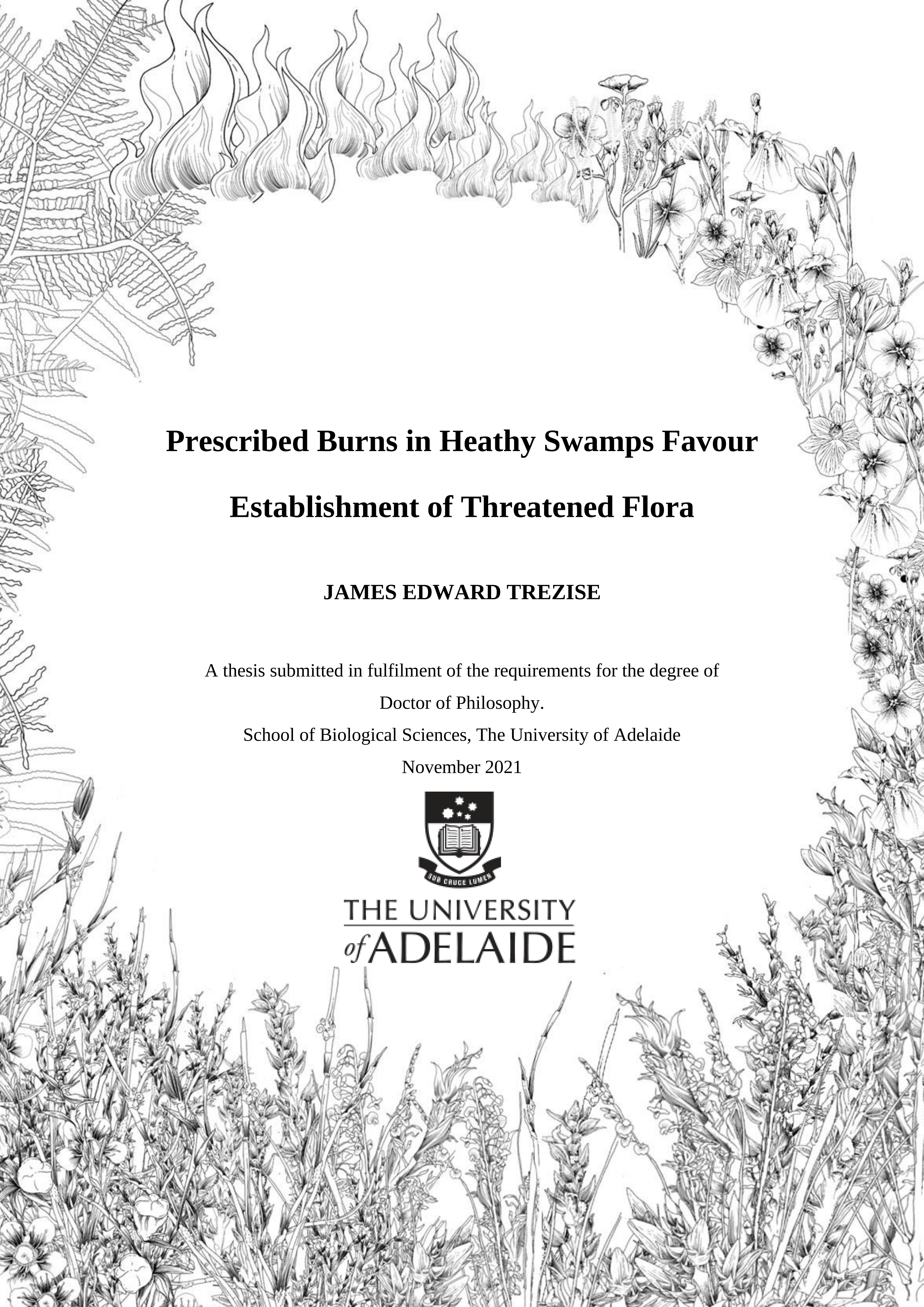

Prescribed Burns in Heathy Swamps Favour Establishment of Threatened Flora

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A thesis submitted in fulfilment of the requirements for the degree of
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Published work included in the thesis

Chapter 3 is the only published chapter related to this thesis. All other chapters are in publication style but have not yet been submitted. Chapter 3 was published in Austral Ecology and can be found online at: https://doi.org/10.1111/aec.12957

Trezise J. E., Facelli J. M., Paton D. C. & Davies R. J.-P. (2021) The effect of heat and smoke on the soil seedbanks of heathlands on permanent freshwater swamps. *Austral Ecology* **46**, 39-51.

Abstract

Long fire-free periods cause heathy swamps to transition into late-successional age classes which are characterised by low species richness and a depauperate understorey. The majority of the critically endangered heathy swamps on the Fleurieu Peninsula are long unburnt and lack 'disturbance dependent' flora, prompting programs to burn some of the long unburnt vegetation. This thesis investigates the utility of fire as a management tool in heathy swamps. I first assessed the influence of heat and smoke on *ex situ* seedling emergence from soil samples. Then, I investigated the seed dormancy mechanisms of a critically endangered species in response to fire cues. Lastly, I conducted experimental burns to evaluate *in situ* plant recovery as a result of fire seasonality and herbivory.

Seedling emergence from the soil samples indicated that fire facilitates the regeneration of threatened ground-stratum natives, including promoting seedling emergence, suppressing competition from dominant species, and providing these threatened ground-stratum natives with opportunities to replenish their seedbanks. Of particular importance, seedling emergence of native shrubs and subshrubs more than doubled with the fire treatment, including the critically endangered *Hibbertia tenuis* which increased 18-fold. By investigating the dormancy mechanisms of *H. tenuis* I then found that germination was negligible without smoke. Prescribed burns were then employed, which initiated a transient successional period with reduced overstorey cover, promotion of the understorey, and increased species richness (7.4 vs 4.5 species m^{-2} in unburnt controls). Within the long-unburnt heathy swamps, 29 % of plant species appearing after burning were absent from the above ground biomass. These plants depend on fire to re-appear above ground, grow, reproduce and replenish their propagule reserves. Populations of *H. tenuis* were declining in the absence of fire and were restricted to a population of 20 plants but have increased to nearly 600 plants since the experimental burns.

The decline of many Fleurieu Peninsula swamp species can be attributed to an imbalance of age classes in the landscape, given that approximately 98 % of the swamps are likely in late-successional stages. With infrequent burning, native ferns and taller shrubs outcompete threatened ground-stratum plant species. I argue that for fire-dependent species, such as *H. tenuis*, local extinctions will occur if the time between fires is greater than the lifespan of the species in both the above- and below-ground vegetation. However, despite potential benefits of prescribed burns, herbivory and fire seasonality can have negative implications for recovery. Herbivory negatively impacts recovery after fire by excluding 12 % of species and slowing the recovery of many others. Native species also had opposing seasonal fire preferences, such that fire in any given season may benefit one species to the detriment of another. In heathy swamps, this thesis supports the utility of prescribed burns for maintaining a balanced spectrum of age classes, but also highlights the importance of mitigating herbivory and considering the effects of fire seasonality.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Front outside cover illustration Anjali Singh.
Front inside cover photo Tim Vale.
Back inside and outside cover photos James Trezise.

Chapter 1. General Introduction

Fire acts as an evolutionary force and disturbance mechanism in flammable ecosystems (Bird *et al.* 2008; Bowman *et al.* 2009; Bradstock *et al.* 2002). Composition of these systems depends on their fire regime, which is the historic pattern of fire season, frequency, severity, intensity, influence and spread within an area (Bond and Keeley 2005; Gill 1975; Gill and Allan 2009). However, with increasing human activity, fire regimes are changing (Bowman *et al.* 2011; Marlon *et al.* 2008; Underwood *et al.* 2009). In Australia, European fire regimes recently (~230 years ago) and abruptly replaced indigenous fire regimes (i.e. aboriginal burning), which previously existed for a period of approximately fifty-thousand years (Bird *et al.* 2008; Bond and Van Wilgen 1996; Bowman *et al.* 2009; Bradstock *et al.* 2002). Dramatic changes to fire regimes, such as in Australia, have negative implications for biodiversity (Keeley and Brennan 2012; Morrison *et al.* 1996; Morrison *et al.* 1995; Quintana-Ascencio *et al.* 2003). For instance, fires which occur too frequently can exhaust seedbanks and resprouting potential (Auld and Denham 2006; Clarke *et al.* 2013; Odion and Tyler 2002), while fires which do not occur frequently enough can lead to senescence and seedbank expiration (Bradstock *et al.* 1995; Lawson *et al.* 2010; Vaughton 1998). Changes to fire seasonality also negatively affect vegetation, as many species have adaptations which are linked to a particular season (e.g. seed dormancy; Jasinge *et al.* 2018; Miller *et al.* 2019; Ooi 2019).

Plants prone to fire have evolved two distinct adaptation types: resprouting (i.e. apical resprouters, epicormic resprouters, geoxyles or geophytes) and seeding (i.e. germination from soil- or canopy-seedbanks), which enables them to survive in fire-prone landscapes (Burrows 2013; El-ahmir *et al.* 2015; Hunter 2003; Keith *et al.* 2002; Pausas and Keeley 2014). Species can rely on one (obligate) or both (facultative) of these methods (Keeley 1986; Pausas and Keeley 2014; Prior and Bowman 2020). For example, species of *Banksia* tolerate fire by protecting seeds in woody canopy fruits which insulate against extreme surface temperatures (> 500 ^{o}C; Huss *et al.* 2019). While soil seedbanks are important for the maintenance of short-lived understorey species that senesce or are outcompeted in the absence of disturbance. For these latter species, the soil seedbank provides a refuge during those above-ground absences (Bond and Keeley 2005; Peterson and Reich 2008; Sparks *et al.* 1998).

In flammable ecosystems, species with soil seedbanks commonly have seed dormancy mechanisms which sense fire (Rawson *et al.* 2013; Staden *et al.* 2000; Thomas *et al.* 2003) because fire is associated with favourable conditions for establishment (Bond and Keeley 2005; Ooi *et al.* 2004; Rocha *et al.* 2015). Species with fire-related seed dormancies commonly rely on physical or chemical cues (e.g. heat or smoke) to break dormancy (Bolin 2009; Jusaitis 1993; Staden *et al.* 2000; Thomas *et al.* 2003; Van Staden *et al.* 2004; Williams *et al.* 2003). Many species also depend on indirect cues related to the combustion of biomass which reduces competition (e.g. temperature stratification or photoperiod; Baskin *et al.* 2008; Hidayati *et al.* 2000; Kettenring and Galatowitsch 2007; Pons 2000; Rokich and Bell 1995; Roy and Arianoutsou-Faraggitaki 1985). Seeds can form persistent soil seedbanks in the absence of these dormancy breaking cues (Bond and Keeley 2005; Bond and Van Wilgen 1996; Brown and Smith 2000; Keeley and Fotheringham 2000a). However, there is a time limit as to how long these seedbanks can persist, with seed half-lives ranging from days to years (Holmes and Newton 2004; Keith *et al.* 2002; Merritt *et al.* 2014).

The success of burning as a restoration tool requires an understanding of soil seedbanks (Ferrandis *et al.* 1999; Penman and Towerton 2008; Pyke *et al.* 2010). The composition of soil seedbanks can be assessed with a variety of methods, including seed counts in soil samples (e.g. Gonzalez and Ghermandi 2012; Mesgaran *et al.* 2007; Price *et al.* 2010), seedling emergence counts from soil samples (e.g. Boedeltje *et al.* 2002; Erfanzadeh *et al.* 2020; Trezise *et al.* 2021), or seedling emergence counts in the field (e.g. Ooi *et al.* 2004; Pavlik *et al.* 1993; Shay *et al.* 2001). These approaches can be used in ecological assessments to estimate the plants likely to re-establish post fire from seedbanks (Boedeltje *et al.* 2002; Cochrane *et al.* 2007; Rawson *et al.* 2013). However, these approaches produce inconsistent results when directly compared to each other (Cardina and Sparrow 1996; Mahé *et al.* 2020; Mesquita *et al.* 2013) and the factors which impact these differences are poorly understood. This limits the certainty of results sourced using these methods in fire-related environmental assessments.

Assessing the impact of fire cues on the dormancy of individual species is also important and can be conducted in a laboratory setting to isolate specific pathways and relationships to environmental conditions (Liyanage and Ooi 2017; Mackenzie *et al.* 2016; Ooi *et al.* 2014). This information can be used to optimise seedling propagation and to inform the prescription of control burns (Bradstock and Auld 1995; Erickson 2015; Penman and Towerton 2008). This is especially important for endangered species which have both a limited supply of seed and complex dormancy requirements. For example, propagation of seedlings for the nationally critically endangered *Hibbertia tenuis* has been severely limited, given that the germination rate of untreated seeds is 2 % and there are only twenty individuals left to source seed from.

Fire dependence for an ecosystem (or a constituent species) can be defined as the requirement for fire to provide the conditions necessary for persistence (e.g. obligate pyrogenic dormancy; Liyanage and Ooi 2017), which cannot otherwise be provided sustainably or realistically by any other disturbance mechanism (Ames *et al.* 2017; Hoffmann and Moreira 2002; Ooi *et al.* 2014). Slashing and other mechanical treatments can be used to reduce fuel loads in a similar capacity to controlled burning (Howard *et al.* 2020; McIver *et al.* 2013; Volkova and Weston 2019), but this lacks ecologically important fire-related cues needed for the seeds of many plants to germinate (e.g. heat and smoke). Furthermore, controlled burning is comparatively cheaper than mechanical treatments, assuming the removed biomass cannot be sold to offset costs (Fernandes *et al.* 1999; Hartsough *et al.* 2008; Rummer 2008; Stephens *et al.* 2012). In southern Australia, government fire management officers argue that in many situations, particularly at large scales, mechanically treating vegetation is either not feasible operationally or is economically unrealistic (T. Groves 2021 pers. comm.). Nevertheless, some fire adapted species will still germinate at low abundances without fire into small gaps, but resulting seedlings often suffer high mortality due to competition (DeSimone and Zedler 1999; Ooi *et al.* 2006; Zhu *et al.* 2003). As such, germination into small gaps in the absence of fire is often insufficient to sustain populations (e.g. Morgan 1997; Skoglund 1992; Trezise *et al.* 2021).

Fire dependent species require fire within a certain period, as individuals within a population can senesce or be outcompeted in conjunction with propagule expiration. This is occurring within the majority of Fleurieu Peninsula Swamps (FPS), as absence of fire has caused the overstorey to dominate and outcompete understorey species (Conservation Council of South Australia 2020; Harding 2005; Trezise *et al.* 2021). On Kangaroo Island (KI), absence of fire is causing senescence of species which comprise the understorey of mallee-dominated vegetation communities (Dowie 2006; Rawson *et al.* 2013; Taylor 2019). Both FPS and KI fire-dependent vegetation communities contain understorey species which are critically endangered and depend on fire for germination (e.g. *H. tenuis* in FPS & *Olearia microdisca* on KI; Davies *et al.* 2013; Johnson 2014; Trezise *et al.* 2021). Such species can become extinct when the time between fires is greater than the lifespan of the species in both the above-ground vegetation and soil seedbank (Bradstock and Kenny 2003; Enright *et al.* 1996; Trezise *et al.* 2021). Hence, the exclusion of fire can cause plant extinctions because younger vegetation age classes are excluded from the landscape (Enright *et al.* 2012; Gosper *et al.* 2011; Tozer and Bradstock 2003). As such, it is important that researchers investigate successional processes and subsequent fire requirements of vegetation (e.g. fire intervals) to improve fire management practices.

Vegetation succession is the sequential change in floristic composition and structure with time since disturbance (Van Andel *et al*. 1993). The successional stage of a vegetation community theoretically reaches equilibrium in the absence of disturbance (Walker and Wardle 2014). A vegetation community's resilience is its capacity to absorb disturbances, reset to an earlier stage and still persist without shifting to an alternative state (Briske *et al* 2017; Holling 1973). For example, while a pristine woodland may be resilient to fire, a woodland degraded by livestock grazing may transition into an exotic grassland after fire (e.g. Taylor 2019). Knowledge of a community's resilience is therefore important in conservation ecology, as it implies that successional pathways can be shifted into undesirable directions without proper management, such as increasing or decreasing historic inter-fire intervals (e.g. Bradstock 2009; Franklin *et al* 2005; Kitzberger *et al* 2016).

Prescribed burns are an ecological tool which can be used to regulate fire-dependent vegetation communities by facilitating successional pathways that benefit threatened species and vegetation communities (Kimura and Tsuyuzaki 2011; Pyke *et al.* 2010; Trezise *et al.* 2021). Despite potential benefits, several factors need to be considered when prescribing fire, including fire seasonality, as species are adapted to a particular fire regime (Keith *et al.* 2020; Miller *et al.* 2019; Tsafrir *et al.* 2019). Fire seasonality needs to be considered because it impacts seed dormancy, cyclic growth stages, and seedling survival (Knox and Clarke 2006b; Laubhan 1995; Roche *et al.* 1998). For example, Ooi (2019) found that an out of season fire resulted in late emergence for a rare *Leucopogon* species. This extended the species' juvenile period, increasing its risk of being killed (e.g. by herbivory) before maturing and replenishing its seedbanks. Likewise, Jasinge *et al.* (2018) found that fire can negatively affect orchid density when out of season burns disrupt active growing seasons. Fire seasonality is therefore an important consideration, given that fire prescribed in the wrong season can negatively impact some species.

Herbivory pressure also affects the recovery of vegetation communities. Recovering vegetation is often more accessible and palatable for herbivores (Smit and Coetsee 2019; Tolsma 2002; Zhao *et al.* 2011) meaning that fire can concentrate herbivores (Letnic 2004; Meers and Adams 2003; Tolsma *et al.* 2007). In southern Australia, the abundance of western grey kangaroos (*Macropus fuliginosus*) has increased since European settlement. This is causing widespread overgrazing of native vegetation (Department for Environment and Water 2019b; Prowse *et al.* 2019). Elsewhere overgrazing by kangaroos and rabbits has caused local plant extinctions (Cohn and Bradstock 2000). However, herbivory pressure can be reduced after fire by limiting access to open water, culling, and fencing (Ford and Grace 1998; Smit and Archibald 2019; Taylor *et al.* 1994). The predicted damage caused by herbivores remains unknown, which is an issue given the high cost of controlling herbivory (Butler *et al.* 2006; Jury and Quarmby 2013; Mawson *et al.* 2016).

Fire regimes, however, largely dictate the type of vegetation present within a landscape. Species recover from fire with a variety of adaptations, ranging from resprouting to germination from seedbanks. Dormancy mechanisms allow some species to take advantage of fire and they can decline in abundance without it. The dormancy mechanisms of individual species can be assessed with laboratory seed germination trials, and the soil seedbanks of vegetation communities can be assessed using seedling emergence approaches. Both can be used to give insight into the fire ecology of an ecosystem which helps drive fire management practices. Understanding seedbank dynamics for a vegetation community and the dormancy mechanisms of individual species is important because the prescription of fire involves controllable factors, such as fire frequency and seasonality.

THESIS AIMS

In this thesis, I investigated the dormancy mechanisms of selected species and the seedbank dynamics of vegetation communities in South Australia which are declining due to inappropriate fire regimes. To address this, I first addressed the following question:

1. What *in situ* and *ex situ* methods are the most appropriate for predicting the response of soil seedbanks to fire?

I further explored the response of seedbanks to fire by determining:

2. What is the effect of heat and smoke on the soil seedbanks of heathlands on permanent freshwater swamps of the Fleurieu Peninsula using an *in situ* seedling emergence approach?
3. What overcomes seed dormancy in the critically endangered *H. tenuis* and what are the implications for propagation and prescribing ecological burns?

After justifying the use of ecological burns in Fleurieu Peninsula swamps, I then:

4. Documented the initial post-fire response of vegetation following ecological burns of heathy swamps within the Fleurieu Peninsula, and the influence of fire season and herbivory on post-fire recovery.

THESIS FORMAT

This thesis is comprised of a series of chapters that have or will be submitted for publication, and so are written as stand-alone papers (Data Chapters 2-5). The exceptions to this are Chapters 1 and 6, the former is a brief review of the background information and the latter is the concluding summary. Each chapter is briefly described below:

Chapter 1. For this introduction chapter, I provide a brief review of the background information established within the data chapters. I define important concepts in the fire ecology and seed dormancy fields, and outline the knowledge gaps this thesis addresses.

Chapter 2. This chapter investigates seedling emergence techniques and the interpretation of fire treatments. I investigated discrepancies between methods by simultaneously conducting an *in situ* and *ex situ* seedling emergence study and comparing the results. Mallee-dominated vegetation communities on KI were studied during this chapter because of ease of access of plant nursery equipment. Results suggested that while *ex situ* studies are more efficient for predicting seedbank response to fire, the simultaneous use of both methods is required to maximise species detection. This information was then used in the design and discussion of subsequent chapters.

Chapter 3. For this chapter, I investigated the effects of fire cues (heat and smoke) on soil seedbanks in Fleurieu Peninsula swamps. These swamps are a critically endangered vegetation community where a suite of species are declining due to lack of fire. The overwhelming majority of these swamps are in a late-successional stage, which is characterised by low species richness and a depauperate understorey. There remains limited research regarding the merit of using prescribed burns in swamps to accomplish restoration outcomes. As such, I replicated the effects of fire on soil seedbanks to inform fire management in swamps. This suggested that several swamp species require fire to replenish their propagule reserves, and that fire provides an opportunity for understorey species to recover after being outcompeted. These findings support the utility of prescribed burning, but they do inform the most beneficial methods for enhancing threatened flora when burning. As such, recommendations could not be made for the season of burn, grazing management, and optimising germination of threatened species. These were investigated in subsequent chapters. This chapter has been published in *Austral Ecology*.

Chapter 4. In this chapter, I investigated the dormancy mechanisms of the critically endangered *Hibbertia tenuis*, which is endemic to FPS. Populations of this species were declining, and restoration works were unsuccessful because its dormancy mechanisms were unknown. This limited the efficiency of *ex situ* propagation and made the prescription of fire questionable, given that the suitable fire regime for the species was not known. Therefore, I conducted laboratory experiments to assess the germination responses of seeds after a variety of fire and environmental treatments. Results showed that typically at least half of the seeds of *H. tenuis* germinated when treated with smoke water and exposed to ambient conditions typical of autumn or spring, and that the season of fire influenced emergence. This research was then used in restoration works to optimise *ex situ* propagation and *in situ* fire management.

Chapter 5. Control burns were implemented for this chapter to assess the effect of fire in swamps of the Fleurieu Peninsula. The use of fire *in situ* was justified given the results of Chapters 3 and 4. I also investigated the influence of fire seasonality and post-fire herbivory, as the literature lacked information regarding the importance of these factors. Results showed that burning initiated a transient successional period of increased plant richness which favoured understorey species. These fires also consumed the majority of the remaining *H. tenuis* individuals (~15 of 20 known plants), but as a result, nearly 600 plants germinated and many have matured saving the species from a likely decline into extinction, assuming these plants can produce a viable seedbank.

Chapter 6. For the concluding chapter I summarise and discuss the importance of understanding soil seedbanks and the seed dormancy mechanisms of plants for prescribing controlled burns. I then discuss the likely successional patterns in heathy swamps after fire and the importance of managing fire intervals, season, and post-fire herbivory. I highlight the key discoveries of this thesis and its contribution to the fire and seed ecology fields. Finally, I discuss the limitations of my study and areas of potential future research.

Chapter 2. Methods for predicting the response of soil seedbanks to fire

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Statement of Authorship

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Publication Details	

Principal Author

Name of Principal Author (Candidate)	James Trezise		
Contribution to the Paper	Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); visualization (lead); writing-original draft (lead); writing-review & editing (equal)		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	10/11/21

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate to include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	**David Paton**		
Contribution to the Paper	Resources (equal); project administration (supporting); supervision (lead); writing-review & editing (equal).		
Signature		Date	29/10/21

Name of Co-Author	**José M. Facelli**		
Contribution to the Paper	Resources (equal); project administration (supporting); supervision (supporting); writing-review & editing (supporting).		
Signature		Date	28/10/21

Name of Co-Author	**Richard Davies**		
Contribution to the Paper	Project administration (supporting); supervision (supporting); writing-review & editing (supporting).		
Signature		Date	28/10/21

ABSTRACT

The composition of soil seedbanks and their response to fire treatments can be measured with *ex situ* counts of germinants from soil samples or *in situ* counts of germinants in the field. We used both methods to produce estimates of seedling abundance, species detection, and the influence of fire on germination. We detected on average 77 seedlings m^{-2} and 6.2 species m^{-2} with an *in situ* seedling emergence approach (144 quadrats) versus 288 seedlings m^{-2} and 4.4 species per tray with an *ex situ* seedling emergence approach (312 trays). Species detection was also different; 76 species were detected *in situ*, 35 of which were unique to this method; 79 species were detected *ex situ*, 38 of which were unique to this method. This was despite both methods producing similar diversity indices. We also assessed species richness as a result of sampling effort with rarefaction. This showed that optimal species detection occurs with 120 *in situ* 1 m^2 quadrats or 130 *ex situ* 0.105 m^2 trays, based on 65 soil samples (volume of 0.0024 m^3 per sample) subsequently split in two. The influence of fire on germination also differed between the methods. The *ex situ* impact of heat plus smoke increased the number of native species which germinated, as well as the seedling abundance of native perennial species and introduced annual/biennial species. Comparatively, the *in situ* fire treatment did not affect the number of species or seedlings which germinated. Differences between species detectability, seedling abundance, and the influence of fire treatments, indicates that one or many factors are influencing these estimates. We found that one such factor was propagule survival, where *in situ* estimates of seedling survival and species detection were limited by herbivory and other environmental stressors. This indicates that the *ex situ* environment is more conducive to seedling survival and therefore seedling detection while the *in situ* method is important for identifying limitations to seedling survival. However, the lower *in situ* estimates of seedling abundance limited our capacity to detect statistical differences in germination because of the fire treatment. Therefore, while we argue that the simultaneous use of both methods is required to maximise species detection and to identify environmental stressors which limit plant survival, *ex situ* studies are better suited to assessing the impact of fire because they require lower sampling replication.

Key terms: seedling emergence, soil seedbank, fire, seed dormancy, methods

INTRODUCTION

Soil seedbanks are the propagule reserves of species that store seed in soil (Gallagher 2013). Soil seedbanks are dynamic and change through time as a consequence of a successional process. Therefore, abiotically similar sites can have dissimilar soil seedbanks because of differences between their disturbance history (e.g. grazing and fire; Milberg 1995; Sternberg *et al.* 2003; Wills and Read 2007). These disturbances (or lack of) therefore dictate the quantity and type of seed available. Fire is an important disturbance which drives succession and seedbank dynamics because too little fire can lead to senescence and too much fire can result in loss of species which are slow to mature. Disturbances can also act synergistically, for example, grazing after fire may limit plant recovery (Foster *et al.* 2016a).

After a disturbance event, as additional species mature and add their seeds to the soil seedbank, the seeds of early post-disturbance colonists become less common (e.g. Bekker *et al.* 2000; Falińska 1999; Grandin and Rydin 1998). Therefore, species' seedbanks are not evenly spread across landscapes (James *et al.* 2007; Matlack and Good 1990; Thompson 1986) and the distribution of seedbanks of rare species often are not homogeneous but are instead isolated to specific microsites (Gosper *et al.* 2020; McCormick and Jacquemyn 2014; Taylor 2008).

Attributes of the seeds within these reserves vary between species, as some germinate almost immediately without stimuli, while others remain dormant until experiencing suitable cues such as smoke from bushfire (Leck *et al.* 1989). The lifespan of seedbanks depends on conditions within the soil and the inherent characteristics of the species (Keith *et al.* 2002). Seed longevity is highly variable between species. For most species, seed half-lives range from a few days to years (Merritt *et al.* 2014). But, in extreme cases, viable seeds have been found several centuries after being deposited (Watson and Riha 2011). Many species have dormancy mechanisms, meaning that germination is restricted until specific conditions occur (Baskin and Baskin 2004), including the occurrence of fire which results in exposure to heat and smoke (Ooi 2007; Staden *et al.* 2000; Van Staden *et al.* 2004).

There is an increasing need to understand the dynamics of soil seedbanks, given the prospects of more severe bushfires (as a consequence of changing climate and land use) and the need to manage fuel loads using fuel reduction burns to help mitigate against those major fires (Lindenmayer *et al.* 2020; Miller *et al.* 2019; Morgan *et al.* 2020; Ooi 2012; Price *et al.* 2010). Burning a site too often or not often enough changes its fire regime and this can have detrimental ecological outcomes, such as local extinctions (Enright *et al.* 2015; Odion and Tyler 2002; Ottewell *et al.* 2011). An understanding of seedbank composition allows for fire managers to sustainably prescribe a burn during a period when the slowest maturing species have sufficiently contributed to their soil seedbanks and the seeds of early post-disturbance colonists are still viable (e.g. Chapters 3 & 5).

The composition of soil seedbanks and their response to treatments can be measured with a variety of methods (Mahé et al. 2020). Primarily, these are *ex situ* seed counts (enumeration) in soil samples (e.g. Gonzalez and Ghermandi 2012; Mesgaran *et al.* 2007; Price *et al.* 2010), *ex situ* counts of germinants from soil samples (e.g. Boedeltje *et al.* 2002; Erfanzadeh *et al.* 2020; Trezise *et al.* 2021), or *in situ* counts of germinants within a given area (e.g. Ooi *et al.* 2004; Pavlik *et al.* 1993; Shay *et al.* 2001). These three approaches allow researchers to assess soil seedbanks but may produce different estimates from one another. Ecological assessments commonly infer species response to fire based on existing literature, but new information should be sought in instances of data deficiencies for threatened vegetation communities (e.g. Kangaroo Island Narrow-leaved Mallee; Taylor 2019). This is also important for individual species, such as the nationally critically endangered *Hibbertia tenuis*, which is threatened by a lack of fire (Chapter 3; Quarmby 2011; Trezise *et al.* 2021).

Seed enumeration involves extracting seeds from the soil by sieving or flotation and then counting and identifying the seeds. This does not determine if these seeds will germinate but the extracted seeds can subsequently be subjected to different experiments to assess their viability (e.g. Collette and Ooi 2020; Le Breton *et al.* 2020; Paroissien *et al.* 2020). Enumeration can result in small seeds being overlooked or seeds being misidentified (Cardina and Sparrow 1996; Ferrandis *et al.* 1999; Gonzalez and Ghermandi 2012). However, unlike other methods, this method detects dormant seeds that would otherwise not be detected using approaches dependent on germination (Brown 1992).

The *ex situ* seedling emergence approach is the identification of seedlings that germinate in soil samples and is often used to assess the impact of treatments on seedling germination (Mahé *et al.* 2020). For instance, the effects of a fire treatment are commonly simulated by applying heat and smoke to soil samples (Boedeltje *et al.* 2002; Cochrane *et al.* 2007; Rawson *et al.* 2013). The emergent seedlings provide a measure of the likely germination of seeds *in situ*. However, these *ex situ* assessments may not provide every cue necessary to break dormancy in every species present in soil samples (Baskin and Baskin 2004; Erfanzadeh *et al.* 2020). Additionally, the process of taking soil cores for a seedling emergence experiment may stimulate the germination of seeds of some species (Courtney 1968; Davies 2005). For example, seeds may become exposed to light cues or become scarified during the mixing process (Table 1).

The *in situ* seedling emergence approach is the identification of seedlings in the field. This method generally investigates the effect of a treatment (e.g. smoke; Tormo *et al.* 2014) or a disturbance (e.g. fire; Vermeire and Rinella 2009) and measures the response of soil seedbanks under natural conditions. The effects of fire on seedling emergence can be extrapolated from *in situ* application of fire cues (Daws *et al.* 2014; Lloyd *et al.* 2000; Pavlik *et al.* 1993) or smaller experimental burns (Kotze 2013; Kral *et al.* 2015; Taylor 2019). These studies are conducted under natural conditions which include environmental stressors that limit survival (e.g. desiccation or herbivory). As such, unless these factors are controlled (e.g. watering and fencing; Cornaglia *et al.* 2005; Taylor 2019), *in situ* estimates of seedling quantity are lower than the true quantity of seed in the soil, and typically lower than equivalent estimates from *ex situ* studies (Cardina and Sparrow 1996; Mesquita *et al.* 2013; Salam *et al.* 2018). As such, *in situ* estimates perhaps provide a more accurate estimate of the seedlings that emerge and survive, given they are subject to environmental stressors. Furthermore, the number of seedlings that ultimately survive until maturity is generally lower (Moles and Westoby 2004; Roche *et al.* 1998; Wellington and Noble 1985). Additionally, the dormancy breaking cues provided within both the *in situ* and *ex situ* methods are different, meaning some species may not be detected using either approach (Cardina and Sparrow 1996). Estimates of soil seedbank composition may differ between *ex situ* seedling emergence and *in situ* seedling emergence approaches, and the factors behind these differences remain poorly understood.

The *in situ* and *ex situ* techniques used to assess the likely functional responses of seedbanks in the soil should provide reasonably comparable estimates of species compositions and relative abundances of seedlings. However, several studies have reported differences between such estimates (Table S11 of Appendix

1). We suggest this is because several factors influence species detection and estimates of seedling abundance. These include seed viability, seed size, specimen identification, propagule availability, propagule/seedling survival, seed dormancy, germination environment, delayed emergence, and seedbank heterogeneity (Table 1). Although several studies compare seed enumeration to *ex situ* seedling emergence (e.g. Gross 1990; Poiani and Johnson 1988; Price *et al.* 2010), to our knowledge, no study compares the effectiveness between *in situ* and *ex situ* emergence techniques for predicting the likely responses of the soil seedbanks to disturbance.

This study documents the seedling emergence of the soil seedbanks of mallee-heath habitats typical of eastern Kangaroo Island in response to fire using both an *ex situ* and an *in situ* approach. The *in situ* approach used burn boxes as described by Pavlik *et al.* (1993) to safely burn small quadrats of vegetation and documenting the plants that established post-fire. The *in situ* study included a soil disturbance treatment and a fenced treatment to exclude herbivory. The *ex situ* approach involved collecting soil samples, exposing these to heat plus smoke and following the subsequent emergence of plants through time within an open nursery.

These studies were undertaken to:

1. Estimate seedling abundances, species richness and species detection from the two techniques and document the differences.
2. Assess the influence of soil disturbance and herbivory on the appearance of seedlings *in situ* post-fire.

We discuss our findings in relation to the factors likely to be influencing the differences in *ex situ* and *in situ* responses, and the implications of these to predicting the likely responses of the soil seedbanks of these mallee-heaths when the above ground vegetation is burnt. We then determine how useful these techniques are for predicting the likely post fire responses of vegetation.

Table 1. Likely influences of nine factors on the ability of three common techniques to assess soil seedbanks (and resprouting from rhizomes and similar propagule reserves): seed enumeration (sorting and identification of seed from soil samples), *ex situ* emergence (seedling emergence of soil samples in a greenhouse/nursery), or *in situ* emergence (monitoring of seedling emergence in the field). Factors can either affect abundance (estimated counts of seed/seedling in samples/quadrats) and/or, detection (the presence of species in samples/quadrats).

Factors and impacted method	Explanation and their influence	Potential improvements, solutions, and considerations
1. **Seed viability** impacts seed enumeration	Does not distinguish between viable and non-viable seeds. This influences abundance (enumeration > emergence).	• Viability can be tested by germinating seeds but does not distinguish between dormant and non-dormant seeds (Bernhardt *et al.* 2008; Gross 1990). • Viability can be tested by cutting seeds and observing embryo fill, but observations are subjective as viability is not ensured for fully filled seeds, and partially attached embryos can still be viable (Crawford *et al.* 2007; Frischie *et al.* 2020; Jorge and Ray 2005).
2. **Seed size** impacts seed enumeration	Species with large seeds favoured. This influences detection and abundance (enumeration < emergence).	• Small seeded species are particularly affected (e.g. orchid seed <0.1 mm; Barthlott *et al.* 2014; Moles *et al.* 2005). • Although some small-seeded species can be detected, not all of their seeds will be detected (Warr *et al.* 1993).
3. **Specimen identification** impacts all methods	Reliably identifiable species are favoured. This influences detection (enumeration < emergence).	• Enumeration biases to detecting the reliably identifiable seeds (Gross 1990; Poiani and Johnson 1988; Price *et al.* 2010). • Machine vision improves seed identification (Granitto *et al.* 2005; Tellaeche *et al.* 2011). • Misidentification of plants occurs in 5-10 % of studies (Łuczaj 2010; Morrison 2016). • Rare species can remain undetected because of misidentification (Archaux *et al.* 2012; Garrard *et al.* 2015; McCarthy *et al.* 2013)
4. **Propagule availability** impacts all methods	A portion of propagules is not captured in samples. This influences detection and abundance (enumeration < *ex situ* emergence < *in situ* emergence)	• Rhizomes and similar propagules can be removed during *ex situ* studies that filter debris from samples (e.g. Cochrane *et al.* 2007; Gonzalez and Ghermandi 2012; Peterson and Baldwin 2004) • Detection of obligate resprouters is particularly affected (Marais *et al.* 2014; Pausas and Keeley 2014; Pausas *et al.* 2016). • Canopy seedbanks can remain undetected (e.g. seed serotiny and fire; Enright *et al.* 1996; Goubitz *et al.* 2004; Keeley and Fotheringham 2000a). • Sampling depth can influence results, as seeds concentrate at different depths (e.g. increased seed depths with soil cracking; Espinar and Clemente 2007; Price *et al.* 2010; Traba *et al.* 2004). • The majority of seeds occur within the top 5 cm of the soil (Auld and Denham 2006; Auld and O'Connell 1991; Wills and Read 2007).

5. **Propagule/ seedling survival** impacts *in situ* emergence	Survival is lower *in situ* compared to *ex situ*. This influences detection and abundance (*in situ* emergence < *ex situ* emergence).	• Conditions for seedling survival are generally better in a greenhouse or glasshouse (Mesquita *et al.* 2013; Salam *et al.* 2018). Seedlings in a greenhouse or glasshouse have a lower risk of desiccation and lower risk of herbivory (e.g. Auld 1995; Bird *et al.* 2012; Engelbrecht *et al.* 2005). • Seed survival is generally better in a greenhouse, as fewer seeds are lost to predation and fungal attack (Blaney and Kotanen 2001; Ghersa and Martınez-Ghersa 2000; Vander Wall *et al.* 2005). • Inter-seedling competition (e.g. competition for light, water, or other resources) can also affect results, this can be controlled by removing seedlings as they emerge (Davies *et al.* 2013; Garwood 1983; Read *et al.* 2000). But removing competition may overestimate the true capacity for vegetation to reseed. • Germination flushes may not be captured from poorly timed surveys as some species rapidly senesce or become outcompeted (e.g. Enright and Lamont 1992; Liu *et al.* 2011; Rutherford *et al.* 2011). • Herbivores target specific species, meaning some species remain undetected (Faast and Facelli 2009; Foster *et al.* 2020; Petit and Dickson 2005).
6. **Seed dormancy** impacts both emergence approaches	Dormant seeds remain undetected. This influences detection and abundance (enumeration > emergence).	• Conditions required for germination may not be met, so emergence techniques give a measure of the minimum number of seeds present as not all seeds will germinate during a single germination event (Erfanzadeh *et al.* 2020). • The dormancy of seeds within a seedbank can vary, as dormancy breaks down over time (Baskin and Baskin 1998; Davies *et al.* 2013; Finkelstein *et al.* 2008). • A portion of dormant seeds remain inactive even after conditions required for germination are met (e.g. bet-hedging; Bell *et al.* 1995; Finkelstein *et al.* 2008; Ooi *et al.* 2009). • 'Dormant' seedbanks can still produce germinants at low abundances in the absence of dormancy breaking cues (DeSimone and Zedler 1999; Ooi *et al.* 2006; Trezise *et al.* 2021).
7. **Germination environment** impacts both emergence approaches	Germination environment between *in situ* and *ex situ* studies are different. This influences detection (*in situ* emergence ≠ *ex situ* emergence).	• Ambient cues are different between *in situ* and *ex situ* studies (e.g. daily light or temperature regimes; Chamorro *et al.* 2018; Ooi *et al.* 2004; Wessels and Schwabe 2008; Yang *et al.* 2020). • Generally, greenhouse samples are regularly irrigated, and this could trigger germination (e.g. dormancy and water availability; Baskin *et al.* 2000; Freas and Kemp 1983; Steadman *et al.* 2004; Ter Heerdt *et al.* 1999). • Treatments that replicate an event may not provide all related dormancy breaking cues. For example, heat plus smoke treatments commonly replicate fire, but maybe lacking all fire cues (e.g. increased light or nitrate levels; Baker *et al.* 2005; Thompson and Ooi 2010; Williams *et al.* 2003). • The process of taking, mixing, and sorting samples may in itself cue emergence by disturbing the soil substrate (e.g. disturbance and light exposure; Davies 2005; Schutte *et al.* 2014; Trezise *et al.* 2021).

		For example, the exposed portion of a soil seedbank is increased when soil samples are spread out over a larger surface area during *ex situ* studies.
8. **Delayed emergence** impacts both emergence approaches	Species that emerge outside of the monitoring period are not detected. This influences detection and abundance (*in situ* emergence ≠ *ex situ* emergence).	• Germination of annuals may be restricted to a season or event (e.g. winter and high rainfall; Carta *et al.* 2013; Dwyer and Erickson 2016; Mott 1974). • Secondary dormancy can delay emergence after primary dormancy is broken (Kleemann and Gill 2013; Ooi 2010; Walck *et al.* 2011). For example, seasonal germination and dormancy cycling (Chamorro *et al.* 2018; Collette and Ooi 2020; Oliveira *et al.* 2017). • Rhizomes and similar propagules can be seasonally dormant (e.g. annual dormancy in orchids; Coates *et al.* 2006; Jasinge *et al.* 2018; Shefferson *et al.* 2005).
9. **Seedbank heterogeneity** impacts all methods	Species which are more evenly spread are more likely to be detected. This influences detection (enumeration ≠ *ex situ* emergence ≠ *in situ* emergence).	• Seedbanks are not evenly spread across vegetation communities (e.g. clumped soil seedbanks and microsites; James *et al.* 2007; Matlack and Good 1990; Thompson 1986). • Rare species may remain undetected when a low number of sample replicates is used (Stark *et al.* 2008). For example, *ex situ* seedling emergence is generally regarded as more time-efficient than enumeration allowing for greater replication (Bekker *et al.* 2000; Warr *et al.* 1993) • Different methods may be better suited to varying levels of seedbank heterogeneity (e.g. Bekker *et al.* 2000; Shun-Li *et al.* 2003)

METHODS

Site

This study was conducted on the north-eastern part of Kangaroo Island (Figure 1), South Australia. This region received an average annual rainfall of 445 mm, based on records from 1995 to 2021 taken at the nearest weather station (Kingscote Airport) in the eastern half of the study area (Bureau of Meteorology 2022). In 2017, when this study was conducted the annual rainfall for Kingscote Airport was 391 mm (Bureau of Meteorology 2022). Seven mallee-heath vegetation sites were selected. Sites are predominantly *Eucalyptus* mallee heathlands with the midstorey consisting of sparse to mid-dense shrubs and a sparse sedge understorey. These sites differed in level of degradation and time since fire (Table 2). Sites were defined as degraded if they had less than 10 % cover of native understorey and were defined as long unburnt if they had no known fire history in government fire records dating back to 1931 (86 years; Department for Environment and Water 2016).

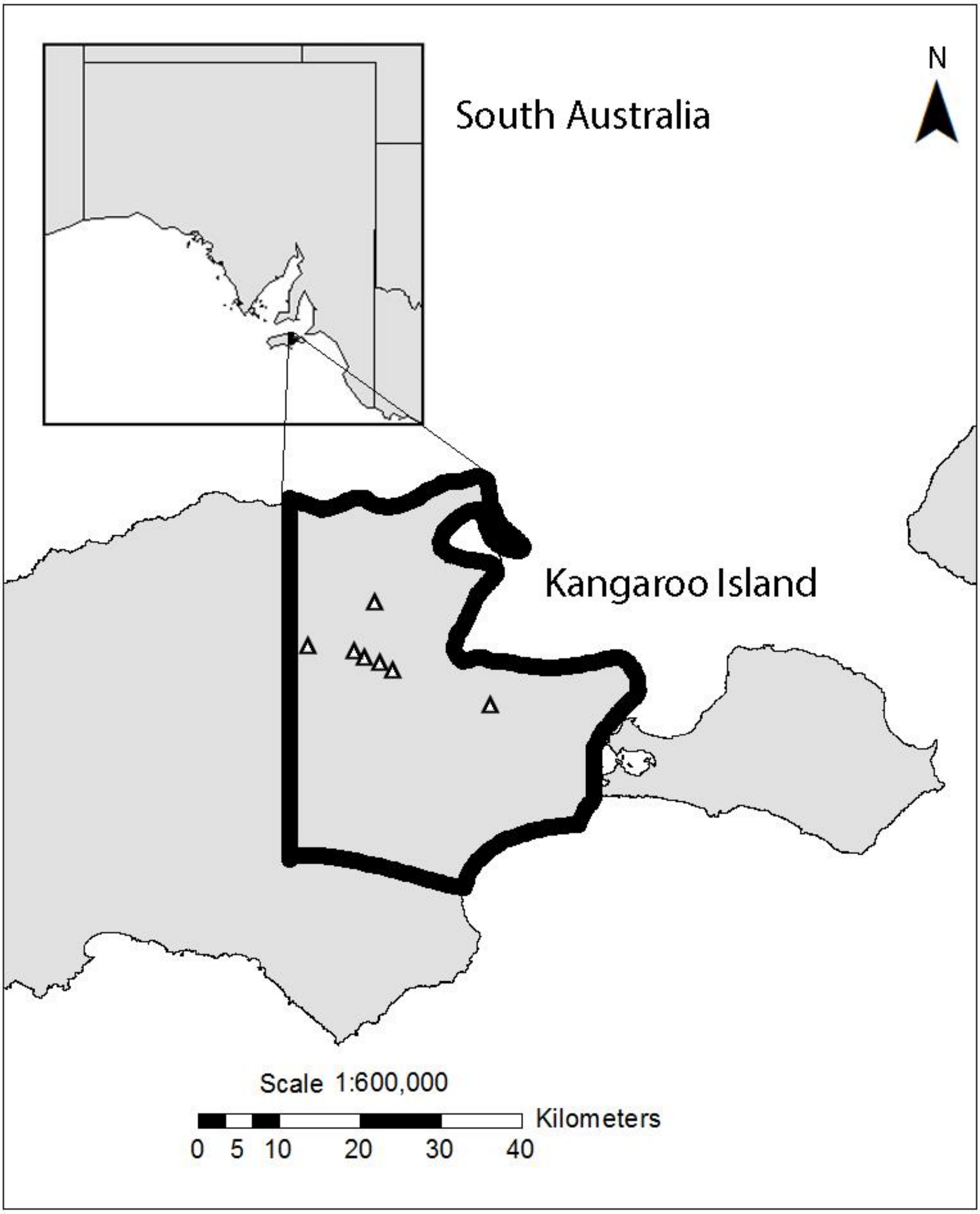

Figure 1. Study boundary in northeastern Kangaroo Island. The seven sites, all classified as mallee-heath, are represented by **Δ**, and exist in a mixture of private property and crown land. Map created using ArcGIS (version 10.3.1) using spatial data from the Department of Planning Transport and Infrastructure (1996).

Table 2. Characteristics of the seven study sites on Kangaroo Island. Descriptions for 'Type', 'Sheep grazing history' and 'Disturbance history' are based on anecdotal observations and communications with landholders. 'Disturbance history' uses government fire records to define sites as long unburnt (Department for Environment and Water 2016). Sites are defined as degraded in the 'Degradation' section if they had less than 10 % cover of native understorey.

Site name	**Acronym**	**Type**	**Sheep grazing history**	**Disturbance history**	**Degradation**
Cygnet Revegetation	CV	Revegetation	Ungrazed	Planted 2011	Healthy
Roadside Vegetation	RV	Remnant	Ungrazed	Burnt 2010	Healthy
Airport Remnant	AR	Remnant	Ungrazed	Long unburnt	Healthy
Heritage Agreement	HA	Remnant	Ungrazed	Long unburnt	Healthy
Spring Rd Remnant	SR	Remnant	Grazed	Long unburnt	Degraded
Redbanks Rd Remnant	RR	Remnant	Grazed	Long unburnt	Degraded
Cygnet Remnant	CR	Remnant	Grazed	Burnt 2010	Degraded

Ex situ experiment

We used an *ex situ* seedling emergence approach to investigate the germinable contents of the soil seedbank and to assess responses to a simulated fire treatment (e.g. Cochrane *et al.* 2007; Davies *et al.* 2013; Rawson *et al.* 2013). Seven sites were selected, and at each site twenty-four 1 m^2 quadrats were randomly allocated using ArcGIS (version 10.3.1). An exception to this was that only 12 quadrats were allocated to the site labelled Cygnet Remnant due to the sites' small size.

In October 2016, a 30 cm diameter auger was used to take a core from the centre of each quadrat to a depth of 5 cm where the majority of seed is held (Auld and Denham 2006; Auld and O'Connell 1991; Wills and Read 2007). Large debris was removed from the cores and the remaining material was then thoroughly mixed and separated into two paired samples. Each sample was spread over growing trays (35 cm × 30 cm × 5 cm deep; drainage holes included) on top of a 1 cm deep layer of sterile drainage sand. This equated to 312 trays, with a total surface area of 32.8 m^2. One tray from each pair was treated with heat plus smoke to simulate fire and the other was not treated (control). Dry heat was administered in an oven at 80 ^{o}C for 60 minutes, thereafter the samples were placed into a smoke tent for 15 minutes (as described by Rawson *et al.* 2013) generated by burning wheat hay in a 200 L barrel drum. Smoke from hay has been shown to promote germination of Kangaroo Island species in similar experiments, likely owing to the production of Karrikin, which is a smoke related compound responsible for plant growth regulation (Davies *et al* 2013; Chiwocha *et al* 2009; Rawson *et al* 2013).

All samples were then randomly placed in an open nursery in October 2016 and their position rotated fortnightly to limit any influence of position. Twenty additional ‘blank’ samples were randomly dispersed among the samples and filled with drainage sand to test for airborne seed contamination. These were monitored alongside all other samples during the study.

The nursery is located within Cygnet Park, Kangaroo Island, which is adjacent to the site named Cygnet Revegetation and is within 20 km of all other sites. To keep the samples damp, watering levels were adjusted throughout the experiment according to local weather forecasts. Such that, watering regimes varied from daily 2 mm applications during dry summer months to weekly 2 mm applications during wet winter months. The accumulated number of seedlings and species that were detected after ~5 months (March 2017) and ~13 months (November 2017) was assessed. The locations of seedlings in trays were noted during the March survey to avoid recounting individuals for a second time during the November survey.

***In situ* experiment**

Three different treatments were employed in a nested design, these being burning, fencing, and disturbance (Figure 2). We investigated six sites, totalling 144 quadrats with a combined surface area of 144 m^2. These were the same quadrats used in the *ex situ* experiment, with the exception of the Cygnet Remnant site. The disturbance treatment was implemented by evenly tilling (to approximately 30 cm soil depth) half of the quadrats for one minute using a hand auger. Ground stratum plant species were churned up during this process (i.e. graminoids and forbs), but care was taken to not remove the above ground material of the middle stratum and upper canopy.

The influence of burning on *in situ* emergence was studied using burn boxes similar to those used by Pavlik *et al.* (1993) in October 2016. The boxes consisted of (2 m x 2 m) squares of corrugated steel (with no lid) and were placed around the quadrats (1 m^2). Fuel was added to the ground layer within boxes. This was comprised of 20 kg of loose wheat hay and any overhanging plant material which was pruned (to a maximum height of 2 m) and placed into the box. Fuel was added to all sites because long unburnt sites had negligible fuel loads due to senescence of the understorey. Temperature monitoring labels (by Thermax) were placed at the surface, at 0.5 cm, 1 cm, and 2 cm in the soil to record the maximum heat achieved at each depth during fires. These were placed in the centre of the boxes. Fires were ignited along the north side of the boxes and allowed to burn until all fuel was consumed (ranging from 1 to 60 minutes), at which point the burnt area was hosed down with a backpack water sprayer to prevent potential re-ignitions. Half of the quadrats were not burnt (unburnt controls) and these were also hosed down to limit the asymmetric effects of watering. Additionally, a fence treatment was implemented, wire mesh fences were erected around six control and six burnt quadrats to restrict herbivory by Western Grey Kangaroos (*Macropus fuliginosus*) and Tammar Wallabies (*M. eugenii*). The fenced area encompassed the entire 1 m^2 quadrat. The fencing material used was 1.8 m tall with 5 cm mesh with no roof. The accumulated number of seedlings and species that were detected after ~5 months (March 2017) and ~13 months (November 2017) were assessed. The locations of seedlings were noted during surveys to avoid recounting the same individual multiple times. As such, additional individuals were counted at later times, and we did not account for losses (e.g. individual seedlings which perished were not removed from our database). Therefore, results give the accumulated effect of grazing after ~13 months of fencing, but results do not show the effect of grazing over time. Additionally, there may have been unknown numbers of germinants appearing and disappearing between the times when monitoring was undertaken.

Six of the seven sites were used for the *in situ* study, as the site labelled Cygnet Remnant was damaged by stock and so all associated *in situ* data were discarded.

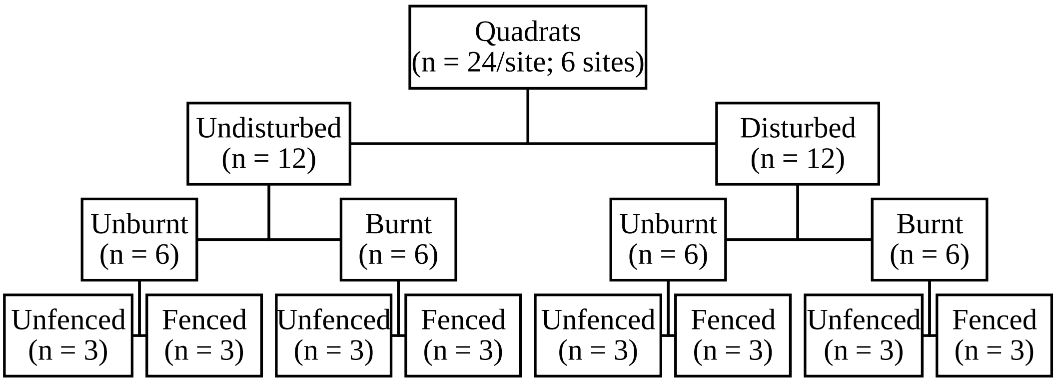

Figure 2. *In situ e*xperimental design showing the nested treatment allocations for each quadrat and the number of replicates within each site.

Comparison between experiments

Inferred differences in germination assume that seedling counts from the two experiments are comparable based on the methods as defined above. Efforts to standardise the two experiments have been made, but they are inherently different due to several factors which do not uniformly influence the two methods (Table 1). For example, the methods have differing watering and grazing regimes. These differences should be acknowledged when interpreting comparisons between the studies. Furthermore, both methods only capture presence of seedlings at 5 and 13 months post treatment, meaning that emergence data during other periods is not considered.

Statistics and nomenclature

We compared the abundance of seedlings and species richness between burnt and unburnt controls, between sites, between disturbed and undisturbed quadrats and between fenced and unfenced controls. Data analyses were performed using the R software in R studio from version 3.5.1 (R Core Team 2019). Generalised linear mixed models were used to predict mean seedling abundances and species richness in samples and quadrats using the R package glmmTMB from version 0.2.0 (Magnusson *et al.* 2017). Simpson and Shannon diversity indices, and the rarefaction plots, were analysed using the R package Vegan from version 2.5-6 (Oksanen *et al.* 2019). Means and *P* values were predicted from the models using the R package emmeans from version 1.7.3 (Lenth *et al.* 2019). These predictions use pairwise methods, including test statistics (t.ratio) to produce *P* vaules. Plots were generated using the R package ggplot2 version 3.3.3 (Wickham *et al.* 2021).

For the *in situ* study, the fire, disturbance, and fencing treatments were considered fixed factors, while site and quadrat were treated as random factors. We classified plants as either seedlings or resprouters and only analysed the seedling data for the present study. Similarly, for the *ex situ* experiment, the fire treatment was considered a fixed factor, while site and quadrat were treated as random factors. For example, model <- glmmTMB(quantity ~ fire + (1|quadrat)+ (1|site), data = data, family = nbinom2. Model selection was determined using an anova function. The distribution and dispersion of the data for each species or life form group informed the response distributions for each model, such that dispersion tests dictated whether the model used either a Poisson or Negative Binomial distribution.

Statistics for individual species and lifeform groups were calculated subject to emergence occurring in either a treated or untreated tray of each pair, such that tray pairs without emergence were excluded from calculations to avoid zero inflation. Furthermore, model summaries and overdispersion checks were produced for models of each species and life form group. All trays/quadrats with ≤ 12 seedlings per tray/quadrat or species present in ≤ 12 trays/quadrats were found to be over-dispersed and so were not reported on in the result.

During both experiments, seedling identification and nomenclature followed the Electronic Flora of South Australia and local plant identification books

(Department for Environment and Water 2020a; Overton and Overton 2012; Prescott 1995).

RESULTS

Ex situ experiment

Differences between sites

We sampled seven separate sites (Table 2), and site as a factor had a significant effect on our models when predicting seedling abundance (χ^2 (6) = 117, *P* = <0.01) and species richness (χ^2(6) = 1524, *P* = <0.01). Seedling abundance and species richness varied between sites; abundance ranged from 923 seedlings m^{-2} for CV quadrats to 53 seedlings m^{-2} for RR quadrats, whereas richness ranged from a mean of 7.4 species in CV quadrats to 2.3 species in RR quadrats (Figure 3 and 4). Furthermore, only four *Avena barbata* seedlings emerged in the blank control trays, indicating contamination was negligible.

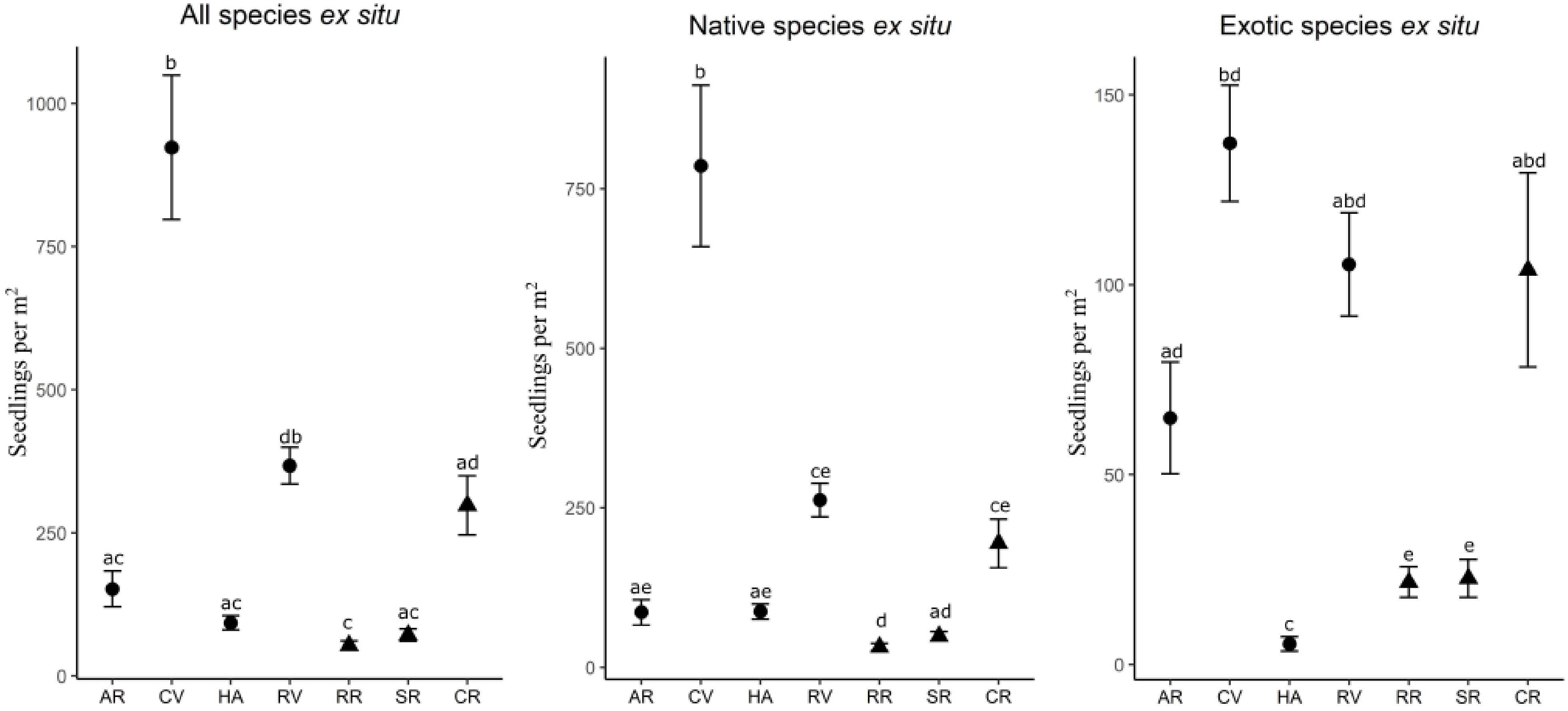

Figure 3. Effect of site on the abundance of extrapolated seedlings emerging from the *ex situ* trays. To convert the *ex situ* abundance (seedlings per tray) to *ex situ* seedlings m^2 multiply by 9.5; given the surface area of the *ex situ* trays are 0.105 m^2 compared to the 1 m^2 *in situ* quadrats. Results are given as mean (± SE) of seedlings per m^2. Circles denote healthy sites (>10 % native understorey), whereas triangles denote a degraded site (<10 % native understorey). The various sites are: Cygnet Revegetation (CV), Roadside Vegetation (RV), Airport Remnant (AR), Heritage Agreement (HA), Spring Road Remnant (SR), Redbanks Rd Remnant (RR), Cygnet Remnant (CR). Different letters represent significant differences as generated using generalised linear mixed models. Additional statistical details can be found in Table S1.1, S1.2 and S1.3 of Appendix 1.

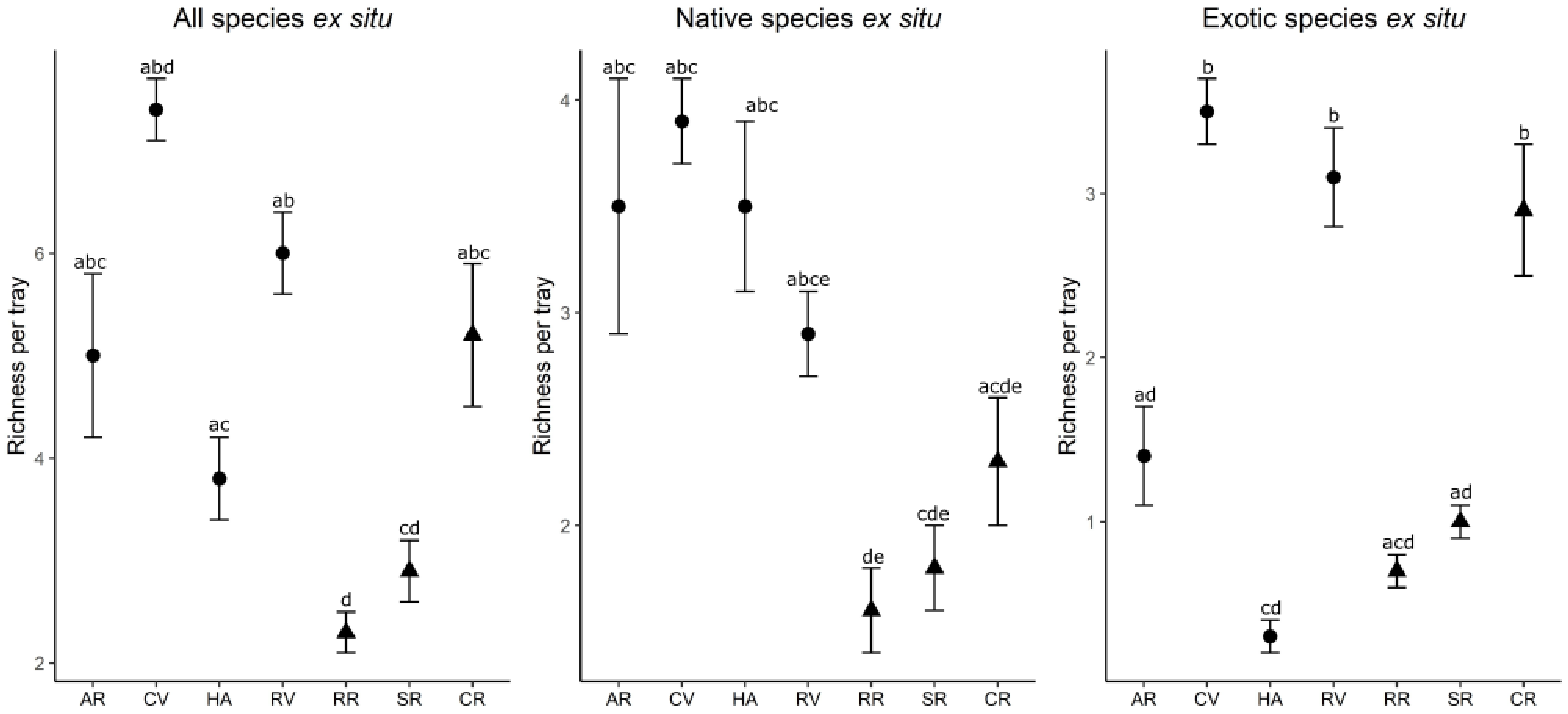

Figure 4. Effect of site on the species richness of seedlings emerging from the *ex situ* trays. Species richness has not been extrapolated, as it does not scale linearly. Significant differences were generated using generalised linear mixed models. Additional statistical details can be found in Table S1.1, S1.2 and S1.3 of Appendix 1. Results are given as mean (± SE) of seedlings per m^2 and number of species per tray/quadrat.

Effect of burning

Application of heat plus smoke (burning treatment) did not significantly increase the number of seedlings of native plants that emerged in trays relative to control trays (Table 3). However, the seedling abundance of native perennials was significantly higher following the burning treatment (burnt 113 seedlings m^{-2} vs unburnt 103 seedlings m^{-2}). As was the case for seven individual species (Table 3). Significant increases in seedling emergence were also detected for introduced species (burnt 70 seedlings m^{-2} vs unburnt 57 seedlings m^{-2}). This was largely due to annuals/biennials (burnt 66 seedlings m^{-2} vs unburnt 54 seedlings m^{-2}) and constituent species *Arctotheca calendula* and *Isolepis marginata* (Table 3).

Table 3. Effect of *ex situ* heat and smoke on the abundances of seedlings emerging from soil samples. To convert the *ex situ* abundance (seedlings per tray) to *ex situ* seedlings m^2 multiply by 9.5; given the surface area of the *ex situ* trays are 0.105 m^2 compared to the 1 m^2 *in situ* quadrats. Significant differences were generated using generalised linear mixed models and only data from paired trays where the target emerged in at least one tray were included in analysis. Additional statistical details can be found in Table S2 of Appendix 1. Mean germinants m^{-2} are given ± standard error.

Longevity & Life form class/species	**Burnt**	**Unburnt**	**Significantly different (*P* value)**
All natives	230.7 ± 44.1	218.8 ± 45.6	
All native annual/biennial	117.5 ± 12.4	115.9 ± 15.0	
Centrolepis strigosa	3.1 ± 0.9	2.5 ± 0.9	
Dysphania pumilio	1.0 ± 0.4	2.5 ± 0.9	Burnt<Unburnt (0.01)
Juncus bufonius	20 ± 4.2	16.4 ± 2.8	
Lachnagrostis filiformis	3.7 ± 1.3	7.4 ± 5.8	
Lythrum hyssopifolia	14.8 ± 4.5	10.6 ± 4.2	Burnt>Unburnt (0.02)
Pseudognaphalium luteoalbum	74.8 ± 8.9	76.6 ± 11.6	
All native perennials	113.2 ± 31.7	102.9 ± 30.6	Burnt>Unburnt (0.01)
Astroloma humifusum	1.3 ± 0.5	0.3 ± 0.2	Burnt>Unburnt (0.02)
Baumea juncea	0.3 ± 0.1	1.1 ± 0.5	Burnt<Unburnt (0.02)
Dodonaea baueri	0.4 ± 0.2	0.4 ± 0.2	
Goodenia varia	0.9 ± 0.3	0.4 ± 0.2	
Hibbertia sp.	2.7 ± 0.9	0.6 ± 0.4	Burnt>Unburnt (<0.01)
Juncus pallidus	91.1 ± 31.9	93.7 ± 30.5	
Lasiopetalum baueri	0.8 ± 0.4	0.1 ± 0.1	Burnt>Unburnt (0.04)
Lepidosperma viscidum	0.8 ± 0.3	0.6 ± 0.3	
Rytidosperma sp.	3.9 ± 1.0	0.8 ± 0.3	Burnt>Unburnt (<0.01)
Schoenus maschalinus	1.5 ± 0.6	1.5 ± 0.7	
Thryptomene ericaea	4.2 ± 1.0	1.7 ± 0.5	Burnt>Unburnt (<0.01)
All introduced species	69.7 ± 7.8	57.3 ± 8.8	Burnt>Unburnt (0.02)
All introduced annual/biennial	66.0 ± 7.0	54.2 ± 7.9	Burnt>Unburnt (0.06)
Aira elegantissima	2.2 ± 1.0	1.6 ± 1.0	
Arctotheca calendula	6.1 ± 1.6	2.0 ± 0.8	Burnt>Unburnt (<0.01)
Avena barbata	20.7 ± 4.7	18.7 ± 5.5	
Centaurium tenuiflorum	1.5 ± 0.8	1.6 ± 0.9	
Ehrharta longiflora	0.8 ± 0.4	1.6 ± 0.8	
Hypochaeris glabra	0.7 ± 0.3	0.4 ± 0.2	
Isolepis marginata	18.7 ± 3.0	12.6 ± 3.0	Burnt>Unburnt (0.05)
Lolium rigidum	0.3 ± 0.1	0.5 ± 0.2	
Sonchus asper	5.6 ± 1.0	7.4 ± 1.7	
Sonchus oleraceus	0.6 ± 0.2	0.5 ± 0.2	
All introduced perennials	3.7 ± 0.8	3.1 ± 0.9	
Cynodon dactylon	2.2 ± 0.7	1.2 ± 0.5	
Solanum nigrum	1.1 ± 0.4	1.1 ± 0.4	

The number of native species emerging from heat plus smoke treated soil (3.1 species per tray) was significantly higher compared to untreated trays (2.4 species per tray; Table 4). Burning also significantly increased the species richness of perennials from 0.9 species per tray to 1.5 species per tray (Table 4). The number of introduced species detected in trays was not influenced by burning (1.8 species in unburnt trays vs 2.0 species in burnt trays; Table 4). The fire treatment also had 17 unique native species that did not emerge in untreated trays, including the nationally endangered *Olearia microdisca*. In comparison, four native species were unique to the untreated trays (Table 5). One introduced species was unique to burnt trays compared to four for controls (Table 6).

Table 4. Effect of heat and smoke on seedling emergency from *ex situ* soil samples. Comparisons of species richness of seedlings emerging from burnt and unburnt treatments for different categories of plants from *ex situ* trials using generalised linear mixed models. Mean richness per tray are given ± standard error. Additional statistical details can be found in Table S3 of Appendix 1.

Longevity & life form class/species	**Burnt**	**Unburnt**	**Significantly different (*P* value)**
All natives	3.1 ± 0.2	2.4 ± 0.2	Burnt>Unburnt (<0.01)
All native perennials	1.5 ± 0.1	0.9 ± 0.1	Burnt>Unburnt (<0.01)
Native annuals/biennials	1.6 ± 0.1	1.5 ± 0.1	
All introduced	2.0 ± 0.1	1.8 ± 0.1	Burnt>Unburnt (0.09)
Introduced perennials	0.2 ± 0.1	0.2 ± 0.1	
Introduced annuals/biennials	1.8 ± 0.1	1.6 ± 0.1	Burnt>Unburnt (0.09)

Table 5. Numbers of trays or quadrats in which one or more seedlings of each native species (or different categories of plants) were detected for 144 quadrats (*in situ* trials) or 312 trays (*ex situ* trials) for all quadrats or all trays combined (A) and for quadrats/trays that were burnt (B), unburnt (UB), fenced (F) or unfenced (UF), disturbed (D) or undisturbed (UD)

	In situ							***Ex situ***		
Longevity & life form class/species (n = 80 species)	**A**	**B**	**UB**	**F**	**UF**	**D**	**UD**	**A**	**B**	**UB**
All natives	101	51	50	52	49	44	57	262	136	126
All native annuals/biennials	21	12	9	12	9	10	11	224	115	109
Centrolepis strigosa (R.Br.) Roem. & Schult.	2	0	2	1	1	1	1	28	16	12
Crassula decumbens Thunb. var. *decumbens*	0	0	0	0	0	0	0	2	2	0
Dysphania pumilio (R.Br.) Mosyakin & Clemants	13	9	4	6	7	5	8	18	7	11
Juncus bufonius L.	0	0	0	0	0	0	0	109	54	55
Lachnagrostis filiformis (G.Forst.) Trin.	1	0	1	0	1	0	1	39	19	20
Lagenophora huegelii Benth.	2	1	1	2	0	2	0	0	0	0
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt	1	0	1	1	0	0	1	178	89	89
Senecio quadridentatus Labill.	2	2	0	1	1	1	1	1	1	0
Wahlenbergia gracilenta Lothian	5	1	4	3	2	4	1	0	0	0
All native perennials	92	48	44	45	47	40	52	189	106	83
Acacia sp.	9	7	2	5	4	5	4	0	0	0
Acacia spinescens Benth.	2	1	1	0	2	0	2	0	0	0
Acrotriche serrulata R.Br.	1	0	1	1	0	0	1	0	0	0
Allocasuarina muelleriana (Miq.) L.A.S.Johnson	3	2	1	2	1	3	0	0	0	0
Astroloma conostephioides (Sond.) F.Muell. ex Benth.	0	0	0	0	0	0	0	4	3	1
Astroloma humifusum (Cavs) R.Br.	7	6	1	6	1	2	5	13	9	4
Atriplex cinerea Poir.	1	1	0	1	0	1	0	0	0	0
Austrostipa sp	24	11	13	18	6	16	8	0	0	0
Baumea juncea	0	0	0	0	0	0	0	13	4	9
Bertya rotundifolia F.Muell.	1	0	1	1	0	0	1	2	1	1
Callistemon rugulosus (D.F.K.Schltdl. ex Link) DC.	9	8	1	5	4	4	5	0	0	0
Calytrix glaberrima	0	0	0	0	0	0	0	6	5	1
Calytrix tetragona Labill.	8	2	6	2	6	2	6	3	2	1
Carex inversa	0	0	0	0	0	0	0	2	2	0
Carpobrotus rossii (Haw.) Schwantes	1	1	0	0	1	0	1	0	0	0

Cassytha pubescens R.Br.	1	1	0	1	0	1	0	0	0	0
Choretrum glomeratum R.Br. var. *glomeratum*	1	1	0	1	0	1	0	2	1	1
Correa reflexa (Labill.) Vent. var. *insularis* P. G.Wilson	8	1	7	5	3	2	6	1	1	0
Daviesia brevifolia Lindl.	1	0	1	0	1	0	1	1	1	0
Dianella brevicaulis (Ostenf.) G.W.Carr & P.F.Horsfall	3	1	2	1	2	2	1	0	0	0
Dichondra repens	0	0	0	0	0	0	0	1	1	0
Dillwynia sericea A.Cunn.	3	1	2	3	0	1	2	1	0	1
Dodonaea baueri Endl.	0	0	0	0	0	0	0	12	7	5
Dodonaea hexandra F.Muell.	5	2	3	2	3	1	4	0	0	0
Dodonaea viscosa	2	1	1	2	0	1	1	0	0	0
Drosera macrantha Endl.	7	3	4	6	1	3	4	0	0	0
Drosera whittakeri Planch.	9	5	4	6	3	3	6	6	1	5
Eucalyptus cneorifolia DC.	26	13	13	17	9	16	10	0	0	0
Eucalyptus cosmophylla F.Muell.	12	4	8	8	4	7	5	0	0	0
Eutaxia diffusa F.Muell.	0	0	0	0	0	0	0	2	1	1
Eutaxia microphylla (R.Br.) C.H.Wright & Dewar.	0	0	0	0	0	0	0	1	1	0
Gonocarpus mezianus (H.Schindl.) Orchard.	0	0	0	0	0	0	0	2	2	0
Goodenia varia R.Br.	0	0	0	0	0	0	0	14	9	5
Grevillea ilicifolia (R.Br.) R.Br. subsp. *ilicifolia*	6	5	1	2	4	2	4	2	1	1
Gyrostemon sp.	0	0	0	0	0	0	0	1	1	0
Hibbertia sp.	11	7	4	7	4	5	6	15	11	4
Ixodia achillaeoides R.Br. subsp. *alata* (Schltdl.) Copley	0	0	0	0	0	0	0	3	3	0
Juncus pallidus R.Br.	19	11	8	9	10	8	11	97	55	42
Juncus subsecundus N.A.Wakef.	13	8	5	4	9	5	8	0	0	0
Lasiopetalum baueri Steetz/L. schulzenii (F.Muell.) Benth.	4	1	3	3	1	3	1	9	7	2
Laxmannia orientalis Keighery.	1	1	0	1	0	1	0	2	2	0
Lepidosperma canescens Boeck.	5	1	4	4	1	3	2	0	0	0
Lepidosperma viscidum R.Br.	11	4	7	9	2	3	8	13	8	5
Logania linifolia Schltdl.	0	0	0	0	0	0	0	7	5	2
Logania ovata R.Br.	0	0	0	0	0	0	0	2	2	0
Lythrum hyssopifolia L.	2	2	0	0	2	1	1	83	51	32
Melaleuca gibbosa Labill.	11	8	3	7	4	5	6	0	0	0
Melaleuca lanceolata Otto.	12	4	8	5	7	7	5	0	0	0

Melaleuca uncinata R.Br.	21	7	14	9	12	9	12	0	0	0
Micrantheum demissum F.Muell.	0	0	0	0	0	0	0	4	3	1
Myoporum sp.	0	0	0	0	0	0	0	2	2	0
Olearia microdisca J.M.Black	0	0	0	0	0	0	0	4	4	0
Orthrosanthus multiflorus	0	0	0	0	0	0	0	2	0	2
Patersonia occidentalis R.Br.	5	2	3	3	2	1	4	0	0	0
Pelargonium australe	0	0	0	0	0	0	0	1	1	0
Pimelea stricta Meisn.	1	0	1	1	0	0	1	0	0	0
Pomaderris paniculosa F.Muell. ex Reissek.	1	1	0	0	1	0	1	0	0	0
Prostanthera sp.	0	0	0	0	0	0	0	4	3	1
Pultenaea acerosa R.Br. ex Benth.	0	0	0	0	0	0	0	1	0	1
Pultenaea daphnoides J.C.Wendl.	2	1	1	2	0	1	1	5	4	1
Rhagodia candolleana Moq.	5	1	4	5	0	2	3	0	0	0
Rytidosperma sp.	13	8	5	6	7	6	7	29	19	10
Schoenus maschalinus Roem. & Schult.	2	0	2	0	2	0	2	14	8	6
Spyridium eriocephalum Fenzl var. *glabrisepalum* J.M.Black	0	0	0	0	0	0	0	5	5	0
Stackhousia aspericocca Schuch.	1	1	0	1	0	1	0	0	0	0
Stackhousia monogyna auct.non Labill	1	1	0	0	1	1	0	0	0	0
Stylidium armeria (Labill.)	1	1	0	1	0	0	1	0	0	0
Thelymitra sp.	2	1	1	1	1	0	2	1	0	1
Thryptomene ericaea F.Muell.	17	7	10	4	13	7	10	42	26	16
Thysanotus patersonii R.Br.	4	3	1	3	1	2	2	1	1	0
Xanthorrhoea semiplana F.Muell. subsp. *tateana* (F.Muell.) Bedford	16	6	10	8	8	7	9	0	0	0
Total richness	56	48	45	48	41	44	48	50	46	33
Number of unique species in treatment or method	30	11	8	15	8	8	12	24	17	4

Table 6. Numbers of trays or quadrats in which one or more seedlings of each introduced species (or different categories of plants) were detected for 144 quadrats (*in situ* trials) or 312 trays (*ex situ* trials) for all quadrats or all trays combined (A) and for quadrats/trays that were burnt (B), unburnt (UB), fenced (F) or unfenced (UF), disturbed (D) or undisturbed (UD).

	In situ							***Ex situ***		
Longevity & life form class/species (n = 34 species)	**A**	**B**	**UB**	**F**	**UF**	**D**	**UD**	**A**	**B**	**UB**
All introduced species	76	43	33	38	38	36	40	204	103	101
All introduced annuals/biennials	70	38	32	41	29	34	36	200	102	98
Aira elegantissima Schur.	1	0	1	1	0	1	0	10	6	4
Arctotheca calendula (L.) Levyns.	14	12	2	8	6	9	5	35	24	11
Avena barbata Pott ex Link.	35	18	17	18	17	19	16	77	43	34
Briza minor L.	0	0	0	0	0	0	0	6	3	3
Bromus diandrus Roth.	0	0	0	0	0	0	0	9	4	5
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch.	0	0	0	0	0	0	0	14	7	7
Cerastium glomeratum Thuill.	0	0	0	0	0	0	0	3	1	2
Cirsium vulgare (Savi) Ten.	1	0	1	0	1	0	1	0	0	0
Cyperus tenellus L.f.	2	2	0	0	2	1	1	9	5	4
Ehrharta longiflora Sm.	5	2	3	3	2	2	3	15	6	9
Ehrharta villosa (L.f.) Schult.f. ex Schult. & Schult.f.	0	0	0	0	0	0	0	1	1	0
Galium murale (L.) All.	0	0	0	0	0	0	0	2	1	1
Hypochaeris glabra L.	17	7	10	10	7	7	10	15	8	7
Isolepis marginata (Thunb.) A.Dietr.	4	1	3	3	1	1	3	110	58	52
Kickxia elatine ssp *crinita*	0	0	0	0	0	0	0	4	2	2
Lagurus ovatus L.	5	1	4	4	1	3	2	5	2	3
Lolium rigidum Gaudin.	0	0	0	0	0	0	0	11	4	7
Polygonum aviculare L.	0	0	0	0	0	0	0	7	2	5
Soliva sessilis Ruiz & Pavs	5	4	1	3	2	2	3	0	0	0
Sonchus asper (L.) Hill	0	0	0	0	0	0	0	95	48	47
Sonchus oleraceus L.	2	0	2	1	1	1	1	15	9	6
Trifolium campestre Schreb.	13	7	6	6	7	5	8	11	9	2
Trifolium subterraneum L.	0	0	0	0	0	0	0	3	0	3
Vulpia bromoides (L.) Gray.	18	14	4	9	9	10	8	40	24	16

All introduced perennials	37	21	16	20	17	17	20	45	25	20
Asparagus asparagoides (L.) Druce f.	11	6	5	5	6	5	6	1	0	1
Conyza sp.	0	0	0	0	0	0	0	1	0	1
Cynodon dactylon (L.) Pers. var. *dactylon*	17	10	7	9	8	10	7	19	11	8
Ehrharta calycina Sm.	4	2	2	3	1	3	1	0	0	0
Malva parviflora L.	0	0	0	0	0	0	0	4	3	1
Oxalis pes-caprae L.	3	1	2	2	1	1	2	1	0	1
Romulea rosea (L.) Eckl.	10	5	5	6	4	3	7	0	0	0
Senecio pterophorus DC.	2	2	0	1	1	1	1	0	0	0
Solanum nigrum L.	8	6	2	5	3	4	4	19	8	11
Taraxacum officinale auct.non F.H.Wigg.	0	0	0	0	0	0	0	5	4	1
Total richness in treatment or method	20	17	18	18	19	19	19	29	25	28
Number of unique species in treatment or method	5	2	3	1	2	1	1	14	1	4

***In situ* experiment**

Differences between sites

Site location significantly influenced abundance of seedlings (χ^2 (5) =88.3, P = <0.01) and species richness (χ^2 (5) = 78, P = <0.01) in quadrats used for the *in situ* study. More native seedlings and native species germinated from the soil seedbank of the revegetation site (CV) compared to nearby remnant roadside vegetation (96 seedlings m^{-2} in CV vs 22 seedlings m^{-2} in RV; 4.5 species m^{-2} in CV vs 2.8 species m^{-2} in RV; Figure 5). We also found that abundance ranged from 146 seedlings m^{-2} in CV quadrats to 4 seedlings m^{-2} in RR quadrats, and that species richness ranged from 7.0 species m^{-2} in CV quadrats to 2.0 species m^{-2} in RR quadrats (Figure 6).

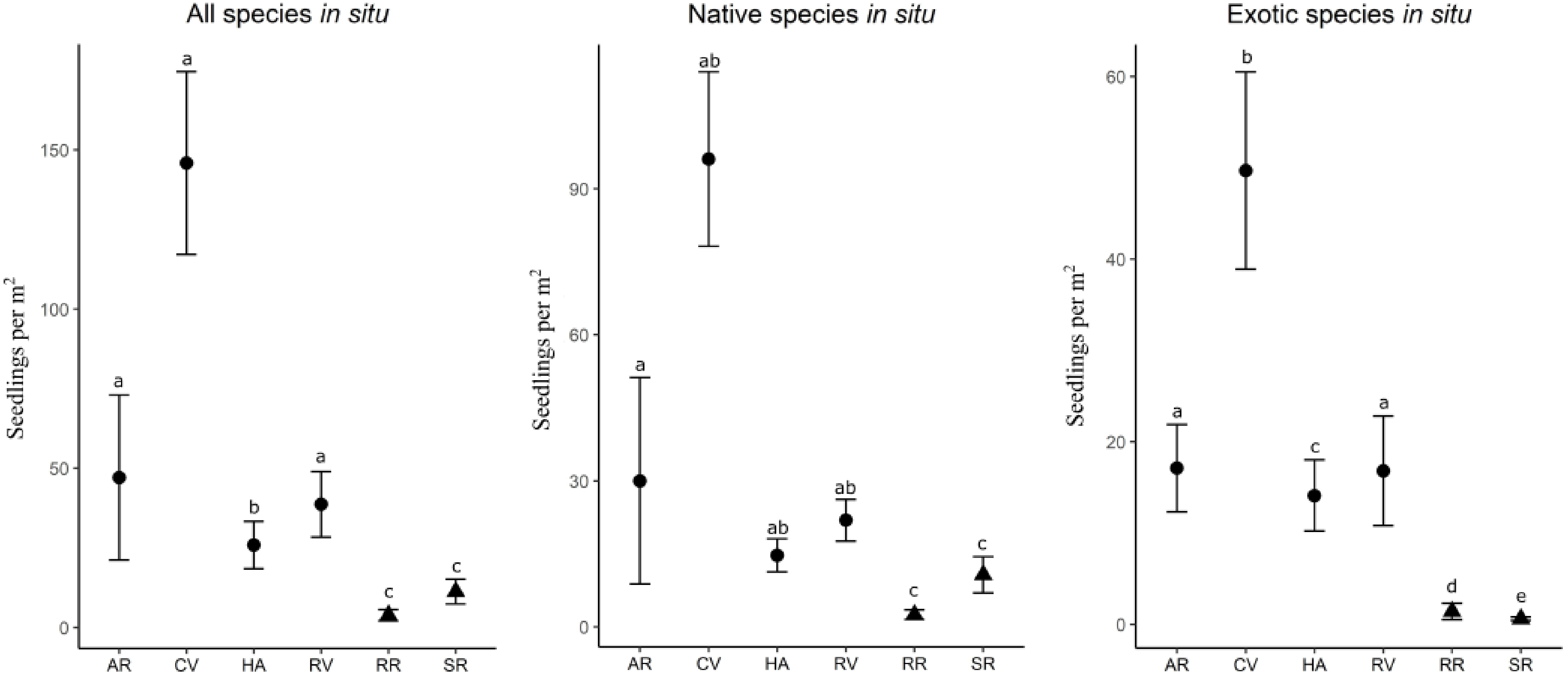

Figure 5. Effect of site on the abundance of seedlings emerging from the *in situ* method. Results are given as mean (± SE) of seedlings per m^2. Circles denote healthy sites (>10 % native understorey), whereas triangles denote a degraded site (<10 % native understorey). The various sites are: Cygnet Revegetation (CV), Roadside Vegetation (RV), Airport Remnant (AR), Heritage Agreement (HA), Spring Road Remnant (SR), Redbanks Rd Remnant (RR). Different letters represent significant differences as generated using generalised linear mixed models. Additional statistical details can be found in Table S4.1, S4.2 and S4.3 of Appendix 1.

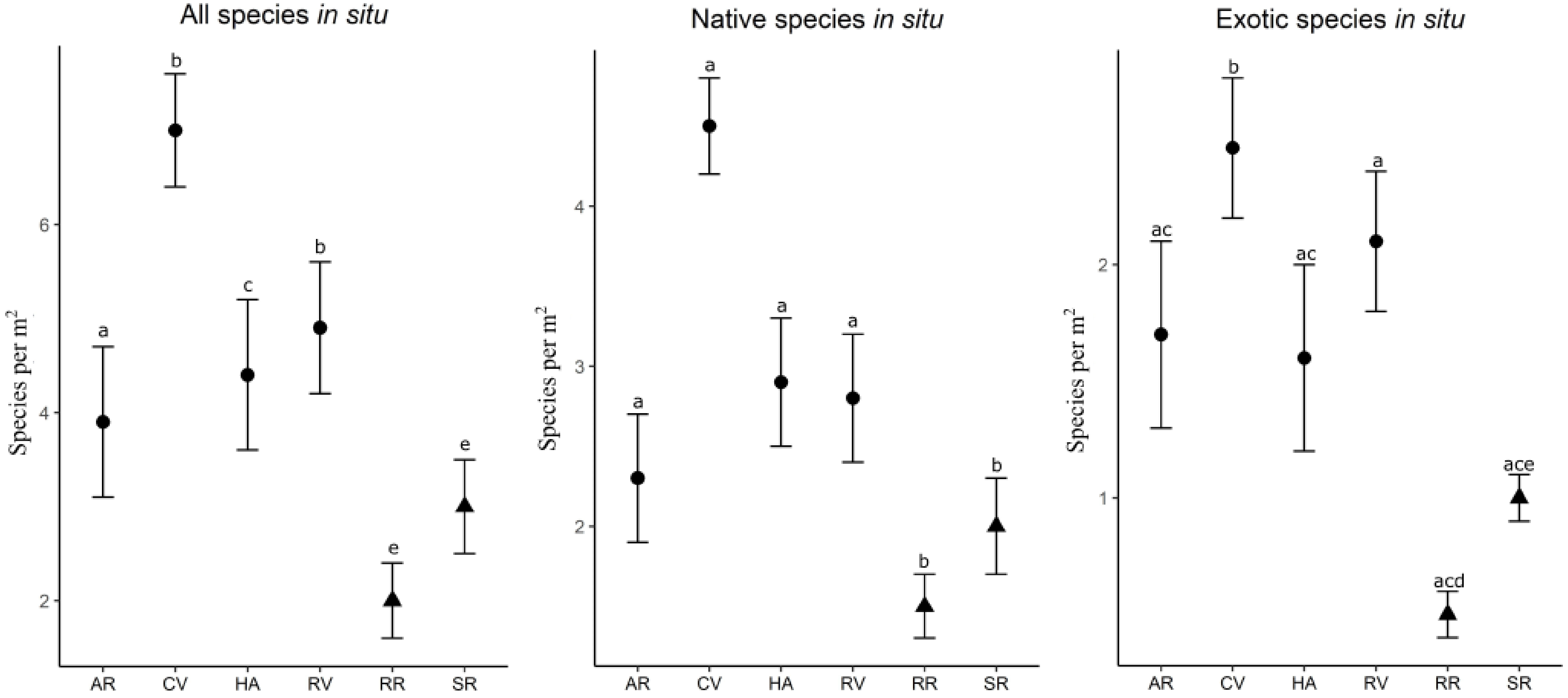

Figure 6. Effect of site on the richness of seedlings from the *in situ* method. Results are given as the number of species (± SE) per m^2. Circles denote healthy sites (>10 % native understorey), whereas triangles denote a degraded site (<10 % native understorey). The various sites are: Cygnet Revegetation (CV), Roadside Vegetation (RV), Airport Remnant (AR), Heritage Agreement (HA), Spring Road Remnant (SR), Redbanks Rd Remnant (RR). Different letters represent significant differences as generated using generalised linear mixed models. Additional statistical details can be found in Table S4.1, S4.2 and S4.3 of Appendix 1.

Effect of burning

The temperatures at the surface and at depths of 0.5 cm, 1 cm, and 2 cm below the surface were 230 ± 3 °C, 169 ± 5 °C, 97 ± 3 °C, and 57 ± 3 °C respectively (mean ± SE). Application of fire using burn boxes did not have a significant effect on the overall number of native seedlings or species richness of seedlings subsequently emerging (Table 7; Table 8). However, there were significantly more native annuals/biennials seedlings in the burnt quadrats (burnt 5 seedlings m^{-2} vs unburnt 1 seedlings m^{-2}; Table 7). Burning did not significantly influence introduced seedling emergence or species richness. However, more introduced perennial seedlings were detected in burnt quadrats (burnt 47 seedlings m^{-2} vs unburnt 10 seedlings m^{-2}; Table 6). This included two introduced perennial species *Cynodon dactylon* and *Romulea rosea* (Table 7).

Table 7. Effect of *in situ* treatments on the abundances of seedlings emerging in quadrats. Treatments include burnt (B), unburnt (UB), fenced (F), unfenced (UF), disturbed (D), and undisturbed (UD). Mean germinants m^{-2} are given ± standard error. Significant differences were generated using generalised linear mixed models and only data from paired quadrats where the target emerged in at least one quadrat were included in the analysis. Additional statistical details can be found in Table S5.1, S5.2, and S5.3 of Appendix 1.

Longevity & life form class/species	**B**	**UB**	**D**	**UD**	**F**	**UF**	**Significance (*P* value)**
All natives	31.5 ± 6.1	26.7 ± 4.0	28.6 ± 5.5	29.8 ± 5.2	33.9 ± 5.8	24.9 ± 4.8	Fenced>Unfenced (0.02)
All native annual/biennial	4.7 ± 1.7	1.2 ± 0.4	3.3 ± 1.4	2.9 ± 1.2	3.0 ± 1.2	3.3 ± 1.5	Burnt>Unburnt (0.01)
Dysphania pumilio	23.4 ± 4.5	na	34.5 ± 0.5	16.2 ± 5.0	20.8 ± 8.4	20.8 ± 5.8	
All native perennials	26.8 ± 4.4	25.5 ± 3.6	25.3 ± 4.1	26.9 ± 4.0	30.9 ± 4.6	21.6 ± 3.3	Fenced>Unfenced (0.06)
Acacia sp.	0.3 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	
Austrostipa sp.	24 ± 12.0	8.0 ± 2.0	16.8 ± 8.6	11.9 ± 5.1	10.7 ± 2.7	36.3 ± 32.3	Burnt>Unburnt (0.01)
Eucalyptus cneorifolia	4.7 ± 1.4	4.3 ± 0.7	5.5 ± 1.2	3.2 ± 0.7	5.1 ± 1.0	3.4 ± 0.9	
Eucalyptus cosmophylla	4.8 ± 3.4	6.6 ± 1.5	6.0 ± 2.0	6.0 ± 2.4	4.6 ± 0.6	8.8 ± 4.2	Unburnt>Burnt (0.06), Unfenced>Fenced (0.05)
Hibbertia sp.	5.6 ± 3.2	4.0 ± 2.7	3.7 ± 2.0	6.3 ± 4.1	6.4 ± 3.6	3.0 ± 2.3	
Juncus pallidus	23.0 ± 4.4	22.4 ± 4.2	18.7 ± 4.5	25.8 ± 3.8	21.9 ± 4.2	23.3 ± 4.3	
Lepidosperma viscidum	26.3 ± 12.2	11.3 ± 4.2	13.3 ± 9.9	18.0 ± 6.6	19.3 ± 6.1	5.0 ± 4.0	
Melaleuca uncinata	3.0 ± 2.0	4.0 ± 1.3	4.3 ± 1.5	3.3 ± 1.6	3.8 ± 1.2	3.7 ± 2.2	
Rytidosperma sp.	6.3 ± 1.7	5.8 ± 2.0	7.6 ± 2.8	5.0 ± 0.9	6.5 ± 0.9	5.7 ± 2.4	
Thryptomene ericaea	9.7 ± 4.1	12.4 ± 4.0	10.1 ± 5.1	12.1 ± 3.5	10.8 ± 3.9	11.5 ± 3.6	Fenced>Unfenced (0.02)
Xanthorrhoea semiplana subsp. *tateana*	5.6 ± 3.1	7.8 ± 3.1	11.0 ± 4.4	4.4 ± 2.0	7.7 ± 3.9	6.3 ± 2.6	
All introduced species	64.5 ± 18.7	28.5 ± 10.3	48.5 ± 15.2	46.4 ± 18.2	45.0 ± 14.2	51.7 ± 19.6	
All introduced annual/biennial	17.1 ± 5.2	18.6 ± 6.4	19.0 ± 6.4	16.8 ± 5.4	23.1 ± 6.7	13 ± 4.9	
Arctotheca calendula	7.6 ± 4.5	10.0 ± 5.0	9.6 ± 5.0	3.7 ± 1.3	6.0 ± 2.5	9.7 ± 6.7	
Avena barbata	24.6 ± 10.3	57.4 ± 23.4	40.2 ± 17.6	38.4 ± 17.1	54.2 ± 19.4	21.4 ± 11.9	Fenced>Unfenced (0.02)
Hypochaeris glabra	3.5 ± 2.2	4.8 ± 1.8	3.8 ± 2.4	4.9 ± 1.6	5.5 ± 2.0	2.6 ± 1.4	
Trifolium campestre	11.1 ± 5.0	9.8 ± 3.4	3.6 ± 1.7	14.9 ± 4.1	15.0 ± 5.4	6.7 ± 2.7	
Vulpia bromoides	28.9 ± 9.4	18.0 ± 6.7	20.7 ± 9.4	34.4 ± 12.0	14.8 ± 3.7	36.7 ± 12.8	
All introduced perennials	47.4 ± 13.5	9.9 ± 3.9	29.5 ± 8.8	29.6 ± 12.8	21.9 ± 7.5	38.7 ± 14.7	Burnt>Unburnt (0.02)
Cynodon dactylon	67.4 ± 14.6	25.4 ± 10.3	54.5 ± 16.2	52.1 ± 17.3	50.0 ± 18.0	56.4 ± 15.5	Burnt>Unburnt (0.06)
Romulea rosea	36.3 ± 27.8	3.7 ± 2.7	13.7 ± 9.8	28.6 ± 27.7	10.0 ± 6.9	42.2 ± 41.6	Burnt>Unburnt (0.05)
Solanum nigrum	3.2 ± 0.8	2.5 ± 1.5	4.0 ± 1.1	2.0 ± 0.6	2.2 ± 0.8	4.3 ± 0.9	

na=Not applicable/insufficient data for analysis.

Table 8. Effect of *in situ* treatments on the richness of germinants in quadrats. Treatments include burnt (B), unburnt (UB), fenced (F), unfenced (UF), disturbed (D), and undisturbed (UD). Significant differences were generated using generalised linear mixed models and only data from paired quadrats where the target emerged in at least one quadrat were included in the analysis. The mean number of species m^{-2} is given ± standard error. Additional statistical details can be found in Table S6.1, S6.2, and S6.3 of Appendix 1.

Longevity & life form class/species	**B**	**UB**	**D**	**UD**	**F**	**UF**	**Significance (*P* value)**
All natives	3.8 ± 0.4	4.2 ± 0.5	4.2 ± 0.5	3.8 ± 0.4	4.6 ± 0.5	3.4 ± 0.4	
All native perennials	3.4 ± 0.3	3.8 ± 0.4	3.8 ± 0.3	3.5 ± 0.3	4.2 ± 0.4	3.0 ± 0.3	Fenced>Unfenced (< 0.01)
All native annuals/biennials	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	
All introduced species	2.4 ± 0.3	1.9 ± 0.3	2.2 ± 0.4	2.1 ± 0.3	2.3 ± 0.3	2.0 ± 0.3	
All introduced perennials	1.3 ± 0.1	1.1 ± 0.2	1.2 ± 0.2	1.2 ± 0.1	1.2 ± 0.2	1.2 ± 0.2	
All introduced annuals/biennials	1.1 ± 0.2	0.9 ± 0.1	1.1 ± 0.2	0.9 ± 0.1	1.1 ± 0.1	0.9 ± 0.1	

Effect of fencing

Fencing after fire significantly increased the number of native seedlings which were recorded in quadrats (fenced 34 seedlings m^{-2} vs unfenced 25 seedlings m^{-2}; Table 7). Similarly, the fenced quadrats also contained more native perennial seedlings (fenced 31 seedlings m^{-2} vs unfenced 22 seedlings m^{-2}; Table 7). The richness of native perennial seedlings was also significantly higher in fenced quadrats (4.2 species m^{-2}) compared to unfenced quadrats (3.0 species m^{-2}; Table 8).

While the overall number of introduced seedlings was not affected by fencing, the abundance of the introduced grass *Avena barbata* increased 2.5-fold in fenced quadrats (Table 7). However, the overall richness of introduced species was not affected by fencing (fenced 2.3 species m^{-2} vs unfenced 2.0 species m^{-2}; Table 8).

Effect of disturbance

The effect of manually tilling quadrats (additional disturbance treatment) did not affect the seedling abundance or the number of species that germinated for both native and introduced species (Table 7; Table 8).

Comparison between *in situ* and *ex situ* experiments

We detected 8770 seedlings from the *in situ* experiment (1 m^2 quadrats), compared to 7025 seedlings from the *ex situ* experiment (0.105 m^2 trays). Across both experiments, a total of 114 species were detected, 35 were unique to the *in situ* method and 38 were unique to the *ex situ* method. A total of 80 native species were detected, 56 of which were detected *in situ* and 50 *ex situ* (Table 5). For introduced species, 34 species were detected overall, 20 *in situ* and 29 *ex situ* (Table 6). We extrapolated the number of seedlings from the surface area of trays 0.105 m^2 to the area of 1 m^2 *in situ* quadrats (9.5-fold increase) to compare the number of seedlings per 1 m^2 between the methods. Seedling abundance estimates from the *ex situ* trays was 288 seedlings m^{-2}, compared with 77 seedlings m^{-2} from the *in situ* quadrats (T (321) = 7.90, P = <0.01).

Rarefaction plots suggest that both methods predict similar total species richness with similar numbers of replicates (~75 species detected with either 120 quadrats *in situ* or 130 trays *ex situ*; Figure 7). However, for the six sites assessed by both methods, the number of replicates (trays/quadrats) required to detect 30 species varied according to site; with the *ex situ* method requiring less replication for three sites, and the *in situ* method requiring less replication for one site, while two sites had similar richness with a similar number of samples (Figures S7.1 and S7.2 in Appendix 1).

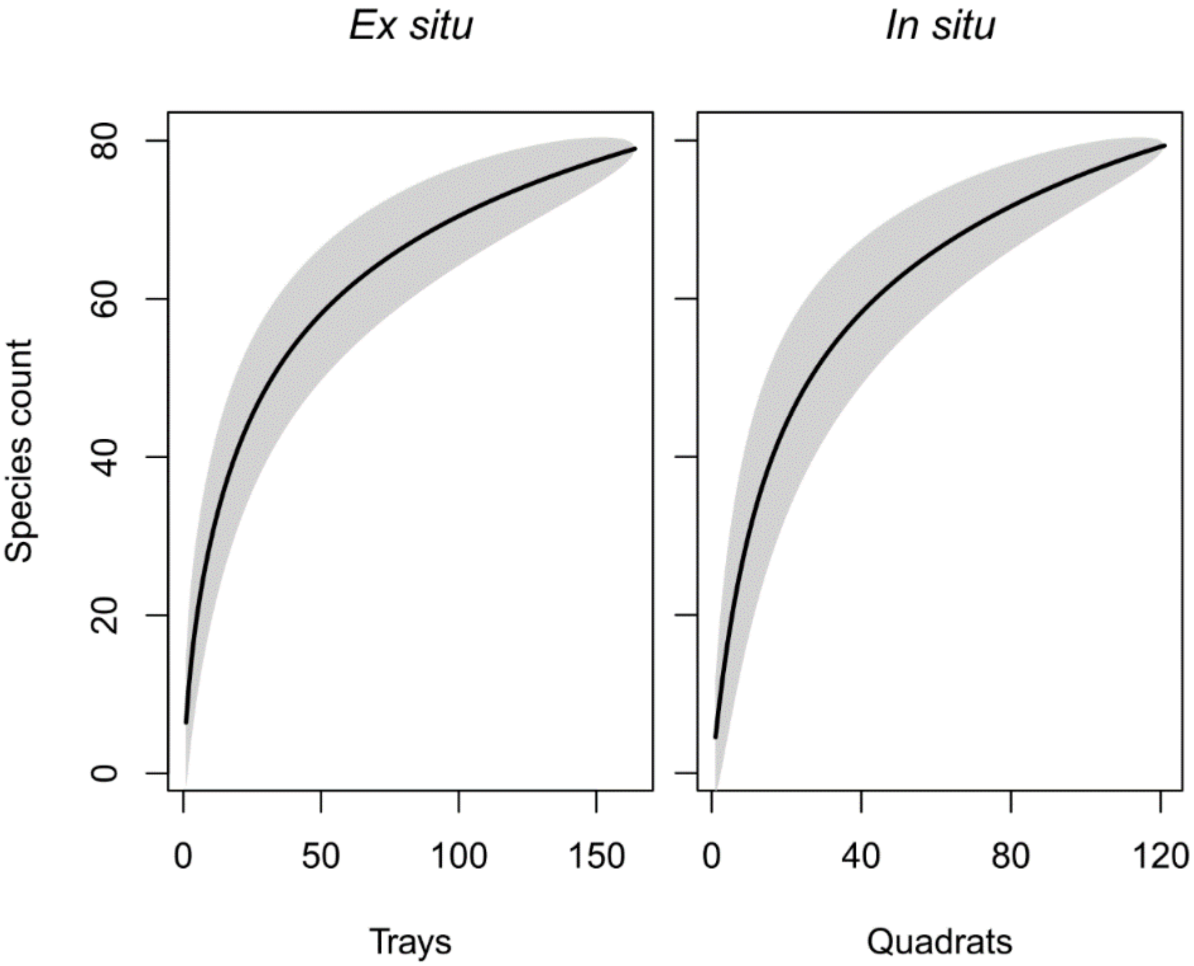

Figure 7. Rarefaction curves showing the relationship between accumulated counts of species and increasing numbers of trays or quadrats for *ex situ* trays and *in situ* quadrats averaged across sites. Figures S7.1 and S7.2 in Appendix 1 show rarefaction plots for each site for both methods. Shaded areas represent 95 % confidence intervals.

For native seedlings, we detected 4070 seedlings from *in situ* quadrats, versus 5962 seedlings from *ex situ* trays. This equated to an average of 225 seedlings m^{-2} *ex situ*, significantly more than the 29 seedlings m^{-2} detected *in situ* (Table 9). This was also the case for native annuals/biennials (*ex situ* 117 seedlings m^{-2} vs *in situ* 3 seedlings m^{-2}; Table 9). Likewise, significantly more *Juncus pallidus* seedlings emerged *ex situ* (Table 9). Similar trends occurred for introduced species. Overall, significantly more seedlings of introduced species appeared *ex situ* (64 seedlings m^{-2}) than *in situ* (47 seedlings m^{-2}; Table 9). This also applied to introduced annual/biennial species (*ex situ* 60 seedlings m^{-2} vs *in situ* 18 seedlings m^{-2}; Table 9).

Table 9. Comparison of seedling abundances between *in situ* 1 m^2 quadrats and *ex situ* 35 × 30 cm trays extrapolated to 1 m^2. To convert the *ex situ* abundance (seedlings per tray) to *ex situ* seedlings m^2 multiply by 9.5; given the surface area of the *ex situ* trays are 0.105 m^2 compared to the 1 m^2 *in situ* quadrats. Significant differences are shown between the *in situ* means and the extrapolated *ex situ* means using generalised linear mixed models. The mean number of seedlings per 1 m^2 are given plus or minus standard error. Additional statistical details can be found in Table S8.1 and S8.2 of Appendix 1.

Longevity & life form class/species	***In situ***	**Extrapolated *ex situ***	**Significantly different (*P* value)**
All species	76.6 ± 15.7	288.2 ± 37.7	*In situ* < Extrapolated *Ex situ* (<0.01)
All natives	29.3 ± 3.8	224.8 ± 31.7	*In situ* < Extrapolated *Ex situ* (<0.01)
All native annuals/biennials	3.1 ± 0.9	116.7 ± 9.7	*In situ* < Extrapolated *Ex situ* (<0.01)
Dysphania pumilio	20.8 ± 4.7	1.7 ± 0.5	
All native perennials	26.2 ± 2.8	108.1 ± 22	
Hibbertia sp.	5.1 ± 2.3	1.7 ± 0.5	
Juncus pallidus	22.7 ± 2.9	92.4 ± 22.0	*In situ* < Extrapolated *Ex situ* (<0.01)
Rytidosperma sp.	6.1 ± 1.2	2.3 ± 0.5	
Thryptomene ericaea	11.3 ± 2.8	3.0 ± 0.6	
All introduced	47.4 ± 11.9	63.5 ± 5.9	*In situ* < Extrapolated *Ex situ* (<0.01)
All introduced annuals/biennials	17.8 ± 4.1	60.1 ± 5.3	*In situ* < Extrapolated *Ex situ* (<0.01)
Arctotheca calendula	8.0 ± 3.7	4.0 ± 0.9	
Avena barbata	39.4 ± 12.1	19.7 ± 3.6	
Hypochaeris glabra	4.4 ± 1.4	0.6 ± 0.2	
All introduced perennials	29.5 ± 7.8	3.4 ± 0.6	
Cynodon dactylon var. *dactylon*	53.4 ± 11.4	1.7 ± 0.4	
Solanum nigrum	3.0 ± 0.7	1.1 ± 0.3	

For all species, the *ex situ* trays contained statistically similar richness to *in situ* quadrats (*ex situ* 4.4 vs *in situ* 6.2; T (355) = -0.78, *P* = 0.44). Species diversity of native species was also statistically similar between the two methods, for both mean Shannon (*ex situ* 0.8 vs *in situ* 0.7; T (196) = 0.60, *P* = 0.55) and mean Simpson diversity indices (*ex situ* 0.6 vs *in situ* 0.7; T (196) = -1.02, *P* = 0.31). However, the *ex situ* method detected significantly more native annual/biennial species than the *in situ* method (*ex situ* 1.5 vs *in situ* 0.4; Table 10), while the opposite was true for native perennials (*ex situ* 1.2 vs *in situ* 3.6; Table 10). Species composition was also different, as each method contained a variety of unique native species, which were not detected by the other method (30 unique species *in situ* vs 24 unique species *ex situ*; with 26 species appearing in both; Table 5).

For introduced species, the average species diversity was also found to be statistically similar for the two methods, with both mean Shannon (*ex situ* 0.3 vs *in situ* 0.3; (T (129) = 0.77, *P* = 0.45) and mean Simpson diversity indices (*ex situ* 0.6 vs *in situ* 0.6; (T (129) = -0.01, *P* = 1.00) being similar. Both methods resulted in statistically similar numbers of introduced species, with *in situ* quadrats containing on average 2.2 species, and *ex situ* soil trays 1.8 species (Table 10). Significantly more introduced perennials were detected *in situ* (1.2) compared to *ex situ* (0.2; Table 10). Species composition was also different between the methods, with the *in situ* quadrats containing 5 unique introduced species and *ex situ* trays containing 14 unique introduced species (Table 6).

Table 10. Comparison between the species richness of different groups between *in situ* 1 x 1 m quadrats and *ex-situ* 35 × 30 cm trays. Means are given plus or minus standard error. Significant differences between the *in situ* and *ex situ* method are analysed using this data subset. Generalised linear mixed models were used for statistical comparisons and means are given plus or minus standard error. Additional statistical details can be found in Table S9 of Appendix 1.

Longevity & life form class/species	***In situ***	***Ex situ***	**Significantly different (*P* value)**
All natives	4.0 ± 0.3	2.7 ± 0.2	
All native annuals/biennials	0.4 ± 0.1	1.5 ± 0.1	*Ex situ* > *In situ* (<0.01)
All native perennials	3.6 ± 0.2	1.2 ± 0.1	*Ex situ* < *In situ* (<0.01)
All introduced	2.2 ± 0.2	1.8 ± 0.1	
All introduced annuals/biennials	1.0 ± 0.1	1.7 ± 0.1	
All introduced perennials	1.2 ± 0.1	0.2 ± 0.1	*Ex situ* < *In situ* (<0.01)

DISCUSSION

Differences between results from the *in situ* and *ex situ* experiment

General differences

In situ and *ex situ* assessments of the soil seedbanks from mallee-heath on eastern Kangaroo Island showed similar levels of species richness but the abundances of seedlings and the species that were detected differed. Overall seedling abundances were 3.8 times higher for the *ex situ* assessments than the *in situ* assessments. This is consistent with other studies that use both methods, typical *ex situ* estimates of seedling emergence are between 3.5 to 6.5 times greater than *in situ* estimates (Akter *et al.* 2018a; Cardina and Sparrow 1996; Hopkins and Parker 1984). Of the 114 species detected emerging from the soil seedbanks of the mallee-heath on eastern Kangaroo Island, 38 were not detected using the *in situ* method and 35 were not detected with the *ex situ* method. Similar studies which employ both methods commonly find species unique to both (Akter *et al.* 2018b; Benvenuti and Pardossi 2017; Graham and Hutchings 1988; Mesquita *et al.* 2015).

Comparing seed enumeration and seedling emergence approaches

Studies that use combinations of seed enumeration and seedling emergence approaches typically report differences in the abundances of seedlings and the species detected. In the present study, we detected on average 288 seedlings m^{-2} with an *ex situ* seedling emergence approach versus 77 seedlings m^{-2} with an *in situ* seedling emergence approach. For comparison, Cardina and Sparrow (1996) investigated annual weed seed abundance in agricultural fields and detected 8900 seeds m^{-2} via seed enumeration, 55200 seedlings m^{-2} with an *ex situ* emergence approach, and 14100 seedlings m^{-2} with an *in situ* seedling emergence approach. We suggest that their estimates of seedling emergence are much greater than ours because they continuously disturbed their soil samples until no more germination occurred, whereas the soil remained undisturbed after the initial treatment in our study. Nevertheless, they argue that while all three approaches are appropriate for studying soil seedbanks, enumeration is significantly more time-consuming.

Studies that compare enumeration to *ex situ* germination are more common and typically find that seedling emergence predicts seedling abundances that are 1.5 to 6 times lower than estimates from enumeration methods (Mahé *et al.* 2020). For instance, Gonzalez and Ghermandi (2012) investigated soil seedbanks from grasslands in Patagonia and detected 9941 seeds m^{-2} via enumeration and 2493 seedlings m^{-2} using *ex situ* seedling emergence. In general, *in situ* seedling emergence studies result in lower overall abundances of seedlings than *ex situ* emergence studies, while enumeration may detect more seed. However, the enumeration technique does not assess the capacity of those seeds to germinate and establish.

Despite the *in situ* and *ex situ* methods producing similar estimates of species richness, and Simpson and Shannon diversity indices, both methods detected a different suite of species. Failing to detect all species with either method is common among studies that compare *in situ* and *ex situ* experiments (e.g. Akter *et al.* 2018b; Benvenuti and Pardossi 2017; Mesquita *et al.* 2015). This can have negative implications for threatened species that remain undetected but that require some mitigation action to persist. In eastern Kangaroo Island mallee vegetation communities, the *ex situ* seedling emergence method failed to detect the threatened species *Xanthorrhoea semiplana* subsp. *tateana*, whereas the threatened *Olearia microdisca*, *Spyridium eriocephalum* and *Logania linifolia* were unique to the *ex situ* trays. Similarly, Davies *et al.* (2013) found 53 species in an *ex situ* emergence study that were not detected in the standing vegetation, three of these species were previously unrecorded from the region indicating that *in situ* surveys of the above ground vegetation can fail to detect a range of species present in the seedbank. This highlights the importance of surveying both the above- and below-ground vegetation during vegetation assessments.

Seedbanks typical of mallee-heath vegetation

Estimates of seedling abundance and richness are typically larger than those presented here (Cardina and Sparrow 1996; Gonzalez and Ghermandi 2012; Ishikawa-Goto and Tsuyuzaki 2004; Taylor 2019). In Australia, seedling abundances have been known to range from < 100 seedlings m^{-2} across 96 taxa in dry mallee heath to > 3000 seedlings m^{-2} across 73 taxa in heathy swamps (Kenny 2012; Trezise *et al.* 2021). Our estimates appear to be typical for Australian mallee-heath vegetation communities when compared to similar research conducted on eastern Kangaroo Island. In our *in situ* quadrats, we found 27 native seedlings m^{-2} in controls and 32 native seedlings m^{-2} after fire, while Taylor (2019) found 25 native plants m^{-2} in controls and between 22 to 41 native seedlings m^{-2} after fire. However, Taylor included all plants that re-established after fire including those that re-sprouted, while we only considered seedlings. In our soil samples, we detected 225 native seedlings m^{-2} and 64 exotic seedlings m^{-2}, whereas Rawson *et al.* (2013) found 199 native seedlings m^{-2} and 173 exotic seedlings m^{-2}. Rawson *et al.* (2013) may have recorded more exotic seedlings because their samples received significantly more water than ours (irrigated daily vs ~weekly) and were kept inside a glasshouse whereas our soil samples were kept in an open-air nursery. This may have resulted in lower seed germination and lower seedling survival of some species. Furthermore, although we sampled the same vegetation community as

Rawson *et al.* (2013), the exact sampling locations differed, and this would have affected results to an unknown degree.

Treatment effects

Fencing and disturbance

Herbivory impacted estimates from our *in situ* seedling emergence study by reducing both the richness and abundance of native species, as well as the abundance of introduced species. We found that fencing significantly increased the number of native perennial species detected in quadrats. In a separate *in situ* seedling emergence study, we found that herbivores preferentially grazed threatened orchids *Spiranthes australis* and *Thelymitra cyanea* making them undetectable in unfenced quadrats (Chapter 5). This is unsurprising given kangaroos have become overabundant since European settlement within southern Australia (including the Kangaroo Island study area), causing widespread overgrazing (Department for Environment and Water 2019b; Grigg and Pople 2001; Prowse *et al.* 2019).

Overgrazing not only reduces the numbers of seedlings that can establish, survive and be detected (Alex and Woinarski 2007; Davies *et al.* 2013; Tolsma 2002) but may also reduce the numbers of seeds in the seedbank by reducing reproductive outputs (Alex and Woinarski 2007; Tiver and Andrew 1997; Vermeire *et al.* 2018). Therefore, it may be necessary to limit herbivory for some years before fire to allow species to accumulate adequate propagule reserves, as well as after fire to reduce the losses of emergent seedlings. Comparable *in situ* studies have also found that herbivory can have negative impacts on native plants by reducing cover and diversity on Kangaroo Island (Taylor 2019) and in eucalypt woodlands with heathy understoreys in south-eastern Australia (Cohn and Bradstock 2000; Meers and Adams 2003; Noble 1989). As such, unless herbivory is mitigated (e.g. through culling and/or fencing), *in situ* estimates of seedling abundance and richness will be lower than *ex situ* estimates, and species that are targeted by herbivores may be undetected as they fail to establish.

Within *in situ* quadrats, we investigated the effects of bioturbation for redistributing seed amongst the soil stratum by manually tilling the soil. Previous studies have found that burrowing animals can increase plant diversity by disturbing soil (Eldridge and James 2009; Fleming *et al.* 2014; Reichman and Seabloom 2002). Bioturbation can alter seedling establishment for a suite of different reasons including, improving microsite availability, providing dormancy breaking cues, altering surface fuel loads, spreading ectomycorrhizal fungi, dispersing seed, trapping seed, reducing competition for seedlings, and increasing soil permeability (Meysman *et al.* 2010; Meysman *et al.* 2006; Pons 2000; Ryan *et al.* 2020; Setterfield 2002; Valentine *et al.* 2017). In the present study, redistributing seeds by tilling did not affect *in situ* seedling emergence estimates, suggesting that our methods may not accurately mimic the effects of digging by animals. We argue that this was because there was not enough time between the fire treatment and the tilling treatment for seeds to become trapped within depressions in the soil; foraging pits are important for trapping seed over time, providing a cache of seeds and a refuge for seedlings to grow (James *et al.* 2009).

Site variation and seedbank heterogeneity

Many of the detected species were only represented by a few seedlings in the *in situ* quadrats; only 4 % of species were detected in twelve or more *in situ* quadrats, compared to 25 % of species in twelve or more *ex situ* trays. This was likely the result of one or several factors affecting seedling survival and detection *in situ* (e.g. herbivory and water availability), the effects of which were less severe in our *ex situ* plant nursery. This is despite our rarefaction plots suggesting greater sampling effort would have resulted in greater species detection in both studies. Low counts and detection are problematic in ecological studies as this limits the detection of treatment differences (Archaux *et al.* 2012; Garrard *et al.* 2015; McCarthy *et al.* 2013). This suggests that substantially more quadrats/trays, with larger surface areas, may be needed to detect rarer species in abundances that are adequate for assessment of treatment effects. This is especially true for *in situ* studies, which often produce lower seedling abundance estimates compared to *ex situ* studies because of added environmental stressors such as grazing and desiccation.

Site was a factor that contributed to the variance of our models, but site more commonly had a significant contribution on model dispersion when analysing *in situ* data compared to *ex* situ data. For instance, rarefaction analyses suggested that the *ex situ* approach required lower sampling replication in three sites and the *in situ* method required lower sampling in one site, and two sites had similar richness with similar sampling effort. We also found that to detect a similar number of species, the *in situ* approach required the monitoring of 8.8 times more surface area of soil than the *ex situ* approach. This was based on maximum species detection, which occurred with 120 *in situ* 1 m^2 quadrats or 130 *ex situ* 0.105 m^2 trays, based on 65 soil samples which were subsequently halved (soil volume of 0.0024 m^3 per sample). The *ex situ* approach can require less replication or monitoring to detect a similar number of species than the *in situ* approach, which may suggest the *ex situ* approach is better suited to sites with higher seed heterogeneity.

Some of the site variance within this study could be explained by differences in grazing and browsing history, and its degrading effect on vegetation. For example, across both studies, native species richness of emergent seedlings in healthy sites was at least double that of degraded sites (<10 % native understorey cover). Similar *in situ* and *ex situ* studies have shown that sites that are degraded by herbivory have lower native species richness and low seedling recruitment (Davies *et al.* 2013; Taylor 2019). Furthermore, the Cygnet Revegetation soil seedbank contained the greatest seed density and species richness, indicating that diverse revegetation which is 6 years old can quickly develop soil seedbanks that are equally as robust at recovering from fire as those of equivalent remnant vegetation.

Fire and the *ex situ* method

Results from the *ex situ* seedling emergence study showed that the burning treatment resulted in more seedlings of native perennials and more native species emerging, than without the treatment. We also found several unique species in the burn treatment, including *Olearia microdisca*, germination of which is known to respond to smoke (Johnson 2014). In a similar *ex situ* study on eastern Kangaroo Island, Rawson *et al.* (2013) also found that fire treatments (heat, smoke, and heat plus smoke) increased the number of native species that emerged, as well as the abundance of native perennial forbs, shrubs and sub-shrubs. Davies *et al.* (2013) also found that heat plus smoke treatments during an *ex situ* study increased the richness of native species emerging from soil seedbanks on eastern Kangaroo Island, but this was only the case for sites with no grazing history. Furthermore, Davies *et al.* (2013) also found that the seeds of a few introduced species were stimulated to germinate following the fire treatment, as was the case for introduced annual/biennial species in our study. For species with soil seedbanks, these *ex situ* studies suggest fire promotes native species richness after 13 months, as well as the abundance of seedlings for native perennial and introduced annual/biennial species.

Fire and the *in situ* method

Assessing results from the *in situ* seedling study gives a different perspective to the *ex situ* findings on the likely effects of fire on the post-fire appearances of plants from the soil seedbank for mallee-heaths on eastern Kangaroo Island. Overall the burning treatment did not influence the overall abundance or richness of native or introduced species that emerged as seedlings. However, burning did increase the overall abundance of native annuals/biennials, including *Dysphania pumilio*, but had no significant effect on any other species or life form group. Taylor (2019) investigated the influence of fire on vegetation in eastern Kangaroo Island *in situ* using controlled burns and found that plots that were burnt contained more native species compared to those left unburnt, provided the post-fire canopy cover was low, pre-fire native seedbank richness was high, pre-fire introduced seedbank richness was low, maximum soil temperature during fire was low, herbivory post-fire was low and proximity to adjacent unburnt remnant vegetation was high.

The *in situ* experiment demonstrates that the soil seedbanks of eastern Kangaroo Island are diverse, but that recovery from a fire can be constrained by environmental factors (Table 1). We found that fenced *in situ* quadrats contained on average 26 perennial native seedlings m^{-2} after a fire, but that these quadrats contained significantly fewer seedlings if exposed to mammalian herbivores. In Australia, seedling survival varies greatly between types of vegetation communities, ranging from 25 % after two years in semi-arid mallee (Wellington and Noble 1985), 3 % to 38 % after one year in sclerophyll woodland (Purdie and Slatyer 1976), and 22 % after one year in *Banksia* woodland (Roche *et al.* 1998). Furthermore, seedling mortality can vary greatly on the conditions after a fire (e.g. climate, grazing and interseedling competition; Chapter 5; Bird *et al.* 2012; Enright *et al.* 2015; Keith 2002; Vaughton 1998). Therefore, the likely consequences of fire on seedling emergence will be highly variable in eastern Kangaroo Island mallee, and that seedling emergence estimates represent some fraction of the total number of plants that will survive and establish into mature plants across an area that is burnt.

Variations in treatment effects between the methods

For the methods we applied, the *ex situ* approach suggests that fire promotes seedling emergence and the *in situ* approach suggests fire does not have a significant effect on seedling richness or abundance. Differences in the interpretation of the effect of fire are influenced by the factors introduced in Table 1, and these should be considered when conducting and interpreting seedling emergence studies with a similar focus. For example, 24 native species were absent from the *in situ* monitoring including the nationally vulnerable and morphophysiologically dormant *Spyridium eriocephalum* var. *glabrisepalum* which only emerged in five *ex situ* soil samples. This was likely the result of poor seedling survival *in situ,* because seedlings were targeted by herbivores or were susceptible to desiccation or other environmental stressors. Therefore, the *ex situ* approach may overestimate the number of seedlings that germinate and subsequently establish. Alternatively, other factors may have influenced detectability and seedling abundance, such as differences in the germination environments between the two studies.

Factors that influence estimates from *in situ* and *ex situ* methods

Specimen identification

Differences in species detectability and seedling abundances between *in situ* and *ex situ* approaches likely reflect differences between the methods (Table 1). A fundamental issue is that many seedlings when they first emerge are hard to identify to species level. Seedlings lack flowers and so often the primary key for confirming identification (e.g. Department for Environment and Water 2020a; Prescott 1994; Rzanny *et al.* 2019). If seedlings fail to survive and grow to a sufficient size to allow identification, then those individuals will not be detected (or may be initially misidentified). During the present study, the identification of seedlings of several species was only possible given that mature flowering individuals were present adjacent to quadrats. Thus, seedlings can be misidentified, resulting in a species not being detected (Factor 3; Table 1). Across both studies, we found that nine species could only be identified to genus level, as these immature plants lacked reproductive organs thus making identification difficult. In addition, some short-lived seedlings may also be missed if they germinate and die between two sampling periods (Factor 8; Table 1; e.g. Facelli and Temby 2002).

Presence of propagules

Propagule availability also influences detection and seedling abundance estimates for *ex situ* emergence studies which filter or sieve soil samples, as this can remove a portion of seeds or rhizomes (Factor 4; Table 1). Therefore, detection of species that depend entirely on resprouting (e.g. from rhizomes) requires *in situ* monitoring (Clarke and Dorji 2008; Kimura and Tsuyuzaki 2011; Måren and Vandvik 2009). Likewise, many species with canopy seedbanks are also unrepresented or undetected during seedling emergence studies because their seed is released in response to plant death and has a short lifespan (Bradstock 1991; Daskalakou and Thanos 1996; Enright *et al.* 2007). For example, of the seven species with canopy seedbanks detected during the study (i.e. *Allocasuarina muelleriana*, *Eucalyptus cneorifolia*, *E. cosmophylla*, *Callistemon rugulosus*, *Melaleuca gibbosa, M. lanceolata*, and *M. uncinata*; Table S10 in the Appendix), all were unique to the *in situ* method and this is unsurprising given these species retain the majority of their seeds in canopy fruits until the vegetative growth supporting the fruits dies (Factor 4; Table 1; Hanley and Lamont 2000; Kim *et al.* 2009; Rayachhetry *et al.* 1998). Although species with canopy soil seedbanks are not the focus of the present study, these species also often have transient soil seedbanks for recovering from disturbances (Daskalakou and Thanos 1996; Keith *et al.* 2002; Lunt 1994). Likewise, many species which rely on seedbanks often also facultatively resprout, and differentiating seedlings and resprouters can often be difficult (Bond and Midgley 2001).

Propagule and seedling survival

Survival of seeds and seedlings between *in situ* and *ex situ* studies are likely to differ because mortality rates of seeds and seedlings are different in the field compared to in a greenhouse or plant nursery. For example, herbivory, desiccation and competition between seedlings is reduced *ex situ* (Factor 5; Table 1; Fenner 1987; Marcora *et al.* 2013; Orrock *et al.* 2006). As such, *ex situ* estimates are generally higher or contain a different suite of species because *in situ* methods account for environmental factors such as herbivory. For instance, we found that 15 species were unique to the fenced quadrats, suggesting that mammalian herbivores target specific species which would result in seedlings of some species being undetected for *in situ* experiments that do not control herbivory (Factor 5; Table 1; Table 5). Thus, propagule and seedling survival can affect estimates of seedling abundance and species detection in seedling emergence studies.

Germination cues and seed dormancy

Seed dormancy mechanisms of species and the environment they are germinated under influences their detection and estimated seedling abundance, even when overall estimates of species diversity are similar (Factor 6 & 7; Table

1). In our study, we found no differences in overall species diversity but found that species were unique to each method. For example, *Goodenia varia* exclusively germinated in 14 soil trays. The seeds of plants in this genus are physiologically dormant and are known to require wet/dry cycles to germinate, and those conditions may have occurred exclusively in the nursery (Hoyle *et al.* 2008a; Hoyle *et al.* 2008b). Similarly, Price *et al.* (2010) attributed differences in the detection of species between different approaches to variances in the seed dormancy mechanisms of different plant species and the absence of appropriate cues to break dormancy in some species. This indicates that a wider range of treatment types and multiple treatment applications may increase the number of species detected and that it is unlikely that any one technique will detect all species within a soil seedbank.

For the mallee-heath systems on Kangaroo Island, we found that native annuals were far more common *ex situ* in the nursery, which indicates that either water availability, exposure to dormancy breaking cues, or both restricted the establishment of some species in the field (Ter Heerdt *et al.* 1999). For example, *Juncus bufonius* occurred in 59 % of trays but was not detected in the field. We suggest this was because more seeds were exposed to dormancy breaking cues as the *ex situ* method of spreading soil samples across a larger area resulted in more seeds being closer to the soil surface. Likewise, water availability was higher in *ex situ* soil trays, which were regularly irrigated.

Future research

Improving the fire and disturbance treatments

Our *in situ* fire treatment (burn box) may not have removed sufficient canopy cover to facilitate seed germination and allow a wider array of plants to re-establish from seeds (Taylor 2019). Canopy cover reduces light and temperature exposure on the soil surface, thus reducing germination rates for seeds that require these germination cues to break dormancy (Gillespie and Allen 2004; Ooi *et al.* 2004; Zhu *et al.* 2003). This may account for the lower detection of species and seedlings *in situ* compared to the *ex situ* estimates and suggests that the burn box method could be improved by mechanically removing all canopy vegetation that shades quadrats.

In the present study, the *in situ* soil disturbance treatment mixed the top 30 cm of soil which would have redistributed seed within the soil stratum. This would have influenced the availability of dormancy breaking stimuli for the redistributed seed and would also have affected the ability of seeds to emerge from different depths. In the present study, soil samples were taken before quadrats were mixed, and so to assess the impact of mixing, future studies could compare mixed samples and undisturbed samples, which are carefully removed from quadrats as to not disturb the soil stratum. Future studies could also incorporate additional treatments that focus on the effects of burrowing animals and their impact on seeds. For example, previous studies have investigated the impacts of bioturbation by replicating foraging pits/burrows, removing surface fuels, altering, and tracking seed availability or by directly comparing the effects of the presence and absence of digging animals with exclosures (Murphy *et al.* 2005; Ross *et al.* 2019; Ryan *et al.* 2020).

Maximising species detection

Future studies could expand on our findings by conducting a seed enumeration study in conjunction with both *in situ* and *ex situ* emergence approaches that include treatments that mimic fire. This would increase species detection and test whether dormancy requirements of some species were not met by either the fire treatment or the other germination cues that are inherent within the *in situ* or *ex situ* approaches. Furthermore, a second round of germination could be instigated by re-treating samples or quadrats in an attempt to stimulate further seeds to germinate and emerge. Likewise, the *ex situ* impact of disturbance caused by the sampling process could be assessed by mixing, processing, and treating samples but then returning them to their origin in the field and then assessing emergence *in situ* while also protecting them from herbivores.

Considerations when using treatments that mimic the influence of fire

We used two separate fire treatments, and these could be made more comparable in future studies by measuring both temperature over time and maximum temperature in both experiments. Soil heating can affect estimates of seedling abundance by breaking seed dormancy (obligate pyrogenic dormancy; Liyanage and Ooi 2017; Moreira and Pausas 2012; Ooi *et al.* 2014) or causing seed mortality (Auld and O'Connell 1991; Tangney *et al.* 2020; Tangney *et al.* 2019). For instance, Taylor (2019) found that native species richness steadily declined as soil temperature increased from 20 ^{o}C at 2 cm depth and that this trend continued even when extreme temperatures were reached (>190 ^{o}C). We measured soil heating *in situ* and this showed that the temperatures detected within our burn boxes were similar to those delivered to the soil during the control burns conducted by Taylor (2019). However, we did not measure soil temperature *ex situ* during the oven heating components of our fire treatment. Therefore, we cannot compare the *ex situ* temperatures to the *in situ* temperatures and make inferences about their effect on germination. Additionally, the period of heating within the burn boxes may not be an accurate depiction of the periods of heating that soil seedbanks experience during a bushfire. For example, heating periods at 2 cm below the surface have been known to exceed 120 ^{o}C for 104 minutes in areas with high fuel loads (Taylor 2019). Future studies could better assess the effect of heating on seedling emergence by measuring temperatures and heating duration within both the *ex situ* and *in situ* experiments. Alternatively, soil samples could be treated *ex situ* to fire treatments and then returned to the field alongside an *in situ* treatment.

Conclusion

Interpreting differences between the *ex situ* and *in situ* method

We investigated the soil seedbanks of mallee-heath from eastern Kangaroo Island using both an *ex situ* and *in situ* seedling emergence method. We found that the methods detected a similar species richness but with different floristic composition, with a suite of species being unique to either approach. Furthermore, the *ex situ* approach produced 3.5 times more seedlings than the *in situ* approach, meaning the *in situ* approach was less useful for detecting treatment effects as there was often insufficient data for analyses. This was despite both methods requiring a similar number of replicates to detect the same number of species. Either method may then be affected by one or many factors, such as lower seedling survival *in situ* (Table 1). For instance, we found that seedling abundance and species detection during the *in situ* seedling emergence study was significantly reduced by post fire herbivory, suggesting that estimates are higher when mammalian herbivores are excluded with fencing.

The number of seedlings that survive until maturity is generally far less than the number of seedlings that emerge soon after a fire (Table S11 of Appendix 1). Therefore, *in situ* studies may provide a better basis for predicting likely outcomes following a fire because they incorporate the effects of stressors (e.g. grazing; Meers and Adams 2003). In general, *ex situ* approaches are likely better for detecting more seedlings and therefore statistical differences between treatment groups, while *in situ* studies may provide a better guide to the likely re-establishment of plants following a fire, and both approaches should be applied to maximise species detection.

Considerations when prescribing fire based on the results of emergence studies

The present study highlights the heterogenicity of soil seedbanks, and the variability in germination response according to the availability of dormancy breaking stimuli. We found that seedling abundance estimates and species detection varied greatly between and among sites. Furthermore, species remained undetected using either approach. High seedbank heterogenicity has been found in similar studies (James *et al.* 2007; Matlack and Good 1990; Thompson 1986) and so land managers should be cautious when prescribing a burn based on information from a single seedling emergence study. We argue that no one method which evaluates soil seedbanks will determine their entire contents. Each will estimate some fraction of it. Thus, at best, the various methods provide only an indication of the capacity of soil seedbanks to re-establish plant populations after a disturbance like fire. Predictions can be improved by using multiple approaches, but not all seeds from all species in the seedbank are expected to germinate following a period of disturbance and the number of these seedlings that survive, establish and mature may be much lower due to post-disturbance conditions (e.g. competition, grazing and rainfall). However, seedling emergence studies do indicate the species likely to establish post disturbance and the appropriate interpretation of these studies depends on the acknowledgement of the factors that influence seedling emergence and survival and the restraints proposed here (Table 1).

Chapter 3. The effect of heat and smoke on the soil seedbanks of heathlands on permanent freshwater swamps

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Name of Principal Author (Candidate)	James Trezise		
Contribution to the Paper	**James Edward Trezise:** Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); visualization (lead); writing-original draft (lead); writing-review & editing (equal)		
Overall percentage (%)	70%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	10/11/21

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate to include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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ABSTRACT

In South Australia, *Swamps of the Fleurieu Peninsula* are critically endangered due to past vegetation clearance and changes in hydrology, but still contain a high diversity of threatened plant species. This vegetation community provides habitat for 82 threatened ground-stratum plant species, including the nationally critically endangered subshrub *Hibbertia tenuis* which is endemic to these swamps. With infrequent burning, native ferns and taller shrubs outcompete these species. We conducted glasshouse trials to determine the potential of fire to regenerate threatened and other swamp plant species. Soil samples from eight swamps were used in germination trials with half of each sample treated with heat plus smoke, and half left untreated. Samples were spread onto trays (n = 188) and seedling emergence was recorded for twelve months. Emergence was dominated by native species (2649 seedlings m^{-2}) compared to introduced (675 seedlings m^{-2}). In total, 48 native and 25 introduced species germinated, with 21 % of germinated native species absent from the above-ground vegetation. The dominant native fern *Gleichenia microphylla* did not emerge from any soil samples, indicating that recovery likely lags behind that of ground-strata species, giving them time to establish and set seed before being outcompeted. Thirty-four rare or threatened species germinated, including five species absent from above-ground vegetation. Of all native species that emerged, only five were confined to heat plus smoke treatments, suggesting most species will regenerate without fire if overstorey competition is reduced. However, seedling emergence of native shrubs/subshrubs more than doubled with fire treatment. Of particular importance, *H. tenuis* showed an 18-fold increase in germination when treated with heat plus smoke. This study supports the utility of ecological burns as a management tool to regenerate threatened plant species in long undisturbed peaty heathlands on permanent swamps.

Key terms: fire, soil seedbank, competition, seedling emergence, swamps

INTRODUCTION

Alteration of natural fire regimes is one of many factors threatening biodiversity in Mediterranean ecosystems (Bond and Van Wilgen 1996; Keith *et al.* 2002; Underwood *et al.* 2009). With the exception of areas deliberately burnt to reduce fuel loads, native vegetation near to agricultural and residential areas is often very infrequently burnt, as managers concentrate more on fire suppression rather than the ecological requirements of biota (Gill and Williams 1996). This is problematic in fire adapted vegetation, as altering fire regimes changes ecosystem structure (Brockway *et al.* 2002; Menges and Hawkes 1998; Peterson and Reich 2001), which can negatively impact biodiversity (Leach and Givnish 1996; Ottewell *et al.* 2011). While most research focuses on adverse effects of high frequency burning (Bradstock *et al.* 1997; Gill and Bradstock 1995), more recent studies document the loss of species diversity due to exclusion of fire (Davies *et al.* 2013; Keith and Bradstock 1994; Keith *et al.* 2002). This applies particularly to small remnants of native vegetation in heavily cleared agricultural and urban landscapes that frequently support high concentrations of threatened flora (Davies *et al.* 2013; Lawson *et al.* 2010; Taylor 2019).

In long unburnt vegetation, overstorey species can outcompete ground-stratum species via both above-ground and below-ground processes (Davies *et al.* 2010), while also restricting seedling establishment (Amarasekare and Possingham 2001; Keeley and Fotheringham 2000a; Keith and Bradstock 1994). Herbaceous understorey species are particularly affected (Bond and Keeley 2005; Sparks *et al.* 1998). Burning not only provides important cues for germination (Downes *et al.* 2014; Kenny 2000; Williams *et al.* 2003) but may also be essential for seedling survival by reducing competition and creating favourable growing conditions (Bond and Keeley 2005; Ooi *et al.* 2004). Some species may persist in the soil seedbank after exclusion from the above-ground vegetation (Hopfensperger 2007; Looney and Gibson 1995; Milberg 1995). These seedbanks are subject to decay as seeds lose viability over time with seedbank half-lives differing between species (e.g. Auld *et al.* 2000; Ooi *et al.* 2007). In the absence of conditions required for seedling recruitment, many mature plants will senesce, and seed production will eventually cease, resulting in declining abundance of viable seed in the soil seedbank. Moreover, when specific conditions (e.g. disturbance) are required to trigger germination, local extinctions may occur if the time between such disturbance events is greater than the lifespan of the species in both the above-ground vegetation and soil seedbank (Bradstock and Kenny 2003; Enright *et al.* 1996).

Seeds of fire adapted plants often require heat and/or smoke to trigger germination (Bell *et al.* 1993; Staden *et al.* 2000). Heat may break physical dormancies, e.g. through high temperatures opening impermeable seed coatings (Tieu *et al.* 2001a), while smoke is an important chemical cue (Staden *et al.* 2000). Fire may also promote recruitment by providing favourable growing conditions such as increased light penetration by removing dense overstorey (Keeley and Fotheringham 2000a; Vaughton 1998). Some fire adapted species will still germinate at low abundances in the absence of fire to enable limited recruitment into small gaps (e.g. DeSimone and Zedler 1999; Ooi *et al.* 2006), but resulting seedlings often suffer high mortality due to competition (e.g. Van Der Meer *et al.* 1999; Zhu *et al.* 2003). As such, germination into small gaps is often insufficient to sustain populations (e.g. Morgan 1997; Skoglund 1992).

The *Swamps of the Fleurieu Peninsula* Ecological Community is confined to the Fleurieu Peninsula of South Australia (Figure 1), and is listed as critically endangered under the Australian *Environment Protection and Biodiversity*

Conservation Act (EPBC Act 1999; Threatened Species Scientific Committee 2013). These permanent freshwater swamps have been extensively cleared and drained since European settlement, and now only 2 % remain in relatively unmodified condition (Harding 2005). Prior to European settlement, these ecosystems were burnt from lightning strikes or from aboriginal burning (Bickford and Gell 2005) but are now threatened by inappropriate fire regimes with fires likely being too infrequent (Duffield and Hill 2002; Quarmby 2011; Threatened Species Scientific Committee 2013). These long unburnt swamps have become dominated by dense coral fern *Gleichenia microphylla*, which outcompetes most ground-stratum species (Conservation Council of South Australia, unpublished database, 2018).

Eighty-four plant species listed as threatened at the national, state or regional level, have been recorded within these swamps and their margins. All but two of which are ground-stratum species (Table S3.1 in Appendix 2) and likely to be adversely affected by coral fern overabundance. One of these, the Yundi guinea flower (*Hibbertia tenuis*), a short-lived perennial subshrub, is listed as critically endangered under the EPBC Act (1999) and is endemic to these swamps (Quarmby 2011). Prior to this study, only 20 individuals were known to occur, all confined to two swamps (Quarmby 2011) where they were restricted to human-cleared trails through dense coral fern (J. Trezise pers. obs., 2018). Fire reduces the dominance of coral fern, leading to a transient period of increased plant richness (Clarkson 1997; Walker and Boneta 1995), particularly of herbs and grasses (Johnson 2001; Timmins 1992). Species richness can decline as time since fire increases (Bond and Van Wilgen 1996) and this successional pattern has been observed in a wide range of ecosystems (e.g. Bohlman *et al.* 2016; Peterson and Reich 2008; Ross *et al.* 2002). The present study aimed to determine the emergence response of *H. tenuis* and other plant species of the Fleurieu Peninsula swamps to fire associated cues of smoke and heat. While previous studies have found that smoke enhances seedling emergence of other *Hibbertia* species (Dixon *et al.* 1995; Hidayati *et al.* 2012), the effect of fire on *H. tenuis* and other threatened flora is poorly understood. We used an *ex situ* seedling emergence approach using soil samples taken from Fleurieu Peninsula swamps including two swamps containing *H. tenuis* and six with suitable habitat for the species.

These samples were exposed to heat and smoke treatments in glasshouse trials aimed to simulate the effect of fire and to determine whether these stimulated the germination of seeds held within the soil seedbank. Smoke and heat treatments enhance germination for many species in fire-prone ecosystems (Morris 2000; Read *et al.* 2000; Reyes and Trabaud 2009) and have been used in seedling emergence studies to replicate the effects of fire on soil seedbanks (Auld and Ooi 2008; Cochrane *et al.* 2007; Rawson *et al.* 2013). In addition to recording the emergence of native swamp species, we also recorded the emergence of introduced species to gain an insight into whether ecological burns were likely to enhance emergence of weeds from pre-existing seedbanks.

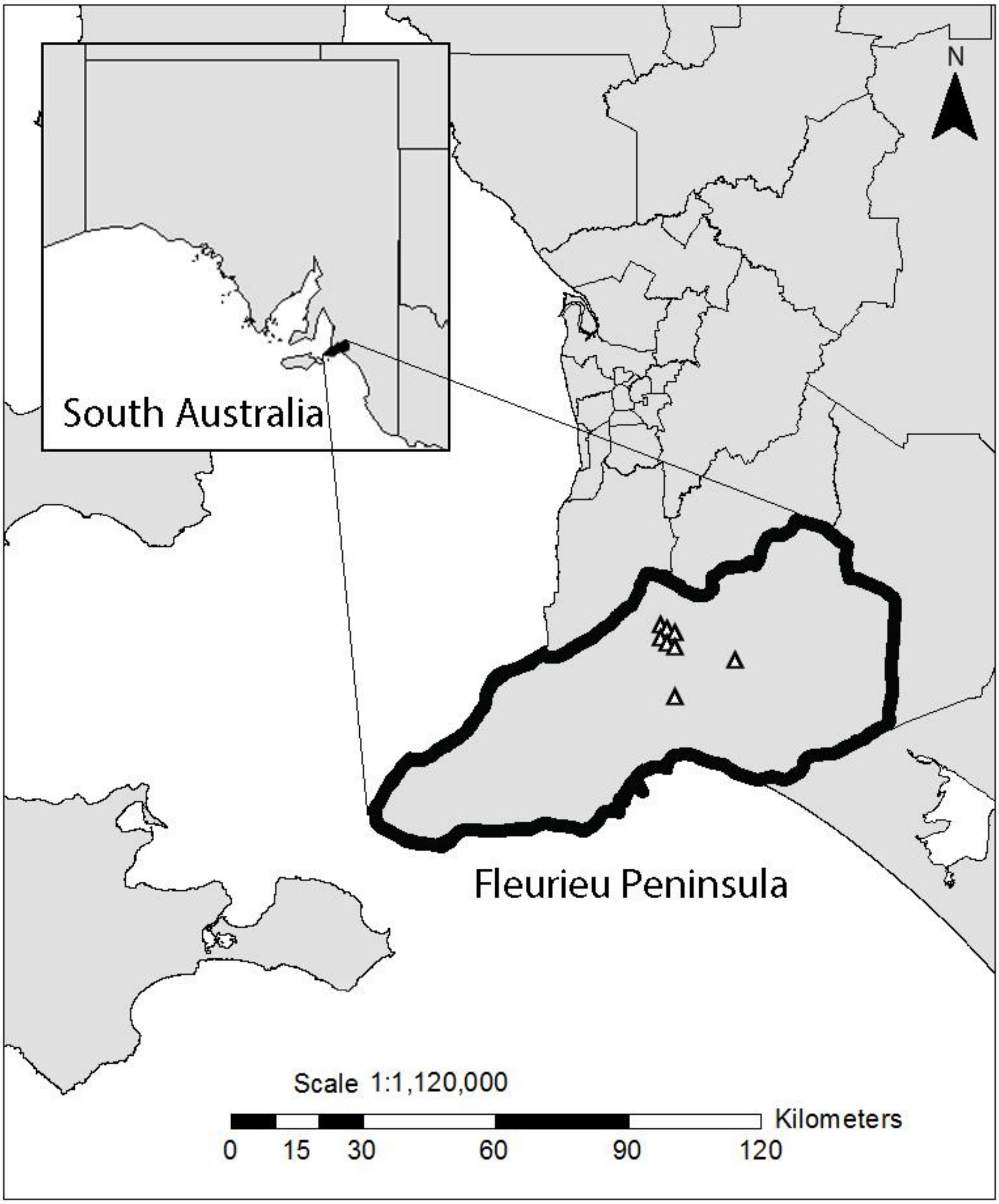

Figure 1. Study boundary in the Fleurieu Peninsula, South Australia. The eight swamps are represented by ∆ which are classified as permanent swamps. Map created using ArcGIS package (version 10.3.1) using spatial data from the Department of Planning Transport and Infrastructure (1996).

METHODS

Study sites

This study was undertaken in eight Fleurieu Peninsula swamps of the Yundi and Nangkita areas on the Fleurieu Peninsula, South Australia (Figure 1). The region has a Mediterranean climate that averages 756 mm of rain per annum (Myponga – Bureau of Meteorology 2022). These heathy, permanently-saturated swamps occur on grey clay soils with high gravel and peat content. Vegetation is predominantly a remnant peat bog ecological community (as defined by Harding 2005), dominated by *G. microphylla* (average 44 % cover) and intermixed with prickly tea-tree *Leptospermum continentale*, native broom *Viminaria juncea*, and other native shrubs and sedges.

All eight swamps were located within a two kilometre radius of historical records of *H. tenuis* (Department for Environment and Water 2020a; Quarmby 2011). Swamps either contained *H. tenuis* or at least suitable habitat for the species. These swamps were unlikely to have been burnt for at least 59 years based on historic imagery dating back to 1958 (Department for Environment and Water 2020c), and have probably not been burnt for at least 86 years using additional information held within government fire records dating back to 1931 (Department for Environment and Water 2016).

Ex situ seedling emergence approach

Eight 1 x 1 m^2 quadrats were randomly allocated, using the ArcGIS package version 10.3.1, in each swamp totalling 64 quadrats. Two of these swamps contained *H. tenuis*, and additional quadrats were erected around every observed individual, totalling 30 quadrats. For each quadrat, percent cover of each species was estimated with the point intercept method, using a 1 x 1 m^2 grid divided into a hundred 10 x 10 cm^2 cells. Percentage cover for each species was estimated by pushing a 2 metre long pin into the north-eastern corner of every cell and recording the percentage of times that species was intercepted by the pin tip. Additional species found within the quadrat, but not intercepted by the pin were given a cover value of 0.1 %, meaning that cover for each species could range from 0.1 % to 100 %.

To quantify the germinable contents of the soil seedbank and assess responses to the fire treatment, we used an *ex situ* seedling emergence approach (e.g. Cochrane *et al.* 2007; Davies *et al.* 2013; Rawson *et al.* 2013). This approach measures the numbers of seedlings that emerge during the monitoring period, but will not detect all seeds present in the soil seedbank (Ter Heerdt *et al.* 1996) and species that may require special germination treatments or take more than a year to emerge. This method was favoured over direct extraction as it is more time efficient (enabling more sampling), avoids bias toward larger seeds (Ferrandis *et al.* 1999; Gonzalez and Ghermandi 2012; Ter Heerdt *et al.* 1996) and differentiates between viable and unviable seed (Hidayati *et al.* 2012).

In August 2017, a 30 cm diameter auger was used to take cores from the centre of each quadrat. Cores were taken to a depth of 5 cm since this is where the majority of seed occurs (Auld and Denham 2006; Auld and O'Connell 1991; Wills and Read 2007). Large debris (e.g. rhizomes) was removed from the cores which were then thoroughly mixed and separated into two paired samples. Mixed samples were then spread into growing trays (33 × 14 × 5 cm^3 with drainage holes) on top of a 1 cm deep layer of sterile drainage sand.

One tray from each pair was treated with heat plus smoke to simulate fire, the other sample being used as a control. Heat was administrated by pouring 200 ml of boiling water evenly on top of the treated samples, compared with 200 ml of water at room-temperature for the control samples. This high temperature (~ 100ºC) is comparable to natural temperatures experienced on and just below soil surfaces during fire (Bradstock and Auld 1995; Bradstock *et al.* 1994; Williams *et al.* 2003) and heat shock commonly has been shown to promote seed germination (Enright *et al.* 1997; Liyanage and Ooi 2015; Wills and Read 2002). This approach was used instead of oven heat treatment because the samples were wet and prolonged exposure to wet-heat can kill seeds (Turner and Dixon 2009). Furthermore, drying samples could be considered an extra treatment as wetting and drying periods are often important mechanisms for breaking seed dormancies (Merritt *et al.* 2007). After water application, treated soil trays were subject to smoke in a smoke tent for 15 minutes. The smoke was generated by burning wheat hay in a 200 L barrel drum, following Rawson *et al.* (2013). Aerosol smoke was used since it is the most effective methods to stimulate germination in fire dependant seeds (Page 2009) and has been widely used in similar studies (e.g. Read *et al.* 2000; Reyes and Trabaud 2009; Thomas *et al.* 2010).

Soil trays were then randomly placed in a greenhouse and were rotated fortnightly around the glasshouse to limit any influence of position. Water was withheld for the first 48 hours, after which trays were automatically watered at intervals adjusted to ensure soils were always waterlogged. Several additional trays filled with drainage sand were randomly placed among the experimental trays to test for airborne seed contamination. Trays were monitored for 12 months, with seedlings recorded and removed immediately after reaching sufficient size for reliable identification. Species that failed to flower in this period were grown on in separate pots to confirm initial identification. When individuals died before flowering or fruiting, they were identified by comparing with other individuals that survived to a point where they could be identified. Seedlings of threatened species were grown and then translocated onto private land and all others were discarded. Nomenclature followed the Electronic Flora of South Australia (Department for Environment and Water 2020a). Where possible, a herbarium voucher specimen was collected and pressed for each species, and these will be submitted to the South Australian Herbarium.

Statistical analysis

We compared the species richness and abundances of key species that emerged in the treated and untreated samples using the R statistical package version 3.5.1 (R Core Team 2019) and the generalised linear mixed model (GLMM) package glmmADMB from version 0.6.5 (Bolker *et al.* 2012). We also used the adonis2 function from the vegan package from version 2.5-2 (Oksanen *et al.* 2019) to assess the difference between species composition in the treated and untreated samples. Treatment was considered a fixed factor, while swamp and quadrat were treated as random factors. Swamp variance did not significantly contribute to our models and therefore we did not compare between them. Furthermore, these swamps were the only sites available and so although they were not selected randomly, they were treated as such in our models. Distribution and dispersion of the data for each species informed the link functions used for each model, such that dispersion tests directed the use of either a Poisson or Negative Binomial distribution. Statistics for individual species and lifeform groups were calculated subject to emergence occurring in either a treated or untreated tray of each pair, such that tray pairs without emergence were excluded from calculations to avoid zero inflation. Mean numbers of seedlings per treatment for each species were extrapolated from the surface area of trays (0.046 m^2) to the surface area of quadrats (1 m^2). Species richness values are given per tray and have not been extrapolated as they do not scale in a linear fashion. GLMMs were also used to compare numbers of species in each lifeform class between treatments.

RESULTS

Effect of the fire treatment on seedling abundance

The heat plus smoke treatment resulted in significantly larger numbers of seedlings of native shrubs/subshrubs (64 seedlings m^{-2}) emerging than from untreated soil (27 m^{-2}; χ^2 (1) = 11.1, P = <0.01; Table 1). Among these, significantly more *H. tenuis* emerged from treated soil (5 m^{-2}) than from untreated soil (< 1 m^{-2}; χ^2 (1) = 16.0, P = <0.01; Table 1) as was the case for *Goodenia ovata* (30 m^{-2} treated vs 9 m^{-2} untreated; χ^2 (1) = 5.6, P = <0.01; Table 1).

However, for all native species together, density of seedlings emerging from heat and smoke treated soil (1274 m^{-2}) did not differ significantly when compared with the numbers emerging from untreated soil (1350 m^{-2}; χ^2 (1) = 0.11, P = 0.74; Table 1). Significant differences were also found for some introduced species. Four times less seedlings of introduced perennial forbs emerged from treated soil (1 m^{-2}) compared with untreated soil (4 m^{-2}; χ^2 (1) = 5.45, P = 0.02; Table 1), while the introduced annual forb *Lysimachia arvensis* had almost half as many seedlings in treated soil (6 m^{-2} treated vs 12 m^{-2} untreated; χ^2 (1) = 1.58, P = 0.02; Table 1). The treatment also appeared to suppress emergence of introduced *Rubus anglocandicans* (4 m^{-2} treated vs 8 m^{-2} untreated; χ^2 (1) = 3.49, P = 0.06; Table 1).

Table 1. Abundance and species richness for lifeform classes in above-ground vegetation compared with seedling emergence Comparisons between numbers of seedlings which emerged from heat plus smoke treated samples (HS) and from control samples (C).

	Above-ground vegetation		**Germinable soil seedbank**						
Longevity & lifeform class/species	**% Cover**	**Richness**	**% Total**	**Richness**	**HS (seedlings m^{-2})**	**C (seedlings m^{-2})**	**P**[‡]	**χ^2**	**n**[§]
All Natives	94.0	71	80.3	48	1273.9 ± 251.2	1349.6 ± 256.7	0.740	0.110	92
All annuals/biennials	1.3	17	39.2	16	608.6 ± 91.1	682.1 ± 109.2	0.762	0.092	86
Forbs	<0.1	8	1	6	20.2 ± 9.4	9.6 ± 3.9	0.178	1.812	20
Grasses	<0.1	1	<0.1	1	0.6 ± 0.4	0.3 ± 0.3	na	na	1
Non-grass graminoids	1.1	8	38.3	9	587.9 ± 81.2	672.1 ± 105.0	0.704	0.144	88
Juncus bufonius	0		8.5		138.2 ± 49.4	236.2 ± 44.6	0.012	5.840	59
All perennials	92.7	54	41.1	32	665.3 ± 160.2	667.5 ± 147.6	0.964	0.002	92
Ferns & clubmosses	45.3	6	<0.1	1	0	0.1 ± 0.1	na	na	3
Gleichenia microphylla	43.7		0		0	0	na	na	0
Forbs	1.1	20	6.9	12	153.8 ± 52.3	76.5 ± 17.4	0.155	2.026	61
Grasses	0.8	3	4.3	1	84.6 ± 33.3	58.4 ± 20.5	0.513	0.428	22
Non-grass graminoids	21.1	11	26.3	8	363.0 ± 58.1	506.0 ± 101.9	0.056	3.642	84
Carex appressa	<0.1		0.6		2.7 ± 1.4	16.6 ± 11.7	0.057	3.615	8
Shrubs/subshrubs	24.3	12	3.4	9	63.8 ± 16.3	26.5 ± 7.6	<0.01	11.082	45
Goodenia ovata	0		1.2		29.5 ± 14.9	9.3 ± 6.6	<0.01	5.626	6
Hibbertia tenuis	8.9		0.2		5.4 ± 2.5	0.3 ± 0.3	<0.01	16.000	8
Leptospermum continentale	5.5		0.3		4.8 ± 2.4	5.7 ± 2.1	0.610	0.257	13
Trees	<0.1	2	<0.1	1	0.1 ± 0.1	0.1 ± 0.1	na	na	2
All Introduced species	6.0	28	19.7	26	332.3 ± 126.3	337.7 ± 128.3	0.827	0.048	71
All annuals/biennials	4.4	14	13.5	15	241.4 ± 59.9	215.8 ± 49.4	0.422	0.646	67
Forbs	0.7	8	9.5	8	174.6 ± 38.0	161.9 ± 34.9	0.442	0.592	60
Lysimachia arvensis	<0.1		0.6		6.3 ± 3.1	11.7 ± 5.2	<0.05	5.484	12
Lotus pedunculatus	0.4		8.3		146.0 ± 36.6	128.8 ± 33.6	0.095	5.484	43
Grasses	3.7	5	3.6	5	66.8 ± 21.9	53.9 ± 14.5	1.000	0.000	39
Briza minor	1.1		0.1		0.1 ± 0.1	na	na	na	3
Non-grass graminoids	<0.1	1	0.4	2	0.3 ± 0.3	0.3 ± 0.3	na	na	4
All perennials	1.6	14	6.2	11	90.9 ± 66.4	121.9 ± 78.9	0.059	3.558	33
Forbs	0.8	7	0.3	6	0.9 ± 0.5	3.6 ± 1.5	<0.05	5.445	10

Grasses	<0.1	1	<0.1	1	0.3 ± 0.3	0	na	na	1
Non-grass graminoids	<0.1	1	<0.1	1	4.2 ± 2.9	8.4 ± 6.4	na	na	1
Shrubs/subshrubs/twiners	0.7	3	5.9	3	85.5 ± 62.7	109.9 ± 71.0	0.214	1.544	28
Genista monspessulana	<0.1		5.6		81.3 ± 62.7	110.5 ± 70.7	0.757	0.094	9
Rubus anglocandicans	0.6		0.4		4.2 ± 1.4	7.8 ± 2.1	0.062	3.490	23
Trees	<0.1	1	0	0	0	0	na	na	0

[‡] Comparison of log transformed data; only data from quadrats where the target emerged in at least one tray were included in analysis; na=not applicable; [§] Number of quadrats in which lifeform class/species emerged in at least one of the two paired trays.

Effect of the fire treatment on species richness and detection

Richness of native species emerging for heat and smoke treated soil (mean: 5.6 species per tray) did not differ significantly from untreated soil (mean: 5.4 species per tray; χ^2 (1) = 0.48, P = 0.49; Table 2). Richness of introduced species was also similar between the treated (mean: 1.8 species per tray) and untreated soil (mean: 1.9 species per tray; χ^2 (1) = 0.21, P = 0.64; Table 2). Species composition did not differ statistically between the treated and untreated samples ($F_{1, 81}$ = 0.72, P = 0.63), but they did contain different species. Of the 48 native species that emerged in the trays, five species (*Acacia verticillata*, *Epilobium billardierianum*, *Eragrostis tenellula*, *Eucalyptus ovata* and *Olearia glandulosa*) emerged only in trays treated with heat plus smoke, while four native species (the perennial forbs *Asperula conferta* and *Lagenifera huegelii*, the fern *Blechnum minus*, and the rush *Juncus caespiticius*) emerged only in untreated trays. Of the 25 introduced species, four were only present in heat plus smoke treated trays while five were only present in untreated trays.

Thirty-four plant species listed as threatened or rare at the national, state or regional level, emerged (Table 3). Nineteen seedlings of the critically endangered species *H. tenuis* were recorded, including from a swamp (from the random samples) where it was previously unknown. Ten native species and eight introduced species that emerged were not found in the above-ground vegetation including five species of conservation concern (Table 3), including *Olearia glandulosa*, a shrub listed as vulnerable at the state level and two regionally threatened species, *Pultenaea dentata* and *Hypericum japonicum*. We recorded 54 perennial and 17 annual native species in the above-ground vegetation, compared to 32 perennial and 16 annual species in the germinable soil seedbank (Table 1). For perennial ferns/clubmosses, only one species of fern *Blechnum minus* emerged from the soil seedbank, despite six species of fern and two species of clubmoss being recorded from the above-ground vegetation (Table S2.1 of Appendix 2).

Table 2. Effect of heat and smoke treatment (HS, C = untreated control) on richness of seedling emergence from the soil seedbank; comparison of numbers of species emerging for each life-history/lifeform class. Analysis is made using GLM models with negative binomial distributions.

	Mean (± SE) number of species per tray		**Significance**[†]	
Longevity & lifeform class/species	**HS**	**C**	χ^2	***P***
All native species	*5.6 ± 0.5*	*5.4 ± 0.3*	*0.482*	*0.488*
All native annuals/biennials	2.6 ± 0.3	2.5 ± 0.2	0.112	0.738
Forbs	0.8 ± 0.4	0.5 ± 0.2	1.982	0.159
Grasses	na	na	na	na
Non-grass graminoid	2.4 ± 0.3	2.4 ± 0.2	0.000	1
All native perennials	3.4 ± 0.4	3.2 ± 0.2	0.398	0.528
Ferns	na	na	na	na
Forbs	1.2 ± 0.2	1.0 ± 0.1	0.368	0.544
Grasses	0.7 ± 0.3	0.8 ± 0.2	0.087	0.768
Non-grass graminoid	1.9 ± 0.3	1.9 ± 0.1	0.004	0.950
Shrubs/subshrubs	1.03 ± 0.3	0.8 ± 0.1	1.556	0.249
Trees	na	na	na	na
All introduced species	*1.8 ± 0.3*	*1.9 ± 0.2*	*0.214*	*0.644*
All introduced annuals/biennials	1.6 ± 0.3	1.5 ± 0.2	0.038	0.845
Forbs	1.2 ± 0.3	1.2 ± 0.2	0.066	0.974
Grass	0.9 ± 0.3	0.9 ± 0.2	0.013	0.908
Non-grass graminoid	0.5 ± 0.6	1.0 ± 0.5	0.680	0.410
All introduced perennials	0.7 ± 0.2	1.0 ± 0.2	2.059	0.151
Ferns	0	0	na	na
Forbs	0.5 ± 0.3	0.9 ± 0.2	1.513	0.219
Grasses	na	na	na	na
Non-grass graminoid	0.7 ± 0.9	0.3 ± 0.3	0.339	0.560
Shrubs/subshrubs	0.6 ± 0.2	0.82± 0.2	1.261	0.261
Trees	0	0	na	na

[†] Comparison of log transformed data; native and introduced species calculated separately ns=$P \geq 0.05$; na=Not applicable/insufficient data for analysis.

Table 3. Frequency of rare and threatened plant species recorded from quadrats. Two comparisons are presented: 1) seed emergence following heat plus smoke treatment (HS), compared with no treatment (C); and 2) present in the above ground vegetation (A) prior to sampling soil and emerging in at least one of the two paired sample trays (S).

			Number of quadrats where species recorded (n=94)			
Family	**Species (Conservation status†)**	**Life-history classes‡**	**HS**	**C**	**A**	**S**
Only recorded from the germinable soil seedbank						
RUBIACEAE	*Asperula conferta* (*ra*)	PFo	0	1	0	1
GUTTIFERAE	*Hypericum japonicum* (r *vu*)	AFo	2	1	0	2
COMPOSITAE	*Olearia glandulosa* (v *en*)	PS	1	0	0	1
LEGUMINOSAE	*Pultenaea dentata* (r *en*)	PS	1	1	0	1
MENYANTHACEAE	*Villarsia umbricola* (*ra*)	PFo	1	1	0	2
Only recorded from the above-ground vegetation						
BLECHNACEAE	*Blechnum wattsii* (r *vu*)	PFe	0	0	1	0
ONAGRACEAE	*Epilobium pallidiflorum* (*ra*)	PFo	0	0	1	0
GLEICHENIACEAE	*Gleichenia microphylla* (r *ra*)	PFe	0	0	37	0
MYRTACEAE	*Leptospermum lanigerum* (*ra*)	PS	0	0	1	0
LYCOPODIACEAE	*Lycopodiella lateralis* (r *cr*)	PFe	0	0	1	0
LYCOPODIACEAE	*Lycopodiella serpentina* (e *cr*)	PFe	0	0	1	0
MYRTACEAE	*Melaleuca squamea* (r *ra*)	PS	0	0	1	0
SCHIZAEACEAE	*Schizaea bifida* (v *en*)	PFe	0	0	1	0
COMPOSITAE	*Senecio glomeratus* (*vu*)	AFo	0	0	1	0
ORCHIDACEAE	*Thelymitra cyanea* (e *en*)	PFo	0	0	1	0
ORCHIDACEAE	*Thelymitra holmesii* (v *en*)	PFo	0	0	1	0
LENTIBULARIACEAE	*Utricularia dichotoma* (*vu*)	PFo	0	0	1	0
LENTIBULARIACEAE	*Utricularia tenella* (*ra*)	PFo	0	0	1	0
XYRIDACEAE	*Xyris operculata* (r *vu*)	PGm	0	0	1	0
Recorded from both the germinable soil seedbank and the above-ground vegetation						
CYPERACEAE	*Baumea rubiginosa* (*ra*)	PGm	14	16	23	23
UMBELLIFERAE	*Centella cordifolia* (*ra*)	PFo	6	7	1	11
CENTROLEPIDACEAE	*Centrolepis fascicularis* (*vu*)	AGm	22	22	1	34
DROSERACEAE	*Drosera binata* (r *vu*)	AFo	5	1	1	5

RESTIONACEAE	*Empodisma minus* (*ra*)	PGm	27	22	6	35
MYRTACEAE	*Eucalyptus ovata* (*vu*)	PT	2	0	1	2
HALORAGACEAE	*Gonocarpus micranthus* (r *vu*)	PFo	20	17	1	31
DILLENIACEAE	*Hibbertia tenuis* (CR e *cr*)	PS	6	1	17	7
UMBELLIFERAE	*Lilaeopsis polyantha* (*vu*)	PFo	2	1	1	2
HALORAGACEAE	*Myriophyllum amphibium* (r *vu*)	PFo	3	3	1	6
IRIDACEAE	*Patersonia occidentalis* (*ra*)	PGm	2	3	8	5
CYPERACEAE	*Schoenus maschalinus* (*vu*)	AGm	26	23	2	39
EPACRIDACEAE	*Sprengelia incarnata* (r *vu*)	PS	5	5	4	6
LEGUMINOSAE	*Viminaria juncea* (r *vu*)	PS	13	10	7	21
VIOLACEAE	*Viola eminens* (*vu*)	PFo	7	4	5	11

[†] CE = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (*EPBC* Act), Lowercase = State (Baker *et al.* 2005), Italics = Regional rating (Gillam and Urban 2014); [‡] *P* = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids.

General findings

A total of 8,748 seedlings of native plants and 2,224 seedlings of introduced plants emerged in the trays, equivalent to 3324 ± 328 (mean ± SE) seedlings emerging per square metre. Averaged across both treatments, the densities of germinating native seed (2649 ± 245 seedlings m^{-2}; 48 species) were significantly greater than for introduced species (675 ± 159 seedlings m^{-2}; 25 species; χ^2 (369) = 15.6, P = <0.01). Emergence was low for most species with more than half of the emerging species producing < 20 seedlings across all trays. Furthermore, no seedlings emerged in the blank control trays, indicating absence of contamination.

DISCUSSION

Differences between the standing vegetation and soil seedbank

In our study of the critically endangered *Swamps of the Fleurieu Peninsula* Ecological Community we germinated 48 native species from the soil seedbank, 21 % of which were absent from the above-ground vegetation. We also germinated 25 introduced species. While the seedbanks of such swamps have not been previously studied, comparisons can be made with similarly designed studies investigating soil seedbanks of ephemeral swamp and dry heath communities in areas of comparable rainfall in southern Australia. Although Nicol *et al.* (2003) recorded fewer (19) native species germinating from the soil seedbank of shallow ephemeral lagoons, seed densities were considerably greater (22,000-78,000 m^{-2}, emergenced monitored for 154 days: Nicol *et al.* 2003) than what we recorded (2996-3652 m^{-2}, 365 days). Similarly, germinable seed densities recorded from soils under dry heath communities were also greater (4,227-12,527 m^{-2}, 150 days: Enright and Kintrup 2001). The comparatively low density of seedlings emerging from the seedbank in long-unburnt Fleurieu Peninsula swamps may be evidence of a diminishing seed input, resulting from the long absence of fire. A persistent soil seedbank requires seed production to balance seed loss. Production of seeds diminishes as vegetation senesces over time, whilst soil borne seeds suffer attrition through decay or predation (Hidayati *et al.* 2012; Roberts 1972; Watson and Riha 2011) with seed viability often following a negative exponential curve (Chambers and MacMahon 1994; Conn *et al.* 2006).

Another factor that may have affected our results was our deliberate bias towards sampling swamp margin habitats containing or likely to contain *H. tenuis*. Thus, wetter microhabitats which possibly contained a greater abundance of seed were not sampled, maybe giving a measure lower than for the swamps as a whole. A separate *in situ* experiment, which monitors the recovery of these swamps after prescribed fire, is being conducted to determine whether low seed abundance is limiting post-fire regeneration and to determine whether other factors may be contributing to this low *ex situ* seedling emergence. Nevertheless, this sampling bias did not affect the other results of the current experiment, quadrats being only assigned to areas of similar vegetation, ensuring sample variation did not significantly influence our models.

Composition of the soil seedbank

Short-lived species comprised the majority of the native soil seedbank in ephemeral gilgai wetlands (Davies *et al.* 2018) and senescent mallee heath communities (Davies *et al.* 2013). In comparison, twice as many perennial natives emerged from the germinable soil seedbank of heath-dominated permanent Fleurieu Peninsula swamps, with approximately equal abundances of seed for each life-history class. This is indicative of the large number of perennial ground-stratum species occurring in such swamps and likely reflects their reproductive strategy of relying on a persistent soil seedbank to survive when outcompeted by dense overstorey species. As in some previous studies (Enright *et al.* 1997; McGraw 1987), the germinable soil seedbank was dominated by both annual and perennial graminoids, predominantly sedges (Cyperaceae) and rushes (Juncaceae) with these comprising 48 % and 32 % of all seedlings respectively. This abundant and readily germinating soil seedbank could represent an adaption to facilitate rapid recolonisation (Bell 2001) and can be attributed to the long-lived nature of their seedbanks (Bakker *et al.* 1996; Leck and Schütz 2005). In contrast, 19 forb, fern and graminoid species which were poorly represented in the above-ground vegetation (< 0.01 % cover) did not emerge from the soil seedbank (Table 3; Table

S2 of appendix 2). Such species may be vulnerable to local extinction in swamps that are left long undisturbed, particularly if seed longevity is less than the inter disturbance period. The paucity of seed of many native species in the germinable soil seedbank (Tables S1.1, S1.2) is consistent with other studies (e.g. Auld 1995; Davies *et al.* 2013) and may result from limited-term seed viability (Auld 1995; Davies 2005) or high rates of seed losses to granivores (Shen *et al.* 2007). Further studies are required to assess how the viability of seeds in the soil seedbank of the Fleurieu Peninsula swamps may deteriorate over time.

Senescence and competition

In the long-unburnt swamps, *G. microphylla* formed a cover dense enough to exclude most ground stratum species. Competition from dense overstoreys in long-undisturbed vegetation, can lead to a loss of species from both the above-ground vegetation as well as the soil seedbank (Bossuyt *et al.* 2006; Davies *et al.* 2013). However, the loss of species from the above-ground vegetation is not necessarily mirrored in the soil seedbank (Amiaud and Touzard 2004) and where species persist in the soil seedbank there is the potential for regeneration burns to at least partially restore above-ground plant diversity (Davies *et al.* 2013). This applied to the heathy swamps we studied, with ten (21 %) of the 48 native species emerging from the sampled soil seedbank being absent from the above-ground vegetation, including five rare or threatened species. This is comparable with other south eastern Australian dry heathlands where 25-32 % of species in the soil seedbank were absent from the above-ground vegetation (Wills and Read 2002; 2007).

In landscapes historically prone to fire, senescence and subsequent declines in species diversity are associated with long fire-free intervals (Cheal 2010;

Shackelford *et al.* 2015). Fire intervals of approximately 45 years generally supports diversity in mallee-heath, heathy dry forests and sandy heathlands (Cheal 2010; Gosper *et al.* 2012; Gosper *et al.* 2011), however, to our knowledge, no studies have assessed maximum recommended fire intervals for heathy swamps. Obligate seeders which require disturbance to break seed dormancy are particularly vulnerable to long-term fire exclusion (Orscheg and Enright 2011). *Pultenaea dentata* and *Olearia glandulosa*, two obligate seeding species which were absent from the above-ground vegetation, emerged from the soil seedbanks taken from the Fleurieu Peninsula swamps. This was despite these swamps being unburnt for at least 59 years. Likewise, *H. tenuis* emerged from soil samples obtained from one swamp where it was also absent in the above-ground vegetation. This indicates the longevity of the soil seedbanks of these species and the potential to establish new populations of obligate species by regenerative burning.

Effects of the fire treatment

Although there was no significant difference in the numbers of native species that emerged from the heat plus smoke and untreated soils, significantly more seedlings of native shrubs and subshrubs emerged. This seems to apply particularly to the dwarf shrub *Goodenia ovata*, a species which also germinates in response to physical disturbance (e.g., bulldozing, J. Trezise pers. obs., 2018). Two other regionally-threatened species found to benefit from fire are the shrub *Viminaria juncea* (Auld and O'Connell 1991; Liyanage and Ooi 2015) and the perennial herb *Gonocarpus micranthus* (Johnson 2001; Timmins 1992), although both species can also emerge in the absence of fire. In contrast, two regionally "near-threatened" species, the fern *Blechnum minus* and the annual rush *Juncus caespiticius*, only germinated from untreated soil. However, one must be cautious extrapolating results of *ex situ* studies to the *in situ* situation, given that the procedure of taking, mixing and spreading the cores of topsoil over the trays, may have in itself stimulated some seeds to germinate (e.g. by providing exposure to light; Davies 2005). Pre-treatments such as specific temperature stratification regimes, which occur naturally, may be required to stimulate germination in smoke treated seed (Hidayati *et al.* 2000). Furthermore, having independent treatments consisting of smoke or heat may have produced different results.

Of greatest importance was the 18-fold increase in emergence of the nationally critically endangered *H. tenuis* in response to the heat plus smoke treatment. This indicates the potential for recovery of this species using ecological burns to both stimulate germination and also to reduce competition by the fern *G. microphylla*, which readily outcompetes *H. tenuis.* Previous recovery actions aimed at increasing the population size of *H. tenuis* by the translocation of tubestock grown from cuttings in unmodified stands of *G. microphylla* (Quarmby 2011), have had limited success with the translocated plants being outcompeted and dying within three years (J. Trezise, pers. obs., 2018). Where the species persists in long unburnt vegetation, it is confined to recently disturbed areas (e.g. tracks), indicating that fire enhances but is not critical for emergence. Despite *G. microphylla* being dominant in the swamps (average 44 % cover), we recorded no plants of this native fern emerging from soil-borne spores. This agrees with previous studies that found the main fire recovery mechanism for *Gleichenia* species is resprouting from rhizomes (Clarkson 1997; McQueen and Forester 2000; Walker and Boneta 1995). Previous burns of *Gleichenia*-dominated wet heath have found fire reduces the biomass for this species for several years (R. Davies, pers. obs., 2017). This is probably due to senescent *G. microphylla* developing adequately dense and dry aboveground fuel to support a burn capable of suppressing its recovery. We suggest that recovery of *G. microphylla* likely lags behind that of ground-strata species, and this gives time for ground-strata species to establish and set seed before being outcompeted.

Our study found a relatively high proportion (90 %) of native species emerged in the absence of heat plus smoke, similar to proportions found from soils under senescent mallee heath (82%; Davies *et al.* 2013). However, emergence rates from untreated soil were lower (36% to 50 %) for seemingly less senescent dry heaths (Auld and Denham 2006; Enright *et al.* 1997; Wills and Read 2007). Relatively high emergence rates in untreated soils may be attributable to the age of the germinable soil seedbank (Davies *et al.* 2013). Morrison *et al.* (1992) found reduced levels of dormancy in older seed, attributing this to factors such as the breakdown of impervious seed coats over time and the leaching of chemicals that inhibit germination (Baskin and Baskin 1998). These processes may be particularly pertinent in permanently water-logged soils. Although the emergence of seedlings from untreated soil suggests some capacity for plants to establish if the competition with other species was removed (e.g. by slashing), the likelihood that these would establish and set seed before the slashed plants had recovered is low. Slashing also lacks important fire-related cues (e.g. heat and smoke). So, fire not only reduces competition by removing biomass but also promotes higher germination rates which is preferable to slashing. Season of burn, intensity and other characteristics of fire will influence the magnitude of the emergence response of the plants (Miller *et al.* 2019).

Considerations when prescribing burns

Despite the observed benefits of fire as a tool to regenerate wet heath, burning can also cause increases in abundance of introduced species that exploit disturbance (Fisher *et al.* 2009; Keeley and Brennan 2012; Milberg and Lamont

1995). The Fleurieu Peninsula swamps are small and embedded within an agricultural landscape and so vulnerable to incursions of weeds following disturbances like fire. That 32 introduced species emerged from the soil seedbanks was not surprising. This included several introduced species that were absent from the above ground vegetation. While most were small short-lived forbs, one such species of concern was the highly invasive perennial grass, *Eragrostis curvula*, which appeared to be promoted by burning, emerging only from heat plus smoke treated soil. A further highly invasive species in these swamps is European blackberry (*Rubus anglocandicans*). While the main post fire strategy for this species is re-sprouting from perennial root stocks, seed dispersal is an important strategy used by the species to invade new areas (e.g. via animal dispersal; Davies 1998). While previous studies (research cited in Davies 2000) have found that the abundance of some introduced species may instead be inhibited by fire, we found this only applied in our study to three species which were abundant (≥7 seedlings) in the soil seedbank (the forbs *Lysimachia arvensis* and *Leontodon saxatilis,* and annual grass *Vulpia bromoides*), none of which are highly competitive. Davies (2000) describes the use of fire to specifically control weeds as being fraught with problems, due to the differing responses of different species to the same treatment, and the ability of weeds to rapidly recover in response to increased nutrients and reduced competition, even where their abundance may have been initially significantly reduced. Thus, while ecological burns of heathy swamps are essential to maintain native plant diversity, they need to be followed up with ongoing, targeted weed management to prevent escalated invasion by such species.

Peat retention needs careful consideration in any fire management in swamps. Many Fleurieu Peninsula swamps contain a substantial peat layer and fire is globally recognised as a threat to peatlands, and is exacerbated by climate change

(Pemberton 2005; Usup *et al.* 2004; Whinam and Hope 2005). Peat accumulation represents a large fraction of global carbon stores (Dise 2009; Page and Hooijer 2016; Page *et al.* 2002.) and so although burning can increase the above ground plant diversity of swamps which contain peat, care is required to minimise combustion of peat. Furthermore, fire can shift ecosystems which support the development of peat, to an alternative state that does not (Frost 1995; Kettridge *et al.* 2015; Turetsky *et al.* 2015). For these reasons, application of fire needs to be conducted in a manner which enables succession but minimises peat combustion and the chance of community shift. These risks can be mitigated by prescribing fire in conditions dry enough to adequately consume aboveground competition, but also wet enough to prevent fire spreading into peat deposits (Prior *et al.* 2020). In southern Australia, these conditions often occur in autumn, but not all seasons are the same and so the moisture content of peat needs to be monitored to confirm this.

Conclusion

In summary, our results suggest that ecological burns may help regenerate populations of threatened plant species in heathlands on permanent swamps, as long as employed periodically at intervals less than the term of their seed viability in the soil seedbank. Prescribed burns offer a range of services likely to facilitate the regeneration of threatened ground-stratum natives in swamp habitats, including promoting seedling emergence, providing gaps in the overstorey, suppressing competition from dominant species, and providing these plants with opportunities to replenish their seedbanks.

Chapter 4. Overcoming seed dormancy in a critically endangered *Hibbertia*: Implications for propagation and ecological burns

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Name of Principal Author (Candidate)	James Trezise		
Contribution to the Paper	Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); visualization (lead); writing-original draft (lead); writing-review & editing (equal).		
Overall percentage (%)	70%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate to include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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ABSTRACT

Many plant species rely on disturbances to recruit and, for threatened species, understanding the precise combination of factors that break seed dormancy is essential for conservation work. The critically endangered subshrub Yundi Guinea-flower (*Hibbertia tenuis*) declines in the absence of disturbance due to competition from dense native ferns and shrubs, including coral fern (*Gleichenia microphylla*) and prickly tea tree (*Leptospermum continentale*). We studied seed dormancy and germination for *H. tenuis* subject to a range of different treatments and combinations of treatments, including smoke and/or heat, gibberellic acid (GA), and varying temperature and light cycles. The percentage of seeds that germinated significantly increased with the application of smoke and GA, indicating a non-complex type of morphophysiological dormancy. Highest germination (> 50 %) occurred after the application of smoke, followed by a daily light/temperature cycle which simulated spring/autumn conditions (22/10 ºC and light/dark, for 12/12h; i.e. 22 ºC in light for 12 hours and 10 ºC in darkness for 12 hours). While no temperature stratification pre-treatments increased germination, seeds exposed to pre-treatments that simulated early spring conditions (15/20 ºC; 2/2 months) inhibited germination, likely because germinating seeds would not have enough time to establish before the hotter and drier summer months. The effect of temperature pre-treatments also varied depending on the presence or absence of light; germination of smoke treated seed when pre-treated with late winter temperatures (5/15 ºC; 2/2 months) was lowest in darkness (17 %) and highest with light exposure (51 %). We propose that this occurs because seeds on the soil surface can rapidly develop roots that infiltrate the damp subsoil before the surface dries out in late spring, but slower establishment rates for buried seed makes them more prone to desiccation thus reducing survival. The confounding effects of temperature stratifications and light exclusion are likely bet-hedging strategies, related to the highly competitive environment *H. tenuis* inhabits and the benefits of retaining dormant seed after a fire in the event of unfavourable conditions for establishment. Hence, ecological burns conducted in autumn provide smoke and stratification cues that maximise both germination and establishment.

Key terms: fire, smoke treatment, seed dormancy, temperature stratification, endangered species

INTRODUCTION

Seed dormancy is an adaptation which enables seeds to delay germination until conditions favour seedling establishment (Finch-Savage and Leubner-Metzger 2006; Jurado *et al.* 2000; Thompson 2000). Species native to fire-prone ecosystems commonly have dormancy requirements that can be broken by smoke and heat (Staden *et al.* 2000; Thomas *et al.* 2003; Tieu *et al.* 2001a). These cues enable rapid germination after fire when there is relatively low competition from other species (Bond and Keeley 2005; Keith and Bradstock 1994; Ooi *et al.* 2004). After being stimulated by smoke and heat, seeds may also require temperature stratifications (i.e. a periodic treatment to temperatures required to break dormancy; Kettenring and Galatowitsch 2007). This enables post-fire recruitment to be delayed until growing conditions are more favourable (Finch-Savage and Leubner-Metzger 2006; Jurado *et al.* 2000), but can lead to complex germination requirements that limit propagation for some species.

Understanding seed dormancy cues can help facilitate *ex-situ* germination (Erickson 2015) and is therefore important for plant restoration programs, particularly for threatened species, where seed may be limited (Tuckett *et al.* 2010; Wilkins *et al.* 2009). Seed dormancy can be classified into hierarchical groups based on how dormancy is maintained and what enhances germination (Baskin and Baskin 2004; Liyanage and Ooi 2016).

Hibbertia seeds have underdeveloped embryos (Hidayati *et al.* 2012), and this indicates morphological dormancy (Geneve 2003). Furthermore, the endotesta (the inner layer of the seed coat) of *Hibbertia* seed are known to contain highly cutinised cells, which prevent water uptake and thus germination, and this is indicative of physiological dormancy (Baskin and Baskin 2004; Schatral 1996). The physiological component of morphophysiological dormancy can be classified as deep, intermediate or non-deep depending upon how seeds react to different treatments such as gibberellic acid (GA) and warm stratifications (Baskin and Baskin 2004).

Stratification periods can prompt internal biosynthesis of the growth hormone GA, which in turn leads to embryo growth and the breaking of dormancy (Finch-Savage and Leubner-Metzger 2006). Exogenous application of GA has been shown to circumvent the need for naturally occurring stratification regimes in many species (Bell *et al.* 1995; Bunker 1994; ChingTe *et al.* 1998; Fang *et al.* 2006; Plummer and Bell 1995; Wardlow *et al.* 1989). Therefore, the exogenous application of GA to seeds can facilitate the study of other dormancy requirements when they occur in combination with the need for stratification.

We studied the germination cues of the nationally listed, critically endangered *Hibbertia tenuis* (Yundi Guinea Flower), a short-lived subshrub confined to three populations in the Fleurieu Peninsula region of South Australia. All populations occur on the margins of the nationally critically endangered *Swamps of Fleurieu Peninsula* (FPS) ecological community. While the germination cues of *H. tenuis* are poorly understood, other more common *Hibbertia* species have been better studied. The *Hibbertia* genus contains many species native to fire-prone ecosystems and as such, they have adaptions to facilitate post-fire regeneration. Many Australian *Hibbertia* species (e.g. *H. acicularis, H. arcuate, H. cistoidea, H. crassifolia, H.depilipes, H. linearis, H. obtusifolia, H. polyancistra, H. pullulan, H. riparia, H. serpyllifolia, H. spanantha* and *H. vestita*) are facultative seeders, such that they can both resprout and germinate from soil seedbanks after fire (Bell and Driscoll 2005; Clarke and Knox 2002; Mappin *et al.* 2003; Thiele 2017; Toelkena and Robinsonb 2015). This contrasts with *H. tenuis* which is an obligate seeder and relies entirely on the soil seedbank to regenerate after fire (J. Trezise pers. obs., 2018).

The FPS community was historically exposed to fire, but it is now threatened by its exclusion (Bickford and Gell 2005; Threatened Species Scientific Committee 2013; Trezise *et al.* 2021). While fire naturally would have occurred mostly in late summer (lowest moisture availability), prescribed burning in southern Australia is limited logistically to autumn and spring, since the heat and lack of rainfall in summer make fires uncontrollable, while winters are too wet. Furthermore, the FPS have a Mediterranean-type climate with hot and dry summers, such that the soil surface temporarily dries out in summer (which can desiccate seedlings) but the substrate below remains wet. *Hibbertia tenuis* is therefore one of many plant species that could be driven to extinction in the absence of fire (Bond and Van Wilgen 1996), but where the season of burn is also an important consideration.

Like other fire adapted species, the dormancy of many species of *Hibbertia* is enhanced by smoke. For example, Cuneo *et al.* (2018) reported an increase in the germination of *Hibbertia puberula* subsp. *glabrescens* from 1 % with untreated seed to 48 % with seed treated with a combination of GA, smoke and alternating temperatures. In fire-prone ecosystems in Mediterranean biomes, aerosol smoke is a common cue that stimulates seed germination in many species (Allan *et al.* 2004; Dixon *et al.* 1995; Hidayati *et al.* 2012). This response is due to chemicals derived from smoke, called karrikinolides (KAR), which release seed from dormancy by interacting with phytohormones such as abscisic acid (ABA), gibberellin and auxin (Meng *et al.* 2017). Gibberellin is a naturally occurring hormone synthesised by plants in response to environmental stimuli, which can inhibit other hormones, such as ABA, which in turn inhibits seed germination (Graeber *et al.* 2012).

Species in the *Hibbertia* genus have seed which is classified as morphophysiologically dormant (Hidayati *et al.* 2012). As well as containing a physical barrier to germination, such as a thick outer coating made of water-resistant cutin (Roche *et al.* 1997), embryo development is dependent on a complex sequence of environmental cues such as seasonal fluctuations in temperature and an interplay with light and smoke (Hidayati *et al.* 2012). In particular, a temperature stratification period is needed to enable seed embryos to ripen and for the radicle to emerge (Hidayati *et al.* 2012), but different *Hibbertia* species have different dormancy-breaking and germination requirements, and the role of cold versus warm stratification is poorly understood (Hidayati *et al.* 2012).

When species, such as some *Hibbertia*, have morphophysiological dormancy mechanisms, *ex-situ* germination for translocation and revegetation programs become extremely difficult and this can severely limit the number of plants propagated (Dixon *et al.* 1995; Finch-Savage and Leubner-Metzger 2006). Plant cuttings are often used as an alternative means of propagation in this case, but as well as being costly and having a lower survival rate (Palma and Laurance 2015), populations are less genetically diverse than populations grown from seed.

This study aims to increase our understanding of fire and other treatments on the germination ecology of native southern Australian plant species by researching the seed germination requirements of *H. tenuis*. Treatments studied included a combination of smoke, GA, temperature and photoperiods, and the need for temperature stratification and light. Results will be used to inform the recovery program for this critically endangered species.

METHODS

Study species

Hibbertia tenuis is a decumbent or scrambling subshrub with a lifespan of approximately a decade (J. Trezise pers. obs., 2022). Leaves grow to 1 cm in length and 2 mm in width and they are shiny green on top, paler underneath, and covered in small, fine, star-shaped hairs. Flowers are terminal, yellow with five petals and are opposite leaves along branches (Toelken 2010). Populations are endemic to the margins of swamp wetlands in the FPS Threatened Ecological Community (TEC). These swamps are highly modified by past drainage and surrounding land use (e.g. dams) and key threats to this TEC includes vegetation clearance, altered hydrology, and inappropriate disturbance regimes such as lack of fire. The main swamp where *H. tenuis* occurs exists in Yundi and contains historic drains and tracks along which most of the *H. tenuis* occurs.

This species flowers predominately in spring and summer (J. Trezise pers. obs., 2018; Quarmby 2011), and shortly after seeds are shed and incorporated into the soil seedbank. The dispersal mechanisms are unknown, but seeds have elaiosomes, meaning transportation by ants and other insects is plausible (Hughes *et al.* 1994; Stebbins and Hoogland 1976). The albuminous seeds are 2.3 mm long by 1.5 mm wide and have rudimentary embryos (Hidayati *et al.* 2012; Johri *et al.* 1992).

Without fire or other disturbance, *H. tenuis* individuals senesce and are rapidly outcompeted by dense shrubs and coral fern (*Gleichenia microphylla*), so between disturbance events, the population persists largely in the soil seedbank. Historic plant counts and records suggest this species was once abundant in these swamps, but in recent years no more than 20 individuals were known, with these plants confined to three swamps along drains and human cleared paths. More current observations suggest numbers are rapidly declining as the last remaining individuals begin to senesce (J. Trezise pers. obs., 2018; Quarmby 2011; Trezise *et al.* 2021).

Seed collection and storage

Seeds of *H. tenuis* were wild collected from the three known populations in October 2018, all populations are within a 2 km radius in Yundi, South Australia (35°18'6"S, 138°37'39"E, approx. 250 m above mean sea level). Seeds were collected in October 2018 using muslin bags which were placed around clumps of flowers and left for two months in the field. It should be noted that this would have restricted pollination during the two month for flowers opening during this period, but the bags also enclosed flowers that had recently finished flowering and were presumably pollinated. Seed from the three populations was then collected and thoroughly mixed. The seed was then separated from debirs (e.g. twigs and other biomass) using sieves and a vacuum separator. The seed was then stored in light-impermeable bags in a low humidity, temperature controlled-environment room (c. 22 ºC) until the experiments commenced in April 2019.

Seed viability

At the start of the experiment, interpretation of viability was made with observations of seed fill determined by an X-Ray machine with a random sample of the captured seed, but identification of a ‘germinable’ embryo was found to be subjective. If a ‘germinable’ embryo is defined as at least 90 % full, with minimal detachment (e.g., A, B, C; Figure 1 in Appendix S3), then average viability was 74.8 % ± 2.6 % (mean seeds with > 90 % fill ± standard error; 5 replicates of 66 seeds). However, germination tests have not been conducted on *H. tenuis* seed to test for viability as a product of embryo fill. It is therefore impossible to know what proportion of the seeds was viable (Frischie *et al.* 2020). For these reasons, results have not been adjusted to exclude non-viable seed.

Experimental design

Two separate experiments were then conducted to assess the impact of different combinations of fire related treatments, temperature stratifications, and photo periods on seed germination. The first experiment applied eight different treatments to batches of seeds, which were then plated and placed into three separate incubation environments. Each treatment was assigned 50 seeds per dish and replicated five times. The second experiment applied two different treatments to groups of seeds, seeds were then plated, and each group was subjected to one of three different temperature pre-treatments, every second dish was sealed in darkness, and then all dishes were placed into the same incubation environment. Fewer seed were available for the second experiment, and so each treatment utilised 40 seeds per dish and was replicated three times. Details regarding these treatments, temperature pre-treatments, incubation conditions, and the light exclusion can be found below, and the order of their application within each experiment is given in Table 1.

Treatments

Within both experiments, treatments were applied first by agitating seeds in beakers in their respective treatment solutions for 24 hours using a laboratory shaker before being placed onto agar plates. Experiment one used all treatments, while experiment two used only smoke and control (Table 1). These treatments were a) untreated control, b) heat shock, c) smoke, d) heat plus smoke, e) GA, f)

GA plus heat, g) GA plus smoke, and h) GA plus heat plus smoke. Each treatment is described below.

a) The untreated control consisted of soaking seed in deionised water.

b) The heat shock treatment (hereafter referred to as “heat”) was applied in an oven (dry heat) for 5 minutes at 90 °C, following Keith (1997). As temperature is lost when opening the oven, we allowed the oven to return to 90 °C before the timing was started. During this period, temperature dropped no less than 10 °C and took no more than 30 seconds to return to 90 °C. When used in combination with other treatments, the heat was applied first, to break impermeable seed coatings (releasing physical dormancies), thus allowing other cues to have an affect (Moreira *et al.* 2010). Heat and smoke treatments were applied individually and together because previous studies have found that combined treatments can result in different outcomes than when they are applied individually (Morris 2000; Thomas *et al.* 2003). All treatments which incorporated heat application were subsequently agitated with deionised water.

c) The smoke treatments consisted of soaking the seed in a premade 10% concentrate smoke solution. The solution was created by passing aerosol smoke (wheat straw burnt in a 44-gallon drum) through a water container for 15 minutes. This is an effective surrogate for aerosol smoke (Staden *et al.* 2000) and has proved effective when applied to other *Hibbertia* species (Hidayati *et al.* 2012).

d) The heat plus smoke treatment consisted of the heat treatment, followed by soaking in the smoke solution.

e) The GA treatment involved soaking seeds in a solution of 500 mg/L of gibberellic acid solution, made by adding 0.5 grams of powdered GA

(Merck KGaA; CAS 77-06-5) into 500 mL of water, which was mixed for 20 minutes.

f) The heat plus GA treatment consisted of the heat treatment, followed by soaking in the GA solution.
g) The smoke plus GA treatment consisted of soaking in a combined mixture of the GA and smoke solutions.
h) The GA plus heat plus smoke treatment consisted of the heat treatment, followed by soaking in a combined mixture of the GA and smoke solutions.

Temperature pre-treatments

Before being incubated, three temperature pre-treatments were applied to the seeds used in experiment two to simulate different seasonal temperatures. No temperature pre-treatments were applied to experiment one (Table 1). Each pretreatment used two different periods of static temperatures, to determine the effect of static temperature stratification:

a) 5 °C for two months followed by 15 °C for two months ("late winter")
b) 15 °C for two months followed by 20 °C for two months ("early spring")
c) 20 °C for two months followed by 15 °C for two months ("late autumn")

Light exclusion

To determine the effect of light exclusion in experiment two, every second plate of seeds was wrapped in aluminium foil before being placed into the incubators.

Incubation

To simulate diurnal temperature ranges and day lengths during different seasons at Yundi (where the seed was collected) germination trials were conducted in temperature- and light-controlled incubators. The day/night alternating temperature cycles approximate the mean daily maximum and minimum air temperature in FPS in winter (15/5 °C), spring/autumn (22/10 °C) and summer (30/15 °C; Myponga - Bureau of Meteorology 2022). These were set to temperature regimes of 15/5 °C, 22/10 °C, or 30/15 °C, for 20/4 h, 12/12 h or 14/10 h, respectively. Length of light exposure (photoperiod) was varied to simulate the three seasons: winter (10/14 h, light/dark), spring/autumn (12/12 h) and summer (14/10 h). All plates were then left to germinate within their respective incubation environment for four months.

Table 1. Two experiments were undertaken using the treatments described in this table. Seeds subjected to "all darkness" were covered in aluminium foil before being incubated[‡]

Component:	**Treatment** (Fire & GA)	**Temperature pre-treatment** (Static stratification; seasons simulated)	**Incubation** (Diurnal temperature cycles; seasons simulated)	**Light treatment** (Diurnal photoperiods; seasons simulated)
Order of application:	1. Applied to seeds before being placed on dishes	2. Applied to seeds after being placed on dishes	3. Applied to seeds on dishes after the temperature pre-treatment	3. Occurring in conjunction with the incubation[‡]
Experiment 1. Aim: Understanding how the interaction between fire treatments, GA, and seasonal diurnal temperature variations, affect germination. Design: 5 reps/treatment with 50 seeds/dish	Control, smoke, heat, smoke plus heat, GA, GA plus smoke, GA plus heat, GA plus smoke plus heat	Nil	30/15 °C for 14/10 h (Summer)	Light/dark for 14/10 h (Summer)
		Nil	22/10 °C for 12/12 h (Spring/autumn)	Light/dark 12/12 h (Spring/autumn)
		Nil	15/5 °C for 20/4 h (Winter)	Light/dark for 10/14 h (Winter)
Experiment 2. Aim: Understanding how interactions between smoke, static seasonal stratification regimes and light exclusion, affect germination Design: 3 reps/treatment 40 seeds/dish	Control, smoke	Late winter (static 5 ºC for 2 months and then 15 ºC for 2 months)	22/10 °C for 12/12 h (Spring/autumn)	All dark[‡]
				Light/dark 12/12 h (Spring/autumn)
		Early spring (static 15 ºC for 2 months and then 20 ºC for 2 months)	22/10 °C for 12/12 h (Spring/autumn)	All dark[‡]
				Light/dark 12/12 h (Spring/autumn)
		Late autumn (static 20 ºC for 2 months and then 15 ºC for 2 months)	22/10 °C for 12/12 h (Spring/autumn)	All dark[‡]
				Light/dark 12/12 h (Spring/autumn)

Incubation and assessment

Treated seeds were placed onto agar dishes that consisted of 1 % agar solution within 9 cm diameter sterile glass petri dishes and transferred into the incubators. All treatments, including changes to temperature and light regimes, were carried out on the seed while on the dishes. The number of seeds that germinated was recorded fortnightly for 28 weeks, at which time no new germinants had been recorded for two consecutive weeks. Germination is given as the mean percentage of the total number of seeds that germinated at the end of the 28 week period. Seeds were considered germinated when the radicle was at least half the length of the seed coat (seed size: 2.3 mm long x 1.5 mm wide) and once scored as germinated, the seed was removed.

Statistics

Statistical differences were calculated between the treatments and stratifications based on the total number of seeds that germinated. Data analyses were performed using the R software in R studio from version 3.5.1 (R Core Team 2019). Our models used binomial distributions with treatment and stratification as fixed factors, and the petri dish replicates as random factors. Model selection was determined using anova and overdispersion functions. Generalised linear mixed models were used to predict mean germination using the R package glmmTMB from version 0.2.0 (Magnusson *et al.* 2017). For example, glmmTMB(seeds ~ treatment * stratification + (1|replicate), data = data, family = "binomial"). Means and *P* values were predicted from the models using the R package emmeans from version 1.7.3 (Lenth *et al.* 2019). These predictions use pairwise methods, including test statistics (t.ratio) to produce *P* vaules.

RESULTS

Experiment 1: Effect of fire, GA, and incubation season on germination

The application of smoke resulted in significantly higher germination in *H. tenuis* compared to controls, regardless of simulated season (Figure 1). The greatest germination at the end of the 28-week scoring period occurred when seeds were incubated under a daily temperature and photoperiod regime that simulated spring/autumn diurnal conditions. Under these conditions mean germination of smoke treated seed (51 % ± 3 %; mean ± 95 % CI) was 21 times greater than for untreated (control) seed (2 % ± 1 %; Z = -8.72, $P < 0.01$). In contrast, heat did not result in increased germination, irrespective of seasonal incubation regimes (Figure 1). Germination with smoke plus heat was not significantly different from germination with only the smoke treatment, irrespective of season (Figure 1).

Application of GA to *H. tenuis* seed resulted in higher mean germination compared to controls, when incubated under spring/autumn conditions (14 % vs 2 %; Z = -4.27, $P < 0.01$) and summer conditions (22 % vs 5 %; Z = -4.91, $P < 0.01$; Figure 1). However, in the case of the spring/autumn incubation, the increase in mean germination from GA application was less than a third of the increase found with smoke treatment (14 % vs 51 %; Z =-8.36, $P = < 0.01$; Figure 1). When GA was added to smoke treated seed it significantly reduced germination (31 % vs 51 %; Z = -4.60, $P = < 0.01$) although this was only the case for seed subjected to spring/autumn incubation (Figure 1). In contrast, applying GA to heat-treated seed significantly increased (doubled) germination under both spring/autumn and winter incubations (Figure 1).

In the absence of GA, the percent of seeds that germinated under winter incubation conditions was fewer than under simulated spring/autumn and summer incubation, across heat, smoke, and heat plus smoke treatments (Figure 1). When only treated with heat, none of the seeds germinated under winter incubation conditions. In contrast, with the addition of GA, mean germination rates for heat-treated seed subject to winter incubation, were not significantly different for similarly treated seed germinated under simulated spring/autumn or summer light and temperature conditions (33 % winter vs 38 % spring/autumn; Z = -1.20, *P* = 0.46; 33 % winter vs 26 % summer; Z = 1.67, *P* = 0.22; Figure 1).

Percent germination under winter incubation conditions with smoke remained significantly less than under spring/autumn and summer incubation, even when GA was added (Figure 1). The highest germination of *H. tenuis* occurred in seed treated with smoke (with or without heat and GA) subject to spring/autumn incubation conditions, namely 10 °C for 12 h in the dark followed by 22 °C in the light for 12 h. After application of the smoke treatment, mean germination under spring incubation conditions (51 % ± 3 %) was significantly greater, than under summer incubation conditions (19 % ± 2 %; Z = 7.70, *P* < 0.01) and winter incubation conditions (9 % ± 2 %; Z = -9.66, *P* < 0.01; Figure 1).

The time taken for germination to plateau (highest germination) for each treatment combination varied with the simulated seasonal conditions (Figure 2). For the “heat plus GA” treatment, time taken to half-highest germination (16 %) took twelve weeks in winter compared to eight weeks in summer or spring/autumn. Likewise, the “heat plus smoke plus GA” treatment took four weeks longer in winter to reach half-highest germination (18 %). However, most germination occurred within the first twelve weeks regardless of treatment except when seeds were exposed to simulated winter conditions

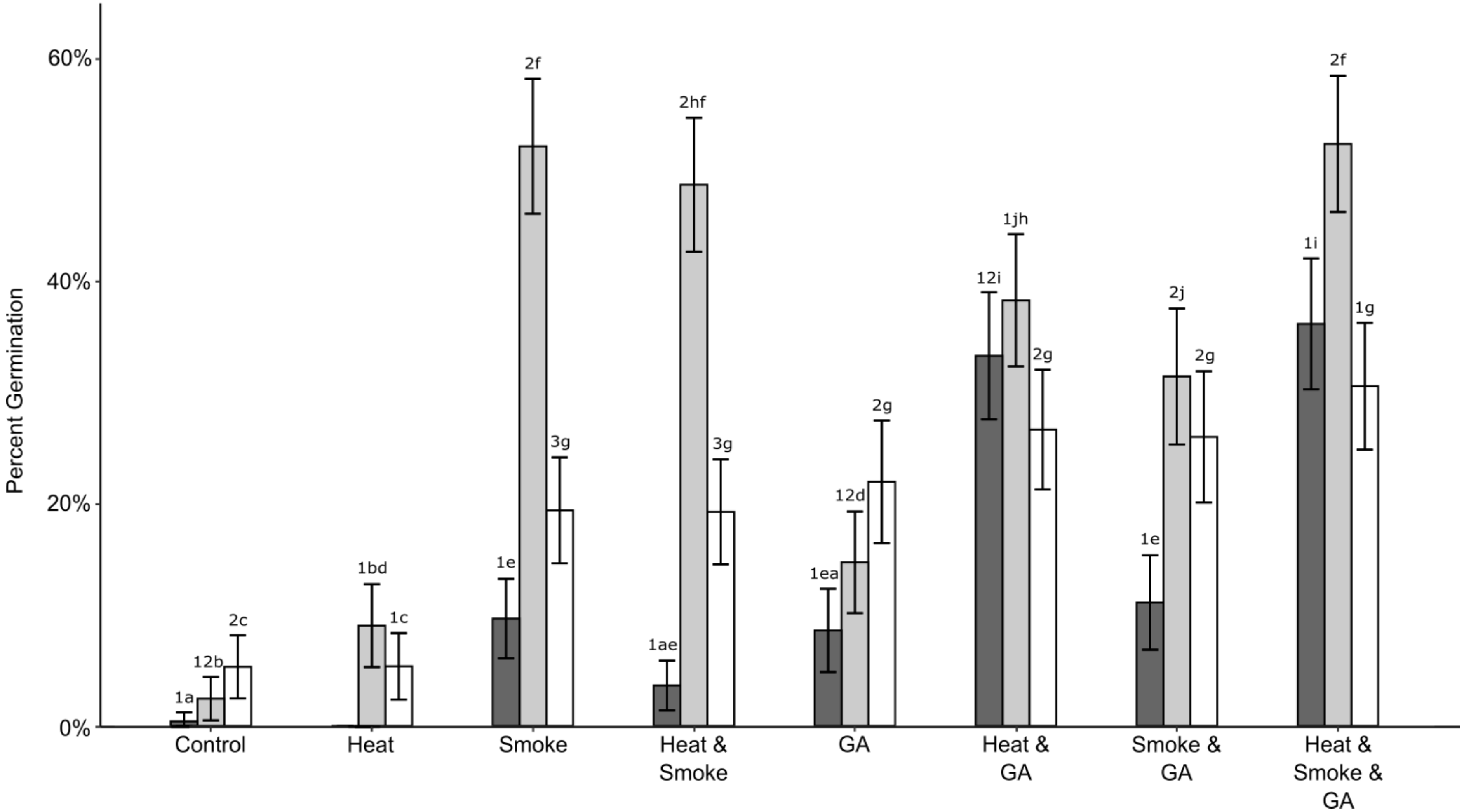

Figure. 1 Effects of the treatments, and photoperiods and maximum/minimum temperature cycles simulating different seasonal conditions: winter (dark grey), spring/autumn (grey), and summer (white), on mean percentage germination of *H. tenuis* seed. Bars represent 95 % confidence intervals. Significant differences ($P \leq 0.05$) in germination between seasons and within treatments are indicated by different numbers. Significant differences between treatments and within the same seasons are indicated by different letters. Statistical details can be found in Tables S2.1 and S2.2 of Appendix 3.

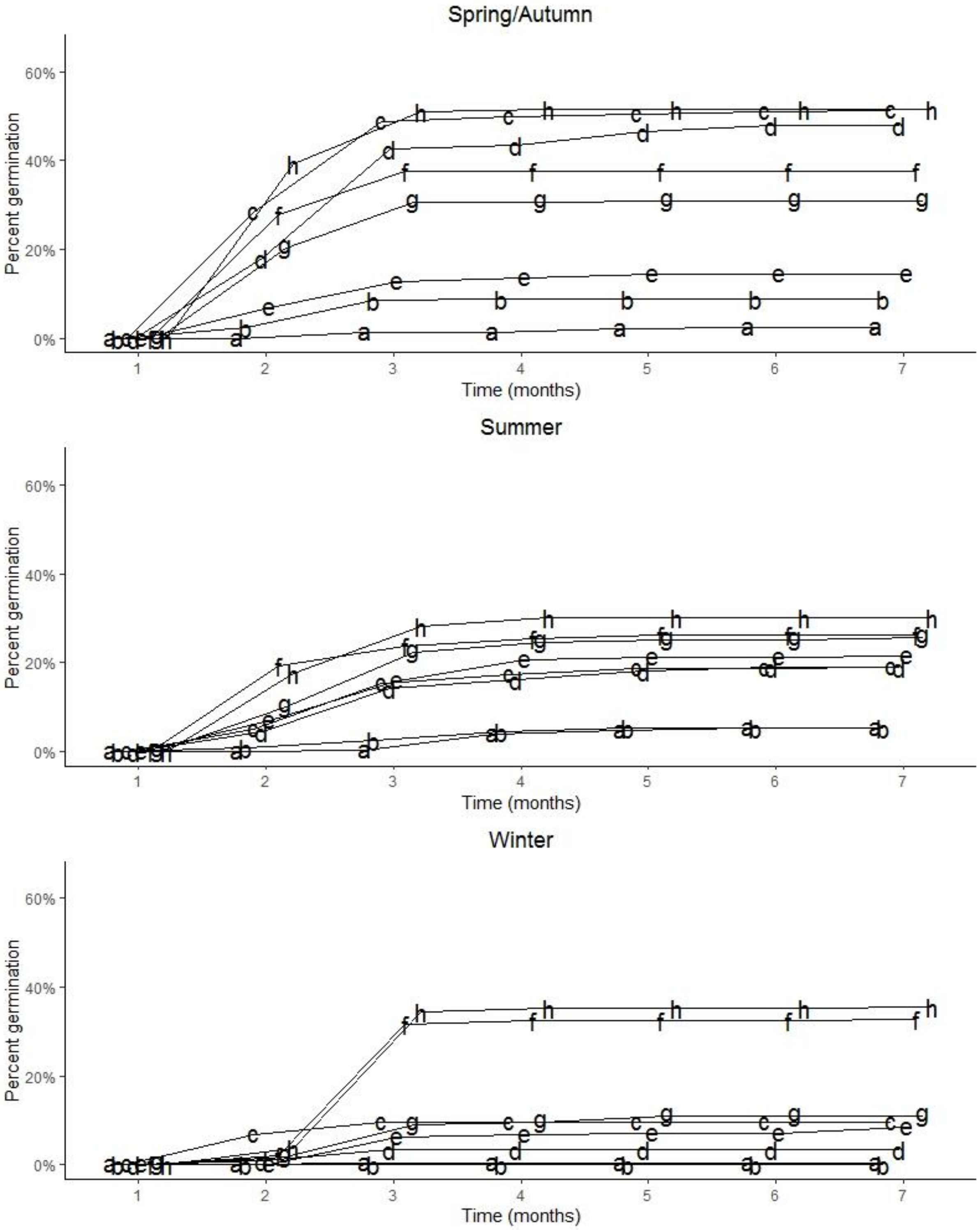

Figure 2. Effect of incubation season on the percentage germination of *H. tenuis* seeds across time, where a = untreated control, b = heat, c = smoke, d = smoke plus heat, e = GA, f = GA plus heat, g = GA plus smoke, and h = heat plus smoke and GA.

Experiment 2: Effect of temperature stratification pre-treatments, smoke treatment and light exclusion

In the absence of a smoke treatment, no significant differences were found between the percent of seed that germinated, regardless of light treatment (light vs dark) and regardless of the different temperature stratification pre-treatments (simulating "late winter" vs "early spring" vs "late autumn"; Figure 3).

In contrast, different temperature stratification pre-treatments significantly affected the germination of smoke treated seeds (Figure 3). Furthermore, differences in germination between pre-treatments varied between light treatments. For instance, under dark conditions, maximum amounts of germination (62 % ± 5 %; mean ± CI) occurred when smoke treated seed was subject to pre-treatment of 20 ºC then 15 ºC pre-treatment ("late autumn"), significantly greater than seed subject to 15 ºC then 20 ºC ("early spring"; 7 % ± 3 %; $Z = -6.60$, $P = < 0.01$) and significantly greater than 5 ºC then 15 ºC ("late winter"; 17 % ± 4 %; $Z = -5.91$, $P = < 0.01$; Figure 3).

In contrast, under light conditions, highest germination (51 % ± 5 %) occurred when the smoke-treated seed was subject to 5 ºC then 15 ºC stratification pre-treatment ("late winter"), significantly greater than when subject to 15 ºC then 20 ºC ("early spring"; 14 % ± 4 %; $Z = 4.97$, $P = < 0.01$; Figure 3). The same mean germination (51 % ± 3 %) was recorded in Experiment 1 for smoke treated seed subject to the same ultimate germination conditions, but without any

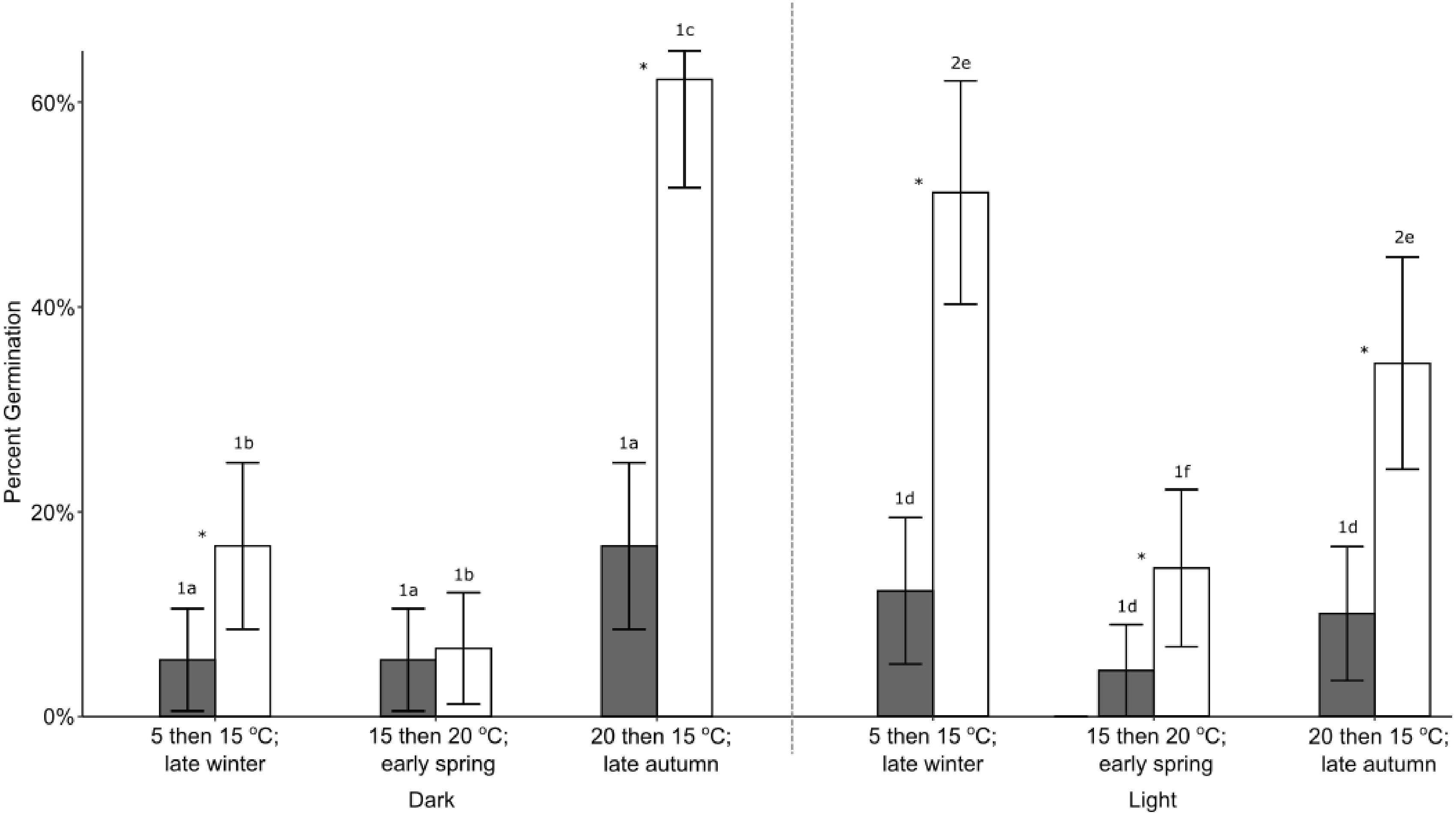

Figure 3. Effects of different static stratification pre-treatments and light exclusion on germination (mean % ± 95% CI) of *H. tenuis* seed either left untreated as controls (grey) or treated with smoke (white). All treatments were then subject to the same maximum/minimum temperature cycle (and in the case of light treated seed, the same photoperiod) which simulated spring/autumn conditions. Significant differences ($P \leq 0.05$) in germination between stratification regimes, with the same treatment and light regime, are indicated by different letters. Differences between light regimes, within stratification and treatments are indicated by different numbers. Differences between treatments, within stratification and light regimes, are indicated by asterisks. Statistical details can be found in Tables S2.3 and S2.4 of Appendix 3.

DISCUSSION

Germination of the morphophysiologically dormant *Hibbertia tenuis* was highest (> 50 %) following a smoke treatment coupled with light and temperature regimes that simulate spring/autumn conditions. Results also show that exogenous application of GA stimulates germination, and this effect is enhanced by heat, however, GA was also found to reduce the positive effects of smoke. Additionally, *H. tenuis* germination was influenced by light availability and seasonal temperatures; high germination in the dark occurred during autumn temperatures, while high germination in the light occurred with late winter temperatures. This indicates a potential bet-hedging mechanism which restricts all seeds from germinating at any one time. This mechanism helps regulate patterns of emergence after a fire in response to unfavourable conditions for establishment, and this has implications for management with prescribed burns.

Effects of fire treatments, gibberellins, and temperature on germination

Smoke

We found that a greater percentage of *H. tenuis* seed germinated (up to 62 %) in treatments that incorporated smoke compared to untreated seed (< 5 %). This aligns with previous research which found that smoke triggers substantial germination in some, but not all, *Hibbertia* species (Hidayati *et al.* 2012). While high amounts of germination were found to depend on diurnal temperature and light cycles that simulated spring or autumn conditions, limited germination was recorded in the control group. In comparison, other *Hibbertia* species have been found to have more complex dependencies to initiate any germination, such as seasonal fluctuations in temperature in conjunction with light and smoke treatments (Hidayati *et al.* 2012). This indicates that *H. tenuis* does not have the same complex physiological barriers to germination found for many other *Hibbertia* species. While *Hibbertia* species have rudimentary embryos (Schatral 1996), which need to grow as a prerequisite for radical emergence, this does not appear to inhibit germination in *H. tenuis*, unlike with other species. We suggest this is because *H. tenuis* seed is adapted to rapid establishment in swamps after the detection of smoke, and so they are not inhibited by physiological barriers.

Following fire in swamps, seedlings are at low risk of desiccation once established due to high water availability in the soil substrate and vegetation recovers quickly as a result. However, competition increases quickly, and it is common for *H. tenuis* to be outcompeted by other species, and as such it largely persists in the soil seedbank after long periods without fire (Clarkson 1997; Conran *et al.* 2017; Hayward *et al.* 2008; Trezise *et al.* 2021). Rapid establishment is critical for survival following fire in highly competitive environments where the soil substrate is permanently saturated (Breen *et al.* 1988; Budelsky and Galatowitsch 2000; Perry *et al.* 2004). The ability to germinate rapidly in response to smoke exposure is, therefore, an important adaptation for *H. tenuis*, given that it occurs in a fire-prone ecosystem where immediate post-fire conditions are the most favorable period for seedling establishment (e.g. Bond and Keeley 2005; Keeley and Fotheringham 2000a; Vaughton 1998).

Gibberellin, heat and smoke

We found that GA stimulated *H. tenuis* germination under all tested seasonal temperature regimes. This effect was significantly greater under summer temperatures than under winter temperatures but effects on germination were inconsistent across the different seasons. The *ex situ* use of GA has been shown to bypass the need for temperature stratifications in several plant species (Bell *et al.* 1995; Bunker 1994; ChingTe *et al.* 1998; Fang *et al.* 2006; Plummer and Bell 1995;

Wardlow *et al.* 1989). This includes some (e.g. *H. huegelii*; Hidayati *et al.* 2012) but not all *Hibbertia* species (e.g. *H. hypericoides*; Schatral 1996).

Heating for 90 °C for 5 minutes did not increase germination of *H. tenuis*, except when also treated with GA. This is most likely due to heat enhancing seed coat permeability, allowing GA to be more readily imbibed. Impermeable seed coats are a characteristic of many *Hibbertia* species, which explains why scarification can enhance germination for some of these species (Allan *et al.* 2004; Bell 1999; Schatral 1996). Heat shock can help to break dormancy in species from fire prone ecosystems, when specific temperature thresholds are needed (e.g. pyrogenic dormancy; Ooi *et al.* 2014), and heat-shock has been shown to promote germination in *H. amplexicaulis* and *H. hypericoides* (Bell 1999).

Interestingly, while the highest germination (51 % when subject to spring/autumn conditions) occured in smoke treated *H. tenuis* seed, adding GA to smoke treated seed subjected to the same temperatures, resulted in significantly reduced germination (31 %; $P = < 0.01$). These results may be due to complex interactions between GA and KAR (from smoke), attributed to “hormone cross talk” where different hormones partially share the same pathways and signalling mechanisms (Guilfoyle *et al.* 2015; Morffy *et al.* 2016). Papenfus *et al.* (2015) describe a similar interaction, whereby a rhizobacterium (bacteria which independently promotes plant growth) and KAR have overlapping modes of action, and cross-talking between hormones within the associated plant, resulting in lower growth.

Temperature

Highest germination was 51 % for smoke- and light-treated seed, under daily temperatures (22/10 ºC for 12/12 h), photoperiod cycles (light/dark for

12/12 h) and after temperature stratifications (5/15 ºC for 2/2 months), which simulated spring conditions. This is possibly an adaption to the swamp margin habitat to which *H. tenuis* is confined, where soil remains moist late into spring despite decreasing rainfall. Germination did occur under winter and summer conditions, albeit at a significantly lower percentage. This may be a bet-hedging strategy, enabling rapid germination of at least some seed to occur, regardless of the time-of-year of when a fire occurs.

Temperature is a well-known factor that influences germination. For example, Davies (2005) showed that the permanent-spring wetland forb *Eriocaulon carsonii* required temperatures corresponding to autumn/spring conditions to overcome dormancy, with no germination occurring under winter or summer temperature conditions. Similar effects have been found with some *Hibbertia* species: neither *H. huegelii* nor *H. hypericoides* have been found to germinate under summer temperature conditions (35 ºC for 28 weeks; Hidayati *et al.* 2012). However, for these and two other *Hibbertia* species (*H. commutata* and *H. racemosa*), the greatest emergence is linked to moisture and temperature regimes correlating to winter conditions (Hidayati *et al.* 2012). This can be explained by the Mediterranean climate and non-swamp habitats in which these later *Hibbertias* occur, where reliably moist conditions for seedling establishment are mostly confined to winter months.

Confounding effects of temperature stratification and light exclusion

Temperature pre-treatments

Germination rates of smoke treated *H. tenuis* seed in the absence of any warm stratification was relatively high (51 %), indicating it does not require a temperature pre-treatment. This is common in species of *Hibbertia* in

Mediterranean climates with hot summers (e.g. *H. huegelii* and *H. hypericoides*; Hidayati *et al.* 2012). If germination of *H. tenuis* seed were dependent on a warm stratification, the species would be at a disadvantage because they rarely experience hot temperatures due to the permanently water-logged subsoil where they grow, which moderates temperature. Nevertheless, alternating temperatures are required to break morphophysiological dormancies in many other species (Baskin and Baskin 2004; Geneve 2003; Graeber *et al.* 2012) as these conditions can relate to favourable climate regimes correlating to specific seasons (Baskin *et al.* 2008; Hidayati *et al.* 2000; Walck *et al.* 2000). For example, Hidayati *et al.* (2012) found warm stratification (35 ºC for 16 weeks) significantly increased germination in *H. commutata* and *H. racemosa*, this being an adaptation to the Mediterranean climate where they occur, where cool wet winters follow hot dry summers. Such species commonly require warm dry stratifications to synchronise germination with the cool wet conditions of the following winter (Baskin and Baskin 1998; Merritt *et al.* 2007).

Light and temperature pre-treatments

Exposure to light was important but not critical for germination in *H. tenuis* depending on other conditions. Increased germination with detection of light has been shown in several plant species (Benvenuti *et al.* 2001; Seo *et al.* 2009; Vazquez-Yanes and Orozco-Segovia 1994) including wetland species (Baskin *et al.* 1989; Davies 2005; Kettenring *et al.* 2006). This is a common mechanism for increasing germination either in gaps or post-fire when there is less competition for light (Baskin *et al.* 1989; Davies 2005; Kettenring *et al.* 2006). However, mechanisms of light-mediated germination can interact with stimuli from smoke (KAR) by inhibiting (rather than stimulating) seed germination in darkness for many of these species. When this occurs, KAR enhances ABA (a plant hormone that regulates dormancy) biosynthesis while impairing GA biogenesis (Meng *et al.* 2017; Nambara *et al.* 2010).

Light and temperature regulated dormancy may be an adaption in *H. tenuis* to avoid germination of seeds that are on the soil surface and have insufficient time to establish before summer; *H. tenuis* is endemic to swamps where the soil surface dries out in summer which can desiccate seedlings. Regardless of light exposure, germination was low for *H. tenuis* seeds exposed to smoke and pre-treatments that simulated early spring conditions, likely because this period is too close to summer. Similar inhibition of germination when seeds are incubated under warm temperatures has previously been found for a wide number of species in Mediterranean-type climates with hot and dry summers (Bell *et al.* 1995; Thanos *et al.* 1989). We also found that germination of smoke treated seed when pre-treated with late winter temperatures was low in darkness (17 %) but was high with light exposure (51 %). Darkness after fire indicates either burial under- soil or -partially burnt swamp vegetation. For example, a patchy fire may kill a parent plant through radiant heat, but the fire may not consume the parent plant or biomass directly above its seed, thus shielding the seed from light. In these dark conditions, germination after late autumn likely provides the best chance of survival because seedlings will have approximately twelve wet winter weeks to mature before summer. Conversely, exposure to light indicates a lack of competition and this coupled with warm spring temperatures allows for seedlings to rapidly established before the onset of summer. Bioturbation may be another explanation of light sensitivity in *H. tenuis* seed, given that digging animals can redistribute seed to soil surface which exposes it to light (Fleming *et al.* 2014).

The different germination responses of the seeds of *H. tenuis* in the dark compared with light is likely a bet-hedging mechanism in response to seed burial depth, as found in other species (Fan *et al.* 2018), to ensure germination occurs where environmental conditions (e.g. season of fire and rainfall) can vary both temporally and spatially. This mechanism allows for a portion of *H. tenuis* seed to germinate after fire under non-ideal conditions (i.e. close to summer) while also ensuring a portion remains dormant for a subsequent opportunity to germinate. Future studies could investigate this strategy further by re-subjecting seeds which did not germinate to a subsequent set of similar treatments. Similar findings have been found in non-swamp *Hibbertia* species (e.g. *H. commutate* & *H. hypericoides*; Schatral 1996; Tieu *et al.* 2001b). For example, Hidayati *et al.* (2012) found high germination in *H. racemosa* seeds subject to a range of seasonal temperatures following warm stratification in darkness. But following stratification under the same conditions but in light, high germination was confined to only winter temperature conditions.

Conservation implications

Propagation

Results from this study can guide *ex situ* propagation, which may be necessary to increase population sizes in extant populations and re-establish ‘new’ populations in areas where it has disappeared. Germination of the morphophysiologically dormant seed of *H. tenuis*’ can be maximised for *ex situ* propagation with the application of smoke water, followed by an incubation period which simulates spring/autumn conditions, corresponding to a 12 hour day and 12 hour night photoperiod, and temperatures oscillating from maximums of 22 °C to 10 °C. Under these conditions more than 50% of the seeds should germinate. Achieving germination rates of 100% is unlikely, either because a portion of the seeds will not be viable, and/or a portion will be in a deeper state of dormancy (e.g. bet-hedging; Bell *et al.* 1995; Finkelstein *et al.* 2008; Ooi *et al.* 2009). Re-exposong seeds to a repeat sequence of stmuli might lead to further seeds germinating. Applying heat on its own, or in unison with any other treatment, under any incubation, will not increase results. Similarly, pre-treating seeds with a temperature and light stratification can inhibit germination and did not increase germination in any of the treatment combinations presented here. Furthermore, application of GA cannot be used to bypass the need for stratification or incubation, as it interacts negatively with the enhancing effects of smoke.

Management of remnant populations

This study has implications for *in situ* management of the three remaining *H. tenuis* populations and indicates that fire is a likely pre-requisite to facilitate germination. Long unburnt FPS with historic *H. tenuis* populations which have disappeared should be a targeted for ecological burns to provide germination cues for dormant seeds of this species potentially hidden in the soil seed bank. These burns should mostly be prescribed in autumn. This is in part because the germination of seeds and growth and establishment of seedlings takes several months such that fires in spring may not provide germinating seedlings with enough time to establish before the hotter and drier summer months. We argue that the highest survival of *H. tenuis* seedlings occurs over winter after an autumn burn due to higher water availability and reduced competition from regenerating larger shrubs, which tend to grow faster in spring when temperatures are warmer and there are more hours of daylight. In addition, autumn burns are often more effective at reducing post-fire competition as spring burns consume less plant biomass (FPS are damper in spring than autumn) and plant biomass can restrict light and heat exposure (Gillespie and Allen 2004; Keeley and Fotheringham 2000a). This makes autumn burning preferable in situations where colder burns could consume insufficient amounts of plant biomass to reduce light competition. Furthermore, *H.*

tenuis mostly flowers across spring and summer, meaning fires during autumn will not disrupt peak flowering, leaving more seed available for recruitment (Miller *et al.* 2019). Results suggest that ecological burning can be instrumental in reversing species decline, however it highlights that careful consideration needs to be taken when prescribing the season of a burn.

Chapter 5. Effect of fire season and herbivory on post-fire succession in an endangered heathy swamp community

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Overall percentage (%)	70%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	10/11/21

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate to include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Signature		Date	28/10/21

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Signature		Date	28/10/21

ABSTRACT

Long periods without fire cause heathy swamps to transition into late-successional age classes, characterised by low species richness and a depauperate understorey. Over 98 % of the Australian nationally critically endangered Fleurieu Peninsula swamps are long unburnt and lack disturbance dependant flora, prompting the use of prescribed burns to achieve a better balance of age classes. We conducted spring and autumn burns to determine the utility of fire as a conservation tool, as well as the importance of fire seasonality and post-fire grazing on plant recovery. Fire prompted a transient successional period of increased richness, reduced overstorey cover and promotion of understorey vegetation. Plant species richness was highest after fire (7.4 species m^{-2}) compared with unburnt quadrats (4.5 species m^{-2}). Moreover, 12 of the 42 detected native species were absent from unburnt quadrats. Many species appeared to require fire to regenerate their propagule reserves, including the nationally critically endangered *Hibbertia tenuis* which increased 8.8-fold in response to burning. These species will become locally extinct if the time between fires is greater than their lifespan in both the above- and below-ground vegetation. Fire seasonality also affected results, as spring burning significantly reduced overall native plant recovery compared to autumn burning. However, some species benefited more from spring burning, suggesting that fire should be prescribed based on the seasonal responses of target species. Grazing decreased plant cover and excluded 12 % of species, including threatened orchids, but may be important during later successional periods. Despite potential benefits of burning, prescription of fire in heathy swamps should consider that different co-occurring species can have opposing seasonal responses and that grazing hinders the initial recovery of vegetation.

Key terms: prescribed burning, season, grazing, fire, heathy swamps, succession

INTRODUCTION

Excluding fire from fire adapted vegetation favours late-successional species (Bond and Keeley 2005; Denslow 1980; Heinl *et al.* 2007). This can result in the local extinction of shorter-lived, early successional species, especially disturbance dependant species (Enright *et al.* 2012; Keeley 1986; Sugihara *et al.* 2006). Thus, at a landscape scale, richness is maximised when a range of age classes are maintained (Gosper *et al.* 2011; Tozer and Bradstock 2003; Watson 2005). The issue of age-class diversity loss applies to landscapes containing long unburnt heathy swamp communities and can be rectified with prescribed burning. Fire returns late-successional vegetation communities to early stages, and in doing so can enhance species richness (Cheal 2010; Shackelford *et al.* 2015; Vandvik *et al.* 2005), alter vegetation structure (Bond and Ladd 2001; Foster *et al.* 2017; Gosper *et al.* 2012) and allow under-represented threatened flora to re-emerge (Cheal 2010; Davis and Davies 2021; Vaughton 1998).

Vegetation succession is the sequential change in composition and structure over time after disturbance, such as fire (Van Andel *et al*. 1993). In heathy swamps this is characterised by short-lived species dominating soon after fire, before these are replaced by heathy shrubs which eventually become outcompeted by ferns or sedges during late successional periods (Cheal 2010). Natural fire regimes in heathy swamps are highly variable, with inter fire periods ranging from 7 to 80 years (Brown and Podger 1982; Cheal 2010; Clarkson 1997; Hayward *et al.* 2008; Walker and Boneta 1995; Wark 1997). Fires occurring outside of this range may cause heathy swamps to transition into alternative vegetation communites.

Long periods without fire in heathy-swamps and heathy-wetlands are associated with floristically simple plant communities (Hayward *et al.* 2008; Kimura and Tsuyuzaki 2011; Timmins 1992), which often become dominated by just a few overstorey species (Harding 2005; Kotze 2013; Pendergrass *et al.* 1998). In such situations, species which characterise the understorey are underrepresented (Clarkson 1997; Martin and Kirkman 2009), as they become outcompeted and lack opportunity for re-establishment (Keeley and Fotheringham 2000b; Middleton 1999). This also applies to the *Swamps of Fleurieu Peninsula* (FPS) ecological community, which is listed as critically endangered under the Australian *Environment Protection and Biodiversity Conservation Act* (EPBC Act 1999) and provides habitat for 84 native plant species which are listed as threatened at the national, state or regional level (Trezise *et al.* 2021). This threatened ecological community is confined to the wettest parts of South Australia where 98 % has been cleared and drained, and now only survives as small, mostly degraded remnant patches (remnants hereafter) surrounded by agricultural land (Harding 2005). Only 2 % of all the 614 surviving remnants have experienced a fire in the last 30 years (Department for Environment and Water 2009; 2016). As a result, most threatened ground-stratum species, such as the nationally critically endangered *H. tenuis,* have all but disappeared (Trezise *et al.* 2021), and now largely only survive in a declining soil seedbank. In an allied study, we showed that 21 % of native species were only present in the soil seedbanks of long unburnt FPS (Chapter 3; Trezise *et al.* 2021). Comparisons can be made with government vegetation surveys which document the presence of species in the long unburnt swamps, this shows that FPS contain between 12 to 78 native species in the above-ground vegetation (n = 25 swamp surveys; Tables S21 & S22 from Appendix 4; Department for Environment and Water 2020b). These swamps would historically have been exposed to more frequent fire (Bickford and Gell 2005; Conran *et al.* 2017), with natural bushfires occurring more regularly in summer and autumn because of the region's Mediterranean climate (Clark 2020). However, fire occurrence in FPS has been actively suppressed to protect surrounding valuable agricultural land (Gill and Williams 1996; Trezise *et al.* 2021), resulting in a substantially reduced proportion of swamps in early successional stages.

Prescribed burning can help mitigate this problem by reducing the cover of dominant flora (e.g. *Gleichenia* spp and *Phragmites australis*) and promoting the establishment of understorey species such as graminoids and forbs (Johnson 2001; Kimura and Tsuyuzaki 2011; Walker and Boneta 1995). For example, small herbaceous species found in the understorey of heathy swamps (e.g. *Drosera* spp and *Thelymitra* spp) have been observed flowering prolifically after fires, but are rarely seen in later successional stages (Timmins 1992; Trezise *et al.* 2021). The seeds of several species of plants in heathy swamps respond to fire-related cues and these species are known to be associated with early post-fire environments, including *Centrolepis aristata, Drosera* spp and *Sprengelia incarnata* (Balmer and Storey 2010; Brown and Podger 1982; Enright and Kintrup 2001; Kenny 2003). Furthermore, in a separate experiment that investigated the dormancy mechanisms of *H. tenuis*, we found that germination was negligible without smoke cues (Chapter 4). Thus, burning can promote germination and establishment of disturbance dependant swamp species (Lugo 1995), many of which are disappearing and possibly becoming locally extinct in its absence (Norton and De Lange 2003; Pendergrass *et al.* 1999; Trezise *et al.* 2021).

Season of fire influences fire behaviour (e.g. seasonal rainfall and temperature trends) which subsequently can interrupt cyclic growth stages (Knox and Clarke 2006b; Laubhan 1995; Roche *et al.* 1998). Prescribed burning is often operationally restricted to autumn or spring in landscapes where summer fires are too dangerous and winter fires are too low in intensity to adequately reduce fuel loads. The ecological consequences of spring and autumn burning can vary greatly;

for instance, autumn burning can enhance the cover of introduced species (Kerns *et al.* 2006) or reduce native cover (Knapp *et al.* 2006). Spring burning promotes *P. australis* growth more so than autumn fire, a species which is known to dominate and subsequently reduce richness in swamps (Kotze 2013), and spring burns interrupt the active growing seasons of many plant species, including many orchids (Jasinge *et al.* 2018). A separate affiliated study on the dormancy of *H. tenuis* seed, suggests that burning in autumn will maximise germination (Chapter 4). Therefore, seasonal effects of fire will likely influence the resulting vegetation structure and composition (Laubhan 1995).

Another factor that commonly influences post-fire regeneration is grazing pressure. In agricultural landscapes, altered land use and vegetation clearance can lead to overgrazing by unnaturally large populations of native grazers (Department for Environment and Water 2019b; Descovich *et al.* 2016; Grigg and Pople 2001; Prowse *et al.* 2019). Furthermore, in southern Australia, western grey kangaroo (*Macropus fuliginosus*) abundance has increased since European settlement, which is causing widespread overgrazing of native vegetation (Department for Environment and Water 2019b; Prowse *et al.* 2019).

Vegetation resprouting or germinating after a fire is often highly accessible and palatable for herbivores. This can be problematic after fire, as grazers can focus on regrowth in burnt areas, which limits the ability of plants to recover (Andruk *et al.* 2014; Letnic 2004; Meers and Adams 2003) and can result in local extinctions (kangaroos and rabbits; Cohn and Bradstock 2000). This effect is exacerbated when burning small areas, as herbivory can become concentrated (Leigh and Holgate 1979). Herbivore exclusion via fencing after a fire has been found to enhance species richness and cover in swamps, by limiting the influence of grazing (Ford and Grace 1998; Taylor *et al.* 1994). In a separate associated study, which assessed the response of grazing on plant recovery after fire, we found that fencing increased both the richness and abundance of native plants (Chapter 2). Season of burn can also affect grazing pressure, with kangaroos more likely to graze regrowth in drier seasons, when surrounding unburnt vegetation is less palatable and more sparse (Tolsma *et al.* 2007). Culling and fencing can be used to mitigate grazing after a fire, and this can improve the recovery of plant communities (Mawson *et al.* 2016; Meers and Adams 2003; Noy-Meir 1995).

The effect of season of burning and subsequent grazing pressure has been well studied in other vegetation communities (e.g. Alex and Woinarski 2007; Fuhlendorf *et al.* 2008; Govender *et al.* 2006; Kerns *et al.* 2006; Knapp *et al.* 2006; Knox and Clarke 2006a; Kraaij *et al.* 2017; Miller *et al.* 2019; Ooi 2010; Tolsma 2002; Tsafrir *et al.* 2019; Whitford and Steinberger 2012; Wright and Clarke 2018) however their effect on heathy swamps is less well understood. Thus, the objective of the current research was to increase our understanding of how the season of burning and subsequent grazing influenced the post-fire recovery of heathy swamps, specifically in senescent examples of the FPS. We conducted plant surveys before and after burns, comparing swamp areas burnt in spring, with areas burnt in autumn and areas left unburnt. We also studied the effect of grazing mammals by setting up exclosures in regenerating swamp vegetation. Our main focus was the effect on the cover and species richness of understorey species, as well as the abundance of *H. tenuis* plants.

METHODS

Study sites

This study was undertaken within three adjacent FPS, in the Yundi area on the Fleurieu Peninsula, in the lower Mount Lofty Ranges of South Australia (Figure

1), which collectively contain the largest known population of *H. tenuis* (Department for Environment and Water 2019a; Quarmby 2011; Trezise *et al.* 2021). These swamps have not been burnt for at least 59 years based on historic imagery dating back to 1958 (Department for Environment and Water 2020c; Trezise *et al.* 2021). Fleurieu Peninsula Swamps occur on permanently saturated peaty subsoils and are often dominated by coral fern (*G. microphylla*) and prickly tea tree (*Leptospermum continentale*) when in late successional stages. The region has a Mediterranean climate that averages 756 mm of rain per annum (Myponga – Bureau of Meteorology 2022).

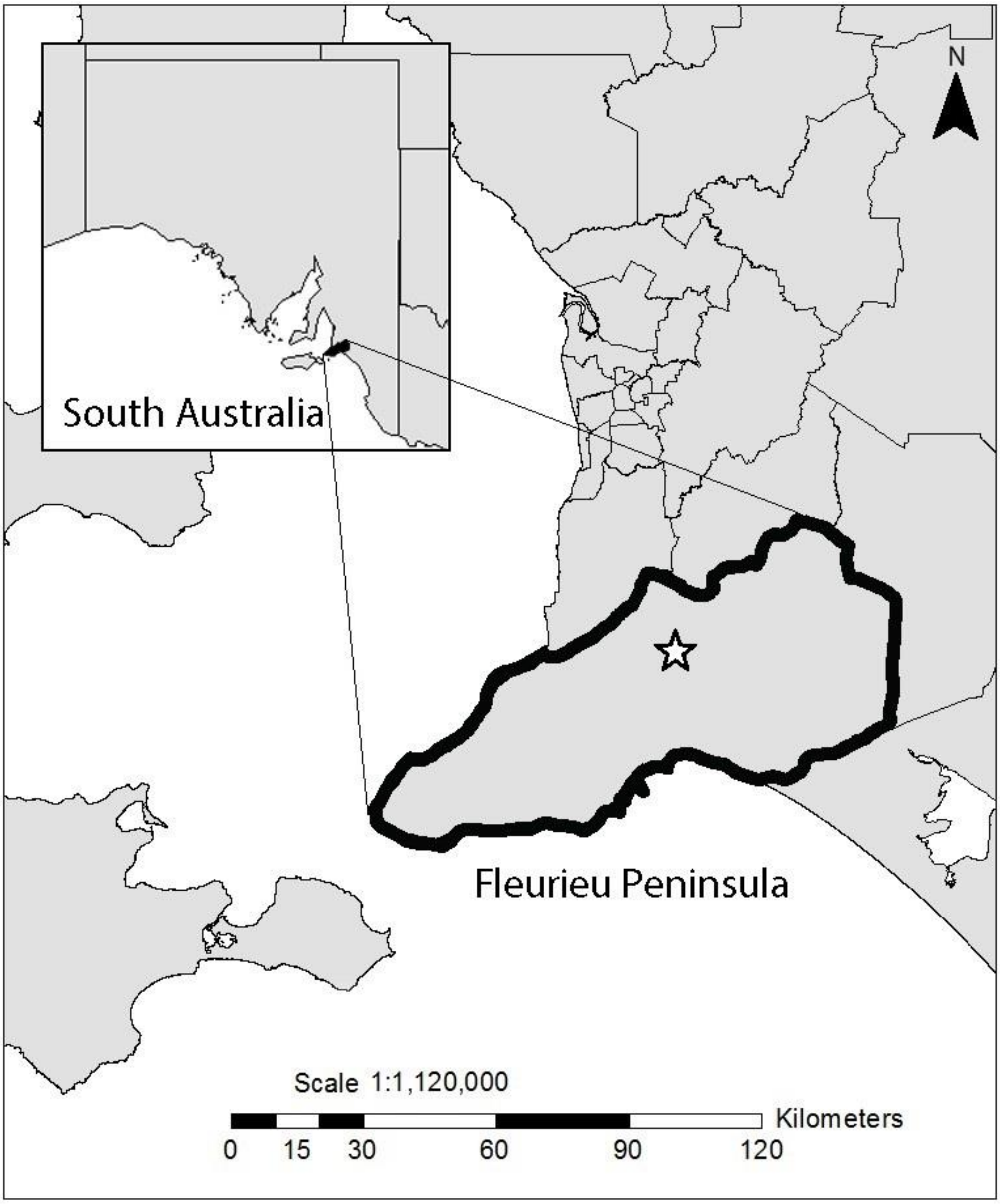


Figure 1. The Fleurieu Peninsula, South Australia. The hollow black star represents the study area. Map created using ArcGIS package (version 10.3.1) using spatial data from the Department of Planning, Transport and Infrastructure (1996).

Ecological burns and fencing

The three swamps were randomly assigned to be burnt either in spring, autumn or left unburnt as a control. Each swamp was then stratified into a core area (> 5 m from the edge of the swampy heath community) and an edge area (≤ 5 m). Eight 1 x 1 m^2 quadrats were then randomly positioned in each of the core and edge areas in each swamp, using the ArcGIS package version 10.3.1 (Esri 2014). For each quadrat, percent cover for every plant species present was estimated using the point intercept method in August 2017 using a 1 x 1 m^2 grid divided into a hundred 10 x 10 cm^2 cells. Percentage cover for each species was estimated by pushing a 2 m long pin into the north-eastern corner of every cell and recording the number of times that species was intercepted by the pin tip. Additional species found within the quadrat, but not intercepted by the pin were given a cover value of 0.1 %, meaning that cover for each species could range from 0.1 % to 100 %. The number of *H. tenuis* plants were also counted in quadrats across the survey dates. As part of a separate unaffiliated survey, the total number of plants were counted within the three swamps (outside and within our quadrats) before the experiment commenced in August 2017 and then again in August 2020 (D. Duval pers. obs., 2020).

The spring burn was conducted in November 2017 and the autumn burn in May 2018. Vegetation surveys occurred 2.5 and 0.5 months before, and 2.5, 4.5, 10 and 18 months after each respective burn, with quadrats in the control swamp being surveyed at the same time as the spring-burnt swamp. Thus there was a seven-month difference between the survey dates conducted in the spring-burnt/control swamp and the autumn swamp. Both burns were ignited using drip torches, and fires were contained using water without retardants or foams. One week after each fire, fenced exclosures were erected around every second quadrat to restrict grazing by *M. fuliginosus* and other herbivores. The fencing material used was 1.8 m tall with 5 cm hexes. The same number of fenced exclosures were also constructed around quadrats in the control swamp, at the same time as for the spring swamps. No fences were erected before burning commenced, and so before and after fire comparisons of quadrats were not possible for fenced quadrats.

Statistical analysis

We compared species richness and cover within quadrats for individual species, and categories based on endemism (native vs introduced), lifespan (annual/biennial vs perennial), and lifeform categories (forb, non-grass graminoid, fern, grass, shrub/subshrub and tree). Data analyses were performed using the R software in R studio from version 3.5.1 (R Core Team 2019). Generalised linear mixed models were used (GLMM) with the R package glmmTMB from version 1.0.2.1 (Magnusson *et al.* 2017), with season and grazing used as fixed factors and quadrat used as random effects. Model selection was determined using anova and overdispersion functions. The variance between the edge and core quadrats did not significantly contribute to our models and therefore we did not compare between them. Distribution and dispersion of the data for each species informed the link functions used for each model, such that dispersion tests directed the use of either a Poisson, Beta or Negative Binomial distribution. For example, the effects of fire on *H. tenuis* cover was modelled as follows: model <- glmmTMB(cover ~ Time since fire * season * fenced + (1|quadrat), data = data , family = beta_family. Means and *P* values were predicted from the models using the R package emmeans from version 1.7.3 (Lenth *et al.* 2019). These predictions used pairwise methods, including test statistics (t.ratio) to produce *P* vaules. Results were then plotted using the R package ggplot2 from version 3.3.3 (Wickham *et al.* 2021).

RESULTS

Effects of fire overtime

Native ferns dominated before the fires which were replaced overtime by native perennials shrubs and non-grass graminoids (Figure 2). The post fire vegetation community also hosted native grasses and forbs which were negligible before fire and in the unburnt control swamp (Figure 2). Furthermore, non-metric multidimensional scaling also showed two distinct groups of species, with minimal species overlap before fire or in controls when compared to burnt quadrats (Figure 3).

The different swamps contained similar numbers of native species and percent plant cover two weeks before fire, comparing the control (3.4 species m^{-2}; 80 %) to autumn (3.6 species m^{-2}; 87 %) and spring quadrats (3.8 native species m^{-2}; 89 %). This was also the case for surveys conducted 2.5 months before fire (Figure 3). Furthermore, *Gleichenia microphylla* dominated before fire, occupying more than 50 % of quadrats in all pre fire surveys and unburnt control quadrats (Table 1 and Figure 3). Comparatively, native annuals/biennials cover was consistently less than 1 % in all unburnt quadrats (Table 1 and Figure 3).

The cover of natives was significantly less 4.5 months after both burns (fenced; 94 % control vs 47 % autumn vs 57 % spring; Table 1). However, at this time the richness of native plants was significantly greater in the autumn (T (296) = -5.92, $P = < 0.01$), when compared to the surveys conducted two weeks before fire. Furthermore, at 4.5 months post-fire, native annuals/biennials richness (fenced; 0.1 control vs 0.8 autumn; Table 3) and cover was significantly greater for the autumn burn relative to unburnt control (fenced; 0.5 % control vs 4.3 % autumn;

Table 3). Burnt quadrats also had significantly greater richness of native perennials after 4.5 months compared to controls (fenced; 6.4 species autumn m^{-2} vs 4.1 species m^{-2} control; Table 3).

The highest recorded value of native richness was 7.4 species m^{-2} recorded at 10 months after the autumn burns compared to 4.5 species m^{-2} in unburnt (fenced; T (254) = 2.81, $P = 0.01$). By the end of the 18-month monitoring period, a total of 42 native plant species had been detected across all quadrats**,** 12 of which were absent without fire compared to 3 previously undetected species in unburnt quadrats (Table S1 in Appendix 4). At this time, there was significantly greater cover of perennial non-grass graminoids (fenced; 20 % control vs 49 % autumn) and shrubs/subshrubs (fenced; 31 % control vs 70 % autumn; Table 2) in burnt quadrats. Additionally, after 18 months, fern re-establishment was negligible, with *G. microphylla* cover being less than 1 % compared to 61 % in unburnt controls (Table 2). At this time, the cover of four native shrubs/subshrubs was significantly greater in burnt quadrats, these were *H. tenuis*, *L. continentale*, *S. incarnata*, and *Viminaria juncea* (Table 2). At 18 months after fire, *H. tenuis* plant counts were significantly greater in burnt quadrats compared to controls (fenced; 5.3 plants autumn vs 0.6 plants control; Table 5). The number of *H. tenuis* plants after 18 months was significantly greater than surveys conducted 2 weeks before fire (autumn; T (235) = -4.13, $P = < 0.01$). However, overall native cover and richness was statistically similar compared to unburnt controls at 18 months (Table 2; Table 4) and pre-fire surveys (Figure 3); the exception was spring burnt quadrats, which never fully recovered to pre-fire levels of cover. Furthermore, cover or species richness for introduced species was not affected by fire when comparing pre-fire surveys to burnt quadrats after 18 months (Figure 4).

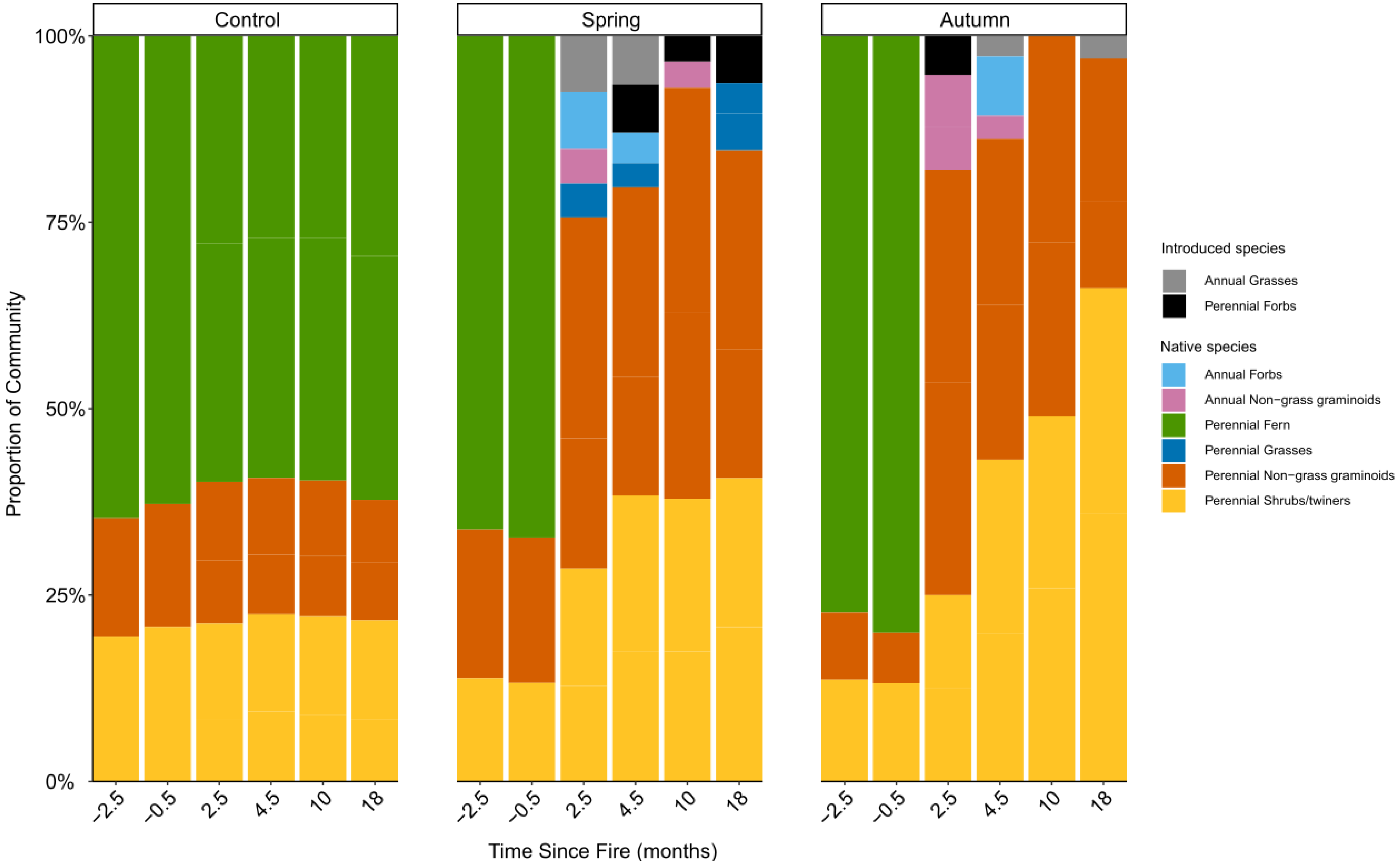


Figure 2. Bar plot showing the relative abundance of each lifeform group over time, after a spring or autumn burn, and within an unburnt control.

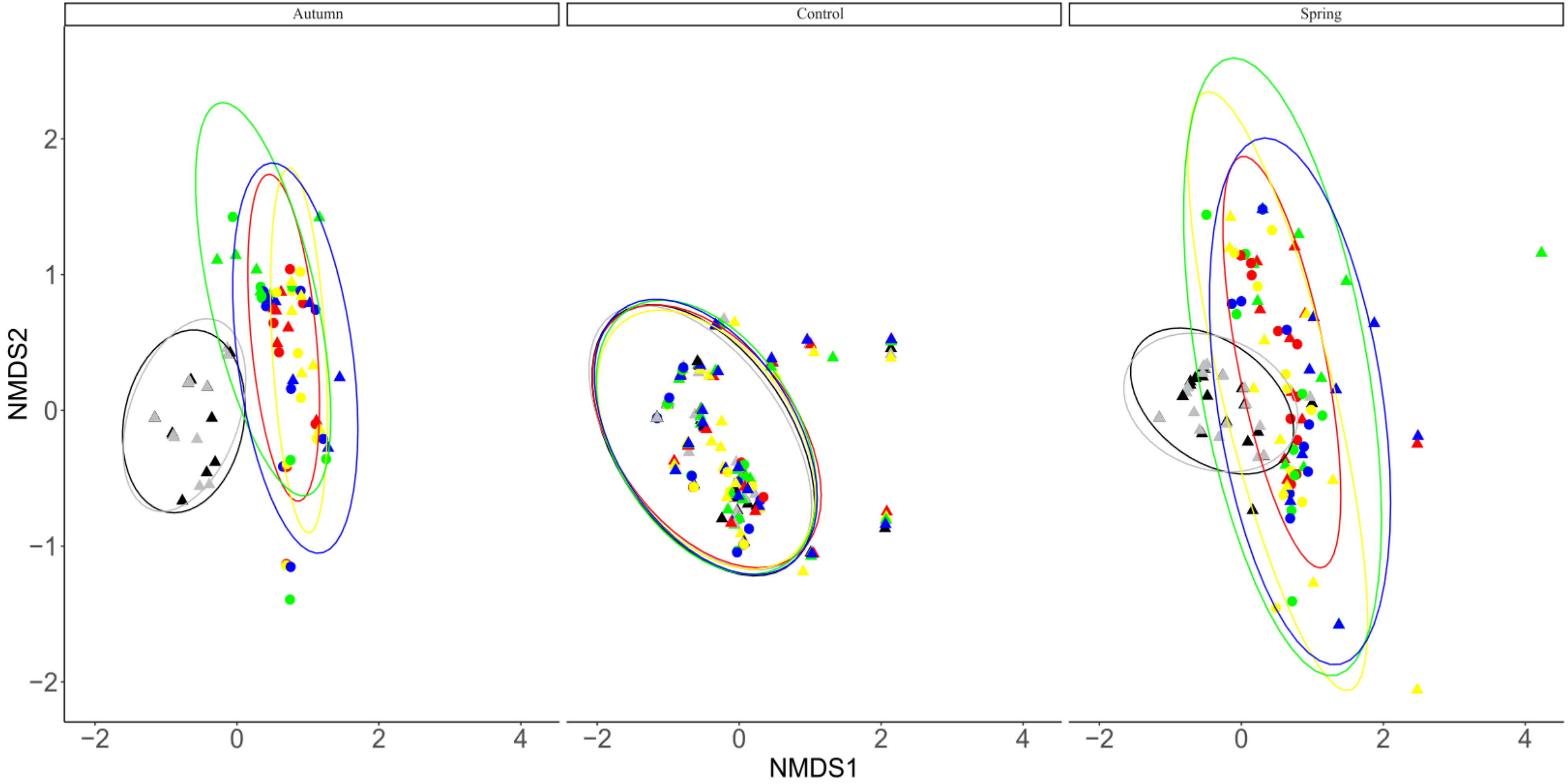


Figure 3. Ordination plot using non-metric multidimensional scaling which shows the grouping of species as a product of time since fire, season of burn and grazing. Times is given as: 2.5 months before fire (grey), 0.5 months before fire (black), 2.5 months after fire (green), 4.5 months after fire (blue), 10 months after fire (red), 18 months after fire (yellow). Differences between the grazing treatment are shown as fenced (circles) and unfenced (triangles).

Table 1. Effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **cover** (Mean ± SE; % plant cover) **4.5 months after fire** using generalised linear mixed models. Additional statistical details can be found in Table S15 of Appendix 4. Significant components denoted with (vs 0) indicates that no values were detected within one of the paired groups.

Longevity & lifeform class/species	**CF**	**CU**	**SF**	**SU**	**AF**	**AU**	**Significance (*P* value)**
All natives	94.4 ± 2.6	89.1 ± 2.9	56.8 ± 12.9	31.2 ± 11.8	47.3 ± 7.8	26.8 ± 10.9	S<C (0.01); A<C (0.01); S(F>UF) (0.04)
All annual/biennial natives	0.5 ± 0.5	0.6 ± 0.4	1.9 ± 0.9	2.1 ± 0.8	4.3 ± 1.2	4.0 ± 1.3	A>C (0.02)
Forbs	<0.1 ± <0.1	0.2 ± 0.2	1.6 ± 0.9	1.8 ± 0.8	1.8 ± 1.2	2.2 ± 1.4	
Non-grass graminoids	0.5 ± 0.5	0.4 ± 0.4	0.3 ± 0.2	0.3 ± 0.3	2.5 ± 1.1	1.8 ± 1.2	
Drosera binata	0	0	1.4 ± 1.0	1.8 ± 0.8	1.8 ± 1.2	2.2 ± 1.4	
All perennial natives	93.9 ± 2.7	88.9 ± 3.0	55.8 ± 12.7	29.3 ± 11.8	43.0 ± 7.5	22.8 ± 10.4	S<C (< 0.01); A<C (<0.01); S(F>UF) (0.07)
Ferns	53.3 ± 12.5	60.3 ± 5.9	0.2 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	S<C (< 0.01); A<C (< 0.01);
Gleichenia microphylla	53.3 ± 12.5	57 ± 6.7	0.2 ± 0.1	<0.1 ± <0.1	0	0	S<C (0.02); A<C (vs 0);
Forbs	0.9 ± 0.6	0.5 ± 0.4	<0.1 ± <0.1	0.4 ± 0.3	1.8 ± 0.9	0.2 ± 0.2	
Grasses	<0.1 ± <0.1	0.8 ± 0.5	4.4 ± 4.2	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	
Non-grass graminoids	21.4 ± 8.6	17.6 ± 4.7	30 ± 11.1	8.7 ± 3.1	15.8 ± 3.3	7.0 ± 1.8	
Baumea rubiginosa	0.9 ± 0.6	2.3 ± 1.0	5.4 ± 3.4	1.7 ± 1.1	3.0 ± 1.1	1.2 ± 0.5	
Baumea tetragona	2.1 ± 1.9	3.8 ± 2.4	1.8 ± 1.1	2.2 ± 1.2	2.4 ± 0.9	1.0 ± 0.3	
Empodisma minus	1.6 ± 1.1	1.0 ± 1.0	2.0 ± 2.0	0.1 ± 0.1	3.1 ± 1.7	1.2 ± 0.3	
Gahnia sieberiana	16.8 ± 8.8	5.0 ± 2.4	17.6 ± 7.9	4.2 ± 2.8	1.6 ± 1.5	0	A(F>UF) (vs 0)
Shrubs/subshrubs	29.0 ± 10.2	19.8 ± 4.4	33.2 ± 11.7	22.9 ± 11.5	25.5 ± 7.6	15.7 ± 8.8	
Acacia provincialis	9.3 ± 4	4.2 ± 1.6	<0.1 ± <0.1	<0.1 ± <0.1	0	0	S<C (< 0.01); A<C (vs 0);
Hibbertia tenuis	11.4 ± 4.3	4.4 ± 1.8	18.7 ± 8.0	5.1 ± 2.7	15.3 ± 6.8	3.2 ± 2.0	
Leptospermum continentale	<0.1 ± <0.1	9.5 ± 4	1.6 ± 1.1	10.9 ± 5.8	4.8 ± 2.1	2.2 ± 0.9	
Sprengelia incarnata	<0.1 ± <0.1	0.4 ± 0.3	0.4 ± 0.4	<0.1 ± <0.1	4.4 ± 2.9	8.5 ± 5.6	
Viminaria juncea	<0.1 ± <0.1	<0.1 ± <0.1	1.7 ± 1.7	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	
Trees	0	0	0	0	0	0	
All introduced	1.5 ± 1.5	2.4 ± 0.6	1.8 ± 1.1	2.2 ± 0.9	1.0 ± 1.0	1.0 ± 1.0	C(F<UF) (0.09)
All annual/biennial introduced	0.9 ± 0.9	1.4 ± 0.3	0.8 ± 0.8	0.8 ± 0.5	0.4 ± 0.4	0.8 ± 0.8	C(F<UF) (0.09)
Forbs	0.3 ± 0.2	0.3 ± 0.1	0 ± 0	0.2 ± 0.1	0 ± 0	0 ± 0	
Leontodon taraxacoides	0.6 ± 0.6	0.1 ± <0.1	0.2 ± 0.2	0.2 ± 0.1	0.3 ± 0.2	0	C(F>UF) (< 0.01); S<C (< 0.01);
Lotus pedunculatus	0.3 ± 0.2	0.2 ± 0.1	<0.1 ± <0.1	0.1 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	

Grasses	0.6 ± 0.6	1 ± 0.2	0.8 ± 0.8	0.6 ± 0.4	0.4 ± 0.4	0.8 ± 0.8	
Holcus lanatus	0.6 ± 0.6	0.6 ± 0.2	0.8 ± 0.8	0.6 ± 0.4	0.4 ± 0.4	0.8 ± 0.8	S>A (0.04)
All perennial introduced	0.6 ± 0.6	1.0 ± 0.4	1.0 ± 0.7	1.4 ± 0.8	0.6 ± 0.6	0.2 ± 0.2	
Forbs	0.6 ± 0.6	0.2 ± 0.1	0.9 ± 0.7	1.0 ± 0.8	0.6 ± 0.6	0.2 ± 0.2	
Shrubs/subshrubs	0.1 ± 0.1	0.9 ± 0.3	0.1 ± 0.1	0.4 ± 0.4	<0.1 ± <0.1	<0.1 ± <0.1	
Rubus anglocandicans	<0.1 ± <0.1	0.8 ± 0.3	<0.1 ± <0.1	0.4 ± 0.4	<0.1 ± <0.1	<0.1 ± <0.1	

Table 2. Effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **cover** (Mean ± SE; % plant cover) **18 months after fire** using generalised linear mixed models. Additional statistical details can be found in Table S16 of Appendix 4. Significant components denoted with (vs 0) indicates that no values were detected within one of the paired groups.

Longevity & lifeform class/species	**CF**	**CU**	**SF**	**SU**	**AF**	**AU**	**Significance (*P* value)**
All natives	98.7 ± 1.0	87.2 ± 3.2	73.9 ± 10.9	31.6 ± 6.5	96.4 ± 3.2	63 ± 13.4	C(F>UF) (0.06); S(F>UF) (< 0.01); A(F>UF) (0.01)
All Annual/biennial natives	<0.1 ± <0.1	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.2	<0.1 ± <0.1	<0.1 ± <0.1	
Forbs	<0.1 ± <0.1	<0.1 ± <0.1	0.3 ± 0.2	0.1 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	
Non-grass graminoids	0	0.1 ± 0.1	0	0.2 ± 0.1	0	0	C(F<UF) (vs 0); S(F<UF) (vs 0)
Drosera binata	0	0	<0.1 ± <0.1	0.1 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	S(F<UF) (0.02)
All perennial natives	98.7 ± 1	87.1 ± 3.2	73.8 ± 10.9	31.3 ± 6.5	96.4 ± 3.2	63 ± 13.4	C(F>UF) (0.06); S(F>UF) (< 0.01); A(F>UF) (0.01)
Ferns	60.5 ± 11.7	60.6 ± 6.0	0.1 ± 0.1	0.8 ± 0.8	<0.1 ± <0.1	<0.1 ± <0.1	S<C (< 0.01); S(F<UF) (0.01); A<C (< 0.01)
Gleichenia microphylla	60.5 ± 11.7	57.2 ± 6.9	<0.1 ± <0.1	0.8 ± 0.8	0	0	S<C (< 0.01); A<C (vs 0)
Forbs	1.3 ± 1.2	0.4 ± 0.4	6.0 ± 5.6	0.1 ± 0.1	1.1 ± 0.6	0.2 ± 0.2	
Grasses	<0.1 ± <0.1	2.2 ± 1.5	9.8 ± 9.0	2.2 ± 1.8	<0.1 ± <0.1	<0.1 ± <0.1	
Non-grass graminoids	19.8 ± 7.7	17.1 ± 4.6	34.9 ± 7.7	9.1 ± 2.8	48.9 ± 13.3	13.7 ± 4.4	A>C (0.02); A(F>UF) (0.01)
Baumea rubiginosa	1.1 ± 1.0	2.5 ± 1.1	7.7 ± 4.9	0.8 ± 0.3	12.8 ± 5.2	5.7 ± 2.4	C(F<UF) (0.03); A>C (0.06); S<A (0.01)
Baumea tetragona	1.9 ± 1.6	3.1 ± 2.0	8.9 ± 4.4	3.1 ± 1.1	2.6 ± 1.9	0.2 ± 0.2	A<C (0.08); S>A (0.03)
Empodisma minus	2.3 ± 1.6	1.1 ± 1.1	5.5 ± 5.5	0.1 ± 0.1	20.8 ± 12.9	4.0 ± 3.2	S(F>UF) (0.06); A(F>UF) (0.05)
Gahnia sieberiana	14.4 ± 7.5	5.4 ± 2.6	12.5 ± 6.4	3.4 ± 2.1	7.3 ± 6.3	0	A(F<UF) (vs 0)
Shrubs/subshrubs	31.3 ± 11	17.5 ± 3.9	47.0 ± 13.7	19 ± 7.3	69.6 ± 11.5	50 ± 13.6	S(F>UF) (0.04); A>C (0.02)
Acacia provincialis	10.4 ± 4.3	4.4 ± 1.6	<0.1 ± <0.1	0.1 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	S<C (< 0.01)
Hibbertia tenuis	11.6 ± 4.2	3.7 ± 1.5	22.2 ± 7.7	0.9 ± 0.4	32.4 ± 13.2	4.8 ± 3.1	S(F>UF) (< 0.01); A>C (0.08); A(F>UF) (0.07)
Leptospermum continentale	<0.1 ± <0.1	8.1 ± 3.3	11.9 ± 5.7	12.6 ± 6.4	16.3 ± 5.4	15.8 ± 4.7	A>C (0.01); C(F<UF) (vs 0)
Sprengelia incarnata	<0.1 ± <0.1	0.3 ± 0.3	4.5 ± 4.5	0.2 ± 0.1	24.6 ± 10.9	25.3 ± 9.9	A>C (0.01); S<A (< 0.01); S(F<UF) (vs 0)
Viminaria juncea	<0.1 ± <0.1	<0.1 ± <0.1	15.9 ± 6.3	<0.1 ± <0.1	0.6 ± 0.6	<0.1 ± <0.1	S(F>UF) (0.06)
Trees	0	0	0	0.1 ± 0.1	0	0	S(F<UF) (vs 0)
All introduced	1.5 ± 1.0	4 ± 1.0	3.6 ± 1.4	2.7 ± 1.1	2.6 ± 2.6	1.8 ± 1.8	
All annual/biennial introduced	1.3 ± 0.9	1.8 ± 0.6	1.4 ± 1.0	0.5 ± 0.4	2.5 ± 2.5	1.7 ± 1.7	
Forbs	0.1 ± 0.1	0.8 ± 0.4	0 ± 0	0.4 ± 0.4	0 ± 0	0 ± 0	
Leontodon taraxacoides	0.3 ± 0.2	0.9 ± 0.4	0.2 ± 0.1	0.7 ± 0.4	0.1 ± 0.1	0	S<C (0.04); A(F<UF) (vs 0)
Lotus pedunculatus	<0.1 ± <0.1	0.8 ± 0.4	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	
Grasses	1.1 ± 0.8	1.0 ± 0.4	1.4 ± 1.0	0.1 ± 0.1	2.5 ± 2.5	1.7 ± 1.7	
Holcus lanatus	1.1 ± 0.8	1.0 ± 0.3	1.4 ± 1.0	<0.1 ± <0.1	2.5 ± 2.5	1.7 ± 1.7	S<C (0.01); A>C (0.02); S<A(< 0.01)

All perennial introduced	0.3 ± 0.2	2.2 ± 0.7	2.3 ± 1.2	2.2 ± 0.9	0.1 ± 0.1	0.2 ± 0.2	
Forbs	0.3 ± 0.2	1.1 ± 0.4	1.1 ± 0.6	1.3 ± 0.6	0.1 ± 0.1	0.2 ± 0.2	
Shrubs/subshrubs	0.1 ± 0.1	1.1 ± 0.5	1.2 ± 0.7	0.9 ± 0.6	<0.1 ± <0.1	<0.1 ± <0.1	
Rubus anglocandicans	<0.1 ± <0.1	0.8 ± 0.3	0.6 ± 0.5	0.9 ± 0.6	<0.1 ± <0.1	<0.1 ± <0.1	

Table 3. Effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **richness** (Mean species m^{-2} ± SE) **4.5 months after fire** using generalised linear mixed models. Additional statistical details can be found in Table S17 of Appendix 4. Significant components denoted with (vs 0) indicates that no values were detected within one of the paired groups.

Longevity & Lifeform class	**CF**	**CU**	**SF**	**SU**	**AF**	**AU**	**Significance (*P* value)**
All natives	4.3 ± 1.0	3.0 ± 0.4	4.7 ± 0.7	3.1 ± 0.8	7.1 ± 1.0	6.8 ± 1.0	A>C (0.01); S<A (0.01)
Annual/biennial natives	0.1 ± 0.1	0.1 ± <0.1	0.6 ± 0.2	0.6 ± 0.2	0.8 ± 0.2	0.7 ± 0.2	S>C (0.08); A>C (0.01)
Forbs	<0.1 ± <0.1	<0.1 ± <0.1	0.3 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	S>C (0.09)
Non-grass graminoids	0.1 ± 0.1	0	0.2 ± 0.1	0.1 ± 0.1	0.5 ± 0.2	0.3 ± 0.2	C(F>UF) (vs 0)
Perennial natives	4.1 ± 0.9	3.0 ± 0.3	4.1 ± 0.5	2.6 ± 0.7	6.4 ± 0.9	6.2 ± 1.0	A>C (0.05); S<A (0.01)
Ferns	1.0 ± <0.1	1.0 ± <0.1	0.2 ± 0.1	0	0	0	S(F>UF) (vs 0)
Forbs	0.3 ± 0.2	0.1 ± <0.1	<0.1 ± <0.1	0.2 ± 0.1	0.8 ± 0.3	0.2 ± 0.2	A>C (0.02); S<A (< 0.01)
Grasses	0	0.1 ± <0.1	0.2 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	A(F<UF) (0.03)
Non-grass graminoids	1.3 ± 0.5	0.9 ± 0.2	2.2 ± 0.3	1.2 ± 0.3	3.5 ± 0.5	3.5 ± 0.6	A(F<UF) (0.06); A>C (< 0.01); S<A (0.02)
Shrubs/subshrubs	1.6 ± 0.6	0.9 ± 0.2	1.4 ± 0.4	1.1 ± 0.5	2.1 ± 0.5	2.5 ± 0.5	
Trees	0	0	0	0	0	0	
All introduced	0.4 ± 0.4	1.2 ± 0.3	0.4 ± 0.2	0.9 ± 0.3	0.4 ± 0.4	0.3 ± 0.3	C(F<UF) (0.07)
Annual/biennial introduced	0.3 ± 0.3	0.8 ± 0.2	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.2 ± 0.2	C(F<UF) (0.04)
Forbs	0.1 ± 0.1	0.3 ± 0.1	<0.1 ± <0.1	0.2 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	
Grasses	0.1 ± 0.1	0.6 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	C(F<UF) (0.02)
Perennial introduced	0.1 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	0.6 ± 0.3	0.3 ± 0.3	0.2 ± 0.2	
Forbs	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.3 ± 0.3	0.2 ± 0.2	
Shrubs/subshrubs	0.1 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	<0.1 ± <0.1	<0.1 ± <0.1	C(F<UF) (0.09)

Table 4. Effect of season (C = "unburnt control", A = "autumn burn", S = "spring burn") and fencing (F = "fenced", U = "unfenced") on plant **richness** (Mean species m^{-2} ± SE) **18 months after fire** using generalised linear mixed models. Additional statistical details can be found in Table S18 of Appendix 4. Significant components denoted with (vs 0) indicates that no values were detected within one of the paired groups.

Longevity & lifeform class	CF	CU	SF	SU	AF	AU	Significance (*P* value)
All natives	4.0 ± 0.8	3.0 ± 0.3	5.0 ± 0.7	4.7 ± 0.7	5.6 ± 0.7	4.8 ± 0.2	
All annual/biennial natives	<0.1 ± <0.1	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	<0.1 ± <0.1	<0.1 ± <0.1	
Forbs	<0.1 ± <0.1	<0.1 ± <0.1	0.2 ± 0.1	0.1 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	
Non-grass graminoids	0	0	0	0.2 ± 0.1	0	0	S(F<UF) (vs 0)
All perennial natives	4.0 ± 0.8	2.9 ± 0.3	4.8 ± 0.7	4.4 ± 0.7	5.6 ± 0.7	4.8 ± 0.2	
Ferns	1.0 ± 0.1	1.0 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0	0	
Forbs	0.1 ± 0.1	<0.1 ± <0.1	0.3 ± 0.1	0.1 ± 0.1	0.5 ± 0.2	0.2 ± 0.2	S(F>UF) (0.06)
Grasses	<0.1 ± <0.1	0.1 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	S>C (0.02); S>A (0.02)
Non-grass graminoids	1.4 ± 0.5	0.9 ± 0.2	2.4 ± 0.4	2.0 ± 0.4	2.6 ± 0.5	2 ± 0.4	S>C (0.10)
Shrubs/subshrubs	1.5 ± 0.5	0.8 ± 0.2	1.7 ± 0.5	1.9 ± 0.4	2.5 ± 0.3	2.7 ± 0.3	
Trees	0	0	0	0.1 ± 0.1	0	0	S(F<UF) (vs 0)
All introduced	0.5 ± 0.3	1.0 ± 0.2	0.9 ± 0.3	1.1 ± 0.4	0.3 ± 0.3	0.3 ± 0.3	
All annual/biennial introduced	0.4 ± 0.3	0.4 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.2 ± 0.2	
Forbs	0.1 ± 0.1	0.1 ± 0.1	<0.1 ± <0.1	0.2 ± 0.2	<0.1 ± <0.1	<0.1 ± <0.1	A<C (< 0.01)
Grasses	0.3 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	
All perennial introduced	0.1 ± 0.1	0.6 ± 0.2	0.7 ± 0.3	0.8 ± 0.2	0.1 ± 0.1	0.2 ± 0.2	C(F<UF) (0.10)
Forbs	0.1 ± 0.1	0.3 ± 0.1	0.5 ± 0.2	0.4 ± 0.2	0.1 ± 0.1	0.2 ± 0.2	
Shrubs/subshrubs	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.2	<0.1 ± <0.1	<0.1 ± <0.1	C(F<UF) (0.09)

Table 5. Effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on *H. tenuis* plant counts (Mean plants ± SE) across each survey date (TSF = “time since fire” in months) using generalised linear mixed models. Additional statistical details can be found in Table S19 of Appendix 4.

TSF	FC	FA	FS	UC	UFA	US	Significance (*P* value)
-2.5	na	na	na	0.58 ± 0.17	0.29 ± 0.23	0.43 ± 0.19	
-0.5	na	na	na	0.62 ± 0.17	0.18 ± 0.25	0.38 ± 0.19	
2.5	2.00 ± 1.46	1.75 ± 0.73	1.08 ± 0.59	0.60 ± 0.44	0.60 ± 0.44	0.67 ± 0.69	
4.5	2.00 ± 1.46	3.25 ± 0.73	2.43 ± 0.62	0.45 ± 0.44	1.50 ± 0.84	1.33 ± 0.75	
10	1.50 ± 1.46	4.75 ± 0.73	3.00 ± 0.59	0.45 ± 0.44	1.67 ± 0.84	1.00 ± 0.69	A(F> UF) (0.01); S(F>UF) (0.03)
18	0.60 ± 0.44	5.25 ± 0.73	2.83 ± 0.59	0.41 ± 0.44	1.67 ± 0.84	0.67 ± 0.69	F(A>C) (<0.01); F(A>S) (0.03); A(F>UF) (<0.01); S(F>UF) (0.02)

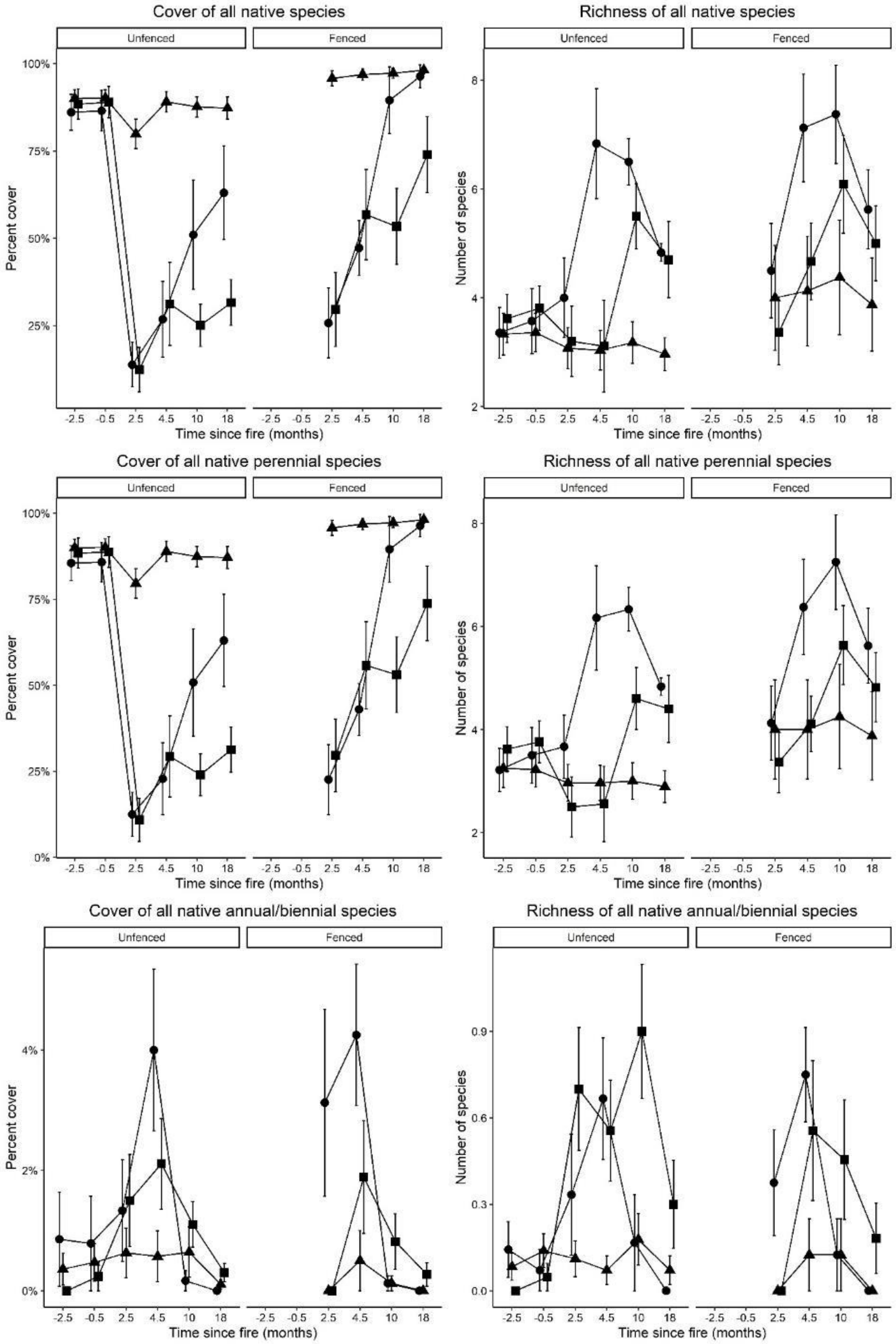


Figure 3. The influence of both season and fencing on percent cover (mean ± SE) and species richness (species m^{-2}) for natives of different lifeform classes. Different seasons are represented by different shapes: circles represent autumn, rectangles represent spring, and triangles represent control quadrats. Percent cover and species richness values, and additional statistical details can be found in Table S3 to Table S8 in Appendix 4.

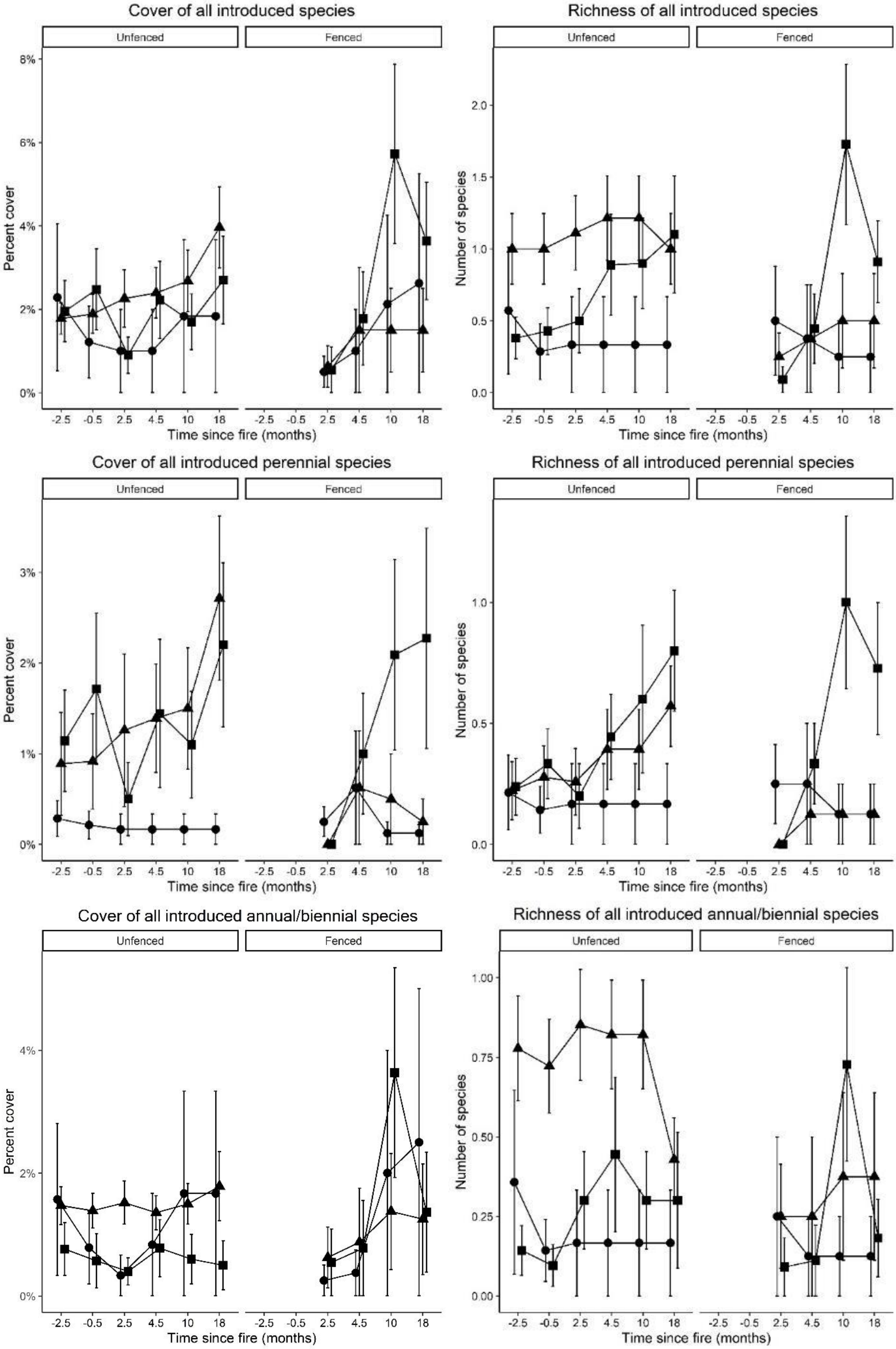


Figure 4. The influence of season and fencing on percent cover (mean ± SE) and species richness (species m^{-2}) for introduced species. Different seasons are represented by different shapes: circles represent autumn, rectangles represent spring, and triangles represent control quadrats. Percent cover and species richness values, and additional statistical details can be found in Table S9 to Table S14 in Appendix 4.

Season

Native plant cover 4.5 months after the fire, was not significantly different between the spring and autumn burnt swamps (57 % spring vs 47 % autumn; Table 1; this and all subsequent comparisons of season are within fenced quadrats only). However, the autumn burnt swamp recovered faster than the spring burnt swamp, containing significantly greater cover after ten months (53 % spring vs 90 % autumn; T (254) = 2.81, *P* = 0.01). Interestingly, there was no significant difference between autumn burnt quadrats and controls quadrats ten months after the burn (90 % autumn vs 95 % control; T (254) = 0.29, *P* = 0.95). In contrast, the spring burnt swamp took 18 months to recover (74 % spring vs 99 % control; Table 2).

Before any burning or fencing, the number of species was on average 3.4 in the control unburnt quadrats, 3.6 in quadrats subsequently burnt in autumn and 3.8 in those to be burnt in spring. Compared with control quadrats, species richness in burnt quadrats was found to be significantly higher 4.5 months after the autumn burn (4.3 control vs 7.1 autumn; Table 3) but not after the spring burn (4.3 control vs 4.7 spring; Table 3). At this time, autumn burnt quadrats contained significantly more species than quadrats burnt in spring (Table 3). However, 18 months after being burnt, native species richness was no longer statistically different than control quadrats even for quadrats burnt in autumn (Table 4). Likewise, the season of burn did not influence richness at this time (Table 4). Despite this, the species composition of swamps was different after 18 months; unburnt quadrats contained three unique species, whereas burnt quadrats contained twelve unique species, eight of which are listed as endangered, vulnerable, or rare at the state level (Table S1 in Appendix 4).

Eighteen months post-fire, total native perennials cover in spring or autumn burnt quadrats was not significantly different to control quadrats (74 % spring vs 96 % autumn vs 99 % control; Table 2). Native perennials recovered faster after autumn burns compared to spring burns (Figure 3). At ten months post fire, percentage perennial cover did not significantly differ between quadrats burnt in autumn and those left unburnt (90 % vs 94 %; T (254) = 0.32, *P* = 0.94) but by this time autumn burnt quadrats had significantly higher cover than spring burnt quadrats (90 % vs 53 %; T (254) = 2.79, *P* = 0.02). Although shrub/subshrub cover as a whole was not significantly greater in autumn compared to spring burnt quadrats, after 18 months (70 % autumn vs 47 % spring; Table 2) it was significantly higher for the regionally vulnerable perennial subshrub *S. incarnata* (25 % autumn vs 5 % spring; Table 2). Similarly, after 18 months, there were more individual *H. tenuis* plants in autumn quadrats compared to spring (5.3 plants autumn vs 2.8 plants spring; Table 5).

While perennial species richness in spring and autumn burnt quadrats was not significantly different from unburnt quadrats after only 2.5 months, by 4.5 months post-fire average richness in the autumn burnt quadrats had increased to 6.4, statistically greater than the measured richness of 4.1 species in spring quadrats (Table 3). Additionally, five species only emerged in the spring burnt quadrats, and three only in the autumn burnt quadrats including the orchid *T. cyanea* which is endangered at the state level (Table S1 in Appendix 4).

Cover of annual native species reached a maximum 4.5 months after fire and had declined to pre-fire levels after 18 months (Figure 3). While annual native cover after 4.5 months was not significantly different between autumn and spring burnt quadrats, the autumn burnt quadrats had significantly higher cover compared to the unburnt controls (4.3 % autumn vs 1.9 % spring vs 0.5 % control; Table 1).

Drosera binata followed a similar trend, the species was not detected without fire and increased to 1.8 % cover after 4.5 months and was negligible after 18 months (Table 1; Table 2).

The richness of native annuals increased after both burns, being higher than the control swamp after 4.5 months in the spring swamp (0.6 spring vs 0.1 controls) and autumn swamp (0.8 autumn vs 0.1 controls; Table 3) but after 10 months these differences were no longer significant. Furthermore, two annual species *S. glomeratus* and *Centrolepis fascicularis* (regionally vulnerable) only emerged in spring burnt quadrats (Table S1 in Appendix 4).

Compared with control quadrats, total cover of introduced species was marginally greater after ten months, in the spring burnt quadrats (5.7 % spring vs 1.5 % control; T (253) = -2.14, *P* = 0.09), but not in the quadrats burnt in autumn (2.1 % autumn vs 1.5 % control; T (253) = -0.06, *P* = 1.0). At this time introduced species cover was significantly greater in the spring burnt quadrats (mean = 5.7 %) than in those burnt in autumn (2.1 %; T (253) = -2.26, *P* = 0.06). However, at 18 months after fire, no significant differences in overall cover of introduced species was detected because of burning or season of fire (Table 2). Nevertheless, after 18 months, the introduced grass *Holcus lanatus* more than doubled in the autumn burnt quadrats relative to unburnt controls (control 1.1 % vs autumn 2.5 %; T (26) = -2.78, *P* = 0.02; Table 2).

The number of introduced species varied as a result of season of burn, with more being detected after ten months in the spring quadrats compared to autumn (1.7 spring vs 0.3 autumn; T (252) = -2.79, *P* = 0.02) and control (1.7 spring vs 0.5 control; T (252) = -2.31, *P* = 0.06). Overall richness then decreased after 18 months becoming equivalent to controls (0.9 spring vs 0.5 control; Table 4). Similar trends were observed for subsets of perennial, annual and individual introduced species but no differences were found to be significant (Table 4). Spring burnt quadrats also had three unique introduced species, with *Solanum nigrum* present in eight quadrats (Table S20 in Appendix 4).

Fencing

Post-fire grazing influenced native vegetation recovery (Figure 3). When quadrats were burnt in spring and then fenced, their cover became similar to controls after 18 months of recovery (74 % spring vs 99 % control; Table 2), those which were left unfenced had significantly less cover (74 % fenced vs 32 % unfenced; Table 2). Recovery of autumn fenced quadrats was faster than spring fenced quadrats, with the former becoming similar to controls after 10 months (90 % vs 95 %; T (254) = 0.30, *P* = 0.95), at this time the difference due to fencing was significant (51 % unfenced vs 90 % fenced; T (254) = -2.9, *P* <0.01). However, fencing did not significantly affect richness for native species after 18 months, in burnt or unburnt quadrats (Table 4).

The richness of native perennial plants in quadrats was not affected by fencing out grazers (Figure 4). However, the cover of perennial natives was higher 18 months after fire in fenced quadrats burnt in spring (31 % unfenced vs 74 % fenced) and autumn (63 % unfenced vs 96 % fenced; Table 4). In control quadrats, richness increased from 3.0 to 4.4 species ten months after fencing (T (254) = -1.8, *P* = 0.08). However, this effect was less pronounced after burning in autumn (10 months; 6.5 unfenced vs 7.4 fenced; T (254) = -0.88, *P* = 0.34) and spring (5.5 unfenced vs 6.1 fenced; T (254) = -1.23, *P* = 0.22).

Several native perennial species only occurred in either fenced or unfenced quadrats (Table S2 in Appendix 4), including threatened orchids in fenced quadrats (e.g. *Spiranthes australis* and *T. cyanea*) and species that are vulnerable at the state level in unfenced quadrats (e.g. *C. fascicularis* and *Utricularia dichotoma*). Recovery of *G. sieberiana* was influenced by grazing, and in autumn burnt quadrats it failed to recover any biomass if left unfenced after 18 months post-fire (0 % unfenced vs 8 % fenced), it also produced significantly less after spring fires (3 % unfenced vs 13 % fenced; Table 4). *Viminaria juncea* was also found to be sensitive to grazing with unfenced quadrats having negligible cover after 18 months of recovery (Table 4).

Similarly, *H. tenuis* cover was higher in fenced quadrats, with the cover being more than six times that of unfenced quadrats at 18 months in autumn (5 % unfenced vs 32 % fenced) and 22 times greater in spring (1 % unfenced vs 22 % fenced; Table 4). Fencing also significantly increased the number of *H. tenuis* plants present in quadrats (autumn; 5.3 plants fenced vs 1.7 plants unfenced; Table 5). However, at no point did fencing affect the number of *H. tenuis* plants in unburnt control quadrats (Table 5). *Empodisma minus* followed a similar trend at 18 months after both autumn (4.0 % unfenced vs 20.8 % fenced) and spring burns (0.1 % unfenced vs 5.5 % fenced; Table 4).

Grazing did not appear to influence the cover of annual natives, but different species existed in fenced and unfenced quadrats (Table S2 in Appendix 4). Three species were only detected in unfenced quadrats, including *C. fascicularis* which was only found in spring burnt quadrats. Similarly, *Senecio glomeratus* was only present in quadrats which were burnt in spring and then fenced. Comparing fenced to unfenced for autumn burnt quadrats at 4.5 months, showed fencing did not influence the cover of native annuals (4.3 % vs 4.0 %; Table 1). Similarly, fencing did not affect the cover of native annuals in spring burnt quadrats (2.3 % vs 0.7 %; Table 1). However, richness in the spring quadrats was lower, with no native annuals occurring at 2.5 months after fire and significantly lower species at 10 months (spring; 0.9 unfenced vs 0.5 fenced; T (254), *P* = 0.01). Fencing had no significant effect on introduced species cover or richness after 18 months (Table 2; Table 4). However, four introduced annuals only occurred in the unfenced quadrats (Table S20 in Appendix 4).

DISCUSSION

Comparison of *in situ* and *ex situ* studies

Previous studies of southern Australian dry heathlands have found 25 % to 32 % of species were absent in the above-ground vegetation but contained propagules in the soil (Wills and Read 2002; 2007). We found a similar situation with swampy heathland, 29 % of all native species only emerged after burning, while not being present before the burns nor in unburnt control quadrats. We also found that the burnt swamps experienced a significant 1.6-fold increase in richness compared to unburnt controls, this occurring 10 months after the fire. This is comparable to findings of a previous *ex situ* study where soil samples from the same swamps were subjected to smoke and heat to simulate burning (Trezise *et al.* 2021). This study found that 21 % of species germinating from the treated soil were absent from the unburnt standing vegetation.

Estimates of plant abundance and species detection from *in situ* studies (such as the present study) are influenced by several factors including propagule availability, propagule/seedling survival, seed dormancy, germination environment, delayed emergence, and seedbank heterogeneity (Chapter 2; Table 1). We suggest that these factors resulted in different estimates for the species studied here, as was the case in similar studies (Cardina and Sparrow 1996; Mesquita *et al.* 2013; Salam *et al.* 2018). Foremost was the emergence of ferns (*G. microphylla* and *Pteridium esculentum*) and orchids (*Spiralis australis* and *Thelymitra cyanea*) after the *in situ* burns but not in the heat and smoke treated soil samples (Chapter 3; Trezise *et al.* 2021). This suggests the lack of a persistent orchid seedbank and fern spores in the soil, at least after the fire if not before. Resprouting underground rhizomes and tubers, respectively, appears to be their primary fire recovery mechanism. The absence of such regeneration in the *ex situ* study can be explained by the sieving process used to remove litter. This is an important finding since it suggests that none of these species will germinate from soil-born seed/spores if fire treatments kill all the underground storage organs. Given the now severely localised, fragmented and mostly degraded nature of the FPS habitat, dispersal of seed and spores from adjacent swamps is not assured. This is an issue since both the orchid species are regionally threatened.

Another species only found to germinate from *in situ* quadrats was the perennial graminoid *Xyris operculata*, which has a state rating of rare. This genus has been found to have physiologically dormant seed which requires stratification periods to germinate (Baskin and Baskin 2003; Garcia *et al.* 2012; Merritt *et al.* 2007; Oliveira and Garcia 2019). Thus the lack of germination *ex situ* within the soil trays (Chapter 3; Trezise *et al.* 2021) may be explained by required stratification conditions not being met in that experiment.

In contrast, several annual graminoids (e.g. *Isolepis* spp and *Juncus* spp) germinated en masse in soil trays but were scarcely detected *in situ*, including after the burns. This may reflect the constant water availability within the greenhouse where the surface of soil samples is kept permanently moist, compared with *in situ* where the soil surface is subject to desiccation over summer. This indicates the value of using both *in situ* and *ex situ* soil seedbank studies to extrapolate total species composition and seed densities in the soil seedbank.

Changes over time following fire

Particularly quick to respond to fire are ephemerals and other short-lived species, which typically dominate shortly after a fire and then disappear from the standing vegetation in subsequent years (Bohlman et al. 2016; Keeley and Fotheringham 2000a; Patykowski et al. 2018). This was particularly the case for heathy swamps, where we found the cover of native annual and biennials to increase on average eight-fold only 4.5 months after the autumn burn. This also applies to species that survive with dormant underground organs, such as orchids and sundews. For example, Timmins (1992) observed a post-fire flush of *D. binata* emergence, and prolific flowering of *Spiranthes* and *Thelymitra* orchid species, in heathy peat swamps of New Zealand, but noted that these species became rare six years after the fire. Our study found an even more rapid turnaround in FPS where *D. binata* emerged en masse only 4.5 months after the fires but was again almost absent eighteen months after the fire.

Although we found the overall cover of native perennial species recovered rapidly following the burns, the composition shifts away from fern dominance to a more diverse and heathier shrub-dominated swamp. This is due to many of the heathy shrub species having seed which is stimulated to germinate by fire (Trezise *et al.* 2021), and the resulting seedlings surviving due to the reduced competition (Battersby et al. 2017; King et al. 2006; Walker and Pate 1986). This is in large part due to perennial ferns, predominately *G. microphylla* which formed dense thickets in the senescent heathy swamps, being slow to regenerate post fire (Brown and Podger 1982; Davis and Davies 2021; Trezise *et al.* 2021; Wark 1997). We found that *G. microphylla* had significantly lower cover after 18 months (< 1 %) compared to unburnt controls (61 %). Previous studies have recorded species of

Gleichenia species taking between seven and 24 years after fire to fully recover (Brown and Podger 1982; Clarkson 1997; Walker and Boneta 1995).

Of particular importance for our study was understanding the fire ecology of the nationally critically endangered *H. tenuis*. Before this study, only 20 individuals were known to occur, all confined to two heathy swamps (Quarmby 2011) where they were restricted to human-cleared trails through dense coral fern (Trezise *et al.* 2021). Our trial burn study area was confined to one of these swamps in an area that contained only 15 *H. tenuis* plants. Two years after our burns, 589 plants had germinated and become established as a result of the burns (D. Duval pers. obs., 2020).

Although our results indicate burning may benefit plant diversity, many other species are disadvantaged by the immediate effects of fire as well as the conditions during early successional periods (Keith et al. 2002). Too frequent fires may result in the loss of such species. Even though *G. microphylla* suppresses most other species when dense, it is still important to not eliminate the species from swamps, as this fern is listed as rare in South Australia. To allow this and other late successional species to sufficiently mature to recover between fires, other studies of swampy heath and damp-heathy scrub have recommended minimal fire intervals ranging from nine to 14 years based on the reestablishment periods of constituent species (Cheal 2010; Clarkson 1997; Hayward et al. 2008). Shorter fire intervals can exclude these species and so prescriptions should be based on the re-establishment period of the slowest maturing species unless a specific ecological outcome requires a shorter interval (Burrows and Wardell-Johnson 2003; Clarkson et al. 2011; Enright et al. 1998). Fire managers should also consider that future fires are likely to be more frequent and hotter, due to climate change (Enright et al. 2015; Fairman et al. 2016; Stevens-Rumann et al. 2018).

Another important consideration is the fire response of introduced species and whether this will affect native plant re-establishment after fire. Previous similar studies of weed-prone native plant communities (e.g. Kerns *et al.* 2006; Lunt 1990; Taylor 2019) have found that introduced species can benefit from fire and this has been identified as a threat to FPS flora (Conservation Council of South Australia 2020; Harding 2005; Threatened Species Scientific Committee 2013). We found that autumn burns doubled the cover of *H. lanatus*, a highly invasive introduced grass that forms dense grassy mats and thus can restrict seedling establishment. A comprehensive survey of the FPS threatened ecological community found this weed grass in every surveyed swamp (Table S23 in Appendix 4; Department for Environment and Water 2020b). On a positive note, we found fires did not promote the overall cover or richness of introduced species in the swamps we studied, although after just 4.5 months these weeds had already re-established to pre-fire levels of cover.

The effect of fire on weed invasion will depend on weeds already present. For example, our study site did not contain the highly invasive, introduced shrub *Ulex europaeus* despite it occurring at 52 % of all surveyed heathy swamps on the Fleurieu Peninsula (Department for Environment and Water 2020b). This species is known to germinate en masse from soil seedbanks after a fire (Table S23 in Appendix 4; Department for Environment and Water 2020b; Pausas *et al.* 2012) suggesting the need for targeted weed management following most burns.

Season of burn

Fire seasonality can have important implications for vegetation recovery (Gillespie and Allen 2004; Knapp *et al.* 2006; Knox and Clarke 2006a). In southern Australia, prescribed burning is often operationally restricted to autumn or spring, as summer burns are too dangerous and winter conditions are too wet to support sufficient fire intensity. Burning heathy swamps in spring and autumn is preferred since the aboveground vegetation is dry enough to carry fire, while the ground is sufficiently wet to prevent fire from spreading into underground peat deposits. In FPS, it is commonly inferred that spring burning may result in fewer species re-appearing than with autumn burns, as the former disrupts peak reproductive periods of 85 % of native species (Table S24 in Appendix 4). Research conducted in similar heathy ecosystems in southern Australia has shown that native plants can be negatively affected by fire which interrupts their flowering periods (e.g. Bowen and Pate 2004; DiTomaso *et al.* 2006; Lamont *et al.* 2000). Additionally, seedlings that emerge shortly after spring fires have a shorter period to establish before the onset of dry summer conditions which can limit establishment (Miller *et al.* 2019).

In the present study, we found that while both spring and autumn burns both significantly increased overall species richness after 4.5 months, different species were favoured by the different burns. For example, the regionally threatened graminoid *C. fascicularis* only emerged in the spring burnt quadrats, while the state-rated endangered orchid *T. cyanea*, only emerged in the autumn burnt quadrats.

Our results suggest that autumn burning results in faster recovery of native perennials in terms of cover and species richness, compared with spring burns (Figure 3). This is despite the autumn and spring burn consuming similar amounts of vegetation. While native annual/biennial cover peaked 4.5 months after both autumn and spring burns, this cover was only significantly higher compared to the unburnt controls only for quadrats burnt in autumn, not those burnt in spring. We also found that cover of the regionally vulnerable *S. incarnata* (rare at the state level) was significantly lower 18 months after the burns, in the spring burnt swamp (5 %) versus the autumn burnt swamp (25 %). This species is a dwarf shrub with morphophysiologically dormant seed (Balmer and Storey 2010). We propose that because this species is adapted to southern Australia's Mediterranean climate, it favours emergence before the winter wet season; seedlings that emerge shortly after spring fires have a shorter period to establish before the onset of dry summer conditions, which can limit establishment (Miller *et al.* 2019).

In contrast, we found the reverse effect on the cover and density of the regionally vulnerable *V. juncea* (rare at the state level), a short-lived shrub with physically dormant seeds (Liyanage and Ooi 2015). After 14 months there was significantly greater cover in fenced spring burnt quadrats (16 %) versus in the fenced autumn burnt quadrats (1 %). Our monitoring indicated that germination and growth mostly occurred over spring and summer. This meant that after the spring burn, heat-primed seed was able to germinate and grow immediately, while after the autumn burn, heat-primed seed (no longer with its hard protective cover) was likely exposed to damage or seed predation for a longer period before germination (e.g. seed predation; Dalling *et al.* 2011; Janzen 1971; Paulsen *et al.* 2013). We argue that in heathy swamps, fire in any given season will not uniformly benefit all species, and so the season of burn should be prescribed based on seasonal vulnerabilities of key target plant species, such as the reproductive periods of threatened species.

While both autumn and spring burns stimulated germination of the critically endangered *H. tenuis*, we found that germination was favoured by autumn burns. After 18 months significantly greater numbers of plants (5.3 plants metre^{-2}) had emerged in fenced quadrats burnt in autumn, with a 31 % greater cover. This compared with 2.8 plants metre^{-2} in fenced spring-burnt quadrats, and only 0.6 plants metre^{-2} in fenced unburnt quadrats. This can be at least partially explained by differences in germination rates. In a previous *ex situ* allied study, we showed that smoke stimulated seed germination. We found significantly higher germination rates occurring when smoke treated seed was subjected to temperature stratification which emulated autumn conditions, than when germinated under those that emulate spring conditions (Chapter 4).

Fire and grazing

Grazing pressure by native herbivores is unnaturally high in southern Australia and this is likely negatively impacting native vegetation (Grigg and Pople 2001) and we suggest these effects are exacerbated after fire in the heathy swamps studied here. Our results show that three understorey species occurred exclusively in at least three fenced quadrats, including the regionally endangered orchid *S. australis,* suggesting these species were targeted by grazers. In the Mount Lofty Ranges in southern Australia, grazers can negatively impact native orchid populations by targeting flowering individuals (Faast and Facelli 2009). Several other Australian studies suggest that overgrazing reduces the cover and diversity of the understorey when herbivores are overabundant (Braden *et al.* 2021; Foster 2015; Mills *et al.* 2020). For example, in arid ephemeral gilgai wetlands, grazing reduces understorey cover when herbivores become concentrated around water sources (Davies *et al.* 2018).

We found such grazing effects in the fragmented heathy swamps in our study area. When fenced, the mean total native vegetation cover in burnt quadrats had reached levels to unburnt quadrats by 18 months after fire. In contrast, where quadrats were left unfenced, total native cover remained low, significantly less than the comparable fenced quadrat. This was especially true for native perennials, which had 33 % less cover in unfenced quadrats than fenced quadrats 18 months after the autumn burn and 43 % less after the spring burn. In a similar study, Meers and Adams (2003) found that grazing significantly reduced the richness and density of shrubs after an ecological burn in dry heathland. Grazing often acts synergistically with fire to reduce plant cover (Foster *et al.* 2016a) and can increase dominance of less palatable species (Foster *et al.* 2016b).

We also found that three native species listed as threatened at least regionally had significantly reduced cover as a result of grazing after being burnt. These included the nationally critically endangered *H. tenuis* where grazing reduced plant counts and cover following both spring and autumn burns. The cover of *E. minus* and *V. juncea* was similarly higher when grazing was excluded.

Results also suggested an interaction between grazing and season of burn. Cover of *S. incarnata* was only significantly reduced by grazing after the spring burn, but not after the autumn burn. We suggest this relates to the Mediterranean climate where FPS exist as water becomes limited during summer and so grazers become concentrated in areas with permanent waterbodies, such as heathy swamps (e.g. Davies *et al.* 2018; James *et al.* 1999; Morris and Reich 2013). This effect can be exacerbated after fire, which increases access to water and understorey species (e.g. Kotze 2013; Murphy and Bowman 2007; Tolsma *et al.* 2007). Alternatively, the effect of overgrazing may be further influenced by the season of burn as regenerating plants are more palatable at some times of year more than others (Zhao *et al.* 2011).

We found that nine species only occurred in unfenced quadrats, including four species that were regionally threatened (*C. fascicularis*, *Eucalyptus ovata*, *Leucopogon hirsutus*, and *U. dichotoma*). Some of these species were represented by single plants, so their occurrence in unfenced quadrats may have been by chance. However, four of the species (*Blechnum minus*, *Euchiton collinus*, *Isolepis inundata*, and *Melaleuca decussata*) occurred in at least three unfenced quadrats each suggesting their absence from fenced quadrats may have been due to increased competition from other species. Grazing can provide important positive impacts to conservation, for instance by preventing overabundance by undesirable species (Conservation Council of South Australia 2020; Lunt *et al.* 2007; Múgica *et al.* 2021). This indicates that although overgrazing needs to be mitigated soon after fire (e.g. by fencing or culling) to prevent the loss of more palatable species and species less tolerant of grazing, further research is needed in FPS to determine if there are species that require some level of browsing (or other disturbance like slashing) to persist.

Conservation implications and considerations

Fire benefited native plant richness in the studied heathy swamps, prompting the need for mosaic burning at the landscape level. We show that burning temporarily suppresses overstorey dominance and in the process benefits understorey species. This transient successional period is important for enabling understorey species to replenish their propagule reserves given that reserves have a finite lifespan. Anthropogenic fire exclusion can cause vegetation communities to shift to alternative states which fire-dependant species cannot inhabit (Briske *et al* 2005, Hanberry 2021, Kitzberger *et al* 2016). However, inter-fire periods need to be balanced, as short inter fire periods may exclude species which typically inhabit the overstorey and have long maturity life-history traits. Such as those which did not reach maturity within the 18 months of monitoring. Additionally, although autumn burning resulted in faster native plant recovery, both spring and autumn burning benefited different individual species. Grazers also impacted results by retarding plant recovery and targeting specific species.

We recommend that heathy swamps should be periodically burnt to establish a balanced distribution of age classes across the landscape. Fire should be employed at intervals greater than the reestablishment period of the slowest maturing species and less than the expiration of the propagule banks of the early successional species. For the FPS studied here, minimum periods of between seven to 24 years will likely allow the reestablishment of *G. microphylla* (Brown and Podger 1982; Clarkson 1997; Walker and Boneta 1995), which we propose to be the slowest maturing species. This assumes that viable rhizomes remain after fire which can reshoot or the distances to unburnt areas are not too great to prevent spores dispersing to allow re-colonisation (Wark 1997). Additionally, grazing should be mitigated (e.g. culling or fencing) immediately after a fire but may be important in maintaining overdominant species during later successional periods. We also suggest prescribing the season of burn based on vulnerabilities of target species (e.g. threatened species; *H. tenuis*), despite autumn burning being favourable in most instances. Fire managers of heathy swamps should: establish a mosaic of age classes, reduce the initial impact of herbivory, and consider the season in which they burn.

Despite the apparent benefits of fire identified from this study, three limitations exist which may confound our recommendations. First, the effect of season may have been influenced by low site replication and so future research should include multiple small patch burns, within multiple swamps, to improve results. Second, grazing appeared to benefit some understorey species, suggesting a moderate degree of grazing may be necessary for maintaining highly competitive overstorey plants after long inter-fire periods (e.g. Fagúndez 2016; López *et al.* 2017; Lunt *et al.* 2007). Last, this study only monitors the early successional period after fire in heathy swamps (up to 18 months) and the time required for late-successional species to re-establish and then dominate could be decades (Brown and Podger 1982; Clarkson 1997; Littlely 1998; Walker and Boneta 1995). Future studies could address this by resurveying the quadrats established in this study at later dates and monitoring similar heathy swamps which have a known fire history.

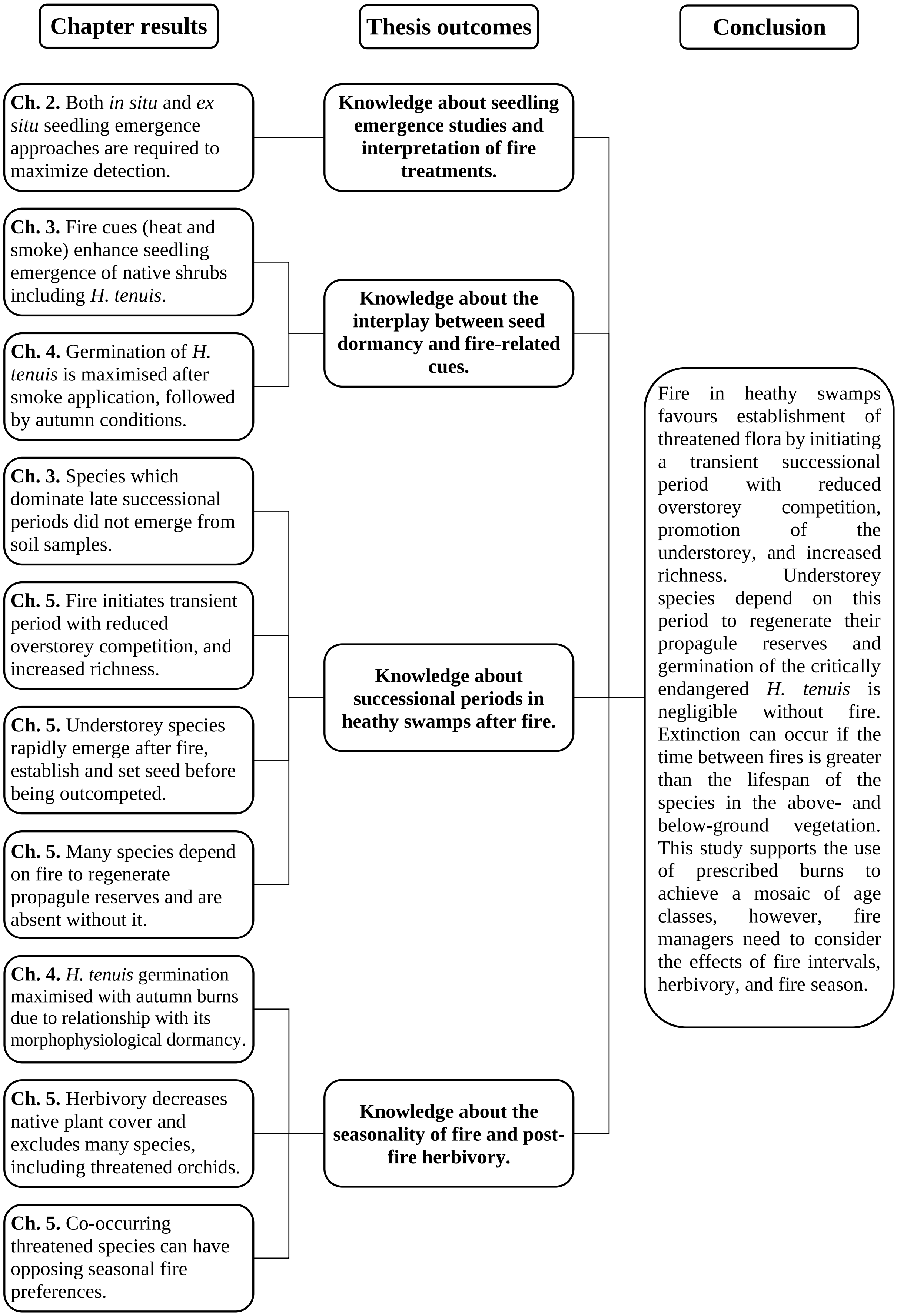
Chapter 6: General discussion

Key results and conclusion

In this thesis, I investigated the response of soil seedbanks to fire. First, I compared *in situ* and *ex situ* methods for evaluating soil seedbanks (Chapter 2). The two methods detected different mixes of species, giving merit to the simultaneous use of both. As such, I used multiple approaches to investigate the impact of fire on heathy swamps, first by using an *ex situ* seedling emergence approach (Chapter 3), then an *ex situ* laboratory germination trial (Chapter 4), and lastly an *in situ* post-fire vegetation survey (Chapter 5).

In southern Australia, most Fleurieu Peninsula swamps (FPS) are in a late-successional age class, characterised by low species richness and a depauperate understorey. This is likely due to 98% of these swamps having not experienced a fire in the last 30 years (Chapter 5). With infrequent burning, native ferns and taller shrubs outcompete threatened ground-stratum species, including the nationally critically endangered subshrub *Hibbertia tenuis* which is endemic to these swamps (Duffield and Hill 2002; Quarmby 2011; Trezise *et al.* 2021). I showed that fire can be used to initiate a transient successional period of increased richness, reduced overstorey cover and subsequent promotion of the understorey (Chapters 3 and 5). I found that 29 % of species were absent without fire, many of which appeared to require fire to regenerate their propagule reserves (Chapter 5). For instance, a much higher proportion of *H. tenuis* seed germinated from soil samples after a heat and smoke treatment (Chapter 3). Likewise, highest germination of seed occurred with conditions that simulated autumn, and germination was negligible without smoke (Chapter 4). There was also marked post-fire establishment of *H. tenuis* following fire, particularly in fenced sections of a swamp burnt in autumn (Chapter 5). As a result of this study, remaining *H. tenuis* populations that were in decline are now growing, with almost six hundred plants now established compared with just twenty plants prior to the fires (D. Duval, pers. obs., 2020).

Despite the potential benefits of burning heathy swamps, fire prescription needs to consider fire intervals, post-fire herbivory, and fire-seasonality. Short fire intervals can exclude species with long maturity life-history traits, while long fire intervals can exclude ‘disturbance dependant’ species (e.g. *H. tenuis*) if the time between fires is greater than the lifespan of the species in both the above- and below-ground vegetation. Herbivory negatively impacted recovery after fire by excluding 12 % of species (inc. threaded orchids) and so should always be mitigated. Cover of co-occurring natives increased in opposing seasons, indicating a fire in any given season will not uniformly benefit all species. Landscape burning regimes should aim to achieve a mosaic of age classes; however, fire managers need to also consider the effects of time since fire, herbivory, and fire seasonality (Figure 1).



Chapter results

Thesis outcomes

Conclusion

Ch. 2. Both *in situ* and *ex situ* seedling emergence approaches are required to maximize detection.

Knowledge about seedling emergence studies and interpretation of fire treatments.

Ch. 3. Fire cues (heat and smoke) enhance seedling emergence of native shrubs including *H. tenuis*.

Ch. 4. Germination of *H. tenuis* is maximised after smoke application, followed by autumn conditions.

Knowledge about the interplay between seed dormancy and fire-related cues.

Ch. 3. Species which dominate late successional periods did not emerge from soil samples.

Ch. 5. Fire initiates transient period with reduced overstorey competition, and increased richness.

Ch. 5. Understorey species rapidly emerge after fire, establish and set seed before being outcompeted.

Ch. 5. Many species depend on fire to regenerate propagule reserves and are absent without it.

Knowledge about successional periods in heathy swamps after fire.

Ch. 4. *H. tenuis* germination maximised with autumn burns due to relationship with its morphophysiological dormancy.

Ch. 5. Herbivory decreases native plant cover and excludes many species, including threatened orchids.

Ch. 5. Co-occurring threatened species can have opposing seasonal fire preferences.

Knowledge about the seasonality of fire and post-fire herbivory.

Fire in heathy swamps favours establishment of threatened flora by initiating a transient successional period with reduced overstorey competition, promotion of the understorey, and increased richness. Understorey species depend on this period to regenerate their propagule reserves and germination of the critically endangered *H. tenuis* is negligible without fire. Extinction can occur if the time between fires is greater than the lifespan of the species in the above- and below-ground vegetation. This study supports the use of prescribed burns to achieve a mosaic of age classes, however, fire managers need to consider the effects of fire intervals, herbivory, and fire season.

Figure 1. Relationship between the results, the thesis outcomes, and the conclusion.

Methods to assess soil seedbanks

The composition of soil seedbanks can be measured with *ex situ* counts of germinants from soil samples, or *in situ* counts of germinants within a given area in the field (Cardina and Sparrow 1996; Mahé *et al.* 2020; Taylor 2019). These approaches allow researchers to assess soil seedbanks concerning fire treatments, but I found they produced different estimates of richness and seedling abundance (Chapter 2). I found that estimates of seedling abundance were 5.5 times higher *ex situ* and that the lower *in situ* estimates limited my capacity to detect statistical differences. This was despite sampling effort being standardised between the methods, suggesting that *ex situ* studies are better suited to assessing treatment effects because they require lower sampling replication. Differences in seedling abundance were likely related to factors which limited seedling survival, such as herbivory. This suggests that prescribed burns should be followed up by management of herbivory and that *in situ* approaches are important for identifying environmental stressors which limit plant replacement after fire. Species composition also differed between methods as each emulated unique germination environments with a different suite of dormancy breaking cues, giving merit to the simultaneous use of both methods to maximise species detection. These findings support the combined use of both *in situ* and *ex situ* methods for assessing soil seedbanks.

Reversing the decline of *Hibbertia tenuis*

By studying the fire ecology of *H. tenuis* and its seed dormancy mechanisms, I observed the decline of remnant and translocated populations because of competition from *Leptospermum continentale* and *Gleichenia microphylla*. At the commencement of this study, only ~20 individuals survived, confined to recently disturbed areas (e.g. tracks). Land managers identified lack of fire as a potential reason for this decline, prompting the need for this study (Duffield and Hill 2002; Harding 2005; Quarmby 2011).

In Chapter 3, I conducted a glasshouse seedling emergence trial to determine if burning swamps could promote *H. tenuis* regeneration. Soil samples were taken from eight different FPS, which either contained the species or had an ideal habitat for it. Germination in the soil samples was then assessed in response to a heat and smoke treatment to simulate fire. The emergence of *H. tenuis* increased 18-fold in fire-treated samples relative to untreated controls. Furthermore, *H. tenuis* was detected in fire treated soil samples from a swamp where the species was previously unknown and not present as standing vegetation. Additionally, no *G. microphylla* plants, a key late successional competitor in these swamps, were detected in samples, and this suggests *H. tenuis* could have reduced competition during the early successional stages after a fire. Periodic fires thus give *H. tenuis* sufficient time to establish and replenish its soil seedbank before being outcompeted again.

In Chapter 4, I investigated the relationship between *H. tenuis'* seed dormancy mechanisms and fire cues. Seeds were collected from remnant plants in the field and exposed to various treatment combinations designed to simulate fire, local climatic conditions, and light restrictions. I found that *H. tenuis* had a morphophysiological dormancy, and that germination was much higher after smoke application, followed by spring/autumn conditions (51 % germination versus 2 % in untreated controls). Light sensing mechanisms were identified which the species uses to avoid conditions after a fire that are unfavourable for establishment (i.e. too close to summer). This suggests that ecological burns conducted in autumn would facilitate good germination and establishment.

Chapters 3 and 4 provided a basis for planning control burns to experimentally determine the impact of *in situ* fires on *H. tenuis*. Hence, for Chapter 5, I conducted two separate burns in swamps containing *H. tenuis* which contained approximately 15 individuals of the 20 known individuals. Burns were conducted in spring 2017 and autumn 2018 to assess the influence of the season of fire on post-fire establishment of *H. tenuis* and other plant species. No *H. tenuis* individuals survived the fires by resprouting, but 589 new plants established across the entire swamp, suggesting the species is a fire-dependent obligate seeder. Within quadrats this translated to an 8.8 fold increase, with an average of 5.3 plants in quadrats burnt in autumn and then fenced. I also found that after 18 months in fenced quadrats, *H. tenuis* cover was significantly greater in the autumn burnt swamp (32 %) compared to in the spring burnt swamp (22 %). Furthermore, compared to fenced quadrats, cover was significantly less in unfenced quadrats burnt in autumn (4.8 %) and spring (1 %). This suggests that establishment of *H. tenuis* is favoured by autumn burning followed by the exclusion of herbivores.

The persistence of *H. tenuis* depends on the appropriate use of fire and future conservation work. This thesis has uncovered three primary findings critical for the conservation of the species:

1. By determining the species dormancy mechanisms, *ex situ* propagation is now a feasible option for restoration. These findings have been used to germinate seedlings grown as tubestock and planted into recently burnt and suitable habitat at Stipiturus Conservation Park, where the species had not been previously recorded (D. Duval pers. comms., 2019).
2. *Hibbertia tenuis* is fire dependant and will only germinate in substantial quantities after fire. Populations were declining in the

absence of fire but have since increased 30-fold after my experimental burns. To my knowledge, this is the first example of a critically endangered plant species in Australia which is no longer declining due to the implementation of a recovery action.

3. Although spring burning is beneficial, establishment is higher following autumn burning and when herbivory is controlled after a fire.

Despite these findings and conservation outcomes, it is imperative that additional populations are established, and any newly established individuals are protected, including those at Yundi where my experimental burns were undertaken. Conservation actions should aim to prevent herbivory, inappropriate fire-regimes, weed incursions, clearance, and changes to hydrology (Quarmby 2011). I also recommend that the seed viability of newly established individuals should be assessed with the seed dormancy methods described in Chapter 4.

Succession in heathy swamps

Species composition and the structure of heathy swamps gradually changes with time. Understorey species typically dominate in the early stages after fire in swamps, and over time they are succeeded by species that progressively dominate in later successional stages (Hayward *et al.* 2008; Kimura and Tsuyuzaki 2011; Timmins 1992). Understorey species then senesce or are outcompeted and are replaced by a smaller number of species which dominate the late-successional stages (Harding 2005; Kotze 2013; Pendergrass *et al.* 1998). Fire may then reboot the process by returning the late-successional vegetation to its earliest stage of development.

Each successional stage hosts a different suite of flora and fauna, meaning that heathy swamps in late-successional stages are not inherently undesirable. But at a landscape scale, biodiversity is maximised when a range of age classes are maintained (Gosper *et al.* 2011; Tozer and Bradstock 2003; Watson 2005). When early vegetation age classes are absent, so too are disturbance-dependent species because they become outcompeted and require a disturbance (like fire) to provide them with an opportunity for re-establishment (Enright *et al.* 2012; Keeley and Fotheringham 2000b; Middleton 1999). Only 2 % of FPS have experienced fire in the last 30 years (Department for Environment and Water 2009; 2016). The resulting imbalance in vegetation age classes is undesirable because habitats which favour disturbance-dependent species are underrepresented.

Fleurieu Peninsula swamps follow successional trends typical of heathy swamps (Figure 2; Chapter 5). My observations and findings from this thesis suggests that three successional stages follow fire in heathy swamps. First, fire prompts an 'early stage' (before ~1 year) of increased richness, reduced overstorey cover and subsequent promotion of the understorey. Species which characterise this early period commonly include *Drosera binata*, *Gonocarpus micranthus, Hibbertia tenuis*, *Prasophyllum murfetii*, *Spiranthes australis*, *Stylidium armeria, Thelymitra cyanea*, *Utricularia dichotoma*, and *Viola eminen*. These species then begin to decline in abundance during the 'intermediate stage' (between ~1 to 5 years) and are succeeded by juvenile shrubs and resprouting sedges. Species which characterise and commonly dominate the intermediate period include *Acacia provincialis, Baumea rubiginosa, Baumea tetragona*, *Emposdisma minus, Gahnia sieberiana*, *L. continentale*, *Patersonia occidentalis*, *Sprengelia incarnata,* and *Viminaria juncea*. Eventually (after ~5 years), species composition and structure begin to transition into a 'late-stage' characterised by the dominance of *G.*

microphylla, senescent *L. continentale*, and occasionally *Blechnum minus*. The post fire successional stages of other heathy swamps and damp-heathy scrub has been described (Cheal 2010; Clarkson 1997; Hayward *et al.* 2008; Wark 1997), however in the FPS, the rate at which the intermediate stage transitions into the late stage is unknown.

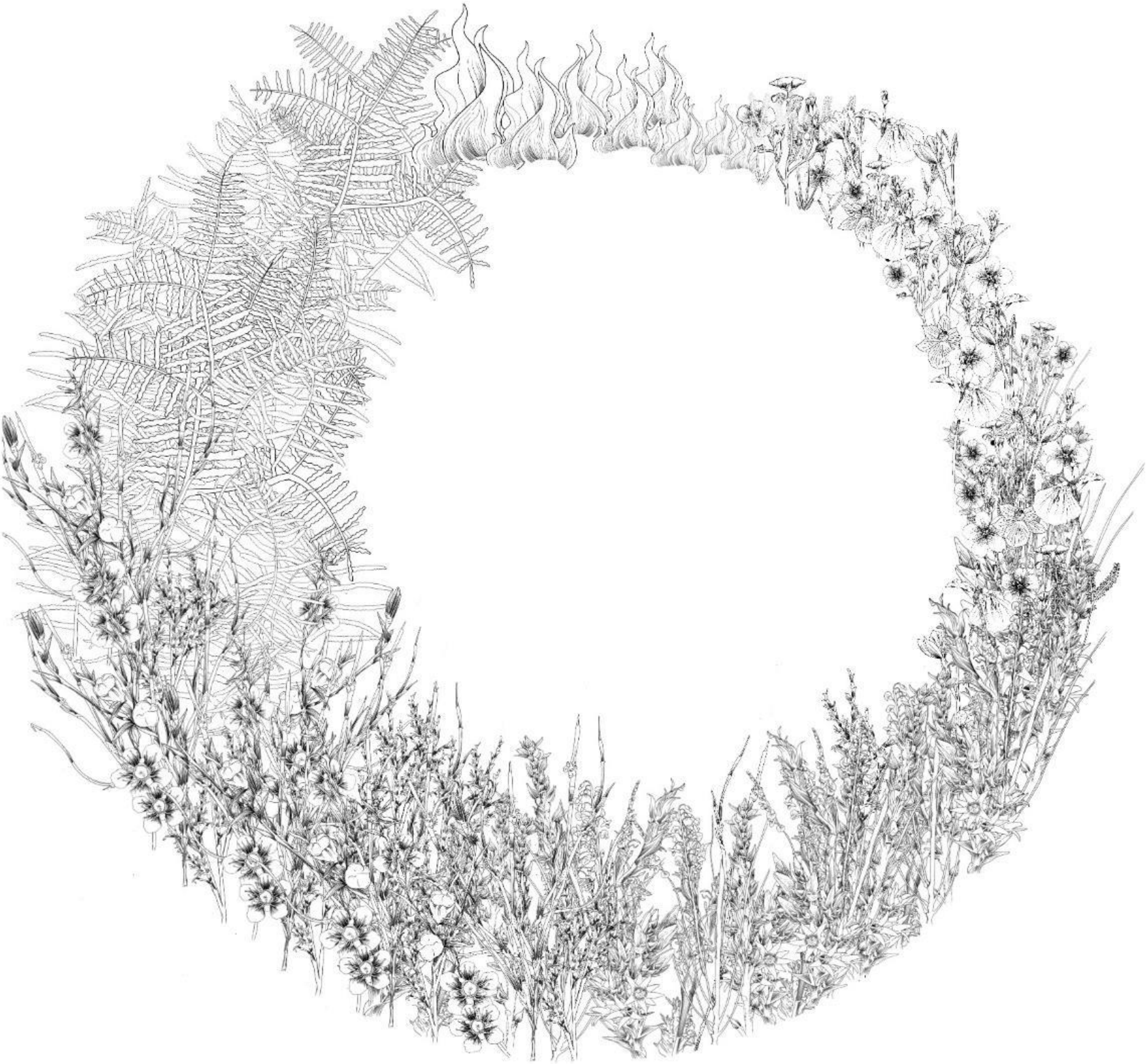


Figure 2. An artistic interpretation of heathy swamp succession, featuring species that characterise different stages after a fire. Understorey species such as *D. binata*, *T. cyanea*, *U. dichotoma*, and *H. tenuis* dominate in the early stages after a fire in swamps (top right corner). Over time they are succeeded by species that progressively dominate in later successional stages, including *P. murfetii*, *B. rubiginosa, V.juncea, and S. incarnata*. Then, during intermediate stages, species such as *G. sieberiana*, *E. minus,* and *L. continentale* typically flourish. These species then senesce or are outcompeted and are replaced by a smaller number of species that dominate the late-successional stages, which commonly is *G. microphylla* (top left corner). Fire may then reboot the process by returning the late-successional vegetation to its earliest stage of development. (Illustration: Anjali Singh)

Recommended fire intervals

I found that species richness was highest in the first year after fire, and that cover is likely to return to pre-fire levels within 1-5 years for these FPS. Despite these findings, the time required for late-successional species to dominate could be decades (Brown and Podger 1982; Clarkson 1997; Littlely 1998; Walker and Boneta 1995). Cheal (2010) recommends that a mosaic of age classes should be maintained in damp heathy scrub, which is a similar vegetation community to the heathy swamps studied here. He suggests that vegetation maturity takes at least 9 years, that individuals of species characteristic of the intermediate stages become uncommon by 25 years (e.g. *E. minus*) and become senesced by 80 years. In Western Australian swamps, Hayward *et al.* (2008) suggests that sites less than 14 years old are more diverse, and that vegetation older than this is often dominated by one or a few species. In the heathy peat swamps of New Zealand, Clarkson (1997) showed that swamps take 12 years to recover to pre-fire conditions, and that species which characterise late-successional periods can take more than 7 years to become common (e.g. *B. minus*). In the Otway Ranges of eastern Australia, Wark (1997) found that heathy peat swamps in gullies took 10 years to recover to pre-fire conditions. These studies suggest that swamp vegetation should be burnt at minimum intervals of 9 to 12 years. In comparison, the Conservation Council of South Australia (2020) suggests that FPS could be considered for repeated burning after 5 to 10 years and suggests minimum fire intervals of at least 8 years. This would maintain desirable floristic diversity and over time would improve the habitat structure for critically endangered Mount Lofty Ranges Southern Emu-wrens (*Stipiturus malachurus intermedius*) by enabling senescent heathy shrubs to re-establish.

For heathy swamps, I argue that inter-fire periods shorter than 7 years could exclude plants which characterise the intermediate or late successional stages. When generalising fire intervals, prescriptions should be based on the re-establishment period of the slowest maturing species, unless a specific ecological outcome requires a shorter interval (Burrows and Wardell-Johnson 2003; Clarkson *et al.* 2011; Enright *et al.* 1998). Fire managers should also consider that minimal fire-free intervals, which are required for species persistence, are predicted to increase with climate change because the speed of re-establishment and production of adequate propagule banks will take longer (Enright *et al.* 2015; Fairman *et al.* 2016; Stevens-Rumann *et al.* 2018). In FPS, the slowest maturing species is likely *G. microphylla*, and species of this genus take between 7 to 24 years to re-establish after fire (Brown and Podger 1982; Clarkson 1997; Walker and Boneta 1995). Furthermore, *G. microphylla* populations can require spore dispersal from adjacent unburnt vegetation when all rhizomes are consumed during a fire (Wark 1997). This indicates that fires prescribed into FPS should maintain an unburnt patch of *G. microphylla* to safeguard its reestablishment.

The maturity of obligate seeders also requires consideration, given these species rely entirely on seed reserves; some non-swamp species can take up to 20 years to mature (Enright *et al.* 2012) and many take more than 5 years (e.g. Edwards and Russell-Smith 2009; Ooi 2019; Wark 1997). To my knowledge, the juvenile period has not been determined for any obligate seeder endemic to FPS. Nevertheless, my results show that obligate seeders in heathy swamps had significantly less cover 18 months after fire, indicating these species may take several years to sufficiently mature and develop a seedbank sufficient to cope with subsequent fires.

Importantly, I found that long unburnt heathy swamps (> 59 years) still contained soil seedbanks of species which were not present in the standing vegetation. This indicates the longevity of the soil seedbanks of these species and the potential for obligate species to survive as propagules in the soil during long inter-fire periods. Various studies have found that species with dormant seeds can persist in soil seedbanks for several decades (Auld *et al.* 2000; Sano *et al.* 2016; Watson and Riha 2011). For these reasons, I argue that FPS should only be considered for repeated burning after 7 years and I suggest fire intervals of 20 years. This would likely allow enough time (for slow maturing species) for the development of adequate propagule reserves, while also ensuring propagule reserves (for species which rapidly establish) remain viable.

Recommended fire intervals should also be verified on-site, given that a large suite of variables influences the fire recovery of vegetation (e.g. post-fire grazing; Alex and Woinarski 2007; Conservation Council of South Australia 2020; Taylor 2019). Burns can also increase the abundance of introduced species by stimulating germination or providing favourable conditions for weeds to invade (Davies *et al.* 2013; Kerns *et al.* 2006; Walck *et al.* 2011). I also argue that long unburnt swamps (i.e. no fire history) should be prioritised before re-burning recently treated swamps, this is especially the case in southern Australia where fire managers concentrate on fuel reduction burning which limits the number of burns that can be conducted entirely for ecological benefits.

The needs of fauna also should be considered when prescribing burns, as fire can have negative effects. For example, by causing direct mortality, increasing predation risk (reduced cover) or limiting food resources (Keith *et al.* 2002). However, some species require fire to maintain suitable habitat. For example, Mount Lofty Ranges Southern Emu-wrens utilise FPS where they inhabit dense heathy vegetation that only exists during intermediate successional stages (Conservation Council of South Australia 2020; Department for Environment and Water 2012; Maguire 2005; 2006; Wilson and Paton 2004). This long unburnt FPS vegetation which is no longer suitable for them could be burnt to provide some suitable habitat for them some years later. However, the early successional periods are not useable and so no one swamp that supports remnant populations of these birds should be totally burnt in any one fire event (Wilson and Paton 2004). Thus, although burning can create favourable conditions, fire regimes need to be managed appropriately (with consideration of fire-intervals and appropriate scales) to ensure animals can re-colonise burnt patches.

Season of fire

In heathy swamps, fire during any given season will not uniformly benefit all species. Results suggest that different species within the same swamp have opposing seasonal preferences, suggesting fire seasonality should be prescribed based on seasonal preferences of target species. For instance, the establishment of the threatened species *H. tenuis* is likely higher from autumn burns. Conversely, the establishment of the threatened species *V. juncea* may be higher following spring burns. Both species co-occur in heathy swamps but may be adapted to different fire regimes, suggesting that burning different sections of swamps in different seasons maximises biodiversity at the landscape level.

In FPS, autumn burning should be prescribed in most instances, but spring burning should not be excluded. I found that autumn burning resulted in faster recovery and higher species richness for perennial natives compared to spring burning. Spring is also a highly productive period for plants, and fires during this period would disrupt the peak reproductive periods of 85 % of species. Seedlings that emerge after autumn burns will also have longer to establish before the onset of dry summer conditions.

Fire seasonality also affects peat consumption during a fire, as seasonal weather conditions can alter moisture content and subsequent fire intensity (Prior *et al.* 2020; Trezise *et al.* 2021). This requires careful consideration because peat accumulation represents a large fraction of global carbon stores and fire is a major threat to deposits (Page and Hooijer 2016; Trezise *et al.* 2021; Usup *et al.* 2004). Hence, I argue that season of burn should be prescribed based on conservation targets, such as avoiding the reproductive periods of threatened species or risk of combusting peat deposits.

Herbivory after fire

Herbivory provides a considerable threat to the recovery of heathy swamps after a fire. I found that 12 % of species did not establish after fire if exposed to mammalian herbivory, including threatened orchid species such as *S. australis* and *T. cyanea*. Perennials also had less cover in unfenced quadrats, including *V. juncea* and *H. tenuis*. Other studies have shown negative effects of herbivory after a fire, with herbivores reducing overall cover or species richness of particular plant species which were targeted by herbivores (Bradstock and Kenny 2003; Cohn and Bradstock 2000; Faast and Facelli 2009). This is unsurprising given that in southern Australia, kangaroo abundance has increased since European settlement, causing widespread overgrazing (Department for Environment and Water 2019b; Prowse *et al.* 2019). Furthermore, herbivores commonly focus on regrowth after a fire, so reducing the ability of plants to recover (Andruk *et al.* 2014; Bradstock and Kenny 2003; Letnic 2004). Grazing and fire can act synergistically to reduce post-fire plant recovery (Foster *et al.* 2016a). This is exacerbated after small burns which can concentrate herbivores (Leigh and Holgate 1979). Fencing after fire enhances species richness and cover in swamps by limiting the influence of herbivory (Ford and Grace 1998; Taylor *et al.* 1994). I suggest that herbivory should be controlled after fire in heathy swamps.

Limitations and further research

In Chapter 2, I compared two approaches to assess the response of soil seedbanks to fire. The *ex situ* approach had twice the number of replicates, despite covering 4-times less soil surface and taking a similar amount of time to conduct. As such, variance in the *in situ* quadrats was higher and the database contained fewer species with sufficient data to produce statistical estimates. A larger number of replicates across methods may have helped address these issues. Other improvements to this Chapter could have resulted from the addition of a seed enumeration component, an improved bioturbation treatment, a comparison between temperatures experienced *in situ* and *ex situ*, and the complete removal of adjacent vegetation which shaded quadrats.

Germination trials are generally limited by time and seed availability, meaning that the number of possible treatments is finite. My work has helped develop an understanding of morphophysiological dormancy of seeds of *H. tenuis* and its relationship to fire, but there are still many unknowns (Chapter 4). I applied several treatments in unison to maximise the use of a limited and finite number of seeds. As such, future studies should independently trial treatments that resulted in high germination, but which were used in unison with other treatments in this study. For example, exposing seeds only to static photoperiod treatments, or only to temperature treatments, may increase knowledge of the relative importance of these factors for breaking dormancy. Future studies should re-subject seeds which did not germinate to a similar set of treatments to further investigate the species potential bet-hedging strategy.

The temperature stratifications used in my experiment to replicate different seasonal conditions simulated air temperatures and not temperatures of the soil. Therefore, improvements could be made by measuring and replicating *in situ* soil temperatures for the temperature stratification treatments. Similarly, the interpretation of the effects of soil temperature on germination would be improved by an *in situ* experiment which compares soil temperature during prescribed burns to seedling germination and establishment.

A further limitation was that I deliberately biased sampling to swamp margin habitats containing or likely to contain *H. tenuis* (Chapter 3). Saturated microhabitats within heathy swamps may respond differently to fire, compared to in the drier (but still permanently moist) microhabitats studied here. Thus, results are less applicable to more saturated wetlands and microhabitats. Additionally, although I studied several swamps in Chapter 3, only two swamps were burnt and assessed in Chapter 5 because of the high expense of conducting control burns. Low site replication reduces detectability of differences between treatments, meaning insight into swamp burning would improve with greater replication. Future studies could improve results by burning additional swamps, without a bias towards *H. tenuis* habitat, and account for some of the environmental variation by distinguishing between permanently saturated and temporarily saturated microhabitats within swamps.

Discussions regarding late succession periods in heathy swamps are restricted to observations and inferences from the literature (Chapter 3 and 5). Given the short monitoring period of this study (< 2 years), I cannot be certain about the recommended 20 year inter-fire period. As such, predictions should be validated by resurveying the quadrats established in this study at later dates. I also recommend that future FPS burns be monitored to assess the impacts of season of burn and check that the succession is occurring as expected (especially given predictions may change because of climate change). Furthermore, similar heathy swamps which have a history of fire (e.g. Stipiturus Conservation Park) could be assessed through time to document the changes in vegetation through time after fire. Improvements to predictions could be made by assessing additional swamps burns, and by conducting future surveys of older successional age classes in the quadrats I established.

Concluding remarks for prescribing fire in heathy swamps

The decline of many FPS species can be attributed to an imbalance of age classes in the landscape, given almost all of these swamps are in late-successional stages. Fire is excluded in most cadastral parcels that contain FPS because they are often fenced and encircled by heavily grazed pasture, which limits the likelihood of bushfire spread. This is problematic as fire-dependent species within FPS will become extinct if burns are not employed before the species expire in both the above- and below-ground vegetation. For instance, the seed dormancy mechanisms of *H. tenuis* are linked to fire, and germination increases 18-fold with smoke exposure. Fire was employed as an ecological tool to stop declining population numbers of this species, which have since increased 30-fold due to the burns conducted during this study. Hence, areas of late successional habitat should be targeted for burning.

In agricultural landscapes, anthropogenic fire exclusion can cause vegetation communities to shift to alternative states (Briske *et al* 2005, Hanberry 2021, Kitzberger *et al* 2016). This occurs because vegetation, including their propagules, senesces over time. The resilience of heathy swamps thus declines after long fire free periods as the successional pathways of constituent species becomes blocked in the absence of fire (Watson 2005, McIver *et al.* 2013). For example, in FPS, long fire free intervals can result in heathy swamps transitioning into fern dominated swamps, coinciding with the loss of shrub species in the above ground vegetation community. Fire is therefore important for conserving species as it enables successional pathways that can benefit underrepresented fire-dependant species.

Despite the likely advantages of burning, fire prescription needs to consider fire intervals, post-fire herbivory, and fire-seasonality. Heathy swamp species with long juvenile periods can be excluded by short fire intervals and so subsequent burns should only be considered after all constituent species are mature and have sufficiently contributed to their propagule reserves. Fire intervals of 20 years are therefore recommended to maximise species retention, and swamps which have not experienced fire for extended periods (< 50 years) should be targeted first. Mammalian herbivory after fire negatively impacted native plants by excluding 12 % of species and limiting the recovery of many others. Additionally, swamp species may have opposing seasonal fire preferences; autumn burning increased *H. tenuis* establishment but decreased *V. juncea* establishment, suggesting that fire in any given season will not uniformly benefit all species. Fire managers of heathy swamps should: establish a mosaic of age classes, reduce the impact of herbivory, and consider the season in which they burn.

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Appendix 1. Supplementary material for Chapter 2

Table S1.1 Effect of site on the abundance and species richness of seedlings **for all species** emerging from the *ex situ* method. To convert the *ex situ* abundance (seedlings per tray) to *ex situ* seedlings m^2 multiply by 9.5; given the surface area of the *ex situ* trays are 0.105 m^2 compared to the 1 m^2 *in situ* quadrats. Species richness has not been extrapolated, as it does not scale linearly. Significant differences were generated using generalised linear mixed models. Results are given as mean (± SE) of seedlings per m^2 and number of species per tray.

Site name	**Quantity**	**Richness**
Cygnet Revegetation^{H} (CV)	922.9 ± 126.0	7.4 ± 0.3
Roadside Vegetation^{H} (RV)	367.3 ± 32.3	6.0 ± 0.4
Airport Remnant^{H} (AR)	152.0 ± 31.3	5.0 ± 0.8
Heritage Agreement^{H} (HA)	92.7 ± 12.5	3.8 ± 0.4
Spring Road Remnant^{D} (SR)	71.6 ± 10.5	2.9 ± 0.3
Redbanks Rd Remnant^{D} (RR)	53.4 ± 8.3	2.3 ± 0.2
Cygnet Remnant (CR)^{D}	298.1 ± 51.7	5.2 ± 0.7
Significant components (*P* value)	AR - CR; T (288) = -1.54, *P* =0.72 AR - CV; T (288) = -5.74, *P* =< 0.01 AR - HA; T (288) = 1.28, *P* =0.86 AR - RR; T (288) = 2.98, *P* =0.05 AR - RV; T (288) = -3.61, *P* =0.01 AR - SR; T (288) = 1.99, *P* =0.42 CR - CV; T (288) = -4.48, *P* =< 0.01 CR - HA; T (288) = 3.21, *P* =0.02 CR - RR; T (288) = 5.08, *P* =< 0.01 CR - RV; T (288) = -2.14, *P* =0.33 CR - SR; T (288) = 4.00, *P* =< 0.01 CV - HA; T (288) = 8.53, *P* =< 0.01 CV - RR; T (288) = 10.68, *P* =< 0.01 CV - RV; T (288) = 2.66, *P* =0.11 CV - SR; T (288) = 9.47, *P* =< 0.01 HA - RR; T (288) = 2.03, *P* =0.4 HA - RV; T (288) = -5.95, *P* =< 0.01 HA - SR; T (288) = 0.84, *P* =0.98 RR - RV; T (288) = -8.08, *P* =< 0.01 RR - SR; T (288) = -1.20, *P* =0.89 RV - SR; T (288) = 6.87, *P* =< 0.01	AR - CR; T (288) = -0.27, *P* =1.00 AR - CV; T (288) = -2.79, *P* =0.08 AR - HA; T (288) = 1.47, *P* =0.76 AR - RR; T (288) = 4.19, *P* =< 0.01 AR - RV; T (288) = -1.39, *P* =0.81 AR - SR; T (288) = 2.98, *P* =0.05 CR - CV; T (288) = -2.77, *P* =0.09 CR - HA; T (288) = 1.92, *P* =0.47 CR - RR; T (288) = 4.85, *P* =< 0.01 CR - RV; T (288) = -1.21, *P* =0.89 CR - SR; T (288) = 3.56, *P* =0.01 CV - HA; T (288) = 5.16, *P* =< 0.01 CV - RR; T (288) = 8.26, *P* =< 0.01 CV - RV; T (288) = 1.78, *P* =0.56 CV - SR; T (288) = 6.94, *P* =< 0.01 HA - RR; T (288) = 3.18, *P* =0.03 HA - RV; T (288) = -3.45, *P* =0.01 HA - SR; T (288) = 1.78, *P* =0.56 RR - RV; T (288) = -6.61, *P* =< 0.01 RR - SR; T (288) = -1.42, *P* =0.79 RV - SR; T (288) = 5.25, *P* =< 0.01

Site^{H} is regarded as healthy (>10 % native understorey); Site^{D} is regarded as degraded (<10 % native understorey).

Table S1.2 Effect of site on the abundance and species richness of seedlings **for native species** emerging from the *ex situ* method. To convert the *ex situ* abundance (seedlings per tray) to *ex situ* seedlings m^2 multiply by 9.5; given the surface area of the *ex situ* trays are 0.105 m^2 compared to the 1 m^2 *in situ* quadrats. Species richness has not been extrapolated, as it does not scale linearly. Significant differences were generated using generalised linear mixed models. Results are given as mean (± SE) of seedlings per m^2 and number of species per tray.

Site name	**Quantity**	**Richness**
Cygnet Revegetation^H (CV)	785.7 ± 126.3	3.9 ± 0.2
Roadside Vegetation^H (RV)	262.0 ± 26.3	2.9 ± 0.2
Airport Remnant^H (AR)	86.3 ± 20.0	3.5 ± 0.6
Heritage Agreement^H (HA)	87.4 ± 11.7	3.5 ± 0.4
Spring Road Remnant^D (SR)	48.9 ± 7.4	1.8 ± 0.2
Redbanks Rd Remnant^D (RR)	31.7 ± 5.9	1.6 ± 0.2
Cygnet Remnant (CR)^D	194.2 ± 38.2	2.3 ± 0.3
Significant components (P value)	AR - CR; T (287) = -1.56, P =0.71	AR - CR; T (287) = 2.15, P =0.33
	AR - CV; T (287) = -5.66, P =< 0.01	AR - CV; T (287) = -0.85, P =0.98
	AR - HA; T (287) = -0.36, P =1.00	AR - HA; T (287) = 0.03, P =1.00
	AR - RR; T (287) = 2.61, P =0.13	AR - RR; T (287) = 4.18, P =< 0.01
	AR - RV; T (287) = -3.68, P =0.01	AR - RV; T (287) = 1.08, P =0.93
	AR - SR; T (287) = 1.11, P =0.92	AR - SR; T (287) = 3.43, P =0.01
	CR - CV; T (287) = -4.39, P =< 0.01	CR - CV; T (287) = -3.36, P =0.02
	CR - HA; T (287) = 1.44, P =0.78	CR - HA; T (287) = -2.44, P =0.19
	CR - RR; T (287) = 4.69, P =< 0.01	CR - RR; T (287) = 1.94, P =0.45
	CR - RV; T (287) = -2.19, P =0.30	CR - RV; T (287) = -1.35, P =0.83
	CR - SR; T (287) = 3.07, P =0.04	CR - SR; T (287) = 1.15, P =0.91
	CV - HA; T (287) = 6.51, P =< 0.01	CV - HA; T (287) = 1.06, P =0.94
	CV - RR; T (287) = 10.07, P =< 0.01	CV - RR; T (287) = 5.87, P =< 0.01
	CV - RV; T (287) = 2.50, P =0.16	CV - RV; T (287) = 2.34, P =0.23
	CV - SR; T (287) = 8.33, P =< 0.01	CV - SR; T (287) = 5.02, P =< 0.01
	HA - RR; T (287) = 3.59, P =0.01	HA - RR; T (287) = 4.83, P =< 0.01
	HA - RV; T (287) = -4.06, P =< 0.01	HA - RV; T (287) = 1.26, P =0.87
	HA - SR; T (287) = 1.79, P =0.56	HA - SR; T (287) = 3.98, P =< 0.01
	RR - RV; T (287) = -7.67, P =< 0.01	RR - RV; T (287) = -3.64, P =0.01
	RR - SR; T (287) = -1.82, P =0.54	RR - SR; T (287) = -0.86, P =0.98
	RV - SR; T (287) = 5.89, P =< 0.01	RV - SR; T (287) = 2.78, P =0.08

Site^H is regarded as healthy (>10 % native understorey); Site^D is regarded as degraded (<10 % native understorey).

Table S1.3 Effect of site on the abundance and species richness of seedlings **for introduced species** emerging from the *ex situ* method. To convert the *ex situ* abundance (seedlings per tray) to *ex situ* seedlings m^2 multiply by 9.5; given the surface area of the *ex situ* trays are 0.105 m^2 compared to the 1 m^2 *in situ* quadrats. Species richness has not been extrapolated, as it does not scale linearly. Significant differences were generated using generalised linear mixed models. Results are given as mean (± SE) of seedlings per m^2 and number of species per tray.

Site name	**Quantity**	**Richness**
Cygnet Revegetation^H (CV)	137.2 ± 15.3	3.5 ± 0.2cc
Roadside Vegetation^H (RV)	105.3 ± 13.6	3.1 ± 0.3
Airport Remnant^H (AR)	64.9 ± 14.7	1.4 ± 0.3
Heritage Agreement^H (HA)	5.4 ± 1.9	0.3 ± 0.1
Spring Road Remnant^D (SR)	22.7 ± 5.0	1.0 ± 0.1
Redbanks Rd Remnant^D (RR)	21.7 ± 4.0	0.7 ± 0.1
Cygnet Remnant (CR)^D	103.9 ± 25.5	2.9 ± 0.4
Significant components (*P* value)	AR - CR; T (288) = -0.96, *P* =0.96 AR - CV; T (288) = -3.13, *P* =0.03 AR - HA; T (288) = 6.39, *P* =< 0.01 AR - RR; T (288) = 3.04, *P* =0.04 AR - RV; T (288) = -2.15, *P* =0.33 AR - SR; T (288) = 3.07, *P* =0.04 CR - CV; T (288) = -2.31, *P* =0.24 CR - HA; T (288) = 7.73, *P* =< 0.01 CR - RR; T (288) = 4.45, *P* =< 0.01 CR - RV; T (288) = -1.23, *P* =0.88 CR - SR; T (288) = 4.47, *P* =< 0.01 CV - HA; T (288) = 10.19, *P* =< 0.01 CV - RR; T (288) = 7.43, *P* =< 0.01 CV - RV; T (288) = 1.23, *P* =0.88 CV - SR; T (288) = 7.45, *P* =< 0.01 HA - RR; T (288) = -4.25, *P* =< 0.01 HA - RV; T (288) = -9.28, *P* =< 0.01 HA - SR; T (288) = -4.16, *P* =< 0.01 RR - RV; T (288) = -6.27, *P* =< 0.01 RR - SR; T (288) = 0.05, *P* =1.00 RV - SR; T (288) = 6.29, *P* =< 0.01	AR - CR; T (288) = -3.16, *P* =0.03 AR - CV; T (288) = -4.28, *P* =< 0.01 AR - HA; T (288) = 4.39, *P* =< 0.01 AR - RR; T (288) = 2.69, *P* =0.10 AR - RV; T (288) = -3.74, *P* =< 0.01 AR - SR; T (288) = 1.33, *P* =0.84 CR - CV; T (288) = -1.21, *P* =0.89 CR - HA; T (288) = 7.42, *P* =< 0.01 CR - RR; T (288) = 6.51, *P* =< 0.01 CR - RV; T (288) = -0.53, *P* =1.00 CR - SR; T (288) = 5.27, *P* =< 0.01 CV - HA; T (288) = 8.43, *P* =< 0.01 CV - RR; T (288) = 7.96, *P* =< 0.01 CV - RV; T (288) = 0.78, *P* =0.99 CV - SR; T (288) = 6.84, *P* =< 0.01 HA - RR; T (288) = -2.24, *P* =0.28 HA - RV; T (288) = -8.00, *P* =< 0.01 HA - SR; T (288) = -3.61, *P* =0.01 RR - RV; T (288) = -7.37, *P* =< 0.01 RR - SR; T (288) = -1.60, *P* =0.68 RV - SR; T (288) = 6.18, *P* =< 0.01

Site^H is regarded as healthy (>10 % native understorey); Site^D is regarded as degraded (<10 % native understorey).

Table S2. Quantity of plants for native species and groups of native species from *ex situ* 35 × 30 cm trays. Modelled means are given plus or minus standard error. Differences between the treatments was analysed subject to plants occurring in either a treated or untreated tray pair using generalised linear models.

Species	**Richness**	**Sum**	**Burnt**	**Unburnt**	**Significance**
All Natives	50	7025	13.9 ± 2.17	11.9 ± 1.86	T (285) = -1.32, *P* = 0.19
All Native Annuals/Biennial	7	3258	7.45 ± 2.57	6.54 ± 2.26	T (251) = -1.52, *P* = 0.13
Centrolepis strigosa (R.Br.) Roem. & Schult.		87	1.79 ± 0.81	1.43 ± 0.67	T (35) = -0.64, *P* = 0.53
Crassula decumbens Thunb. var. decumbens		2	na	na	na
Dysphania pumilio (R.Br.) Mosyakin & Clemants		54	1.01 ± 0.32	2.67 ± 0.65	T (19) = 2.68, *P* = 0.01
Juncus bufonius L.		584	2.77 ± 0.67	2.54 ± 0.61	T (153) = -0.41, *P* = 0.68
Lachnagrostis filiformis (G.Forst.) Trin.		172	1.68 ± 0.59	2.83 ± 0.98	T (51) = 1.06, *P* = 0.29
Lagenifera huegelii auct.non Benth.		0	0	0	0
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt		2358	7.28 ± 1.71	7.5 ± 1.75	T (207) = 0.2, *P* = 0.84
Senecio quadridentatus Labill. (r)		1	na	na	na
Wahlenbergia gracilenta Lothian		0	0	0	0
All Native Perennials	43	3767	6.29 ± 1.52	4.02 ± 0.98	T (235) = -2.59, *P* = 0.01
Acacia sp.		0	0	0	0
Acacia spinescens Benth.		0	0	0	0
Acrotriche serrulata R.Br.		0	0	0	0
Allocasuarina muelleriana (Miq.) L.A.S.Johnson		0	0	0	0
Astroloma conostephioides (Sond.) F.Muell. ex Benth.		7	na	na	na
Astroloma humifusum (Cavs) R.Br.		26	1.59 ± 0.45	0.38 ± 0.19	T (21) = -2.52, *P* = 0.02
Atriplex cinerea Poir.		0	0	0	0
Austrostipa sp.		0	0	0	0
Baumea juncea (R.Br.) Palla		21	0.3 ± 0.16	1.27 ± 0.38	T (19) = 2.43, *P* = 0.03
Bertya rotundifolia F.Muell.		4	na	na	na
Callistemon rugulosus (D.F.K.Schltdl. ex Link) DC.		0	0	0	0
Calytrix glaberrima (F.Muell.) Craven		6	na	na	na
Calytrix tetragona Labill.		4	na	na	na
Carex inversa R.Br.		3	na	na	na
Carpobrotus rossii (Haw.) Schwantes		0	0	0	0
Cassytha pubescens R.Br.		0	0	0	0

Choretrum glomeratum R.Br. var. glomeratum		3	na	na	na
Correa reflexa (Labill.) Vent. var. *insularis* Paul G.Wilson		1	na	na	na
Daviesia brevifolia Lindl.		1	na	na	na
Dianella brevicaulis (Ostenf.) G.W.Carr & P.F.Horsfall		0	0	0	0
Dichondra repens J.R.Forst. & G.Forst.		3	na	na	na
Dillwynia sericea A.Cunn.		1	na	na	na
Dodonaea baueri Endl.		14	0.7 ± 0.265	0.7 ± 0.265	T (16) = 0.01, *P* = 1
Dodonaea hexandra F.Muell.		0	0	0	0
Dodonaea viscosa Jacq.		0	0	0	0
Drosera macrantha Endl.		0	0	0	0
Drosera whittakeri Planch.		6	na	na	na
Eucalyptus cneorifolia DC.		0	0	0	0
Eucalyptus cosmophylla F.Muell.		0	0	0	0
Eutaxia diffusa F.Muell.		3	na	na	na
Eutaxia microphylla (R.Br.) C.H.Wright & Dewar		2	na	na	na
Gonocarpus mezianus (H.Schindl.) Orchard		2	na	na	na
Goodenia varia R.Br.		23	1.08 ± 0.29	0.54 ± 0.2	T (23) = -1.5, *P* = 0.15
Grevillea ilicifolia (R.Br.) R.Br. subsp. *ilicifolia*		5	na	na	na
Gyrostemon sp.		1	na	na	na
Hibbertia sp.		52	3.04 ± 0.71	0.72 ± 0.26	T (20) = -4.08, *P* = <0.01
Ixodia achillaeoides R.Br. subsp. *alata* (Schltdl.) Copley		3	na	na	na
Juncus pallidus R.Br.		2879	5.1 ± 1.69	5.26 ± 1.73	T (133) = -0.11, *P* = 0.91
Juncus subsecundus N.A.Wakef.		0	0	0	0
Lasiopetalum baueri Steetz / L. schulzenii (F.Muell.) Benth.		14	1.4 ± 0.53	0.23 ± 0.18	T (12) = -2.35, *P* = 0.04
Laxmannia orientalis Keighery		2	na	na	na
Lepidosperma canescens Boeck.		0	0	0	0
Lepidosperma viscidum R.Br.		21	1.2 ± 0.4	0.9 ± 0.33	T (16) = -0.58, *P* = 0.57
Logania linifolia Schltdl. (r)		8	na	na	na
Logania ovata R.Br.		2	na	na	na
Lythrum hyssopifolia L.		396	2.13 ± 0.71	1.2 ± 0.41	T (119) = -2.29, *P* = 0.02
Melaleuca gibbosa Labill.		0	0	0	0
Melaleuca lanceolata Otto		0	0	0	0
Melaleuca uncinata R.Br.		0	0	0	0

Micrantheum demissum F.Muell.		5	na	na	na
Myoporum sp.		3	na	na	na
Olearia microdisca J.M.Black (E e e)		5	na	na	na
Orthrosanthus multiflorus Sweet		2	na	na	na
Patersonia occidentalis R.Br.		0	0	0	0
Pelargonium australe		1	na	na	na
Pimelea stricta Meisn.		0	0	0	0
Pomaderris paniculosa F.Muell. ex Reissek		0	0	0	0
Prostanthera sp.		6	na	na	na
Pultenaea acerosa R.Br. ex Benth.		1	na	na	na
Pultenaea daphnoides J.C.Wendl.		10	na	na	na
Rhagodia candolleana Moq.		0	0	0	0
Rytidosperma sp.		73	2.07 ± 0.51	0.46 ± 0.16	T (45) = -4.24, *P* = <0.01
Schoenus maschalinus Roem. & Schult.		47	2.07 ± 0.73	2.03 ± 0.71	T (17) = -0.03, *P* = 0.97
Spyridium eriocephalum Fenzl var. *glabrisepalum* J.M.Black (V v v)		7	na	na	na
Stackhousia aspericocca Schuch.		0	0	0	0
Stackhousia monogyna auct.non Labill		0	0	0	0
Stylidium armeria (Labill.) Labill		0	0	0	0
Thelymitra sp.		1	na	na	na
Thryptomene ericaea F.Muell.		92	2.07 ± 0.36	0.86 ± 0.2	T (57) = -3.05, *P* = <0.01
Thysanotus patersonii R.Br.		1	na	na	na
Xanthorrhoea semiplana F.Muell. subsp. *tateana* (F.Muell.) Bedford (r)		0	0	0	0
All introduced species	29	1996	5.97 ± 1.95	4.49 ± 1.48	T (242) = -2.22, *P* = 0.03
All introduced annuals/biennial	22	1890	5.78 ± 1.89	4.45 ± 1.47	T (241) = -1.89, *P* = 0.06
Aira elegantissima Schur		60	3.13 ± 1.89	2.48 ± 1.46	T (15) = -0.28, *P* = 0.78
Arctotheca calendula (L.) Levyns		126	3.16 ± 0.67	0.99 ± 0.26	T (49) = -3.55, *P* = < 0.01
Avena barbata Pott ex Link		614	5.25 ± 1.16	4.68 ± 1.04	T (105) = -0.37, *P* = 0.72
Briza minor L.		8	na	na	na
Bromus diandrus Roth		12	na	na	na
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch.		49	2.18 ± 0.98	2.28 ± 1.02	T (17) = 0.07, *P* = 0.95
Cerastium glomeratum Thuill.		7	na	na	na
Cirsium vulgare (Savi) Ten.		0	0	0	0
Cyperus tenellus L.f.		17	na	na	na

Ehrharta longiflora Sm.		37	0.86 ± 0.36	1.79 ± 0.66	T (23) = 1.3, *P* = 0.21
Ehrharta villosa (L.f.) Schult.f. ex Schult. & Schult.f.		6	na	na	na
Galium murale (L.) All.		3	na	na	na
Hypochaeris glabra L.		18	0.91 ± 0.28	0.58 ± 0.22	T (20) = -0.93, *P* = 0.36
Isolepis marginata (Thunb.) A.Dietr.		493	3.19 ± 0.66	2.07 ± 0.43	T (167) = -1.95, *P* = 0.05
Kickxia elatine ssp *crinita*		11	na	na	na
Lagurus ovatus L.		20	na	na	na
Lolium rigidum Gaudin		12	0.4 ± 0.2	0.79 ± 0.28	T (16) = 1.13, *P* = 0.27
Polygonum aviculare L.		7	na	na	na
Soliva sessilis Ruiz & Pavs		0	0	0	0
Sonchus asper (L.) Hill		203	1.08 ± 0.22	1.39 ± 0.27	T (129) = 1.31, *P* = 0.19
Sonchus oleraceus L.		17	0.64 ± 0.21	0.57 ± 0.2	T (24) = -0.24, *P* = 0.81
Trifolium campestre Schreb.		17	na	na	na
Trifolium subterraneum L.		5	na	na	na
Vulpia bromoides (L.) Gray		148	na	na	na
All introduced perennials	7	106	1.46 ± 0.29	1.29 ± 0.26	T (65) = -0.45, *P* = 0.65
Asparagus asparagoides (L.) Druce f.		1	na	na	na
Conyza sp.		8	na	na	na
Cynodon dactylon (L.) Pers. var. *dactylon*		53	2.23 ± 0.54	1.23 ± 0.35	T (23) = -1.64, *P* = 0.11
Ehrharta calycina Sm.		0	0	0	0
Malva parviflora L.		4	na	na	na
Oxalis pes-caprae L.		1	na	na	na
Romulea rosea (L.) Eckl.		0	0	0	0
Senecio pterophorus DC.		0	0	0	0
Solanum nigrum L.		34	0.94 ± 0.3	0.95 ± 0.3	T (31) = 0.02, *P* = 0.99
Taraxacum officinale auct.non F.H.Wigg.		5	na	na	na

na=insufficient data to calculate statistic

Table S3. Richness of species and groups of species from e*x situ* 35 × 30 cm trays. Modelled means are given plus or minus standard error. Differences between the treatments was analysed subject to plants occurring in either a treated or untreated tray pair using generalised linear models.

Species	**Richness**	**Burnt**	**Unburnt**	**Significance**
All Natives	52	2.98 ± 0.36	2.26 ± 0.28	T (284) =-3.89, *P* = < 0.01
Native Perennials	9	1.70 ± 0.24	0.99 ± 0.15	T (236) =-4.84, *P* = < 0.01
Native Annuals/Biennials	43	1.70 ± 0.23	1.57 ± 0.22	T (252) =-0.88, *P* = 0.37
All Introduced	27	1.88 ± 0.42	1.63 ± 0.36	T (243) =-1.65, *P* = 0.09
Introduced Perennials	20	0.74 ± 0.14	0.68 ± 0.14	T (66) =-0.28, *P* = 0.77
Introduced Annuals/Biennials	7	1.75 ± 0.38	1.51 ± 0.33	T (242) =-1.65, *P* = 0.09

Table S4.1 Effect of site on seedling abundance and species richness from the *in situ* method for **all species**. Means are given as the number of germinants/species m^{-2} ± standard error.

Site name	**Quantity**	**Richness**
Cygnet Revegetation^{H} (CV)	145.8 ± 28.7	7.0 ± 0.6
Roadside Vegetation^{H} (RV)	38.7 ± 10.3	4.9 ± 0.7
Airport Remnant^{H} (AR)	47.1 ± 25.9	3.9 ± 0.8
Heritage Agreement^{H} (HA)	28.8 ± 7.4	4.4 ± 0.8
Spring Road Remnant^{D} (SR)	11.3 ± 3.9	3.0 ± 0.5
Redbanks Rd Remnant^{D} (RR)	3.9 ± 1.8	2.0 ± 0.4
Significant components (*P* value)	AR - CV; T (264) = -1.27, *P* =0.80 AR - HA; T (264) = 3.14, *P* =0.02 AR - RR; T (264) = 6.90, *P* =< 0.01 AR - RV; T (264) = 0.75, *P* =0.98 AR - SR; T (264) = 5.40, *P* =< 0.01 CV - HA; T (264) = 6.60, *P* =< 0.01 CV - RR; T (264) = 11.06, *P* =< 0.01 CV - RV; T (264) = 2.85, *P* =0.05 CV - SR; T (264) = 9.42, *P* =< 0.01 HA - RR; T (264) = 5.46, *P* =< 0.01 HA - RV; T (264) = -3.23, *P* =0.02 HA - SR; T (264) = 3.39, *P* =0.01 RR - RV; T (264) = -7.92, *P* =< 0.01 RR - SR; T (264) = -2.18, *P* =0.25 RV - SR; T (264) = 6.14, *P* =< 0.01	AR - CV; T (265) = -1.64, *P* =0.58 AR - HA; T (265) = 2.97, *P* =0.04 AR - RR; T (265) = 4.98, *P* =< 0.01 AR - RV; T (265) = 0.18, *P* =< 0.01 AR - SR; T (265) = 4.26, *P* =< 0.01 CV - HA; T (265) = 7.27, *P* =< 0.01 CV - RR; T (265) = 8.89, *P* =< 0.01 CV - RV; T (265) = 2.71, *P* =0.08 CV - SR; T (265) = 8.32, *P* =< 0.01 HA - RR; T (265) = 3.07, *P* =0.03 HA - RV; T (265) = -3.95, *P* =< 0.01 HA - SR; T (265) = 2.04, *P* =0.32 RR - RV; T (265) = -6.21, *P* =< 0.01 RR - SR; T (265) = -1.08, *P* =0.89 RV - SR; T (265) = 5.43, *P* =< 0.01

Site^{H} is regarded as healthy (>10 % native understorey); Site^{D} is regarded as degraded (<10 % native understorey).

Table S4.2 Effect of site on seedling abundance and species richness from the *in situ* method for **native species**. Means are given as the number of germinants/species m^{-2} ± standard error.

Site name	**Quantity**	**Richness**
Cygnet Revegetation^{H} (CV)	96.1 ± 17.9	4.5 ± 0.3
Roadside Vegetation^{H} (RV)	21.9 ± 4.3	2.8 ± 0.4
Airport Remnant^{H} (AR)	30.0 ± 21.2	2.3 ± 0.4
Heritage Agreement^{H} (HA)	14.7 ± 3.4	2.9 ± 0.4
Spring Road Remnant^{D} (SR)	10.7 ± 3.7	2.0 ± 0.3
Redbanks Rd Remnant^{D} (RR)	2.5 ± 1.0	1.5 ± 0.2
Significant components (*P* value)	AR - CV; T (265) = -0.12, *P* =1.00 AR - HA; T (265) = 1.60, *P* =0.6 AR - RR; T (265) = 5.90, *P* =< 0.01 AR - RV; T (265) = 0.28, *P* =1.00 AR - SR; T (265) = 5.90, *P* =< 0.01 CV - HA; T (265) = 2.20, *P* =0.24 CV - RR; T (265) = 7.31, *P* =< 0.01 CV - RV; T (265) = 0.51, *P* =1.00 CV - SR; T (265) = 7.46, *P* =< 0.01 HA - RR; T (265) = 5.38, *P* =< 0.01 HA - RV; T (265) = -1.58, *P* =0.61 HA - SR; T (265) = 5.5, *P* =< 0.01 RR - RV; T (265) = -6.56, *P* =< 0.01 RR - SR; T (265) = < 0.01, *P* =1.00 RV - SR; T (265) = 6.70, *P* =< 0.01	AR - CV; T (265) = 0.86, *P* =0.96 AR - HA; T (265) = 2.79, *P* =0.06 AR - RR; T (265) = 5.84, *P* =< 0.01 AR - RV; T (265) = 1.08, *P* =0.89 AR - SR; T (265) = 5.86, *P* =< 0.01 CV - HA; T (265) = 2.77, *P* =0.07 CV - RR; T (265) = 6.43, *P* =< 0.01 CV - RV; T (265) = 0.39, *P* =1.00 CV - SR; T (265) = 6.57, *P* =< 0.01 HA - RR; T (265) = 4.29, *P* =< 0.01 HA - RV; T (265) = -2.16, *P* =0.26 HA - SR; T (265) = 4.37, *P* =< 0.01 RR - RV; T (265) = -5.83, *P* =< 0.01 RR - SR; T (265) = -0.06, *P* =1.00 RV - SR; T (265) = 5.95, *P* =< 0.01

Site^{H} is regarded as healthy (>10 % native understorey); Site^{D} is regarded as degraded (<10 % native understorey).

Table S4.3 Effect of site on seedling abundance and species richness from the *in situ* method for **introduced species**. Means are given as the number of germinants/species m^{-2} ± standard error.

Site name	**Quantity**	**Richness**
Cygnet Revegetation^{H} (CV)	49.7 ± 10.8	2.5 ± 0.3
Roadside Vegetation^{H} (RV)	16.8 ± 6.0	2.1 ± 0.3
Airport Remnant^{H} (AR)	17.1 ± 4.8	1.7 ± 0.4
Heritage Agreement^{H} (HA)	14.1 ± 3.9	1.6 ± 0.4
Spring Road Remnant^{D} (SR)	0.6 ± 0.2	1.0 ± 0.1
Redbanks Rd Remnant^{D} (RR)	1.4 ± 0.9	0.5 ± 0.1
Significant components (*P* value)	AR - CV; T (265) = -3.65, *P* =< 0.01 AR - HA; T (265) = 3.45, *P* =0.01 AR - RR; T (265) = 3.66, *P* =< 0.01 AR - RV; T (265) = -0.55, *P* =0.99 AR - SR; T (265) = 0.81, *P* =0.96 CV - HA; T (265) = 8.82, *P* =< 0.01 CV - RR; T (265) = 8.55, *P* =< 0.01 CV - RV; T (265) = 4.18, *P* =< 0.01 CV - SR; T (265) = 6.17, *P* =< 0.01 HA - RR; T (265) = 0.50, *P* =1.00 HA - RV; T (265) = -4.94, *P* =< 0.01 HA - SR; T (265) = -3.42, *P* =0.01 RR - RV; T (265) = -5.05, *P* =< 0.01 RR - SR; T (265) = -3.65, *P* =< 0.01 RV - SR; T (265) = 1.81, *P* =0.46	AR - CV; T (265) = -3.87, *P* =< 0.01 AR - HA; T (265) = 1.67, *P* =0.55 AR - RR; T (265) = 1.73, *P* =0.52 AR - RV; T (265) = -1.58, *P* =0.61 AR - SR; T (265) = -0.62, *P* =0.99 CV - HA; T (265) = 9.28, *P* =< 0.01 CV - RR; T (265) = 7.26, *P* =< 0.01 CV - RV; T (265) = 5.66, *P* =< 0.01 CV - SR; T (265) = 7.26, *P* =< 0.01 HA - RR; T (265) = 0.28, *P* =1.00 HA - RV; T (265) = -5.13, *P* =< 0.01 HA - SR; T (265) = -3.55, *P* =0.01 RR - RV; T (265) = -4.33, *P* =< 0.01 RR - SR; T (265) = -3.13, *P* =0.02 RV - SR; T (265) = 1.84, *P* =0.44

Site^{H} is regarded as healthy (>10 % native understorey); Site^{D} is regarded as degraded (<10 % native understorey).

Table S5.1 Quantity of plants for native species and groups of native species from *in situ* 1 x 1 m quadrats. Modelled means are given plus or minus standard error. Differences between the fire treatments was analysed subject to plants occurring in either a burn or unburnt quadrat pair using generalised linear models. Na, not applicable or insufficient data to calculate statistic.

Species	**Richness**	**Sum**	**Burnt**	**Unburnt**	**Significance**
All natives	56	4070	13.5 ± 5.0	9.9 ± 3.7	T (90) = -1.37, *P* = 0.17
Native annuals/biennial	7	240	15.3 ± 3.8	3.9 ± 1.3	T (14) = -3.21, *P* = 0.01
Centrolepis strigosa (R.Br.) Roem. & Schult.		2	na	na	na
Crassula decumbens Thunb. var. *decumbens*	0	0	0	0	0
Dysphania pumilio (R.Br.) Mosyakin & Clemants		194	21.3 ± 4.4	2.2 ± 2.2	T (2) = 0.00, *P* = 1.00
Juncus bufonius L.	0	0	0	0	0
Lachnagrostis filiformis (G.Forst.) Trin.		4	na	na	na
Lagenophora huegelii Benth.		4	na	na	na
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt		1	na	na	na
Senecio quadridentatus Labill. (r)		9	na	na	na
Wahlenbergia gracilenta Lothian		26	na	na	na
Native perennials	49	3830	17.3 ± 7.2	17.4 ± 6.7	T (81) = 0.02, *P* = 0.99
Acacia sp.		30	2.4 ± 0.6	2.0 ± 1.1	T (3) = -0.33, *P* = 0.76
Acacia spinescens Benth.		16	na	na	na
Acrotriche serrulata R.Br.		3	na	na	na
Allocasuarina muelleriana (Miq.) L.A.S.Johnson		5	na	na	na
Astroloma conostephioides (Sond.) F.Muell. ex Benth.		0	0	0	0
Astroloma humifusum (Cavs) R.Br.		111	na	na	na
Atriplex cinerea Poir.		2	na	na	na
Austrostipa sp.		451	27.1 ± 13.5	4.8 ± 2.1	T (13) = -2.94, *P* = 0.01
Baumea juncea (R.Br.) Palla		0	0	0	0
Bertya rotundifolia F.Muell.		4	na	na	na
Callistemon rugulosus (D.F.K.Schltdl. ex Link) DC.		32	na	na	na
Calytrix glaberrima		0	0	0	0
Calytrix tetragona Labill.		56	na	na	na
Carex inversa R.Br.		0	0	0	0
Carpobrotus rossii (Haw.) Schwantes		3	na	na	na
Cassytha pubescens R.Br.		1	na	na	na
Choretrum glomeratum R.Br. var. *glomeratum*		1	na	na	na
Correa reflexa (Labill.) Vent. var. *insularis* Paul G.Wilson		38	na	na	na

Daviesia brevifolia Lindl.		1	na	na	na
Dianella brevicaulis (Ostenf.) G.W.Carr & P.F.Horsfall		12	na	na	na
Dichondra repens J.R.Forst. & G.Forst.		0	0	0	0
Dillwynia sericea A.Cunn.		6	na	na	na
Dodonaea baueri Endl.		0	0	0	0
Dodonaea hexandra F.Muell.		50	na	na	na
Dodonaea viscosa Jacq.		2	na	na	na
Drosera macrantha Endl.		46	na	na	na
Drosera whittakeri Planch.		132	na	na	na
Eucalyptus cneorifolia DC.		187	2.0 ± 0.9	3.6 ± 0.9	T (16) = 1.36, *P* = 0.19
Eucalyptus cosmophylla F.Muell.		136	2.3 ± 1.3	9.2 ± 2.5	T (6) = 2.33, *P* = 0.06
Eutaxia diffusa F.Muell.		0	0	0	0
Eutaxia microphylla (R.Br.) C.H.Wright & Dewar		0	0	0	0
Gonocarpus mezianus (H.Schindl.) Orchard		0	0	0	0
Goodenia varia R.Br.		0	0	0	0
Grevillea ilicifolia (R.Br.) R.Br. subsp. *ilicifolia*		8	na	na	na
Gyrostemon sp.		0	0	0	0
Hibbertia sp.		71	1.7 ± 1.4	2.1 ± 1.6	T (5) = 0.15, *P* = 0.89
Ixodia achillaeoides R.Br. subsp. *valata* (Schltdl.) Copley		0	0	0	0
Juncus pallidus R.Br.		904	22.1 ± 4.0	18.4 ± 3.4	T (6) = -0.71, *P* = 0.50
Juncus subsecundus N.A.Wakef.		242	na	na	na
Lasiopetalum baueri Steetz / L. schulzenii (F.Muell.) Benth.		28	na	na	na
Laxmannia orientalis Keighery		2	na	na	na
Lepidosperma canescens Boeck.		33	na	na	na
Lepidosperma viscidum R.Br.		372	19.1 ± 8.7	7.7 ± 2.8	T (7) = -1.55, *P* = 0.17
Logania linifolia Schltdl.		0	0	0	0
Logania ovata R.Br.		0	0	0	0
Lythrum hyssopifolia L.		6	na	na	na
Melaleuca gibbosa Labill.		53	4.0 ± 1.6	1.0 ± 0.7	na
Melaleuca lanceolata Otto		72	na	na	na
Melaleuca uncinata R.Br.		138	2.1 ± 1.3	3.9 ± 1.1	T (2) = 0.9, *P* = 0.46
Micrantheum demissum F.Muell.		0	0	0	0
Myoporum sp.		0	0	0	0
Olearia microdisca J.M.Black (E e)		0	0	0	0

Orthrosanthus multiflorus Sweet		0	0	0	0
Patersonia occidentalis R.Br.		16	na	na	na
Pelargonium australe		0	0	0	0
Pimelea stricta Meisn.		3	na	na	na
Pomaderris paniculosa F.Muell. ex Reissek		3	na	na	na
Prostanthera sp.		0	0	0	0
Pultenaea acerosa R.Br. ex Benth.		0	0	0	0
Pultenaea daphnoides J.C.Wendl.		9	na	na	na
Rhagodia candolleana Moq.		8	na	na	na
Rytidosperma sp.		83	6.6 ± 0.9	4.2 ± 1.3	T (2) = -1.31, *P* = 0.32
Schoenus maschalinus Roem. & Schult.		8	na	na	na
Spyridium eriocephalum Fenzl var. *glabrisepalum* J.M.Black (V v)		0	0	0	0
Stackhousia aspericocca Schuch.		9	na	na	na
Stackhousia monogyna auct.non Labill		1	na	na	na
Stylidium armeria (Labill.) Labill		2	na	na	na
Thelymitra sp.		6	na	na	na
Thryptomene ericaea F.Muell.		203	7.3 ± 4.7	4.2 ± 2.8	T (11) = -1.03, *P* = 0.32
Thysanotus patersonii R.Br.		7	na	na	na
Xanthorrhoea semiplana F.Muell. subsp. *tateana* (F.Muell.) Bedford (r)		218	2.6 ± 1.5	4.4 ± 1.8	T (7) = 0.75, *P* = 0.48
All introduced species	20	4700	13.7 ± 6.9	10.4 ± 5.2	T (65) = -1.21, *P* = 0.23
Introduced annuals/biennial	13	2804	11.8 ± 5.0	10.1 ± 4.4	T (59) = -0.51, *P* = 0.61
Aira elegantissima Schur		15	na	na	na
Arctotheca calendula (L.) Levyns		105	3.3 ± 1.4	6.4 ± 6.4	T (5) = 0.00, *P* = 1.00
Avena barbata Pott ex Link		1739	4.5 ± 2.6	6.9 ± 4.1	T (21) = 0.98, *P* = 0.34
Briza minor L.		0	0	0	0
Bromus diandrus Roth		0	0	0	0
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch.		0	0	0	0
Cerastium glomeratum Thuill.		0	0	0	0
Cirsium vulgare (Savi) Ten.		1	na	na	na
Cyperus tenellus L.f.		7	na	na	na
Ehrharta longiflora Sm.		51	na	na	na
Ehrharta villosa (L.f.) Schult.f. ex Schult. & Schult.f.		0	0	0	0
Galium murale (L.) All.		0	0	0	0
Hypochaeris glabra L.		118	2.0 ± 1.1	3.1 ± 1.2	T (7) = 0.68, *P* = 0.52

Isolepis marginata (Thunb.) A.Dietr.		8	na	na	na
Kickxia elatine ssp *crinita*		0	0	0	0
Lagurus ovatus L.		19	na	na	na
Lolium rigidum Gaudin		0	0	0	0
Polygonum aviculare L.		0	0	0	0
Soliva sessilis Ruiz & Pavs		75	na	na	na
Sonchus asper (L.) Hill		0	0	0	0
Sonchus oleraceus L.		2	na	na	na
Trifolium campestre Schreb.		192	6.3 ± 2.4	7.1 ± 2.8	T (7) = 0.21, *P* = 0.84
Trifolium subterraneum L.		0	0	0	0
Vulpia bromoides (L.) Gray		472	16.4 ± 5.1	9.2 ± 9.2	T (7) = 0.00, *P* = 1.00
Introduced perennials	7	1896	16.3 ± 13.9	7.4 ± 6.4	T (26) = -2.42, *P* = 0.02
Asparagus asparagoides (L.) Druce f.		27	na	na	na
Conyza sp.		0	0	0	0
Cynodon dactylon (L.) Pers. var. *dactylon*		1329	46 ± 10.9	16.9 ± 5.9	T (5) = -2.37, *P* = 0.06
Ehrharta calycina Sm.		43	na	na	na
Malva parviflora L.		0	0	0	0
Oxalis pes-caprae L.		67	na	na	na
Romulea rosea (L.) Eckl.		404	64.6 ± 46.2	5.4 ± 4.8	T (3) = -3.18, *P* = 0.05
Senecio pterophorus DC.		2	na	na	na
Solanum nigrum L.		24	3.4 ± 0.8	2.0 ± 1.1	T (2) = -0.86, *P* = 0.48
Taraxacum officinale auct.non F.H.Wigg.		0	0	0	0

Table S5.2 Quantity of plants for native species and groups of native species from *in situ* 1 x 1 m quadrats. Modelled means are given plus or minus standard error. Differences between the fenced treatment was analysed subject to plants occurring in either a fenced or unfenced quadrat pair using generalised linear models. Na, not applicable or insufficient data to calculate statistic.

Species	**Richness**	**Sum**	**Fenced**	**Unfenced**	**Significance**
All natives	56	4070	15.4 ± 5.7	8.6 ± 3.2	T (90) = -2.44, *P* = 0.02
Native annuals/biennial	7	240	8.9 ± 2.3	6.7 ± 2.3	T (14) = -0.65, *P* = 0.53
Centrolepis strigosa (R.Br.) Roem. & Schult.		2	na	na	na
Crassula decumbens Thunb. var. *decumbens*		0	0	0	0
Dysphania pumilio (R.Br.) Mosyakin & Clemants		194	6.7 ± 3.1	7.0 ± 7.0	T (2) = 0.00, *P* = 1.00
Juncus bufonius L.		0	0	0	0
Lachnagrostis filiformis (G.Forst.) Trin.		4	na	na	na
Lagenophora huegelii Benth.		4	na	na	na
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt		1	na	na	na
Senecio quadridentatus Labill. (r)		9	na	na	na
Wahlenbergia gracilenta Lothian		26	na	na	na
Native perennials	49	3830	21.7 ± 8.2	13.8 ± 5.9	T (81) = -1.87, *P* = 0.06
Acacia sp.		30	1.5 ± 0.8	3.3 ± 1.0	T (3) = 1.28, *P* = 0.29
Acacia spinescens Benth.		16	na	na	na
Acrotriche serrulata R.Br.		3	na	na	na
Allocasuarina muelleriana (Miq.) L.A.S.Johnson		5	na	na	na
Astroloma conostephioides (Sond.) F.Muell. ex Benth.		0	0	0	0
Astroloma humifusum (Cavs) R.Br.		111	na	na	na
Atriplex cinerea Poir.		2	na	na	na
Austrostipa sp.		451	7.5 ± 2.3	17.2 ± 10.6	T (13) = 1.29, *P* = 0.22
Baumea juncea (R.Br.) Palla		0	0	0	0
Bertya rotundifolia F.Muell.		4	na	na	na
Callistemon rugulosus (D.F.K.Schltdl. ex Link) DC.		32	na	na	na
Calytrix glaberrima		0	0	0	0
Calytrix tetragona Labill.		56	na	na	na
Carex inversa R.Br.		0	0	0	0
Carpobrotus rossii (Haw.) Schwantes		3	na	na	na
Cassytha pubescens R.Br.		1	na	na	na
Choretrum glomeratum R.Br. var. *glomeratum*		1	na	na	na
Correa reflexa (Labill.) Vent. var. *insularis* Paul G.Wilson		38	na	na	na

Daviesia brevifolia Lindl.		1	na	na	na
Dianella brevicaulis (Ostenf.) G.W.Carr & P.F.Horsfall		12	na	na	na
Dichondra repens J.R.Forst. & G.Forst.		0	0	0	0
Dillwynia sericea A.Cunn.		6	na	na	na
Dodonaea baueri Endl.		0	0	0	0
Dodonaea hexandra F.Muell.		50	na	na	na
Dodonaea viscosa Jacq.		2	na	na	na
Drosera macrantha Endl.		46	na	na	na
Drosera whittakeri Planch.		132	na	na	na
Eucalyptus cneorifolia DC.		187	4.0 ± 1.2	1.8 ± 0.8	T (16) = -1.65, *P* = 0.12
Eucalyptus cosmophylla F.Muell.		136	2.2 ± 1.2	9.6 ± 2.9	T (6) = 2.48, *P* = 0.05
Eutaxia diffusa F.Muell.		0	0	0	0
Eutaxia microphylla (R.Br.) C.H.Wright & Dewar		0	0	0	0
Gonocarpus mezianus (H.Schindl.) Orchard		0	0	0	0
Goodenia varia R.Br.		0	0	0	0
Grevillea ilicifolia (R.Br.) R.Br. subsp. *ilicifolia*		8	na	na	na
Gyrostemon sp.		0	0	0	0
Hibbertia sp.		71	2.6 ± 1.9	1.4 ± 1.2	T (5) = -0.57, *P* = 0.60
Ixodia achillaeoides R.Br. subsp. *alata* (Schltdl.) Copley		0	0	0	0
Juncus pallidus R.Br.		904	17.2 ± 3.4	23.6 ± 4.1	T (6) = 1.21, *P* = 0.27
Juncus subsecundus N.A.Wakef.		242	na	na	na
Lasiopetalum baueri Steetz / L. schulzenii (F.Muell.) Benth.		28	na	na	na
Laxmannia orientalis Keighery		2	na	na	na
Lepidosperma canescens Boeck.		33	na	na	na
Lepidosperma viscidum R.Br.		372	na	na	na
Logania linifolia Schltdl.		0	0	0	0
Logania ovata R.Br.		0	0	0	0
Lythrum hyssopifolia L.		6	na	na	na
Melaleuca gibbosa Labill.		53	na	na	na
Melaleuca lanceolata Otto		72	na	na	na
Melaleuca uncinata R.Br.		138	3.9 ± 1.4	2.1 ± 1.2	T (2) = -0.95, *P* = 0.44
Micrantheum demissum F.Muell.		0	0	0	0
Myoporum sp.		0	0	0	0
Olearia microdisca J.M.Black (E e)		0	0	0	0

Orthrosanthus multiflorus Sweet		0	0	0	0
Patersonia occidentalis R.Br.		16	na	na	na
Pelargonium australe		0	0	0	0
Pimelea stricta Meisn.		3	na	na	na
Pomaderris paniculosa F.Muell. ex Reissek		3	na	na	na
Prostanthera sp.		0	0	0	0
Pultenaea acerosa R.Br. ex Benth.		0	0	0	0
Pultenaea daphnoides J.C.Wendl.		9	na	na	na
Rhagodia candolleana Moq.		8	na	na	na
Rytidosperma sp.		83	6.8 ± 1.1	4.1 ± 1.2	T (2) = -1.55, *P* = 0.26
Schoenus maschalinus Roem. & Schult.		8	na	na	na
Spyridium eriocephalum Fenzl var. *glabrisepalum* J.M.Black (V v)		0	0	0	0
Stackhousia aspericocca Schuch.		9	na	na	na
Stackhousia monogyna auct.non Labill		1	na	na	na
Stylidium armeria (Labill.) Labill		2	na	na	na
Thelymitra sp.		6	na	na	na
Thryptomene ericaea F.Muell.		203	14.0 ± 10.0	2.2 ± 1.5	T (11) = -2.74, *P* = 0.02
Thysanotus patersonii R.Br.		7	na	na	na
Xanthorrhoea semiplana F.Muell. subsp. *tateana* (F.Muell.) Bedford (r)		218	2.9 ± 1.6	3.9 ± 1.7	T (7) = 0.43, *P* = 0.68
All introduced species	20	4700	11.4 ± 5.9	12.4 ± 6.2	T (65) = 0.34, *P* = 0.73
Introduced annuals/biennial	13	2804	13.6 ± 5.7	8.8 ± 4.0	T (59) = -1.31, *P* = 0.20
Aira elegantissima Schur		15	na	na	na
Arctotheca calendula (L.) Levyns		105	4.6 ± 2.3	4.7 ± 4.7	T (5) = 0.00, *P* = 1.00
Avena barbata Pott ex Link		1739	9.8 ± 5.5	3.1 ± 1.9	T (21) = -2.53, *P* = 0.02
Briza minor L.		0	0	0	0
Bromus diandrus Roth		0	0	0	0
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch.		0	0	0	0
Cerastium glomeratum Thuill.		0	0	0	0
Cirsium vulgare (Savi) Ten.		1	na	na	na
Cyperus tenellus L.f.		7	na	na	na
Ehrharta longiflora Sm.		51	na	na	na
Ehrharta villosa (L.f.) Schult.f. ex Schult. & Schult.f.		0	0	0	0
Galium murale (L.) All.		0	0	0	0
Hypochaeris glabra L.		118	4.1 ± 1.6	1.5 ± 0.8	T (7) = -1.47, *P* = 0.18

Isolepis marginata (Thunb.) A.Dietr.		8	na	na	na
Kickxia elatine ssp *crinita*		0	0	0	0
Lagurus ovatus L.		19	na	na	na
Lolium rigidum Gaudin		0	0	0	0
Polygonum aviculare L.		0	0	0	0
Soliva sessilis Ruiz & Pavs		75	na	na	na
Sonchus asper (L.) Hill		0	0	0	0
Sonchus oleraceus L.		2	na	na	na
Trifolium campestre Schreb.		192	9.8 ± 3.8	4.6 ± 1.8	T (7) = -1.39, *P* = 0.21
Trifolium subterraneum L.		0	0	0	0
Vulpia bromoides (L.) Gray		472	13.2 ± 13.2	11.5 ± 11.5	T (7) = 0.00, *P* = 1.00
Introduced perennials	7	1896	10.1 ± 8.7	12.0 ± 10.3	T (26) = 0.54, *P* = 0.60
Asparagus asparagoides (L.) Druce f.		27	na	na	na
Conyza sp.		0	0	0	0
Cynodon dactylon (L.) Pers. var. *dactylon*		1329	23 ± 6.9	33.9 ± 10.1	T (5) = 0.93, *P* = 0.40
Ehrharta calycina Sm.		43	na	na	na
Malva parviflora L.		0	0	0	0
Oxalis pes-caprae L.		67	na	na	na
Romulea rosea (L.) Eckl.		404	9.1 ± 7.7	38.4 ± 29.6	T (3) = 1.79, *P* = 0.17
Senecio pterophorus DC.		2	na	na	na
Solanum nigrum L.		24	1.6 ± 0.8	4.2 ± 1.3	T (2) = 1.63, *P* = 0.24
Taraxacum officinale auct.non F.H.Wigg.		0	0	0	0

Table S5.3 Quantity of plants for native species and groups of native species from *in situ* 1 x 1 m quadrats. Modelled means are given plus or minus standard error. Differences between the disturbance treatments was analysed subject to plants occurring in either a disturbed or undisturbed quadrat pair using generalised linear models. Na, not applicable or insufficient data to calculate statistic.

Species	**Richness**	**Sum**	**Disturbed**	**Undisturbed**	**Significance**
All natives	56	4070	11.8 ± 4.5	11.3 ± 4.1	T (90) = -0.19, *P* = 0.85
Native annuals/biennial	7	240	na	na	na
Centrolepis strigosa (R.Br.) Roem. & Schult.		2	na	na	na
Crassula decumbens Thunb. var. *decumbens*		0	0	0	0
Dysphania pumilio (R.Br.) Mosyakin & Clemants		194	na	na	na
Juncus bufonius L.		0	0	0	0
Lachnagrostis filiformis (G.Forst.) Trin.		4	na	na	na
Lagenophora huegelii Benth.		4	na	na	na
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt		1	na	na	na
Senecio quadridentatus Labill. (r)		9	na	na	na
Wahlenbergia gracilenta Lothian		26	na	na	na
Native perennials	49	3830	16.7 ± 6.4	18.0 ± 7.5	T (81) = 0.36, *P* = 0.72
Acacia sp.		30	na	na	na
Acacia spinescens Benth.		16	na	na	na
Acrotriche serrulata R.Br.		3	na	na	na
Allocasuarina muelleriana (Miq.) L.A.S.Johnson		5	na	na	na
Astroloma conostephioides (Sond.) F.Muell. ex Benth.		0	0	0	0
Astroloma humifusum (Cavs) R.Br.		111	na	na	na
Atriplex cinerea Poir.		2	na	na	na
Austrostipa sp.		451	na	na	na
Baumea juncea (R.Br.) Palla		0	0	0	0
Bertya rotundifolia F.Muell.		4	na	na	na
Callistemon rugulosus (D.F.K.Schltdl. ex Link) DC.		32	na	na	na
Calytrix glaberrima		0	0	0	0
Calytrix tetragona Labill.		56	na	na	na
Carex inversa R.Br.		0	0	0	0
Carpobrotus rossii (Haw.) Schwantes		3	na	na	na
Cassytha pubescens R.Br.		1	na	na	na
Choretrum glomeratum R.Br. var. *glomeratum*		1	na	na	na
Correa reflexa (Labill.) Vent. var. *insularis* Paul G.Wilson		38	na	na	na

Daviesia brevifolia Lindl.		1	na	na	na
Dianella brevicaulis (Ostenf.) G.W.Carr & P.F.Horsfall		12	na	na	na
Dichondra repens J.R.Forst. & G.Forst.		0	0	0	0
Dillwynia sericea A.Cunn.		6	na	na	na
Dodonaea baueri Endl.		0	0	0	0
Dodonaea hexandra F.Muell.		50	na	na	na
Dodonaea viscosa Jacq.		2	na	na	na
Drosera macrantha Endl.		46	na	na	na
Drosera whittakeri Planch.		132	na	na	na
Eucalyptus cneorifolia DC.		187	na	na	na
Eucalyptus cosmophylla F.Muell.		136	na	na	na
Eutaxia diffusa F.Muell.		0	0	0	0
Eutaxia microphylla (R.Br.) C.H.Wright & Dewar		0	0	0	0
Gonocarpus mezianus (H.Schindl.) Orchard		0	0	0	0
Goodenia varia R.Br.		0	0	0	0
Grevillea ilicifolia (R.Br.) R.Br. subsp. *ilicifolia*		8	na	na	na
Gyrostemon sp.		0	0	0	0
Hibbertia sp.		71	na	na	na
Ixodia achillaeoides R.Br. subsp. *alata* (Schltdl.) Copley		0	0	0	0
Juncus pallidus R.Br.		904	15.8 ± 3.3	25.7 ± 4.0	T (6) = 1.87, *P* = 0.11
Juncus subsecundus N.A.Wakef.		242	na	na	na
Lasiopetalum baueri Steetz / L. schulzenii (F.Muell.) Benth.		28	na	na	na
Laxmannia orientalis Keighery		2	na	na	na
Lepidosperma canescens Boeck.		33	na	na	na
Lepidosperma viscidum R.Br.		372			
Logania linifolia Schltdl.		0	0	0	0
Logania ovata R.Br.		0	0	0	0
Lythrum hyssopifolia L.		6	na	na	na
Melaleuca gibbosa Labill.		53	na	na	na
Melaleuca lanceolata Otto		72	na	na	na
Melaleuca uncinata R.Br.		138	na	na	na
Micrantheum demissum F.Muell.		0	0	0	0
Myoporum sp.		0	0	0	0
Olearia microdisca J.M.Black (E e)		0	0	0	0

Orthrosanthus multiflorus Sweet		0	0	0	0
Patersonia occidentalis R.Br.		16	na	na	na
Pelargonium australe		0	0	0	0
Pimelea stricta Meisn.		3	na	na	na
Pomaderris paniculosa F.Muell. ex Reissek		3	na	na	na
Prostanthera sp.		0	0	0	0
Pultenaea acerosa R.Br. ex Benth.		0	0	0	0
Pultenaea daphnoides J.C.Wendl.		9	na	na	na
Rhagodia candolleana Moq.		8	na	na	na
Rytidosperma sp.		83	5.4 ± 1.5	5.2 ± 1.0	T (2) = -0.14, *P* = 0.90
Schoenus maschalinus Roem. & Schult.		8	na	na	na
Spyridium eriocephalum Fenzl var. *glabrisepalum* J.M.Black (V v)		0	0	0	0
Stackhousia aspericocca Schuch.		9	na	na	na
Stackhousia monogyna auct.non Labill		1	na	na	na
Stylidium armeria (Labill.) Labill		2	na	na	na
Thelymitra sp.		6	na	na	na
Thryptomene ericaea F.Muell.		203	na	na	na
Thysanotus patersonii R.Br.		7	na	na	na
Xanthorrhoea semiplana F.Muell. subsp. *tateana* (F.Muell.) Bedford (r)		218	na	na	na
All introduced species	20	4700	10.9 ± 5.6	12.9 ± 6.4	T (65) = 0.74, *P* = 0.46
Introduced annuals/biennial	13	2804	9.3 ± 4.0	12.9 ± 5.7	T (59) = 1.04, *P* = 0.30
Aira elegantissima Schur		15	na	na	na
Arctotheca calendula (L.) Levyns		105	na	na	na
Avena barbata Pott ex Link		1739	5.7 ± 3.3	5.4 ± 3.2	T (21) = -0.12, *P* = 0.91
Briza minor L.		0	0	0	0
Bromus diandrus Roth		0	0	0	0
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch.		0	0	0	0
Cerastium glomeratum Thuill.		0	0	0	0
Cirsium vulgare (Savi) Ten.		1	na	na	na
Cyperus tenellus L.f.		7	na	na	na
Ehrharta longiflora Sm.		51	na	na	na
Ehrharta villosa (L.f.) Schult.f. ex Schult. & Schult.f.		0	0	0	0
Galium murale (L.) All.		0	0	0	0
Hypochaeris glabra L.		118	na	na	na

Isolepis marginata (Thunb.) A.Dietr.		8	na	na	na
Kickxia elatine ssp *crinita*		0	0	0	0
Lagurus ovatus L.		19	na	na	na
Lolium rigidum Gaudin		0	0	0	0
Polygonum aviculare L.		0	0	0	0
Soliva sessilis Ruiz & Pavs		75	na	na	na
Sonchus asper (L.) Hill		0	0	0	0
Sonchus oleraceus L.		2	na	na	na
Trifolium campestre Schreb.		192	na	na	na
Trifolium subterraneum L.		0	0	0	0
Vulpia bromoides (L.) Gray		472	11.1 ± 3.7	13.6 ± 13.6	T (7) = 0.00, *P* = 1.00
Introduced perennials	7	1896	12.2 ± 10.6	9.9 ± 8.4	T (26) = -0.63, *P* = 0.53
Asparagus asparagoides (L.) Druce f.		27	na	na	na
Conyza sp.		0	0	0	0
Cynodon dactylon (L.) Pers. var. *dactylon*		1329	25.8 ± 7.9	30.2 ± 8.7	T (5) = 0.38, *P* = 0.72
Ehrharta calycina Sm.		43	na	na	na
Malva parviflora L.		0	0	0	0
Oxalis pes-caprae L.		67	na	na	na
Romulea rosea (L.) Eckl.		404	na	na	na
Senecio pterophorus DC.		2	na	na	na
Solanum nigrum L.		24	na	na	na
Taraxacum officinale auct.non F.H.Wigg.		0	0	0	0

Table S6.1 Richness of species and groups of species from *in situ* 1 x 1 m quadrats. Modelled means are given plus or minus standard error. Differences between the fire treatments was analysed subject to plants occurring in either a burnt or unburnt quadrat pair using generalised linear models. Na, not applicable or insufficient data to calculate statistic.

Species	**Richness**	**Burnt**	**Unburnt**	**Significance**
All Natives	56	3.1 ± 0.3	2.9 ± 0.3	T (91) = -0.66, *P* = 0.51
Native perennials	49	3.1 ± 0.5	3.5 ± 0.5	T (82) = 0.91, *P* = 0.37
Native annuals/biennials	7	1.2 ± 0.3	1.3 ± 0.4	T (17) = 0.17, *P* = 0.87
All introduced	20	2.2 ± 0.3	2.4 ± 0.3	T (66) = 0.58, *P* = 0.56
Introduced perennials	7	1.3 ± 0.3	1.2 ± 0.3	T (27) = -0.26, *P* = 0.80
Introduced annuals/biennials	13	1.7 ± 0.3	1.6 ± 0.3	T (60) = -0.33, *P* = 0.74

Table S6.2 Richness of species and groups of species from *in situ* 1 x 1 m quadrats. Modelled means are given plus or minus standard error. Differences between the fence treatments was analysed subject to plants occurring in either a fenced or unfenced quadrat pair using generalised linear models. Na, not applicable or insufficient data to calculate statistic.

Species	**Richness**	**Fenced**	**Unfenced**	**Significance**
All natives	56	3.3 ± 0.4	2.7 ± 0.3	T (66) = -0.6, *P* = 0.55
Native perennials	49	4.0 ± 0.6	2.7 ± 0.4	T (82) = -3.06, *P* = < 0.01
Native annuals/biennials	7	na	na	na
All introduced	20	2.4 ± 0.3	2.2 ± 0.3	T (66) = -0.6, *P* = 0.55
Introduced perennials	7	1.3 ± 0.3	1.2 ± 0.3	T (27) = -0.21, *P* = 0.83
Introduced annuals/biennials	13	1.5 ± 0.2	1.7 ± 0.3	T (60) = 0.68, *P* = 0.50

Table S6.3 Richness of species and groups of species from *in situ* 1 x 1 m quadrats. Modelled means are given plus or minus standard error. Differences between the disturbance treatment was analysed subject to plants occurring in either a disturbed or undisturbed quadrat pair using generalised linear models. Na, not applicable or insufficient data to calculate statistic.

Species	**Richness**	**Disturbed**	**Undisturbed**	**Significance**
All natives	56	3.1 ± 0.4	2.9 ± 0.3	T (91) = -0.48, *P* = 0.63
Native perennials	49	3.4 ± 0.5	3.2 ± 0.5	T (82) = -0.44, *P* = 0.66
Native annuals/biennials	7	na	na	na
All introduced	20	2.3 ± 0.3	2.3 ± 0.3	T (66) = 0.03, *P* = 0.98
Introduced perennials	7	1.3 ± 0.3	1.3 ± 0.3	T (27) = 0.03, *P* = 0.97
Introduced annuals/biennials	13	1.7 ± 0.3	1.6 ± 0.3	T (60) = -0.09, *P* = 0.93

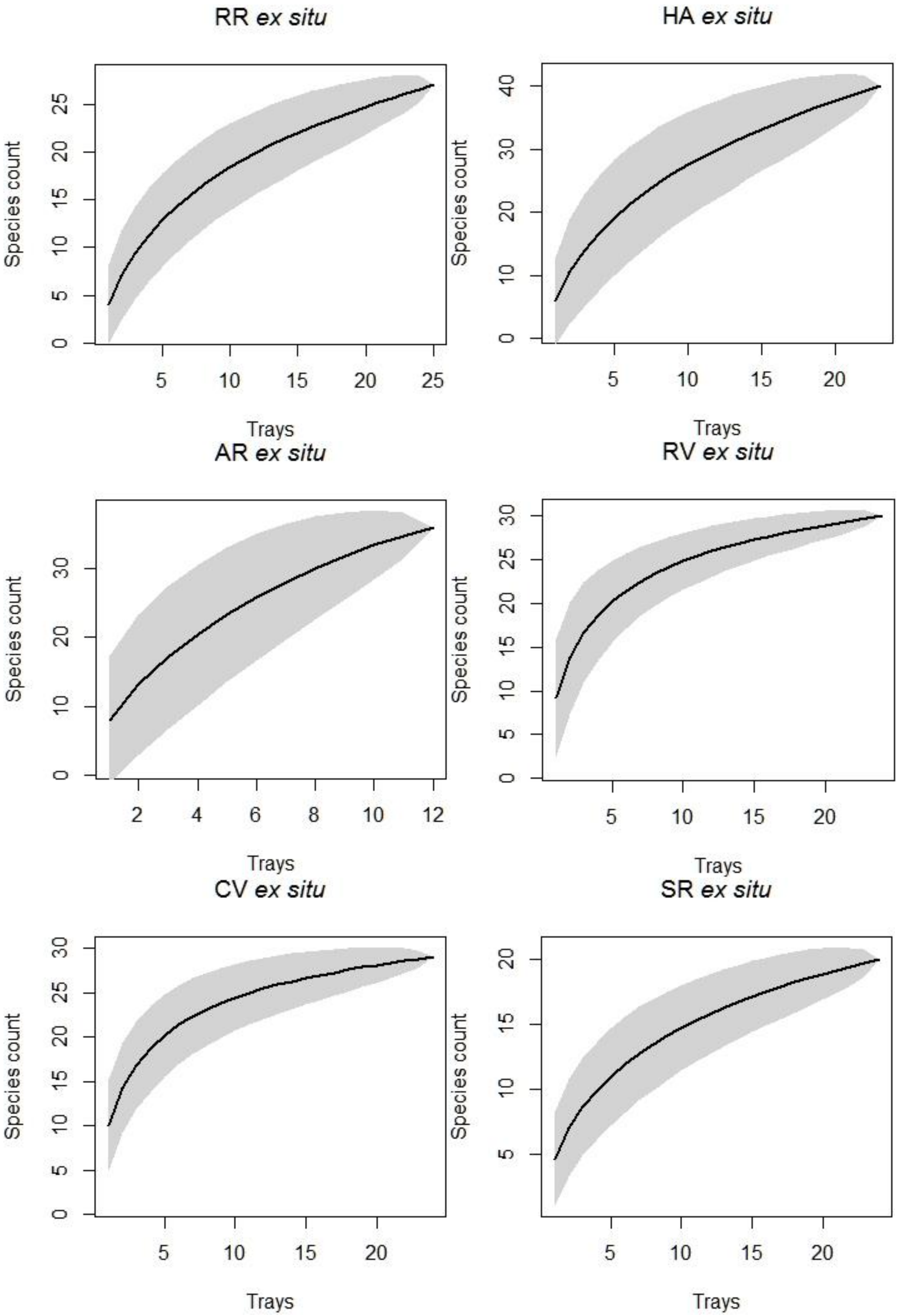

Figure S7.1 Rarefaction curves showing the relationship between counts of species and increased sampling effort within ***ex situ*** trays and different sites (AR ="Airport Remnant^{H}", CV ="Cygnet Revegetation^{H}", HA ="Heritage Agreement^{H}", RR ="Redbanks Road Remnant^{D} ", RV ="Roadside Vegetation^{H}", and SR ="Spring Road Remnant^{D}”). Shaded areas represent 95 % confidence intervals. ^{H}Healthy; ^{D}Degraded.

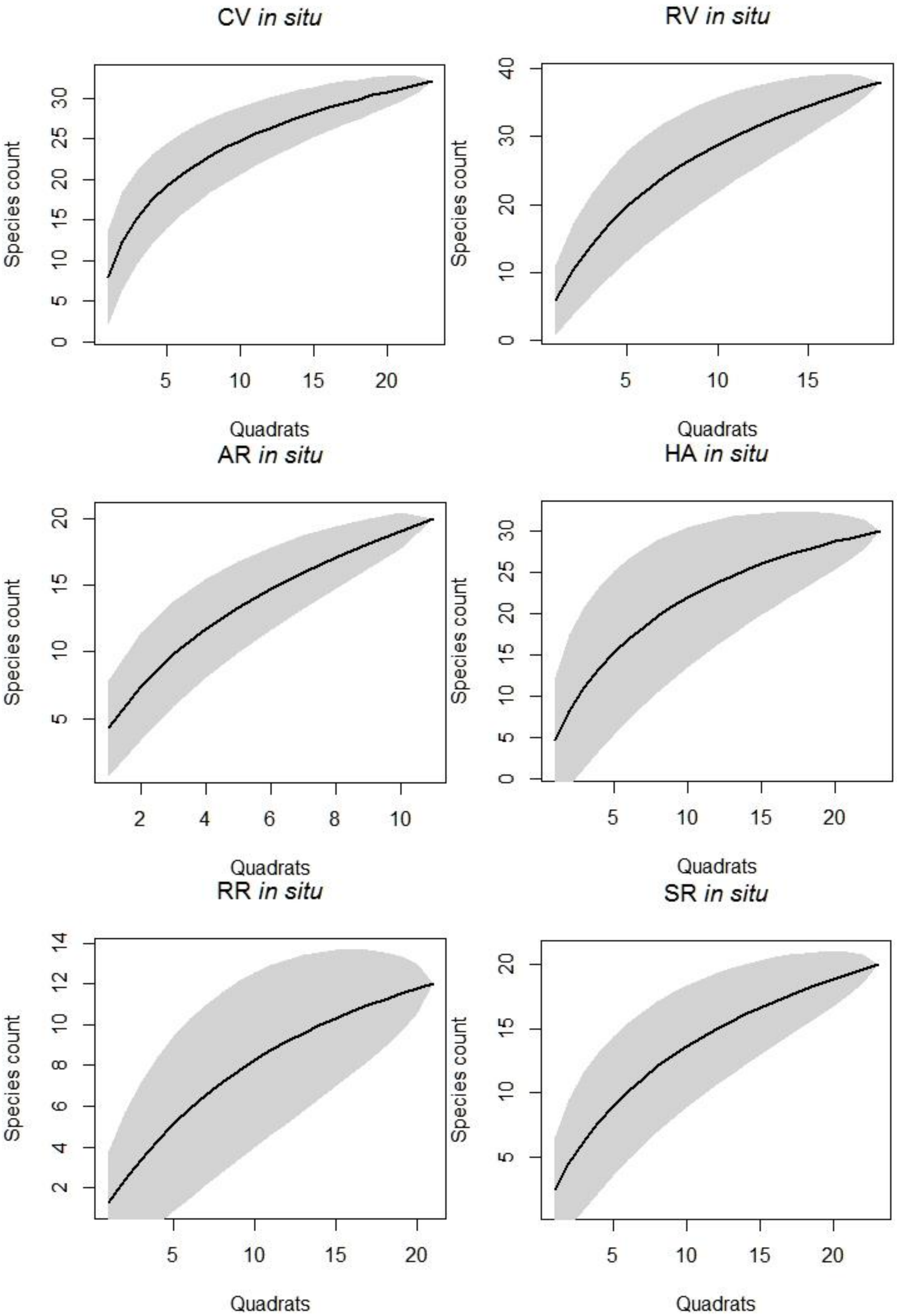

Figure S7.2 Rarefaction curves showing the relationship between counts of species and increased sampling effort within ***in situ*** trays and different sites (AR ="Airport Remnant^{H}", CV ="Cygnet Revegetation^{H}", HA ="Heritage Agreement^{H}", RR ="Redbanks Road Remnant^{D} ", RV ="Roadside Vegetation^{H}", and SR ="Spring Road Remnant^{D}”). Shaded areas represent 95 % confidence intervals. ^{H}Healthy; ^{D}Degraded.

Table S8.1 Comparison between quantity of seedlings for species and groups between *in situ* 1 x 1 m quadrats and *ex situ* 35 × 30 cm trays. Modelled means are given plus or minus standard error. Table utilises a database subset which excludes data from the last *in situ* survey date. Each extrapolated *ex situ* mean is a 9.5-fold increase of the *ex situ* mean counterparts.

	In situ			*Ex situ*			
Species	Sum	n	Mean ± SE	Sum	n	Mean ± SE	Extrapolated (Mean ± SE)
All Species	8770	121	24.1 ± 10.5	7025	242	13.5 ± 6.1	133.0 ± 60.3
All natives	4070	89	15.7 ± 7.3	5962	240	9.6 ± 4.7	99.1 ± 49.3
All native annuals/biennials	240	51	1.3 ± 0.5	2364	212	6.1 ± 2.7	59.9 ± 28.2
Dysphania pumilio (R.Br.) Mosyakin & Clemants	164	7	61.8 ± 21.9	46	28	0.4 ± 0.2	9.3 ± 10.7
All native perennials	3830	66	16.9 ± 7.2	3154	214	2.4 ± 1.2	33.4 ± 20.0
Hibbertia sp.	63	9	2.7 ± 1.8	52	30	1.1 ± 0.8	29.4 ± 46.9
Juncus pallidus R.Br.	217	10	1.6 ± 1.3	2737	108	3.7 ± 3.8	49.3 ± 64.5
Rytidosperma sp.	61	10	4.4 ± 1.7	64	54	0.4 ± 0.2	4.0 ± 3.7
Thryptomene ericaea F.Muell.	128	11	10.9 ± 4.8	80	66	0.7 ± 0.5	11.4 ± 12.6
All introduced	4700	85	11.1 ± 4.3	1507	219	4.9 ± 2.1	45.7 ± 20.9
All introduced annuals/biennials	2804	78	11.0 ± 4.2	1400	206	3.3 ± 1.4	30.8 ± 13.5
Arctotheca calendula (L.) Levyns	88	11	4.7 ± 2.6	120	62	0.6 ± 0.4	3.5 ± 3.8
Avena barbata Pott ex Link	933	23	21.8 ± 12.8	392	102	1.4 ± 0.9	15.8 ± 12.7
Hypochaeris glabra L.	36	9	0.6 ± 0.9	13	32	0.1 ± 0.1	1.2 ± 1.5
All introduced perennials	1896	29	17.7 ± 8.9	89	88	0.7 ± 0.4	11.2 ± 9.1
Cynodon dactylon (L.) Pers. var. *dactylon*	725	12	44.1 ± 11.9	49	34	0.9 ± 0.4	48.6 ± 29.3
Solanum nigrum L.	24	8	5.3 ± 3.3	26	40	0.5 ± 0.4	3.8 ± 5.1

Table S8.2 Comparison between quantity of seedling between *in situ* 1 x 1 m quadrats and *ex situ* 35 × 30 cm trays. Means are given plus or minus standard error. Table utilises a database subset which excludes data from the last *in situ* survey date. Each extrapolated *ex situ* mean is a 9.5-fold increase of the *ex situ* mean counterparts. Significant differences are given between both *in situ* means versus *ex situ* means and *in situ* means versus extrapolated *ex situ* means.

Species	***In situ* vs *ex situ***	***In situ* vs extrapolated (*ex situ*)**
All species	T (355) = -3.31, *P* = 0.01	T (355) = 8.68, *P* = < 0.01
All natives	T (321) = -2.46, *P* = 0.01	T (321) = 7.90, *P* = < 0.01
Native annuals/biennials	T (255) = 4.98, *P* = < 0.01	T (255) = 10.1, *P* = < 0.01
Dysphania pumilio (R.Br.) Mosyakin & Clemants	T (28) = -7.24, *P* = < 0.01	T (27) = -0.88, *P* = 0.38
Native perennials	T (272) = -6.36, *P* = < 0.01	T (272) = 0.39, *P* = 0.15
Hibbertia sp.	T (32) = -2.02, *P* = 0.05	T (31) = 1.15, *P* = 0.26
Juncus pallidus R.Br.	T (110) = 0.81, *P* = 0.42	T (110) = 3.08, *P* = < 0.01
Rytidosperma sp.	T (60) = -3.90, *P* = < 0.01	T (60) = 0.02, *P* = 0.98
Thryptomene ericaea F.Muell.	T (69) = -3.03, *P* = <0.01	T (69) = 0.06, *P* = 0.95
All introduced	T (295) = -2.86, *P* = < 0.01	T (295) = 0.35, *P* = < 0.01
Introduced annuals/biennials	T (276) = -4.80, *P* = < 0.01	T (276) = 3.39, *P* = < 0.01
Arctotheca calendula (L.) Levyns	T (65) = -2.86, *P* = < 0.01	T (65) = -0.42, *P* = 0.67
Avena barbata Pott ex Link	T (118) = -4.74, *P* = < 0.01	T (118) = -0.60, *P* = 0.55
Hypochaeris glabra L.	T (34) = -6.03, *P* = <0.01	T (33) = -0.65, *P* = 0.52
Introduced perennials	T (109) = -6.73, *P* = < 0.01	T (109) = -0.99, *P* = 0.33
Cynodon dactylon (L.) Pers. var. *dactylon*	T (39) = -9.82, *P* = < 0.01	T (38) = -0.70, *P* = 0.49
Solanum nigrum L.	T (40) = -2.88, *P* = < 0.01	T (40) = -0.95, *P* = 0.35

Table S9. Comparison between the richness of different groups between *in situ* 1 x 1 m quadrats and *ex situ* 35 × 30 cm trays. Modelled means are given plus or minus standard error. Table utilises a database subset which excludes data from the last *in situ* survey date. Significant differences are given between both *in situ* means versus *ex situ* means and *in situ* means versus extrapolated *ex situ* means.

	In situ			***Ex situ***			
Species	**Sum**	**n**	**Mean ± SE**	**Sum**	**n**	**Mean ± SE**	**Significance**
All species	513	121	3.8 ± 0.7	1088	242	3.6 ± 0.7	T (355) = -0.78, *P* = 0.44
All natives	241	89	2.4 ± 0.4	679	240	2.1 ± 0.4	T (322) = -1.00, *P* = 0.32
Native annuals/biennials	21	51	0.3 ± 0.1	378	212	1.7 ± 0.5	T (256) = 5.06, *P* = < 0.01
Native perennials	235	66	2.8 ± 0.4	301	214	0.9 ± 0.2	T (273) = -9.48, *P* = < 0.01
All introduced	141	85	1.3 ± 0.3	409	221	1.4 ± 0.4	T (299) = 0.38, *P* = 0.70
Introduced annuals/biennials	92	78	0.9 ± 0.2	371	206	1.2 ± 0.3	T (277) = 2.07, *P* = 0.40
Introduced perennials	39	29	1.4 ± 0.2	37	88	0.4 ± 0.1	T (110) = -4.10, *P* = < 0.01

Table S10. The fire response of species detected during the study. Information sourced from an unpublished Department for Environment and Water database, the Electronic Flora of South Australia at flora.sa.gov.au, expert advice, and observations during the experiment.

Species	**Fire Response**	**Seed storage/resprouting mechanism**
All Natives		
All Native Annuals/Biennial		
Centrolepis strigosa (R.Br.) Roem. & Schult.	Sr	Transient Soil
Crassula decumbens Thunb. var. decumbens	S	Transient Soil
Dysphania pumilio (R.Br.) Mosyakin & Clemants	S^{A}	Transient Soil
Juncus bufonius L.	S^{A}	Transient Soil
Lachnagrostis filiformis (G.Forst.) Trin.	Rs	Rhizome
Lagenifera huegelii auct.non Benth.	Rs^{A}	Basal/Persistent Soil
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt	S	Persistent Soil
Senecio quadridentatus Labill. (r)	S	Persistent Soil
Wahlenbergia gracilenta Lothian	S	Persistent Soil
All Native Perennials		
Acacia sp.	Sr^{A}	Persistent Soil
Acacia spinescens Benth.	Sr	Persistent Soil
Acrotriche serrulata R.Br.	Rs	Lignotuber
Allocasuarina muelleriana (Miq.) L.A.S.Johnson	Sr	Canopy
Astroloma conostephioides (Sond.) F.Muell. ex Benth.	Rs^{A}	Basal/Persistent Soil^{A}
Astroloma humifusum (Cavs) R.Br.	Rs	Lignotuber
Atriplex cinerea Poir.	RS	Basal/Persistent Soil
Austrostipa sp.	RS^{A}	Basal/Persistent Soil
Baumea juncea (R.Br.) Palla	Rs	Rhizome
Bertya rotundifolia F.Muell.	S	Persistent Soil
Callistemon rugulosus (D.F.K.Schltdl. ex Link) DC.	Rs	Lignotuber/Serotinous canopy
Calytrix glaberrima (F.Muell.) Craven	SR	Basal/Persistent Soil
Calytrix tetragona Labill.	SR	Basal/Persistent Soil
Carex inversa R.Br.	Rs^{A}	Basal/Persistent Soil
Carpobrotus rossii (Haw.) Schwantes	S	Persistent Soil
Cassytha pubescens R.Br.	S	Persistent Soil
Choretrum glomeratum R.Br. var. glomeratum	S	Persistent Soil^{A}
Correa reflexa (Labill.) Vent. var. *insularis* Paul G.Wilson	RS^{A}	Basal/Persistent Soil
Daviesia brevifolia Lindl.	Rs	Lignotuber/Persistent Soil
Dianella brevicaulis (Ostenf.) G.W.Carr & P.F.Horsfall	Rs	Rhizome/Persistent Soil
Dichondra repens J.R.Forst. & G.Forst.	Sr	Persistent Soil/Basal^{A}
Dillwynia sericea A.Cunn.	Sr	Basal/Persistent Soil
Dodonaea baueri Endl.	RS^{A}	Basal/Persistent Soil
Dodonaea hexandra F.Muell.	RS^{A}	Basal/Persistent Soil
Dodonaea viscosa Jacq.	RS^{A}	Basal/Persistent Soil
Drosera macrantha Endl.	Rs^{A}	Tuber/Persistent Soil
Drosera whittakeri Planch.	Rs^{A}	Tuber/Persistent Soil
Eucalyptus cneorifolia DC.	Rs	Lignotuber/Serotinous canopy
Eucalyptus cosmophylla F.Muell.	Rs	Lignotuber/Serotinous canopy

Eutaxia diffusa F.Muell.	Sr	Persistent Soil
Eutaxia microphylla (R.Br.) C.H.Wright & Dewar	Sr	Persistent Soil
Gonocarpus mezianus (H.Schindl.) Orchard	Sr	Persistent Soil/Rhizome
Goodenia varia R.Br.	Sr	Persistent Soil/Basal
Grevillea ilicifolia (R.Br.) R.Br. subsp. *ilicifolia*	Rs	Basal/Persistent Soil
Gyrostemon sp.	Sr^{A}	Persistent Soil/Basal
Hibbertia sp.	Sr^{A}	Basal/Persistent Soil
Ixodia achillaeoides R.Br. subsp. *alata* (Schltdl.) Copley	Sr^{A}	Basal/Persistent Soil^{A}
Juncus pallidus R.Br.	Rs^{A}	Rhizome/Transient soil
Juncus subsecundus N.A.Wakef.	Rs^{A}	Rhizome/Transient soil
Lasiopetalum baueri Steetz / L. schulzenii (F.Muell.) Benth.	SR^{A}	Basal/Persistent Soil
Laxmannia orientalis Keighery	S^{A}	Persistent Soil
Lepidosperma canescens Boeck.	Rs^{A}	Rhizome/Persistent Soil
Lepidosperma viscidum R.Br.	Rs	Basal/Persistent Soil
Logania linifolia Schltdl. (r)	SR^{A}	Basal/Persistent Soil
Logania ovata R.Br.	SR^{A}	Basal/Persistent Soil
Lythrum hyssopifolia L.	S	Persistent Soil^{A}
Melaleuca gibbosa Labill.	Rs	Lignotuber/Serotinous canopy
Melaleuca lanceolata Otto	Rs	Lignotuber/Serotinous canopy
Melaleuca uncinata R.Br.	Rs	Lignotuber/Serotinous canopy
Micrantheum demissum F.Muell.	Sr^{A}	Basal/Persistent Soil
Myoporum sp.	Sr^{A}	Persistent Soil/Basal
Olearia microdisca J.M.Black (E e e)	Sr^{A}	Persistent Soil/Basal
Orthrosanthus multiflorus Sweet	Rs^{A}	Rhizome/Persistent Soil^{A}
Patersonia occidentalis R.Br.	Rs^{A}	Rhizome/Persistent Soil
Pelargonium australe	Rs	Rhizome/Persistent Soil^{A}
Pimelea stricta Meisn.	S	Persistent Soil
Pomaderris paniculosa F.Muell. ex Reissek	S	Persistent Soil
Prostanthera sp.	S	Persistent Soil
Pultenaea acerosa R.Br. ex Benth.	S^{A}	Persistent Soil
Pultenaea daphnoides J.C.Wendl.	S	Persistent Soil
Rhagodia candolleana Moq.	S	Transient Soil
Rytidosperma sp.	Rs^{A}	Rhizome/Persistent Soil
Schoenus maschalinus Roem. & Schult.	Rs	Basal/Persistent Soil
Spyridium eriocephalum Fenzl var. *glabrisepalum* J.M.Black (V v v)	Sr^{A}	Persistent Soil/Basal
Stackhousia aspericocca Schuch.	Rs^{A}	Rhizome/Persistent Soil
Stackhousia monogyna auct.non Labill	SR	Persistent Soil/Basal
Stylidium armeria (Labill.) Labill	Rs^{A}	Basal/Persistent Soil
Thelymitra sp.	Rs^{A}	Rhizome/Persistent Soil
Thryptomene ericaea F.Muell.	Sr^{A}	Persistent Soil/Basal
Thysanotus patersonii R.Br.	Rs	Rhizome/Persistent Soil
Xanthorrhoea semiplana F.Muell. subsp. *tateana* (F.Muell.) Bedford (r)	R	Basal
All introduced species		
All introduced annuals/biennial		
Aira elegantissima Schur	S	Transient Soil
Arctotheca calendula (L.) Levyns	S	Transient Soil

Avena barbata Pott ex Link	S	Transient Soil
Briza minor L.	S	Transient Soil
Bromus diandrus Roth	S	Transient Soil
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch.	S	Transient Soil
Cerastium glomeratum Thuill.	S	Transient Soil[A]
Cirsium vulgare (Savi) Ten.	Sr	Transient Soil/Basal[A]
Cyperus tenellus L.f.	S	Transient Soil
Ehrharta longiflora Sm.	S	Transient Soil
Ehrharta villosa (L.f.) Schult.f. ex Schult. & Schult.f.	S[A]	Transient Soil
Galium murale (L.) All.	Sr	Transient Soil/basal
Hypochaeris glabra L.	S	Transient Soil[A]
Isolepis marginata (Thunb.) A.Dietr.	Rs	Rhizome/Transient soil
Kickxia elatine ssp *crinita*	S	Transient Soil[A]
Lagurus ovatus L.	Sr[A]	Transient Soil/Basal[A]
Lolium rigidum Gaudin	S	Transient Soil[A]
Polygonum aviculare L.	S[A]	Transient Soil[A]
Soliva sessilis Ruiz & Pavs	Sr[A]	Transient Soil/Basal[A]
Sonchus asper (L.) Hill	S	Transient Soil[A]
Sonchus oleraceus L.	Sr	Transient Soil/Basal[A]
Trifolium campestre Schreb.	S	Transient Soil[A]
Trifolium subterraneum L.	S[A]	Transient Soil[A]
Vulpia bromoides (L.) Gray	S	Transient Soil[A]
All introduced perennials		
Asparagus asparagoides (L.) Druce f.	Rs	Rhizome/Transient soil
Conyza sp.	S	Transient Soil[A]
Cynodon dactylon (L.) Pers. var. *dactylon*	Rs	Rhizome/Transient soil
Ehrharta calycina Sm.	Rs	Basal/Transient soil
Malva parviflora L.	S	Transient Soil[A]
Oxalis pes-caprae L.	Rs	Rhizome/Transient soil
Romulea rosea (L.) Eckl.	Rs	Rhizome/Transient soil
Senecio pterophorus DC.	S	Transient soil
Solanum nigrum L.	S	Persistent Soil
Taraxacum officinale auct.non F.H.Wigg.	SR	Basal/Transient soil

[A] The fire response or seed storage/resprouting mechanism has been assumed based on the response a species in the same genus or per observations; Fire response is given as R = primarily resprouts, S = primarily recovers from seeds, Rs = primarily resprouts but known to recover from seed, Sr = primarily recovers from seed but has been known to resprout; Seed storage or resprouting mechanism lists the primary response post fire as observed in the field or as identified in government fire response databases (J. Trezise pers. obs., 2020; Abley 2014; Kenny *et al.* 2014).

Table S11. Examples of the abundance and richness of soil seed banks and plant survival from the literature where at least two paired methods are utilised. Abundance estimates for seed enumeration are given as the number of seeds per meter^{-2} unless otherwise specified. Abundance estimates for emergence techniques are given as seedlings per meter^{-2}. However, for enumeration and emergence methods, richness values are given as the total number of species detected (as richness does not scale linearly and therefore could not be standardised).

Plant community/species	**Treatment**	**Abundance**	**Richness**	**Source**
Seed enumeration				
Annually ploughed field, Michigan, USA	Washed; 0-2 cm depth	880 m^{-2}	na	(Gross 1990)
Semi-arid ephemeral wetlands, NSW, Australia	Washed; 0-5 cm depth;	97 100g soil^{-1}	na	(Price *et al.* 2010)
Wetlands, North Dakota, USA	Washed; 0-5 cm depth	706 m$^{-2\dagger}$	17	(Poiani and Johnson 1988)
Annual grasses, non-tilled agricultural fields, Ohio USA	Washed; 0-7.5 cm depth	8900 m^{-2}	na	(Cardina and Sparrow 1996)
Fire-prone grassland, Bariloche, Patagonia	0-10 cm depth; sodium chloride wash	9941 m^{-2}	8	(Gonzalez and Ghermandi 2012)
Soil deposits, Mount Usu volcano, Japan	0-10 cm depth; washed	1702 m$^{-2\dagger}$	30	(Ishikawa-Goto and Tsuyuzaki 2004)
***Ex situ* seedling emergence**				
Annually ploughed field, Michigan, USA	Washed; 0-2 cm depth; cold-stratification	4880 m^{-2}	na	(Gross 1990)
Semi-arid ephemeral wetlands, NSW, Australia	Washed; 0-2 cm depth;	94 100g soil^{-1}	na	(Price *et al.* 2010)
Wetlands, North Dakota, USA	0-5 cm depth	1177 m$^{-2\dagger}$	19	(Poiani and Johnson 1988)
Annual grasses, non-tilled agricultural fields, Ohio USA	0-7.5 cm depth	55200 m^{-2}	na	(Cardina and Sparrow 1996)
Fire-prone grassland, Bariloche, Patagonia	0-10 cm depth; cold-stratification	2493 m^{-2}	10	(Gonzalez and Ghermandi 2012)
Soil deposits, Mount Usu volcano, Japan	0-10 cm depth	659 m$^{-2\dagger}$	23	(Ishikawa-Goto and Tsuyuzaki 2004)
Weeds only, agriculture field, Bacabal, Brazil	0-3 cm depth	3206 m^{-2}	50	(Mesquita *et al.* 2013)
Weeds only, agriculture field, Lago Verde County, Brazil	0-3 cm depth	372 m^{-2}	29	(Mesquita *et al.* 2015)
Weeds only, agriculture field	0-15 cm depth	2721 m^{-2}	33	(Akter *et al.* 2018b)
Mallee-heath, eastern Kangaroo Island, Australia	0-5 cm depth	371 m$^{-2\dagger}$	86	(Rawson *et al.* 2013)‡
Mallee-heath, eastern Kangaroo Island, Australia	0-5 cm depth	133 m^{-2}	79	Chapter 2
***In situ* seedling emergence**				
Annual grasses, non-tilled agricultural fields, Ohio USA		14100 m^{-2}	na	(Cardina and Sparrow 1996)
Weeds only, agriculture field, Bacabal, Brazil		653 m^{-2}	34	(Mesquita *et al.* 2013)
Weeds only, agriculture field, Lago Verde County, Brazil		183 m^{-2}	29	(Mesquita *et al.* 2015)
Weeds only, agriculture field		700 m^{-2}	31	(Akter *et al.* 2018b)

Mallee-heath, eastern Kangaroo Island, Australia		24 m^{-2}	76	Chapter 2
Mallee-heath, eastern Kangaroo Island, Australia	Low intensity fire	22 m$^{-2\dagger}$	13	(Taylor 2019)[‡]
Mallee-heath, eastern Kangaroo Island, Australia	High intensity fire	41 m$^{-2\dagger}$	13	(Taylor 2019)[‡]
Mallee-heath, eastern Kangaroo Island, Australia	Unburnt control	4 m$^{-2\dagger}$	4	(Taylor 2019)[‡]
***In situ* monitoring of seedling survival**				
Sclerophyll shrubland, Ku-ring-gai Chase National Park, Australia	Survey 6 months after fire	1358 seedlings total	na	(Moles and Westoby 2004)
Sclerophyll shrubland, Ku-ring-gai Chase National Park, Australia	Survey at 1 year after fire	577 seedlings total	na	(Moles and Westoby 2004)
Eucalyptus species, Wyperfeld National Park, Australia	Survey 2 months after fire	1 m$^{-2\dagger}$	na	(Wellington and Noble 1985)
Eucalyptus species, Wyperfeld National Park, Australia	Survey 2 years after fire	0.25 m$^{-2\dagger}$	na	(Wellington and Noble 1985)
Banksia woodland, Forrestdale, Australia	Survey 1 year after fire	365 m$^{-2\dagger}$	na	(Roche *et al.* 1998)
Banksia woodland, Forrestdale, Australia	Survey after 2 years after fire	68 m$^{-2\dagger}$	na	(Roche *et al.* 1998)

[†] = reported value has been extrapolated to m^{-2}; na = value was not reported or is not compatible to other literature presented here. [‡] Studies are affiliated and utilise the same sites.

Appendix 2. Supplementary material for Chapter 3

Table S1.1 Frequency of native species that germinated from soil collected from the 94 Fleurieu Peninsula swamp quadrats. Two comparisons are presented: 1) seed germinating following heat plus smoke treatment (HS), compared with no treatment (C); and 2) present in the above ground vegetation (A) prior to sampling soil and emerging in at least one of the two paired sample trays (S).

Family	Species (Conservation status†)	Life-history & lifeform class‡	Number of samples where species recorded (N=94)			
			HS	C	A	S
Only germinated from heat plus smoke treated (HS) soil						
LEGUMINOSAE	*Acacia verticillata* C. L. Willdenow (*nt*)	PS	4	0	6	4
ONAGRACEAE	*Epilobium billardierianum* L., Sp. Pl. (*nt*)	AFo	3	0	1	3
GRAMINEAE	*Eragrostis tenellula* (Kunth) Steud.	AG	1	0	1	1
MYRTACEAE	*Eucalyptus ovata* Labill. (*vu*)	PT	2	0	1	2
COMPOSITAE	*Olearia glandulosa* (Labill.) Benth. (v *en*)	PS	1	0	0	1
Only germinated from untreated (C) soil (and not heat plus smoke treated (HS) soil)						
RUBIACEAE	*Asperula conferta* Hook.f (*ra*)	PFo	0	1	0	1
BLECHNACEAE	*Blechnum minus* (R.Br.) Ettingsh (*nt*)	PFe	0	3	1	3
JUNCACEAE	*Juncus caespiticius* E.Mey. (*nt*)	AGm	0	3	0	3
COMPOSITAE	*Lagenophora huegelii* Benth.	PFo	0	1	1	1
Germinated from both heat plus smoke treated (HS) & control (C) soils						
LEGUMINOSAE	*Acacia provincialis* A.Camus	PS	16	17	15	25
CYPERACEAE	*Baumea juncea* (R.Br.) Palla	PGm	45	43	8	60
CYPERACEAE	*Baumea rubiginosa* (Spreng.) Boeckeler (*ra*)	PGm	14	16	23	23
CYPERACEAE	*Baumea tetragona* (Labill.) S.T.Blake (*nt*)	PGm	6	8	21	10
CALLITRICHACEAE	*Callitriche umbonata* Hegelm	PFo	3	2	0	4
CYPERACEAE	*Carex appressa* R.Br.	PGm	5	6	1	8
UMBELLIFERAE	*Centella cordifolia* (Hook.f.) Nannf. (*ra*)	PFo	6	7	1	11
CENTROLEPIDACEAE	*Centrolepis aristata* (R.Br.) Roem. & Schult.	AGm	1	2	1	2
CENTROLEPIDACEAE	*Centrolepis fascicularis* Labill. (*vu*)	AGm	22	22	1	34
CYPERACEAE	*Cyperus tenellus* L.f.	AGm	47	40	3	55
DROSERACEAE	*Drosera binata* Labill. (r *vu*)	AFo	5	1	1	5
DROSERACEAE	*Drosera pygmaea* DC (*nt*)	AFo	1	1	1	2
RESTIONACEAE	*Empodisma minus* (Hook.f.) L.A.S.Johnson & D.F.Cutler (*ra*)	PGm	27	22	6	35
COMPOSITAE	*Euchiton collinus* Cass	PFo	2	6	1	7

CYPERACEAE	*Gahnia sieberiana* Kunth (*nt*)	PGm	14	13	19	21
HALORAGACEAE	*Gonocarpus micranthus* Thunb. (r *vu*)	PFo	20	17	1	31
GOODENIACEAE	*Goodenia ovata* Sm.	PS	6	4	0	6
SCROPHULARIACEAE	*Gratiola peruviana* L.	PFo	8	10	1	15
DILLENIACEAE	*Hibbertia tenuis* Toelken & R.J.Bates (CR e *cr*)	PS	6	1	17	7
GUTTIFERAE	*Hypericum japonicum* Thunb. (r *vu*)	AFo	2	1	0	2
CYPERACEAE	*Isolepis cernua* (Vahl) Roem. & Schult.	AGm	12	20	0	24
CYPERACEAE	*Isolepis inundata* R.Br.	AGm	52	51	1	68
JUNCACEAE	*Juncus bufonius* L.	AGm	43	45	0	59
JUNCACEAE	*Juncus planifolius* R.Br. (*nt*)	PGm	58	56	3	72
MYRTACEAE	*Leptospermum continentale* Joy Thomps.	PS	7	10	19	13
UMBELLIFERAE	*Lilaeopsis polyantha* (Gand.) H.Eichler (*vu*)	PFo	2	1	1	2
CAMPANULACEAE	*Lobelia anceps* L.f.	PFo	14	8	3	18
LYTHRACEAE	*Lythrum hyssopifolia* L.	AFo	5	6	1	10
HALORAGACEAE	*Myriophyllum amphibium* Labill. (r *vu*)	PFo	3	3	1	6
IRIDACEAE	*Patersonia occidentalis* R.Br. (*ra*)	PGm	2	3	8	5
GRAMINEAE	*Poa labillardieri* Steud. (*nt*)	PG	24	26	9	34
LEGUMINOSAE	*Pultenaea dentata* Labill. (r *en*)	PS	1	1	0	1
CYPERACEAE	*Schoenus apogon* Roem. & Schult.	AGm	1	1	4	2
CYPERACEAE	*Schoenus maschalinus* Roem. & Schult. (*vu*)	AGm	26	23	2	39
COMPOSITAE	*Senecio picridioides* (Turcz.) M.E.Lawr.	AFo	3	2	1	4
EPACRIDACEAE	*Sprengelia incarnata* Sm. (r *vu*)	PS	5	5	4	6
MENYANTHACEAE	*Villarsia umbricola* (Aston) Tippery & Les (*ra*)	PFo	1	1	0	2
LEGUMINOSAE	*Viminaria juncea* (Schrad. & J.C.Wendl.) Hoffmanns. (r *vu*)	PS	13	10	7	21
VIOLACEAE	*Viola eminens* K.R.Thiele & Prober (*vu*)	PFo	7	4	5	11

CE[†] = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (*EPBC* Act), Lowercase = State rating (Barker et al. 2005), Italics = Regional rating (Gillam & Urban 2014); P[‡] = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub/twiner, Fo = Forb, Fe = Fern/clubmosses', G = Grass, Gm = Non-grass graminoid

Table S1.2 Native species from above-ground vegetation in the 94 Fleurieu Peninsula Swamp quadrats, but not from the germinable soil seed bank.

Family	Species (Conservation status[†])	Life-history & lifeform class[‡]	Number of quadrats where species recorded (n=94)
LEGUMINOSAE	*Acacia myrtifolia* C. L. Willdenow	PS	1
BLECHNACEAE	*Blechnum wattsii* Tindale (r *vu*)	PFe	1
ONAGRACEAE	*Epilobium pallidiflorum* Sol. ex A.Cunn. (*ra*)	PFo	1
GRAMINEAE	*Eragrostis tenellula* (Kunth) Steud.	AG	1
MYRTACEAE	*Eucalyptus cosmophylla* F.Muell.	PT	1
GLEICHENIACEAE	*Gleichenia microphylla* R.Br. (r *ra*)	PFe	37
JUNCACEAE	*Juncus pallidus* R.Br.	PGm	1
JUNCACEAE	*Juncus sarophorus* L.A.S.Johnson	PGm	1
CYPERACEAE	*Lepidosperma longitudinale* Labill. (*nt*)	PGm	1
MYRTACEAE	*Leptospermum lanigerum* (Sol. ex Aiton) Sm. (*ra*)	PS	1
LINDSAEACEAE	*Lindsaea linearis* Sw. (*nt*)	PFe	1
LYCOPODIACEAE	*Lycopodiella lateralis* (R.Br.) B.Ollg. (r *cr*)	PFe	1
LYCOPODIACEAE	*Lycopodiella serpentina* (Kunze) B.Ollg. (e *cr*)	PFe	1
MYRTACEAE	*Melaleuca decussata* R.Br. (*nt*)	PS	1
MYRTACEAE	*Melaleuca squamea* Labill. (r *ra*)	PS	1
GRAMINEAE	*Microlaena stipoides* (Labill.) R.Br.	PG	1
POLYGONACEAE	*Persicaria decipiens* (R.Br.) K.L.Wilson	PFo	1
DENNSTAEDTIACEAE	*Pteridium esculentum* (G.Forst.) Cockayne	PFe	3
GRAMINEAE	*Phragmites australis* (Cavs) Trin. ex Steud.	PG	1
SCHIZAEACEAE	*Schizaea bifida* Willd. (v *en*)	PFe	1
COMPOSITAE	*Senecio glomeratus* Desf. ex Poir. (*vu*)	AFo	1
COMPOSITAE	*Senecio minimus* Poir. (*nt*)	AFo	1
STYLIDIACEAE	*Stylidium armeria* (Labill.)	PFo	1
ORCHIDACEAE	*Thelymitra cyanea* (Lindl.) Benth. (e *en*)	PFo	1
ORCHIDACEAE	*Thelymitra holmesii* Nicholls (v *en*)	PFo	1
LENTIBULARIACEAE	*Utricularia dichotoma* Labill. (*vu*)	PFo	1
LENTIBULARIACEAE	*Utricularia tenella* R.Br. (*ra*)	PFo	1
XYRIDACEAE	*Xyris operculata* Labill. (r *vu*)	PGm	1

CE[†] = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (*EPBC* Act), Lowercase = State rating (Barker et al. 2005), Italics = Regional rating (Gillam & Urban 2014); P[‡] = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Ferns/clubmosses’, G = Grass, Gm = Non-grass graminoid’

Table S1.3. Introduced species which germinated from soil, collected from the 94 Fleurieu Peninsula Swamp quadrats. Two comparisons are presented: 1) seed germinating from the soil seed bank following heat plus smoke treatment (HS) compared with the untreated control (C); and 2) present in the above ground vegetation (A) prior to sampling soil and emerging in at least one of the two paired sample trays (S).

Family	Species	Life-history & lifeform class†	Number of samples where species recorded (n=94)			
			HS	C	A	S
Only germinated from heat plus smoke treated (H) soil						
GRAMINEAE	*Briza minor* L.	AG	3	0	6	3
COMPOSITAE	*Cirsium vulgare* (Savi) Ten.	PFo	1	0	1	1
GRAMINEAE	*Cynodon dactylon* L.	AG	1	0	0	1
GRAMINEAE	*Eragrostis curvula* (Schrad.) Nees	PG	1	0	0	1
Only germinated from untreated (C) soil and no treated (HS) soil						
CYPERACEAE	*Isolepis marginata* (Thunb.) A.Dietr.	AGm	0	1	1	1
COMPOSITAE	*Leontodon saxatilis* Lam.	PFo	0	5	7	5
COMPOSITAE DC.	*Senecio pterophorus* DC.	PFo	0	2	1	2
LEGUMINOSAE	*Ulex europaeus* L.	PS	0	1	1	1
GRAMINEAE	*Vulpia bromoides* (L.) Gray	AG	0	1	2	1
Germinated from both heat plus smoke treated (HS) & control (C) soils						
GRAMINEAE	*Aira cupaniana* Guss	AG	5	6	1	10
PRIMULACEAE	*Lysimachia arvensis* U.Manns & Anderb	AFo	6	9	1	12
GENTIANACEAE	*Centaurium erythraea* Rafn	AFo	5	7	0	9
LEGUMINOSAE	*Genista monspessulana* (L.) L.A.S.Johnson	PS	7	6	3	9
GRAMINEAE	*Holcus lanatus* L.	AG	24	28	14	34
COMPOSITAE	*Hypochaeris glabra* L.	AFo	2	1	0	3
JUNCACEAE	*Juncus articulatus* L.	PGm	2	1	1	3
JUNCACEAE	*Juncus capitatus* Weigel	AGm	2	3	0	4
LEGUMINOSAE	*Lotus pedunculatus* Schkuhr	AFo	37	30	7	43
LABIATAE	*Prunella vulgaris* L.	PFo	2	1	1	3
ROSACEAE	*Rubus anglocandicans* A.Newton	PS	9	16	8	23
SOLANACEAE	*Solanum nigrum* L.	AFo	5	6	0	8
COMPOSITAE	*Sonchus asper* (L.) Hill	AFo	6	8	11	11
COMPOSITAE	*Taraxacum officinale*	AFo	1	1	0	1
LEGUMINOSAE	*Trifolium* Spp	AFo	13	10	0	18
COMPOSITAE	*Vellereophyton dealbatum* (Thunb.) Hilliard & B.L.Burtt	AFo	1	2	1	2

P† = Perennial, A = Annual/biennial; T = Tree/mallee, S = Shrub/subshrub/vine, F = Forb, G = Grass, Gm = Non-grass graminoids

Table S1.4. Introduced species recorded from above ground vegetation in the 49 Fleurieu Peninsula Swamp quadrats, but not from the germinable soil seed bank.

Family	Species	Life-history & lifeform class†	Number of quadrats where species recorded (n=94)
GRAMINEAE	*Anthoxanthum odoratum* L.	PG	1
COMPOSITAE	*Arctotheca calendula* Levyns	AFo	1
IRIDACEAE	*Freesia laxa* (Thunb.) Goldblatt & J.C.Manning	PFo	1
GERANIACEAE	*Geranium* Spp	PFo	1
PINACEAE	*Pinus radiata* D.Don	PT	1
PLANTAGINACEAE	*Plantago* spp	PFo	1
COMPOSITAE	*Soliva sessilis* Ruiz & Pavs	AFo	1

P† = Perennial, A = Annual/biennial; T = Tree/mallee, S = Shrub/subshrub/vine, F = Forb, G = Grass, Gm = Non-grass graminoid

Table S2.1 Results for native species in the above ground vegetation (AGV) and germinable soil seed bank (SSB) are given. 1) Total percent cover is given for the AGV for individual species and all life-history/lifeform classes. 2) Total number of seedlings which germinated in the experiment is given and comparisons are made between the heat plus smoke treatment (HS) compared with the control (C); differences between the treatments was analysed subject to germination occurring in either a treated or untreated tray of each pair using generalised linear models.

		Above-ground vegetation	**Seeds germinating from SSB**				
Life-history classes	**Lifeform class/species**	**% Cover (Mean ± SE)**	**HS†**	**C†**	**P**	**χ^2**	**n‡**
Annual and biennial	**Forbs**	0.14	**70**	**35**	**0.178**	**1.812**	**20**
	Drosera binata Labill. (r *vu*)	0.02	25	4	na	na	5
	Drosera pygmaea DC (*nt*)	0.03	1	1	na	na	2
	Epilobium billardierianum L., Sp. Pl. (*nt*)	0	3	0	na	na	3
	Hypericum japonicum Thunb. (r *vu*)	0	2	1	na	na	2
	Lythrum hyssopifolia L.	0.03	36	26	0.950	0.004	10
	Senecio glomeratus Desf. ex Poir. (*vu*)	0.02	0	0	na	na	0
	Senecio minimus Poir. (*nt*)	0.02	0	0	na	na	0
	Senecio picridioides (Turcz.) M.E.Lawr.	0.02	3	3	na	na	4
	Grasses	0.02	**4**	**0**	**na**	**na**	**1**
	Eragrostis tenellula (Kunth) Steud.	0.02	4	0	na	na	1
	Non-grass graminoids	1.14	**1953**	**2237**	**0.704**	**0.144**	**88**
	Centrolepis aristata (R.Br.) Roem. & Schult.	0.02	1	5	na	na	2
	Centrolepis fascicularis Labill. (*vu*)	0.02	172	144	0.642	0.214	34
	Cyperus tenellus L.f.	0.34	746	670	0.088	2.790	55
	Isolepis cernua (Vahl) Roem. & Schult.	0.02	90	222	0.890	0.021	24
	Isolepis inundata R.Br.	0.09	364	460	0.740	0.110	55
	Juncus bufonius L.	0	353	576	0.012	5.840	59
	Juncus caespiticius E.Mey. (*nt*)	0	0	5	na	na	3
	Schoenus apogon Roem. & Schult.	0.62	2	2	na	na	2
	Schoenus maschalinus Roem. & Schult. (*vu*)	0.03	225	153	0.560	0.340	39
Perennial	**Ferns & clubmosses'**	45.32	**0**	**8**	**na**	**na**	**3**
	Blechnum minus (R.Br.) Ettingsh (*nt*)	0.68	0	8	na	na	3
	Blechnum wattsii Tindale (r *vu*)	0.02	0	0	na	na	0
	Gleichenia microphylla R.Br. (r *ra*)	43.65	0	0	na	na	0
	Lindsaea linearis Sw. (*nt*)	0.02	0	0	na	na	0

	Lycopodiella lateralis (R.Br.) B.Ollg. (r *cr*)	0.02	0	0	na	na	0
	Lycopodiella serpentina (Kunze) B.Ollg. (e *cr*)	0.02	0	0	na	na	0
	Pteridium esculentum (G.Forst.) Cockayne	0.90	0	0	na	na	0
	Schizaea bifida Willd. (v *en*)	0.02	0	0	na	na	0
	Forbs	1.11	**508**	**251**	**0.1546**	**2.026**	**61**
	Asperula conferta Hook.f (*ra*)	0	0	2	na	na	1
	Callitriche umbonata Hegelm	0	9	5	na	na	4
	Centella cordifolia (Hook.f.) Nannf. (*ra*)	0.02	29	41	0.6418	0.2142	11
	Epilobium pallidiflorum Sol. ex A.Cunn. (*ra*)	0.02	0	0	na	na	0
	Euchiton collinus Cass	0	7	9	na	na	7
	Gonocarpus micranthus Thunb. (r *vu*)	0.02	318	93	0.095	2.672	31
	Gratiola peruviana L.	0.02	22	18	0.760	0.097	15
	Lagenophora huegelii Benth.	0.02	0	1	na	na	1
	Lilaeopsis polyantha (Gand.) H.Eichler (*vu*)	0.02	2	1	na	na	2
	Lobelia anceps L.f.	0.22	54	54	0.747	0.110	18
	Thelymitra cyanea (Lindl.) Benth. (e *en*)	0.02	0	0	na	na	0
	Thelymitra holmesii Nicholls (v *en*)	0.02	0	0	na	na	0
	Utricularia dichotoma Labill. (*vu*)	0.02	0	0	na	na	0
	Utricularia tenella R.Br. (*ra*)	0.02	0	0	na	na	0
	Myriophyllum amphibium Labill. (r *vu*)	0.02	49	3	na	na	6
	Persicaria decipiens (R.Br.) K.L.Wilson	0.02	0	0	na	na	0
	Stylidium armeria (Labill.)	0.05	0	0	na	na	0
	Villarsia umbricola (Aston) Tippery & Les (*ra*)	0	1	1	na	na	2
	Viola eminens K.R.Thiele & Prober (*vu*)	0.59	17	23	0.680	0.167	11
	Grasses	0.78	**281**	**194**	**0.513**	**0.428**	**22**
	Microlaena stipoides (Labill.) R.Br.	0	0	0	na	na	0
	Phragmites australis (Cavs) Trin. ex Steud.	0.02	0	0	na	na	0
	Poa labillardieri Steud. (*nt*)	0.76	281	194	0.513	0.428	34
	Non-grass graminoids	21.10	**1206**	**1622**	**0.056**	**3.642**	**84**
	Baumea juncea (R.Br.) Palla	3.16	257	233	0.540	0.378	60
	Baumea rubiginosa (Spreng.) Boeckeler (*ra*)	3.05	53	52	0.464	0.539	23
	Baumea tetragona (Labill.) S.T.Blake (*nt*)	2.46	19	14	0.690	0.159	10
	Carex appressa R.Br.	0.02	9	55	0.057	3.612	8
	Empodisma minus (Hook.f.) L.A.S.Johnson & D.F.Cutler (*ra*)	1.06	337	607	0.810	0.060	35

	Gahnia sieberiana Kunth (*nt*)	9.93	36	46	0.740	0.111	21
	Juncus pallidus R.Br.	0.02	0	0	na	na	3
	Juncus planifolius R.Br. (*nt*)	0.17	493	653	0.180	1.772	72
	Juncus sarophorus L.A.S.Johnson	0.02	0	0	na	na	0
	Lepidosperma longitudinale Labill. (*nt*)	0.02	0	0	na	na	0
	Patersonia occidentalis R.Br. (*ra*)	0	2	14	na	na	5
	Xyris operculata Labill. (r *vu*)	0.02	0	0	na	na	0
	Shrubs/subshrubs	24.34	**251**	**126**	**0.001**	**11.082**	**45**
	Acacia myrtifolia C. L. Willdenow	0.02	0	0	na	na	0
	Acacia provincialis A.Camus	5.39	35	38	0.600	0.281	25
	Acacia verticillata C. L. Willdenow (*nt*)	0.69	5	0	na	na	4
	Goodenia ovata Sm.	0	98	31	0.001	5.626	6
	Hibbertia tenuis Toelken & R.J.Bates (CR e *cr*)	8.93	18	1	0.007	16	8
	Leptospermum continentale Joy Thomps.	5.48	16	19	0.610	0.257	13
	Leptospermum lanigerum (Sol. ex Aiton) Sm. (*ra*)	0.02	0	0	na	na	0
	Melaleuca decussata R.Br. (*nt*)	0.02	0	0	na	na	0
	Melaleuca squamea Labill. (r *ra*)	0.14	0	0	na	na	0
	Olearia glandulosa (Labill.) Benth. (v *en*)	0	1	0	na	na	1
	Pultenaea dentata Labill. (r *en*)	0	16	1	na	na	1
	Sprengelia incarnata Sm. (r *vu*)	0.45	26	18	0.575	0.3106	6
	Viminaria juncea (Schrad. & J.C.Wendl.) Hoffmanns. (r *vu*)	1.30	36	18	0.080	2.940	21
	Trees	0.03	**2**	**0**	**na**	**na**	**2**
	Eucalyptus cosmophylla F.Muell.	0.02	0	0	na	na	0
	Eucalyptus ovata Labill. (*vu*)	0.02	2	0	na	na	2

Total number of seedlings emerging in samples[†] Number of quadrats in which lifeform class/species germinated in at least one of the two paired trays[‡]; na=insufficient data to calculate statistic

Table S2.2 Results for introduced species in the above ground vegetation (AGV) and germinable soil seed bank (SSB) are given. 1) Total percent cover is given for the AGV for individual species and all life-history/lifeform classes. 2) Total number of seedlings which germinated in the experiment is given and comparisons are made between the heat plus smoke treatment (HS) compared with the control (C); differences between the treatments was analysed subject to germination occurring in either a treated or untreated tray of each pair using generalised linear models.

		Above-ground vegetation	**Seeds germinating from SSB**				
Life-history classes	**Lifeform class/species**	**% Cover (Mean ± SE)**	**HS†**	**C†**	**P**	**χ^2**	**n‡**
Annual and biennial	**Forbs**	0.71	**571**	**524**	**0.442**	**0.592**	**60**
	Lysimachia arvensis U.Manns & Anderb	0.02	21	39	0.022	1.58	12
	Arctotheca calendula Levyns	0.02	0	0	na	na	0
	Centaurium erythraea Rafn	0	19	24	0.5337	0.3874	9
	Hypochaeris glabra L.	0	4	2	na	na	2
	Lotus pedunculatus Schkuhr	0.40	485	429	0.095	5.484	43
	Soliva sessilis Ruiz & Pavs	0.14	0	0	na	na	0
	Sonchus asper (L.) Hill	0.07	6	11	na	na	11
	Trifolium Spp	0.02	24	15	0.150	2.096	18
	Vellereophyton dealbatum (Thunb.) Hilliard & B.L.Burtt	0.02	12	4	na	na	2
	Grasses	3.71	**216**	**179**	**1.000**	**0.000**	**39**
	Aira cupaniana Guss	0.02	11	14	0.690	0.161	10
	Briza minor L.	1.13	9	0	na	na	3
	Cynodon dactylon L.	0	1	0	na	na	1
	Holcus lanatus L.	2.16	195	156	0.603	0.270	34
	Vulpia bromoides (L.) Gray	0.38	0	9	na	na	1
	Non-grass graminoids	0.02	**12**	**28**	**na**	**na**	**4**
	Isolepis marginata (Thunb.) A.Dietr.	0	0	1	na	na	1
	Juncus capitatus Weigel	0	12	27	na	na	4
Perennial	**Forbs**	0.83	**10**	**26**	**0.020**	**5.445**	**10**
	Cirsium vulgare (Savi) Ten.	0.05	1	0	na	na	1
	Freesia laxa (Thunb.) Goldblatt & J.C.Manning	0.02	0	0	na	na	0
	Geranium spp.	0.02	0	0	na	na	0
	Leontodon saxatilis Lam.	0.73	0	7	na	na	5
	Plantago spp	0.02	0	0	na	na	0

	Prunella vulgaris L.	0.02	2	3	na	na	3
	Senecio pterophorus DC.	0.02	0	2	na	na	2
	Solanum nigrum L.	0	6	13	0.120	2.372	8
	Taraxacum officinale	0	1	1	na	na	1
	Grasses	0.02	**4**	**0**	**na**	**na**	**1**
	Anthoxanthum odoratum L.	0.02	0	0	na	na	0
	Eragrostis curvula (Schrad.) Nees	0	4	0	na	na	1
	Non-grass graminoids	0.02	**2**		**0.450**	**0.570**	
	Juncus articulatus L.	0.02	2	1	na	na	3
	Shrubs/twiners	0.69	**284**	**365**	**0.214**	**1.544**	**28**
	Genista monspessulana (L.) L.A.S.Johnson	0.03	270	338	0.757	0.094	9
	Rubus anglocandicans A.Newton	0.64	14	26	0.062	3.490	23
	Ulex europaeus L.	0.02	0	1	na	na	1
	Trees	0.02	**0**	**0**	**na**	**na**	**0**
	Pinus radiata D.Don	0.02	0	0	na	na	0

Total number of seedlings emerging in samples[†] Number of quadrats in which lifeform class/species germinated in at least one of the two paired trays; na=insufficient data to calculate statistic[‡]

Table S3.1 Threatened plant species occurring in, or at the margins of, permanent freshwater swamps or springs in the Adelaide and Mount Lofty Ranges Region of South Australia (Department for Environment and Water 2020a). Life-history and lifeform class descriptions for each species, and whether they are confined to the ground stratum and thus susceptible to being outcompeted by dominant ferns and shrubs.

			Conservation status[†]			**Life-history & lifeform class[¶]**	**Ground Stratum?**
Family	**Plant species**	**Common names**	**AUST[‡]**	**SA[§]**	**AMLR[‖]**		
DILLENIACEAE	*Hibbertia tenuis*	Fleurieu Peninsula Guinea-flower	CR	EN	CR	PS	Yes
ORCHIDACEAE	*Prasophyllum murfetii*	Maroon Leek-orchid	CR	EN	CR	PFo	Yes
ORCHIDACEAE	*Corybas fordhamii*	Swamp Helmet-orchid		EN	CR	PFo	Yes
ORCHIDACEAE	*Genoplesium ciliatum*	Swamp Midge-orchid		EN	CR	PFo	Yes
LYCOPODIACEAE	*Lycopodiella serpentina*	Bog Clubmoss		EN	CR	PFe	Yes
ORCHIDACEAE	*Pterostylis uliginosa*			EN	CR	PFo	Yes
ORCHIDACEAE	*Thelymitra circumsepta*	Naked Sun-orchid		EN	CR	PFo	Yes
JUNCACEAE	*Juncus prismatocarpus*	Branching Rush		EN	EN	PGm	Yes
ORCHIDACEAE	*Pterostylis falcata*	Forked Greenhood		EN	EN	PFo	Yes
ORCHIDACEAE	*Thelymitra cyanea*	Veined Sun-orchid		EN	EN	PFo	Yes
OSMUNDACEAE	*Todea barbara*	King Fern		EN	EN	PFe	No
DICKSONIACEAE	*Dicksonia antarctica*	Soft Tree-fern		EN	DD	PFe	No
CYPERACEAE	*Isolepis producta*	Nutty Club-rush		VU	RE	AGm	Yes
ORCHIDACEAE	*Cryptostylis subulata*	Moose Orchid		VU	CR	PFo	Yes
CYPERACEAE	*Eleocharis atricha*	Tuber Spike-rush		VU	CR	PGm	Yes
LENTIBULARIACEAE	*Utricularia lateriflora*	Small Bladderwort		VU	CR	PFo	Yes
ADIANTACEAE	*Adiantum capillus-veneris*	Dainty Maiden-hair		VU	EN	PFe	Yes
JUNCACEAE	*Juncus amabilis*			VU	EN	PGm	Yes
SCROPHULARIACEAE	*Mazus pumilio*	Swamp Mazus		VU	EN	PFo	Yes
ORCHIDACEAE	*Microtis orbicularis*	Swamp Onion-orchid		VU	EN	PFo	Yes
PORTULACACEAE	*Montia fontana ssp. chondrosperma*	Waterblinks		VU	EN	AFo	Yes
COMPOSITAE	*Olearia glandulosa*	Swamp Daisy-bush		VU	EN	PS	Yes
CAMPANULACEAE	*Pratia puberula*	White-flower Matted Pratia		VU	EN	PFo	Yes

SCHIZAEACEAE	*Schizaea bifida*	Forked Comb-fern		VU	EN	PFe	Yes
SCHIZAEACEAE	*Schizaea fistulosa*	Narrow Comb-fern		VU	EN	PFe	Yes
ORCHIDACEAE	*Thelymitra holmesii*	Blue Star Sun-orchid		VU	EN	PFo	Yes
HALORAGACEAE	*Myriophyllum crispatum*	Upright Milfoil		VU	?	PFo	Yes
CAMPANULACEAE	*Isotoma fluviatilis ssp. australis*	Swamp Isotome		RA	RE	PFo	Yes
HALORAGACEAE	*Myriophyllum papillosum*	Robust Milfoil		RA	RE	PFo	Yes
HALORAGACEAE	*Myriophyllum variifolium*	Varied Milfoil		RA	RE	PFo	Yes
LYCOPODIACEAE	*Lycopodiella lateralis*	Slender Clubmoss		RA	CR	PFe	Yes
ORCHIDACEAE	*Microtis rara*	Sweet Onion-orchid		RA	CR	PFo	Yes
RUTACEAE	*Boronia parviflora*	Swamp Boronia		RA	EN	PFo	Yes
SCROPHULARIACEAE	*Gratiola pumilo*	Dwarf Brooklime		RA	EN	PFo	Yes
ORCHIDACEAE	*Prasophyllum australe*	Austral Leek-orchid		RA	EN	PFo	Yes
PTERIDACEAE	*Pteris tremula*	Tender Brake		RA	EN	PFe	Yes
LEGUMINOSAE	*Pultenaea dentata*	Clustered Bush-pea		RA	EN	PS	Yes
RANUNCULACEAE	*Ranunculus inundatus*	River Buttercup		RA	EN	PFo	Yes
CYPERACEAE	*Schoenus tesquorum*	Grassy Bog-rush		RA	EN	PGm	Yes
ORCHIDACEAE	*Spiranthes australis*	Austral Lady's Tresses		RA	EN	PFo	Yes
CYPERACEAE	*Baumea acuta*	Pale Twig-rush		RA	VU	PGm	Yes
CYPERACEAE	*Baumea gunnii*	Slender Twig-rush		RA	VU	PGm	Yes
CYPERACEAE	*Baumea laxa*	Lax Twig-rush		RA	VU	PGm	Yes
BLECHNACEAE	*Blechnum wattsii*	Hard Water-fern		RA	VU	PFe	Yes
CYPERACEAE	*Carex gunniana*	Mountain Sedge		RA	VU	PGm	Yes
CYPERACEAE	*Cyperus sanguinolentus*	Dark Flat-sedge		RA	VU	PGm	Yes
DROSERACEAE	*Drosera binata*	Forked Sundew		RA	VU	PFo	Yes
ELATINACEAE	*Elatine gratioloides*	Waterwort		RA	VU	AFo	Yes
HALORAGACEAE	*Gonocarpus micranthus ssp. micranthus*	Creeping Raspwort		RA	VU	PFo	Yes
HALORAGACEAE	*Haloragis brownii*	Swamp Raspwort		RA	VU	PFo	Yes
GUTTIFERAE	*Hypericum japonicum*	Matted St John's Wort		RA	VU	AFo	Yes

DENNSTAEDTIACEAE	*Hypolepis rugosula*	Ruddy Ground-fern		RA	VU	PFe	Yes
EPACRIDACEAE	*Leucopogon hirsutus*	Hairy Beard-heath		RA	VU	PS	Yes
HALORAGACEAE	*Myriophyllum amphibium*	Broad Milfoil		RA	VU	PFo	Yes
HALORAGACEAE	*Myriophyllum integrifolium*	Tiny Milfoil		RA	VU	PFo	Yes
EPACRIDACEAE	*Sprengelia incarnata*	Pink Swamp-heath		RA	VU	PS	Yes
JUNCAGINACEAE	*Triglochin alcockiae*	Alcock's Water-ribbons		RA	VU	PGm	Yes
LEGUMINOSAE	*Viminaria juncea*	Native Broom		RA	VU	PS	No
ORCHIDACEAE	*Spiranthes sp. Late selfing white (R.Bates 909)*	Austral Lady's Tresses			CR	PFo	Yes
ORCHIDACEAE	*Eriochilus sp. Swamp*				EN	PFo	Yes
GOODENIACEAE	*Goodenia humilis*	Swamp Goodenia			EN	PFo	Yes
UMBELLIFERAE	*Hydrocotyle pterocarpa*	Wing Pennywort			EN	PFo	Yes
GRAMINEAE	*Isachne globosa*	Swamp Millet			EN	PG	Yes
POLYGONACEAE	*Persicaria praetermissa*	Spotted Knotweed			EN	PFo	Yes
AZOLLACEAE	*Azolla pinnata*	Ferny Azolla			VU	PFe	Yes
CENTROLEPIDACEAE	*Centrolepis fascicularis*	Tufted Centrolepis			VU	AGm	Yes
ZANNICHELLIACEAE	*Lepilaena cylindrocarpa*	Long-fruit Water-mat			VU	AFo	Yes
UMBELLIFERAE	*Lilaeopsis polyantha*	Australian Lilaeopsis			VU	PFo	Yes
SCROPHULARIACEAE	*Limosella australis*	Australian Mudwort			VU	AFo	Yes
HALORAGACEAE	*Myriophyllum salsugineum*	Lake Milfoil			VU	PFo	Yes
HALORAGACEAE	*Myriophyllum simulans*	Amphibious Milfoil			VU	PFo	Yes
HALORAGACEAE	*Myriophyllum simulans*	Amphibious Milfoil			VU	PFo	Yes
IRIDACEAE	*Patersonia fragilis*	Short Purple-flag			VU	PGm	Yes
POTAMOGETONACEAE	*Potamogeton pectinatus*	Fennel Pondweed			VU	PFo	Yes
POTAMOGETONACEAE	*Potamogeton tepperi*	Tepper's Pondweed			VU	PFo	Yes
POTAMOGETONACEAE	*Potamogeton tricarinatus*	Floating Pondweed			VU	PFo	Yes
RANUNCULACEAE	*Ranunculus pumilio var. pumilio*	Ferny Buttercup			VU	AFo	Yes
GRAMINEAE	*Rytidosperma semiannulare*	Wetland Wallaby-grass			VU	PG	Yes
CYPERACEAE	*Schoenus carsei*	Wiry Bog-rush			VU	PGm	Yes

CYPERACEAE	*Schoenus maschalinus*	Leafy Bog-rush			VU	AGm	Yes
COMPOSITAE	*Senecio glomeratus ssp. longifructus*	Swamp Groundsel			VU	AFo	Yes
LENTIBULARIACEAE	*Utricularia dichotoma*	Purple Bladderwort			VU	PFo	Yes
HYDROCHARITACEAE	*Vallisneria australis*	River Eel-grass			VU	PFo	Yes
MENYANTHACEAE	*Villarsia reniformis*	Running Marsh-flower			VU	PFo	Yes

[†]CE = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; [‡]National rating (*EPBC* Act), [§]State rating (Gillam & Urban 2014), [‖]Regional rating (Gillam & Urban 2014); [¶]*P* = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoid

Appendix 3. Supplementary material for Chapter 4

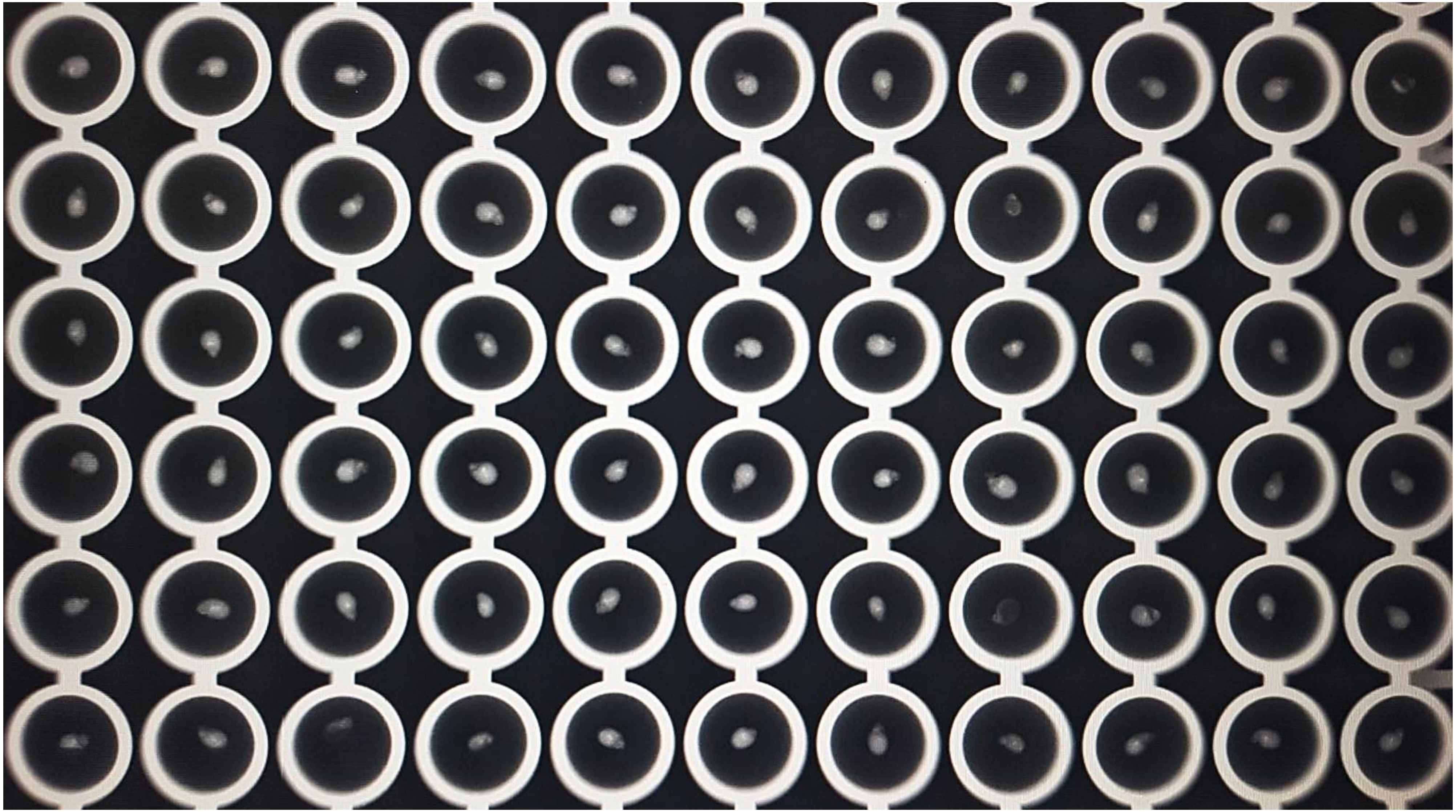

Figure S1.1 Photo of *Hibbertia tenuis* seed taken with an X-Ray machine to determine ‘seed fill’ and viability.

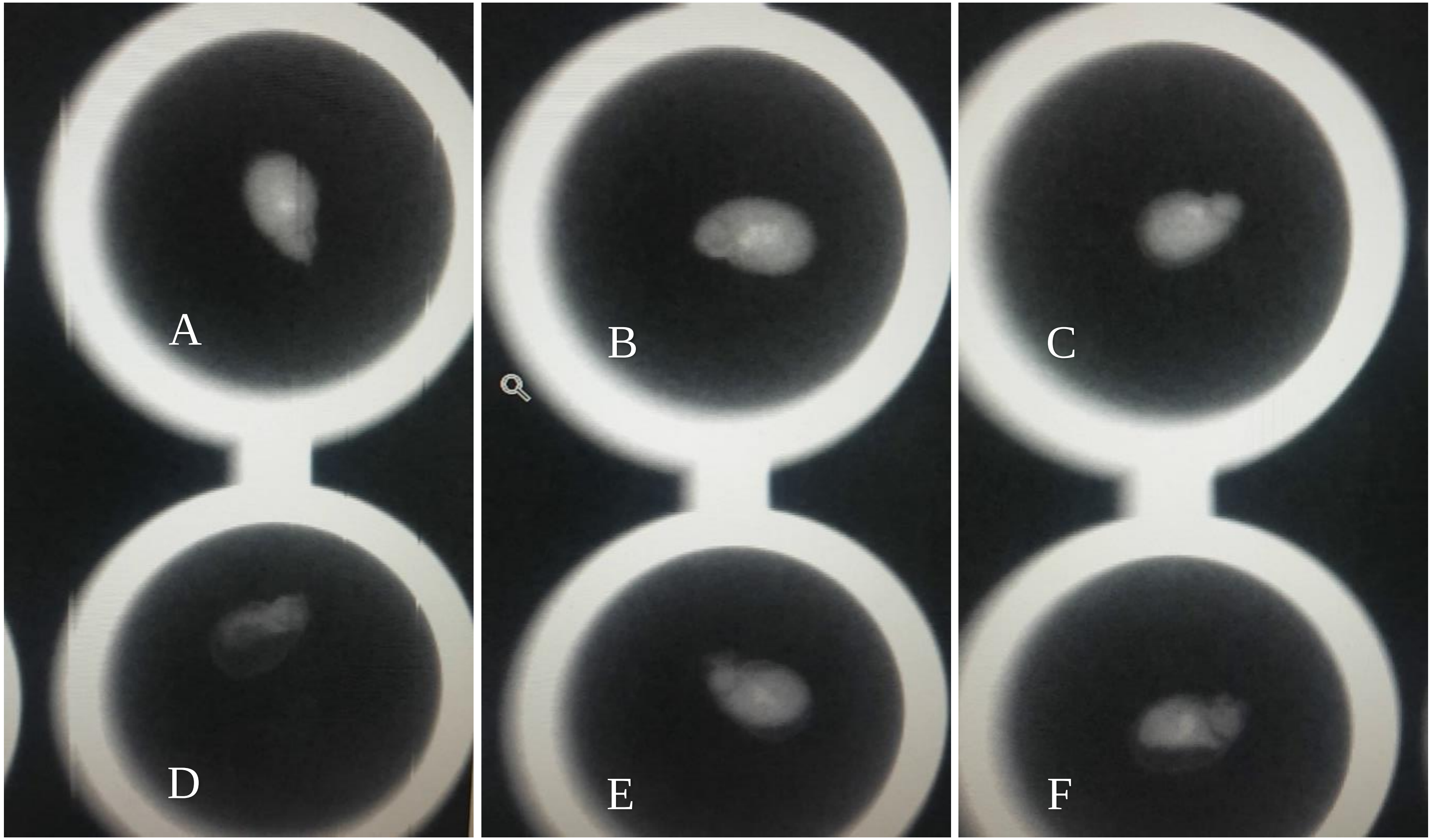

Figure S1.2 Photo of *Hibbertia tenuis* seed taken with an X-Ray machine to determine ‘seed fill’ and viability. The image is a close up of the bottom left corner of Figure 1 and shows the spectrum of potentially ‘germinable’ embryos, which ranges from empty (D) to partially detached (E, F), to mostly attached (C) to fully intact (A, B). Determination of ‘seed fill’ and viability, as determined by X-Ray photography. Observations of ‘seed fill’ were determined using an X-Ray machine, using 5 image replicates of plates which each held 66 seeds (Figure 1). If a ‘germinable’ embryo is defined as at least 90 % full, with minimal detachment (e.g. A, B, C; Figure 2), then we found that average viability was 74.8 % ± 2.6 % (mean ± standard error).

Table S2.1 The effect of treatments and seasonal temperature regimes on percent germination (mean % ± 95 % CI), with statistical comparisons between seasonal temperature regimes.

Treatment	**Autumn/ Spring**	**Autumn/ Spring vs Summer**	**Summer**	**Autumn/ Spring vs Winter**	**Winter**	**Summer vs Winter**
	% Germination	**Significance**	**% Germination**	**Significance**	**% Germination**	**Significance**
Control	2.40 ± 0.97	χ^2 (95) = -1.61, *P* = 0.25	5.22 ± 1.41	χ^2 (95) = -1.67, *P* = 0.22	< 0.01 ± < 0.01	χ^2 (95) = -2.51, *P* = 0.04
GA	14.46 ± 2.26	χ^2 (95) = -2, *P* = 0.12	21.59 ± 2.73	χ^2 (95) = -2.01, *P* = 0.12	8.44 ± 1.85	χ^2 (95) = -3.78, *P* = < 0.01
GA & heat	37.64 ± 2.94	χ^2 (95) = 2.84, *P* = 0.01	26.2 ± 2.67	χ^2 (95) = -1.2, *P* = 0.46	32.73 ± 2.83	χ^2 (95) = 1.67, *P* = 0.22
GA & smoke	30.9 ± 3.03	χ^2 (95) = 1.26, *P* = 0.42	25.56 ± 2.92	χ^2 (95) = -5.01, *P* = < 0.01	10.91 ± 2.1	χ^2 (95) = -3.89, *P* = < 0.01
GA, smoke & heat	51.47 ± 3.03	χ^2 (95) = 4.99, *P* = < 0.01	30.04 ± 2.83	χ^2 (95) = -3.72, *P* = < 0.01	35.56 ± 2.91	χ^2 (95) = 1.35, *P* = 0.37
Heat	8.86 ± 1.85	χ^2 (95) = 1.49, *P* = 0.3	5.26 ± 1.48	χ^2 (95) = < 0.01, *P* = < 0.01	< 0.01 ± < 0.01	χ^2 (95) = < 0.01, *P* = < 0.01
Smoke	51.26 ± 3.00	χ^2 (95) = 7.7, *P* = < 0.01	19.06 ± 2.36	χ^2 (95) = -9.66, *P* = < 0.01	9.49 ± 1.77	χ^2 (95) = -3.16, *P* = 0.01
Smoke & heat	47.86 ± 2.99	χ^2 (95) = 7.06, *P* = < 0.01	18.93 ± 2.34	χ^2 (95) = -9.34, *P* = < 0.01	3.57 ± 1.11	χ^2 (95) = -5.17, *P* = < 0.01

Table S2.2 The effect of static stratification pre-treatments (with or without light) and smoke on germination.

Treatment	**Spring**	**Summer**	**Winter**
Control - GA	χ^2 (95) = -4.27, P = < 0.01	χ^2 (95) = -4.91, P = < 0.01	χ^2 (95) = -3.04, P = 0.06
Control - GA & heat	χ^2 (95) = -7.41, P = < 0.01	χ^2 (95) = -5.88, P = < 0.01	χ^2 (95) = -4.75, P = < 0.01
Control - GA & smoke	χ^2 (95) = -6.64, P = < 0.01	χ^2 (95) = -5.65, P = < 0.01	χ^2 (95) = -3.33, P = 0.03
Control - GA & smoke & heat	χ^2 (95) = -8.74, P = < 0.01	χ^2 (95) = -6.52, P = < 0.01	χ^2 (95) = -4.87, P = < 0.01
Control - heat	χ^2 (95) = -2.91, P = 0.08	χ^2 (95) = -0.02, P = 1.00	χ^2 (95) = < 0.01, P = 1.00
Control - smoke	χ^2 (95) = -8.73, P = < 0.01	χ^2 (95) = -4.5, P = 1.00	χ^2 (95) = -3.19, P = 0.04
Control - smoke & heat	χ^2 (95) = -8.41, P = < 0.01	χ^2 (95) = -4.47, P = < 0.01	χ^2 (95) = -2.11, P = 0.42
GA - GA & heat	χ^2 (95) = -5.74, P = < 0.01	χ^2 (95) = -1.20, P = 0.93	χ^2 (95) = -6.11, P = 0.00
GA - GA & smoke	χ^2 (95) = -4.2, P = < 0.01	χ^2 (95) = -0.99, P = 0.97	χ^2 (95) = -0.88, P = 0.99
GA - GA & smoke & heat	χ^2 (95) = -8.37, P = < 0.01	χ^2 (95) = -2.12, P = 0.41	χ^2 (95) = -6.59, P = < 0.01
GA - heat	χ^2 (95) = 1.89, P = 0.56	χ^2 (95) = 4.74, P = < 0.01	χ^2 (95) = < 0.01, P = 1.00
GA - smoke	χ^2 (95) = -8.36, P = < 0.01	χ^2 (95) = 0.70, P = 1.00	χ^2 (95) = -0.41, P = 1.00
GA - smoke & heat	χ^2 (95) = -7.74, P = < 0.01	χ^2 (95) = 0.74, P = 1.00	χ^2 (95) = 2.27, P = 0.32
GA & heat - GA & smoke	χ^2 (95) = 1.58, P = 0.76	χ^2 (95) = 0.16, P = 1.00	χ^2 (95) = 5.48, P = < 0.01
GA & heat - GA & smoke & heat	χ^2 (95) = -3.23, P = 0.03	χ^2 (95) = -0.99, P = 0.98	χ^2 (95) = -0.70, P = 1.00
GA & heat - heat	χ^2 (95) = 7.00, P = < 0.01	χ^2 (95) = 5.67, P = < 0.01	χ^2 (95) = < 0.01, P = 1.00
GA & heat - smoke	χ^2 (95) = -3.20, P = 0.04	χ^2 (95) = 1.99, P = 0.49	χ^2 (95) = 6.32, P = < 0.01
GA & heat - smoke & heat	χ^2 (95) = -2.42, P = 0.24	χ^2 (95) = 2.04, P = 0.46	χ^2 (95) = 7.43, P = < 0.01
GA & smoke - GA & smoke & heat	χ^2 (95) = -4.63, P = < 0.01	χ^2 (95) = -1.09, P = 0.96	χ^2 (95) = -6.00, P = < 0.01
GA & smoke - heat	χ^2 (95) = 5.67, P = < 0.01	χ^2 (95) = 5.45, P = < 0.01	χ^2 (95) = < 0.01, P = 1.00
GA & smoke - smoke	χ^2 (95) = -4.60, P = < 0.01	χ^2 (95) = 1.74, P = 0.66	χ^2 (95) = 0.52, P = 1.00
GA & smoke - smoke & heat	χ^2 (95) = -3.88, P = < 0.01	χ^2 (95) = 1.78, P = 0.63	χ^2 (95) = 3.08, P = 0.05
GA & smoke & heat - heat	χ^2 (95) = 9.23, P = < 0.01	χ^2 (95) = 6.28, P = < 0.01	χ^2 (95) = < 0.01, P = 1.00
GA & smoke & heat - smoke	χ^2 (95) = 0.05, P = 1.00	χ^2 (95) = 2.95, P = 0.07	χ^2 (95) = 6.86, P = < 0.01
GA & smoke & heat - smoke & heat	χ^2 (95) = 0.85, P = 0.99	χ^2 (95) = 3.00, P = 0.07	χ^2 (95) = 7.80, P = < 0.01
Heat - smoke	χ^2 (95) = -9.22, P = < 0.01	χ^2 (95) = -4.33, P = < 0.01	χ^2 (95) = < 0.01, P = 1.00
Heat - smoke & heat	χ^2 (95) = -8.70, P = < 0.01	χ^2 (95) = -4.30, P = < 0.01	χ^2 (95) = < 0.01, P = 1.00
Smoke - smoke & heat	χ^2 (95) = 0.80, P = 0.99	χ^2 (95) = 0.04, P = 1.00	χ^2 (95) = 2.72, P = 0.13

Table S2.3 The effect of smoke and static stratification pre-treatments (with or without light) on percent germination (mean % ± 95 % CI), with statistical comparisons between smoke and untreated controls.

Treatment	Control	Smoke	Significance
Dark; 15 then 20 °C	5.56 ± 2.41	6.67 ± 2.63	χ^2 (23) = -0.31, *P* = 0.76
Dark; 20 then 15 °C	16.67 ± 3.93	62.22 ± 5.11	χ^2 (23) = -5.91, *P* = < 0.01
Dark; 5 then 15 °C	5.56 ± 2.41	16.67 ± 3.93	χ^2 (23) = -2.27, *P* = 0.03
Light; 15 then 20 °C	4.44 ± 2.17	14.44 ± 3.71	χ^2 (23) = -2.17, *P* = 0.04
Light; 20 then 15 °C	10.00 ± 3.16	34.44 ± 5.01	χ^2 (23) = -3.74, *P* = < 0.01
Light; 5 then 15 °C	12.22 ± 3.45	51.11 ± 5.27	χ^2 (23) = -5.24, *P* = < 0.01

Table S2.4 The effect of static stratification pre-treatments (with or without light) and smoke on percent germination (mean % ± 95 % CI), with statistical comparisons between the pre-treatments.

Treatment	**Control**	**Smoke**
Dark; 15 then 20 °C - Dark; 20 then 15 °C	χ^2 (23) = -2.27, P = 0.25	χ^2 (23) = -6.6, P = < 0.01
Dark; 15 then 20 °C - Dark; 5 then 15 °C	χ^2 (23) = < 0.01, P = 1.00	χ^2 (23) = -2.02, P = 0.36
Dark; 15 then 20 °C - Light; 15 then 20 °C	χ^2 (23) = 0.34, P = 1.00	χ^2 (23) = -1.66, P = 0.57
Dark; 15 then 20 °C - Light; 20 then 15 °C	χ^2 (23) = -1.1, P = 0.88	χ^2 (23) = -4.18, P = < 0.01
Dark; 15 then 20 °C - Light; 5 then 15 °C	χ^2 (23) = -1.53, P = 0.65	χ^2 (23) = -5.68, P = < 0.01
Dark; 20 then 15 °C - Dark; 5 then 15 °C	χ^2 (23) = 2.27, P = 0.25	χ^2 (23) = 5.91, P = < 0.01
Dark; 20 then 15 °C - Light; 15 then 20 °C	χ^2 (23) = 2.50, P = 0.17	χ^2 (23) = 6.15, P = < 0.01
Dark; 20 then 15 °C - Light; 20 then 15 °C	χ^2 (23) = 1.30, P = 0.78	χ^2 (23) = 3.68, P = 0.01
Dark; 20 then 15 °C - Light; 5 then 15 °C	χ^2 (23) = 0.85, P = 0.96	χ^2 (23) = 1.50, P = 0.67
Dark; 5 then 15 °C - Light; 15 then 20 °C	χ^2 (23) = 0.34, P = 1.00	χ^2 (23) = 0.41, P = 1.00
Dark; 5 then 15 °C - Light; 20 then 15 °C	χ^2 (23) = -1.10, P = 0.88	χ^2 (23) = -2.69, P = 0.12
Dark; 5 then 15 °C - Light; 5 then 15 °C	χ^2 (23) = -1.53, P = 0.65	χ^2 (23) = -4.69, P = < 0.01
Light; 15 then 20 °C - Light; 20 then 15 °C	χ^2 (23) = -1.40, P = 0.72	χ^2 (23) = -3.04, P = 0.06
Light; 15 then 20 °C - Light; 5 then 15 °C	χ^2 (23) = -1.81, P = 0.48	χ^2 (23) = -4.97, P = < 0.01
Light; 20 then 15 °C - Light; 5 then 15 °C	χ^2 (23) = -0.47, P = 1.00	χ^2 (23) = -2.25, P = 0.26

Appendix 4. Supplementary material for Chapter 5

Table S1. Frequency of native species recorded from in seasons unburnt controls, spring burnt and autumn burnt quadrats.

Species[†]	Class[‡]	Control	Spring	Autumn
Only detected in control unburnt quadrats				
Blechnum minus (R.Br.) Ettingsh (*nt*)	PGm	4	0	0
Drosera pygmaea DC (*nt*)	AFo	1	0	0
Viola eminens K.R.Thiele & Prober (*vu*)	PFo	9	0	0
Only detected in Autumn burnt quadrats				
Melaleuca decussata R.Br. (*nt*)	PS	0	0	5
Spiranthes australis (R.Br.) Lindl. (r *en*)	PFo	0	0	4
Thelymitra cyanea (Lindl.) Benth. (E en)	PFo	0	0	1
Only detected in Spring burnt quadrats				
Centrolepis fascicularis Labill. (*vu*)	AGm	0	1	0
Eucalyptus ovata Labill. (*vu*)	PT	0	1	0
Euchiton collinus Cass	PFo	0	3	0
Leucopogon hirsutus Sond. (r *vu*)	PS	0	1	0
Microlaena stipoides (Labill.) R.Br.	PG	0	3	0
Senecio glomeratus Desf. ex Poir. (*vu*)	AFo	0	4	0
Utricularia dichotoma Labill. (*vu*)	PFo	0	1	0
All other species				
Acacia myrtifolia C. L. Willdenow	PS	0	2	0*
Acacia provincialis A. Camus	PS	41	4	0
Acacia verticillata C. L. Willdenow	PS	12	0	1
Baumea juncea (R.Br.) Palla	PGm	16	8	32
Baumea rubiginosa (Spreng.) Boeckeler (*ra*)	PGm	32	53	37
Baumea tetragona (Labill.) S.T.Blake (*nt*)	PGm	32	59	33
Cyperus tenellus L.f.	AGm	0	3	0*
Drosera binata Labill. (r *vu*)	AFo	0	17	6
Gahnia sieberiana Kunth (*nt*)	PGm	44	30	7
Gleichenia microphylla R.Br. (r *ra*)	PF	127	5	0
Gonocarpus micranthus Thunb. (r *vu*)	PFo	3	6	0
Goodenia ovata Sm.	PS	8	0	4
Gratiola peruviana L.	PFo	0	1	0*
Hibbertia tenuis Toelken & R.J.Bates (CR e *cr*)	PS	44	40	23
Isolepis inundata R.Br.	AGm	0	5	0*
Juncus planifolius R.Br. (*nt*)	PGm	3	4	5
Leptospermum continentale Joy Thomps.	PS	47	29	45
Lobelia anceps L.f.	PFo	4	0	4
Lythrum hyssopifolia L.	AFo	4	1	0
Melaleuca squamea Labill. (r *ra*)	PS	0	0*	5
Patersonia occidentalis R.Br. (*ra*)	PGm	10	7	1
Poa labillardieri Steud. (*nt*)	PG	11	13	0
Pteridium esculentum (G.Forst.) Cockayne	PF	12	1	0
Schoenus apogon Roem. & Schult.	AGm	5	2	1
Schoenus maschalinus Roem. & Schult. (*vu*)	AGm	4	3	10
Sprengelia incarnata Sm. (r *vu*)	PS	7	6	22
Stylidium armeria (Labill.)	PFo	0	0*	14
Viminaria juncea (Schrad. & J.C.Wendl.) Hoffmanns. (r *vu*)	PS	3	41	19
Xyris operculata Labill. (r ra)	PGm	0*	1	19

[†] Brackets represents conservation status: CE = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (*EPBC* Act), Lowercase = State rating (Barker et al. 2005), Italics = Regional rating (Gillam & Urban 2014); [‡] Class represents the Longevity and lifeform class of each species, such that: P = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids. *Species occurred in at least one quadrat before it was burnt.

Table S2. Frequency of native species recorded from fenced or unfenced quadrats.

Species[†]	Class[‡]	Fenced	Unfenced
Only detected in fenced quadrats			
Thelymitra cyanea (Lindl.) Benth. (E *en*)	PFo	1	0
Gratiola peruviana L.	PFo	1	0
Microlaena stipoides (Labill.) R.Br.	PG	3	0
Senecio glomeratus Desf. ex Poir. (*vu*)	AFo	4	0
Spiranthes australis (R.Br.) Lindl.	PFo	4	0
Only detected in unfenced quadrats			
Blechnum minus (R.Br.) Ettingsh (*nt*)	PGm	0	4
Centrolepis fascicularis Labill. (*vu*)	AGm	0	1
Drosera pygmaea DC (*nt*)	AFo	0	1
Eucalyptus ovata Labill. (*vu*)	PT	0	1
Euchiton collinus Cass	PFo	0	3
Isolepis inundata R.Br.	AGm	0	5
Leucopogon hirsutus Sond. (r *vu*)	PS	0	1
Melaleuca decussata R.Br. (*nt*)	PS	0	5
Utricularia dichotoma Labill. (*vu*)	PFo	0	1
Detected in either fenced or unfenced quadrats			
Acacia myrtifolia C. L. Willdenow	PS	1	1
Acacia provincialis A.Camus	PS	17	28
Acacia verticillata C. L. Willdenow	PS	9	4
Baumea juncea (R.Br.) Palla	PGm	28	28
Baumea rubiginosa (Spreng.) Boeckeler (*ra*)	PGm	64	58
Baumea tetragona (Labill.) S.T.Blake (*nt*)	PGm	56	68
Cyperus tenellus L.f.	AGm	1	2
Drosera binata Labill. (r *vu*)	AFo	7	16
Gahnia sieberiana Kunth (*nt*)	PGm	42	39
Gleichenia microphylla R.Br. (r *ra*)	PF	36	96
Gonocarpus micranthus Thunb. (r *vu*)	PFo	3	6
Goodenia ovata Sm.	PS	4	8
Hibbertia tenuis Toelken & R.J.Bates (CR e *cr*)	PS	62	45
Juncus planifolius R.Br. (*nt*)	PGm	7	5
Leptospermum continentale Joy Thomps.	PS	40	81
Lobelia anceps L.f.	PFo	4	4
Lythrum hyssopifolia L.	AFo	1	4
Melaleuca squamea Labill. (r *ra*)	PS	4	1
Patersonia occidentalis R.Br. (*ra*)	PGm	3	15
Poa labillardieri Steud. (*nt*)	PG	8	16
Pteridium esculentum (G.Forst.) Cockayne	PF	1	12
Schoenus apogon Roem. & Schult.	AGm	4	4
Schoenus maschalinus Roem. & Schult. (*vu*)	AGm	7	10
Sprengelia incarnata Sm. (r *vu*)	PS	18	17
Stylidium armeria (Labill.)	PFo	10	4
Viminaria juncea (Schrad. & J.C.Wendl.) Hoffmanns. (r *vu*)	PS	34	29
Viola eminens K.R.Thiele & Prober (*vu*)	PFo	7	2
Xyris operculata Labill. (r *ra*)	PGm	12	8

[†] Brackets represents the species conservation status, such that: CE = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (*EPBC* Act), Lowercase = State rating (Barker et al. 2005), Italics = Regional rating (Gillam & Urban 2014);

[‡] Class represents the Longevity and lifeform class of each species, such that: P = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids.

Table S3.1 **Cover** of **native** flora in the **control** quadrats (% plant cover ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	88.9 ± 2.4	89.3 ± 2.4	79.9 ± 4.2	89.1 ± 2.9	87.6 ± 2.9	87.2 ± 3.2	93.5 ± 2.6	94.4 ± 2.6	94.5 ± 2.4	98.7 ± 1
Annual/biennial	All	0.4 ± 0.3	0.5 ± 0.3	0.6 ± 0.4	0.6 ± 0.4	0.6 ± 0.4	0.1 ± 0.1	0	0.5 ± 0.5	0.1 ± 0.1	0
	Forbs	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	0	0	0 ± 0	0 ± 0	0
	Non-grass graminoids	0.3 ± 0.3	0.4 ± 0.3	0.4 ± 0.4	0.4 ± 0.4	0.5 ± 0.4	0.1 ± 0.1	0 ± 0	0.5 ± 0.5	0.1 ± 0.1	0
Perennial	All	88.9 ± 2.4	89.2 ± 2.4	79.6 ± 4.3	88.9 ± 3	87.4 ± 2.9	87.1 ± 3.2	93.5 ± 2.6	93.9 ± 2.7	94.4 ± 2.5	98.7 ± 1
	Ferns	58.2 ± 5.1	58.1 ± 5.2	56.4 ± 6.1	60.3 ± 5.9	60.4 ± 6	60.6 ± 6	52.5 ± 11.6	53.3 ± 12.5	52.5 ± 12.8	60.5 ± 11.7
	Forbs	0.9 ± 0.5	0.9 ± 0.5	0.8 ± 0.6	0.5 ± 0.4	0.8 ± 0.5	0.4 ± 0.4	0.9 ± 0.6	0.9 ± 0.6	1.9 ± 1.3	1.3 ± 1.2
	Grasses	0.7 ± 0.4	0.7 ± 0.4	0.7 ± 0.5	0.8 ± 0.5	0.7 ± 0.5	2.2 ± 1.5	0	0	0	0
	Non-grass graminoids	16.5 ± 3.9	17.4 ± 3.9	15 ± 4	17.6 ± 4.7	16.9 ± 4.4	17.1 ± 4.6	21.8 ± 8.7	21.4 ± 8.6	21 ± 8.5	19.8 ± 7.7
	Shrubs/subshrubs	20.3 ± 3.9	21.7 ± 3.8	16.2 ± 3.5	19.8 ± 4.4	18 ± 3.8	17.5 ± 3.9	28.1 ± 9.7	29 ± 10.2	29.5 ± 10.5	31.3 ± 11
	Tree	0	0	0	0	0	0	0	0	0	0

Table S3.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for native species in the control quadrats for plant cover. Na, not applicable.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = 0.13, *P* = 1.00	T (254) = 1.98, *P* = 0.11	T (254) = -1.88, *P* = 0.06
Annual/biennial	All	T (295) = 0.31, *P* = 1.00	T (254) = -0.38, *P* = 0.92	T (254) = 0.162, *P* = 0.87
	Forbs	T (295) = 0.11, *P* = 1.00	T (254) = -0.43, *P* = 0.90	T (254) = 0.09, *P* = 0.93
	Non-grass graminoids	na	na	na
Perennial	All	T (295) = 0.16, *P* = 1.00	T (254) = 2.01, *P* = 0.11	T (254) = -1.89, *P* = 0.06
	Ferns	T (295) = -0.76, *P* = 0.97	T (254) = 5.40, *P* = <0.01	T (254) = 0.59, *P* = 0.56
	Forbs	T (295) = 0.64, *P* = 0.99	T (254) = -0.40, *P* = 0.91	T (254) = -0.27, *P* = 0.79
	Grasses	na	na	na
	Non-grass graminoids	T (295) = -0.15, *P* = 1.00	T (254) = -1.25, *P* = 0.43	T (254) = -0.23, *P* = 0.82
	Shrubs/subshrubs	T (295) = 0.57, *P* = 0.99	T (254) = -1.55, *P* = 0.27	T (254) = -0.88, *P* = 0.38
	Tree	na	na	na

Table S4.1 **Cover** of **native** flora in the **autumn** burnt quadrats (% plant cover ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	86.1 ± 5.2	86.5 ± 5.8	13.8 ± 6.4	26.8 ± 10.9	51 ± 15.6	63 ± 13.4	25.8 ± 10	47.3 ± 7.8	89.5 ± 9.5	96.4 ± 3.2
Annual/biennial	All	0.9 ± 0.8	0.8 ± 0.8	1.3 ± 0.8	4 ± 1.3	0.2 ± 0.2	0	3.1 ± 1.6	4.3 ± 1.2	0.1 ± 0.1	0
	Forbs	0.1 ± 0.1	0	0	2.2 ± 1.4	0.2 ± 0.2	0	0 ± 0	1.8 ± 1.2	0.1 ± 0.1	0
	Non-grass graminoids	0.8 ± 0.8	0.8 ± 0.8	1.3 ± 0.8	1.8 ± 1.2	0	0	3.1 ± 1.6	2.5 ± 1.1	0	0
Perennial	All	85.5 ± 5.1	85.8 ± 5.7	12.5 ± 6.5	22.8 ± 10.4	50.8 ± 15.6	63 ± 13.4	22.6 ± 10.2	43 ± 7.5	89.5 ± 9.5	96.4 ± 3.2
	Ferns	71.4 ± 7	73.6 ± 6.9	0	0	0	0	0	0	0	0
	Forbs	1.2 ± 0.9	1.3 ± 0.9	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.8 ± 0.5	1.8 ± 0.9	1.3 ± 0.8	1.1 ± 0.6
	Grasses	0	0	0	0	0	0	0	0	0	0
	Non-grass graminoids	8.9 ± 3.7	8 ± 3.9	4.7 ± 1.1	7 ± 1.8	27 ± 12.2	13.7 ± 4.4	17 ± 8.7	15.8 ± 3.3	56 ± 13.6	48.9 ± 13.3
	Shrubs/subshrubs	14.1 ± 3.9	13.6 ± 4.1	7.7 ± 6.7	15.7 ± 8.8	29.2 ± 10.2	50 ± 13.6	4.9 ± 1.7	25.5 ± 7.6	50.4 ± 11.3	69.6 ± 11.5
	Tree	0	0	0	0	0	0	0	0	0	0

Table S4.2. Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for native species in the autumn quadrats for plant cover. Na, not applicable.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = 2.22, *P* = 0.23	T (254) = <0.01, *P* = 1.00	T (254) = -2.62, *P* = 0.01
Annual/biennial	All	T (295) = 0.19, *P* = 1.00	T (254) = <0.01, *P* = 1.00	T (254) = <0.01, *P* = 1.00
	Forbs	T (295) = <0.01, *P* = 1.00	T (254) = <0.01, *P* = 1.00	T (254) = <0.01, *P* = 1.00
	Non-grass graminoids	na	na	na
Perennial	All	T (295) = 1.56, *P* = 0.63	T (254) = -0.05, *P* = 1.00	T (254) = -2.59, *P* = 0.01
	Ferns	T (295) = 17.7, *P* = <0.01	T (254) = -5.01, *P* = 0.01	T (254) = 0.02, *P* = 0.98
	Forbs	T (295) = 2.19, *P* = 0.25	T (254) = 0.81, *P* = 0.70	T (254) = -0.76, *P* = 0.45
	Grasses	na	na	na
	Non-grass graminoids	T (295) = -5.01, *P* = 0.01	T (254) = 2.67, *P* = 0.02	T (254) = -2.55, *P* = 0.01
	Shrubs/subshrubs	T (295) = -5.96, *P* = 0.01	T (254) = 2.68, *P* = 0.02	T (254) = -0.66, *P* = 0.51
	Tree	na	na	na

Table S5.1 **Cover** of **native** flora in the **spring** burnt quadrats (% plant cover ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	88.4 ± 4.4	89 ± 4.5	12.4 ± 6.4	31.2 ± 11.8	25.1 ± 6.1	31.6 ± 6.5	29.6 ± 10.6	56.8 ± 12.9	53.4 ± 10.9	73.9 ± 10.9
Annual/biennial	All	0 ± 0	0.2 ± 0.2	1.5 ± 0.8	2.1 ± 0.8	1.1 ± 0.4	0.3 ± 0.2	0 ± 0	1.9 ± 0.9	0.8 ± 0.5	0.3 ± 0.2
	Forbs			0.6 ± 0.3	1.8 ± 0.8	0.4 ± 0.2	0.1 ± 0.1		1.6 ± 0.9	0.6 ± 0.5	0.3 ± 0.2
	Non-grass graminoids	0	0.2 ± 0.2	0.9 ± 0.8	0.3 ± 0.3	0.7 ± 0.4	0.2 ± 0.1	0	0.3 ± 0.2	0.2 ± 0.2	0
Perennial	All	88.4 ± 4.4	88.7 ± 4.5	10.9 ± 6.3	29.3 ± 11.8	24 ± 6.1	31.3 ± 6.5	29.6 ± 10.6	55.8 ± 12.7	53.1 ± 10.9	73.8 ± 10.9
	Ferns	62.3 ± 6.8	63.6 ± 6.6	0	0	0	0.8 ± 0.8	0.2 ± 0.1	0.2 ± 0.1	0	0.1 ± 0.1
	Forbs	0	0	0.1 ± 0.1	0.4 ± 0.3	1.3 ± 1.1	0.1 ± 0.1	0	0	3.3 ± 3.3	6 ± 5.6
	Grasses	0.7 ± 0.4	0.4 ± 0.3	0	0	1.2 ± 1	2.2 ± 1.8	1.5 ± 1.4	4.4 ± 4.2	2.3 ± 2.1	9.8 ± 9
	Non-grass graminoids	22 ± 5.6	21.3 ± 5.4	4.6 ± 2.3	8.7 ± 3.1	9.2 ± 2.3	9.1 ± 2.8	18.1 ± 7.4	30 ± 11.1	26.9 ± 8.6	34.9 ± 7.7
	Shrubs/subshrubs	18.4 ± 6.2	17.8 ± 6	6.2 ± 4.4	22.9 ± 11.5	12.3 ± 5.4	19 ± 7.3	10.9 ± 4.7	33.2 ± 11.7	31.2 ± 9.6	47 ± 13.7
	Tree	0	0	0	0	0	0.1 ± 0.1	0	0	0	0

Table S5.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for native species in the spring quadrats for plant cover. Na, not applicable.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = 9.96, *P* = <0.01	T (254) = 1.96, *P* = 0.12	T (254) = -4.03, *P* = 0.01
Annual/biennial	All	T (295) = -0.63, *P* = 0.99	T (254) = -0.38, *P* = 0.92	T (254) = 0.26, *P* = 0.80
	Forbs	T (295) = -0.28, *P* = 1.00	T (254) = -0.43, *P* = 0.90	T (254) = -0.23, *P* = 0.82
	Non-grass graminoids	na	na	na
Perennial	All	T (295) = 9.96, *P* = <0.01	T (254) = 1.94, *P* = 0.13	T (254) = -4.0, *P* = <0.01
	Ferns	T (295) = 21.9, *P* = <0.01	T (254) = -0.07, *P* = 0.10	T (254) = -2.45, *P* = 0.01
	Forbs	T (295) = -0.45, *P* = 1.00	T (254) = 0.46, *P* = 0.89	T (254) = -0.58, *P* = 0.56
	Grasses	na	na	na
	Non-grass graminoids	T (295) = 2.62, *P* = <0.01	T (254) = 1.47, *P* = 0.31	T (254) = -1.79, *P* = 0.07
	Shrubs/subshrubs	T (295) = -0.71, *P* = 0.98	T (254) = 1.41, *P* = 0.34	T (254) = -2.06, *P* = 0.04
	Tree	na	na	na

Table S6.1 Species **richness** of **native** flora in the **control** quadrats (mean species ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	3.3 ± 0.4	3.4 ± 0.4	3.1 ± 0.4	3 ± 0.4	3.2 ± 0.4	3 ± 0.3	4.1 ± 0.9	4.3 ± 1	4.5 ± 1	4 ± 0.8
Annual/biennial	All	0.1 ± 0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0	0.2 ± 0.1	0.1 ± 0	0	0.1 ± 0.1	0.1 ± 0.1	0
	Forbs	0	0.1 ± 0	0	0	0.1 ± 0	0	0	0	0	0
	Non-grass graminoids	0.1 ± 0	0.1 ± 0	0.1 ± 0.1	0	0.1 ± 0.1	0	0	0.1 ± 0.1	0.1 ± 0.1	0
Perennial	All	3.3 ± 0.4	3.2 ± 0.3	3 ± 0.4	3 ± 0.3	3 ± 0.4	2.9 ± 0.3	4.1 ± 0.9	4.1 ± 0.9	4.4 ± 1	4 ± 0.8
	Ferns	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0
	Forbs	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0	0.1 ± 0.1	0	0.3 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.1
	Grasses	0.1 ± 0	0.1 ± 0	0.1 ± 0.1	0.1 ± 0	0.1 ± 0.1	0.1 ± 0.1	0	0	0	0
	Non-grass graminoids	1.1 ± 0.2	0.9 ± 0.2	0.9 ± 0.1	0.9 ± 0.2	0.9 ± 0.2	0.9 ± 0.2	1.3 ± 0.5	1.3 ± 0.5	1.5 ± 0.5	1.4 ± 0.5
	Shrubs/subshrubs	1 ± 0.2	1.1 ± 0.2	0.9 ± 0.2	0.9 ± 0.2	0.9 ± 0.2	0.8 ± 0.2	1.6 ± 0.6	1.6 ± 0.6	1.6 ± 0.6	1.5 ± 0.5
	Tree	0	0	0	0	0	0	0	0	0	0

Table S6.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for richness of native flora.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = 1.01, *P* = 0.91	T (254) = -1.05, *P* = 0.55	T (254) = -0.34, *P* = 0.74
Annual/biennial	All	T (295) = 1.24, *P* = 0.82	T (254) = -1.00, *P* = 0.60	T (254) = 0.44, *P* = 0.66
	Forbs	T (295) = 0.37, *P* = 1.00	T (254) = 0.70, *P* = 0.76	T (254) = 0.12, *P* = 0.91
	Non-grass graminoids	na	na	na
Perennial	All	T (295) = 0.71, *P* = 0.98	T (254) = -0.91, *P* = 0.63	T (254) = -1.43, *P* = 0.15
	Ferns	na	na	na
	Forbs	T (295) = 0.65, *P* = 0.99	T (254) = -0.84, *P* = 0.68	T (254) = < -0.01, *P* = 1.00
	Grasses	T (295) = -0.92, *P* = 0.94	T (254) = -2.81, *P* = 0.02	T (254) = 1.28, *P* = 0.20
	Non-grass graminoids	T (295) = 0.04, *P* = 1.0	T (254) = -2.06, *P* = 0.10	T (254) = -1.16, *P* = 0.25
	Shrubs/subshrubs	T (295) = 1.38, *P* = 0.74	T (254) = -0.41, *P* = 0.91	T (254) = -1.42, *P* = 0.16
	Tree	na	na	na

Table S7.1 Species **richness** of **native** flora in the **autumn** burnt quadrats (mean species ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	3.4 ± 0.5	3.6 ± 0.6	4 ± 0.7	6.8 ± 1	6.5 ± 0.4	4.8 ± 0.2	4.5 ± 0.9	7.1 ± 1	7.4 ± 0.9	5.6 ± 0.7
Annual/biennial	All	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.7 ± 0.2	0.2 ± 0.2	0	0.4 ± 0.2	0.8 ± 0.2	0.1 ± 0.1	0
	Forbs	0.1 ± 0.1	0	0	0.3 ± 0.2	0.2 ± 0.2	0	0	0.3 ± 0.2	0.1 ± 0.1	0
	Non-grass graminoids	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.2	0	0	0.4 ± 0.2	0.5 ± 0.2	0	0
Perennial	All	3.3 ± 0.4	3.6 ± 0.5	3.7 ± 0.6	6.2 ± 1	6.3 ± 0.4	4.8 ± 0.2	4.1 ± 0.7	6.4 ± 0.9	7.3 ± 0.9	5.6 ± 0.7
	Ferns	1 ± 0	1 ± 0	0	0	0	0	0	0	0	0
	Forbs	0.2 ± 0.1	0.4 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.5 ± 0.3	0.8 ± 0.3	0.6 ± 0.3	0.5 ± 0.2
	Grasses	0	0	0	0	0	0	0	0	0	0
	Non-grass graminoids	1 ± 0.3	1.1 ± 0.3	2.7 ± 0.5	3.5 ± 0.6	3.2 ± 0.6	2 ± 0.4	2.5 ± 0.5	3.5 ± 0.5	3.6 ± 0.5	2.6 ± 0.5
	Shrubs/subshrubs	1.1 ± 0.2	1.1 ± 0.2	0.8 ± 0.3	2.5 ± 0.5	3 ± 0.4	2.7 ± 0.3	1.1 ± 0.3	2.1 ± 0.5	3 ± 0.5	2.5 ± 0.3
	Tree	0	0	0	0	0	0	0	0	0	0

Table S7.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for richness of native flora.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = -2.24, *P* = 0.22	T (254) = 1.59, *P* = 0.25	T (254) = -0.72, *P* = 0.47
Annual/biennial	All	T (295) = 1.10, *P* = 0.88	T (254) = < -0.01, *P* = 1.00	T (254) = < -0.01, *P* = 1.0
	Forbs	T (295) = 1.52, *P* = 0.65	T (254) = -0.65, *P* = 0.79	T (254) = < 0.01, *P* = 1.00
	Non-grass graminoids	na	na	na
Perennial	All	T (295) = -2.89, *P* = 0.05	T (254) = 1.69, *P* = 0.21	T (254) = -0.76, *P* = 0.45
	Ferns	na	na	na
	Forbs	T (295) = 2.19, *P* = 0.25	T (254) = 1.97, *P* = 0.12	T (254) = < -0.01, *P* = 0.81
	Grasses	na	na	na
	Non-grass graminoids	T (295) = -3.02, *P* = 0.03	T (254) = 2.42, *P* = 0.04	T (254) = -1.12, *P* = 0.26
	Shrubs/subshrubs	T (295) = -7.26, *P* = < 0.01	T (254) = 1.68, *P* = 0.22	T (254) = 0.26, *P* = 0.80
	Tree	na	na	na

Table S8.1 Species **richness** of **native** flora in the **spring** burnt quadrats (mean species ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	3.6 ± 0.4	3.8 ± 0.4	3.2 ± 0.6	3.1 ± 0.8	5.5 ± 0.6	4.7 ± 0.7	3.4 ± 0.6	4.7 ± 0.7	6.1 ± 0.9	5 ± 0.7
Annual/biennial	All	0	0	0.7 ± 0.2	0.6 ± 0.2	0.9 ± 0.2	0.3 ± 0.2	0	0.6 ± 0.2	0.5 ± 0.2	0.2 ± 0.1
	Forbs	0	0	0.4 ± 0.2	0.4 ± 0.2	0.4 ± 0.2	0.1 ± 0.1	0	0.3 ± 0.2	0.4 ± 0.2	0.2 ± 0.1
	Non-grass graminoids	0	0	0.3 ± 0.2	0.1 ± 0.1	0.5 ± 0.2	0.2 ± 0.1	0	0.2 ± 0.1	0.1 ± 0.1	0
Perennial	All	3.6 ± 0.4	3.8 ± 0.4	2.5 ± 0.6	2.6 ± 0.7	4.6 ± 0.6	4.4 ± 0.7	3.4 ± 0.6	4.1 ± 0.5	5.6 ± 0.8	4.8 ± 0.7
	Ferns	1 ± 0	1 ± 0	0	0	0	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0	0.1 ± 0.1
	Forbs	0	0	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0	0	0.1 ± 0.1	0.3 ± 0.1
	Grasses	0.1 ± 0.1	0.1 ± 0.1	0	0	0.3 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.4 ± 0.2
	Non-grass graminoids	1.8 ± 0.3	2 ± 0.2	1.3 ± 0.3	1.2 ± 0.3	2.5 ± 0.3	2 ± 0.4	1.9 ± 0.4	2.2 ± 0.3	3.1 ± 0.3	2.4 ± 0.4
	Shrubs/subshrubs	0.7 ± 0.2	0.7 ± 0.2	1.1 ± 0.4	1.1 ± 0.5	1.5 ± 0.4	1.9 ± 0.4	1.1 ± 0.4	1.4 ± 0.4	2.2 ± 0.6	1.7 ± 0.5
	Tree	0	0	0	0	0	0.1 ± 0.1	0	0	0	0

Table S8.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for richness of native flora.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = -1.80, *P* = 0.47	T (254) = 0.66, *P* = 0.79	T (254) = -0.18, *P* = 0.87
Annual/biennial	All	T (295) = -2.35, *P* = 0.18	T (254) = -0.97, *P* = 0.60	T (254) = 0.67, *P* = 0.51
	Forbs	T (295) = -0.94, *P* = 0.94	T (254) = < 0.01, *P* = 1.00	T (254) = 1.19, *P* = 0.24
	Non-grass graminoids	na	na	na
Perennial	All	T (295) = -1.32, *P* = 0.77	T (254) = 0.90, *P* = 0.64	T (254) = -0.50, *P* = 0.62
	Ferns	na	na	na
	Forbs	T (295) = -0.45, *P* = 1.00	T (254) = 1.29, *P* = 0.40	T (254) = -1.91, *P* = 0.06
	Grasses	T (295) = -1.08, *P* = 0.90	T (254) = -2.81, *P* = 0.02	T (254) = -1.34, *P* = 0.18
	Non-grass graminoids	T (295) = -0.73, *P* = 0.98	T (254) = 0.54, *P* = 0.85	T (254) = -0.81, *P* = 0.42
	Shrubs/subshrubs	T (295) = -5.17, *P* = < 0.01	T (254) = 1.40, *P* = 0.35	T (254) = 0.33, *P* = 0.74
	Tree	na	na	na

Table S9.1 **Cover** of **introduced** species in the **control** quadrats (% plant cover ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	1.8 ± 0.4	1.9 ± 0.5	2.3 ± 0.7	2.4 ± 0.6	2.7 ± 0.7	4 ± 1	0.6 ± 0.5	1.5 ± 1.5	1.5 ± 1	1.5 ± 1
Annual/biennial	All	1.5 ± 0.3	1.4 ± 0.3	1.5 ± 0.4	1.4 ± 0.3	1.5 ± 0.3	1.8 ± 0.6	0.6 ± 0.5	0.9 ± 0.9	1.4 ± 0.9	1.3 ± 0.9
	Forbs	0.4 ± 0.2	0.3 ± 0.1	0.4 ± 0.2	0.3 ± 0.1	0.5 ± 0.2	0.8 ± 0.4	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.1
	Grasses	1.1 ± 0.2	1.1 ± 0.2	1.1 ± 0.3	1 ± 0.2	1 ± 0.2	1 ± 0.4	0.5 ± 0.5	0.6 ± 0.6	1.1 ± 0.7	1.1 ± 0.8
Perennial	All	0.3 ± 0.2	0.5 ± 0.3	0.7 ± 0.5	1 ± 0.4	1.2 ± 0.5	2.2 ± 0.7	0 ± 0	0.6 ± 0.6	0.1 ± 0.1	0.3 ± 0.2
	Forbs	0.1 ± 0.1	0.1 ± 0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	1.1 ± 0.4	0 ± 0	0.6 ± 0.6	0.1 ± 0.1	0.3 ± 0.2
	Shrubs/subshrubs	0.2 ± 0.1	0.4 ± 0.3	0.6 ± 0.4	0.9 ± 0.3	1.0 ± 0.4	1.1 ± 0.5	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1

Table S9.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for introduced species in the control quadrats for plant cover.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = -0.18, *P* = 1.0	T (254) = -1.30, *P* = 0.40	T (254) = 1.29, *P* = 0.20
Annual/biennial	All	T (295) = -2.58, *P* = 0.11	T (254) = 0.32, *P* = 0.95	T (254) = 0.31, *P* = 0.76
	Forbs	T (295) = -0.14, *P* = 1.0	T (254) = 0.28, *P* = 0.96	T (254) = 0.16, *P* = 0.87
	Grasses	T (295) = 3.92, *P* = < 0.01	T (254) = 0.18, *P* = 0.98	T (254) = -0.06, *P* = 0.95
Perennial	All	T (295) = -2.57, *P* = 0.11	T (254) = -1.65, *P* = 0.23	T (254) = 1.43, *P* = 0.15
	Forbs	T (295) = -1.70, *P* = 0.54	T (254) = -0.96, *P* = 0.61	T (254) = 0.57, *P* = 0.57
	Shrubs/subshrubs	T (295) = -1.71, *P* = 0.53	T (254) = -0.74, *P* = 0.73	T (254) = 0.66, *P* = 0.51

Table S10.1 **Cover** of **introduced** species in the **autumn** burnt quadrats (% plant cover ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	Lifeform class	Unfenced						Fenced			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	2.3 ± 1.8	1.2 ± 0.9	1 ± 1	1 ± 1	1.8 ± 1.8	1.8 ± 1.8	0.5 ± 0.4	1 ± 1	2.1 ± 2.1	2.6 ± 2.6
Annual/biennial	All	1.6 ± 1.2	0.8 ± 0.6	0.3 ± 0.3	0.8 ± 0.8	1.7 ± 1.7	1.7 ± 1.7	0.3 ± 0.2	0.4 ± 0.4	2 ± 2	2.5 ± 2.5
	Forbs	0.7 ± 0.7	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0
	Grasses	0.9 ± 0.6	0.6 ± 0.6	0.3 ± 0.3	0.8 ± 0.8	1.7 ± 1.7	1.7 ± 1.7	0.1 ± 0.1	0.4 ± 0.4	2 ± 2	2.5 ± 2.5
Perennial	All	0.7 ± 0.5	0.4 ± 0.3	0.7 ± 0.7	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.6 ± 0.6	0.1 ± 0.1	0.1 ± 0.1
	Forbs	0.4 ± 0.3	0.4 ± 0.3	0.7 ± 0.7	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.6 ± 0.6	0.1 ± 0.1	0.1 ± 0.1
	Shrubs/subshrubs	0.3 ± 0.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Table S10.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for introduced species in the autumn quadrats for plant cover.

Longevity	Lifeform class	0.5 before vs 18 after (Unfenced; Control)	Control vs Spring (Fenced; 18 months)	Fenced vs Unfenced (Control; 18 months)
All	All	T (295) = 0.26, *P* = 1.0	T (254) = 0.04, *P* = 1.0	T (254) = -0.04, *P* = 0.97
Annual/biennial	All	T (295) = 0.51, *P* = 1.0	T (254) = 0.15, *P* =0.99	T (254) = -0.06, *P* = 0.95
	Forbs	T (295) = 0.44, *P* = 1.0	T (254) = -0.26, *P* =0.96	T (254) = < 0.01, *P* = 1.0
	Grasses	T (295) = -0.65, *P* = 0.99	T (254) = 0.38, *P* =0.92	T (254) = -0.10, *P* = 0.92
Perennial	All	T (295) = 0.51, *P* =1.0	T (254) = -0.06, *P* = 1.0	T (254) = 0.11, *P* = 0.91
	Forbs	T (295) = 0.43, *P* =1.0	T (254) = -0.03, *P* =1.0	T (254) = 0.08, *P* = 0.94
	Shrubs/subshrubs	T (295) = 0.04, *P* =1.0	T (254) = < 0.01, *P* = 1.0	T (254) = < 0.01, *P* = 1.0

Table S11.1 **Cover** of **introduced** species in the **spring** burnt quadrats (% plant cover ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	2 ± 0.7	2.5 ± 1	0.9 ± 0.4	2.2 ± 0.9	1.7 ± 0.7	2.7 ± 1.1	0.5 ± 0.5	1.8 ± 1.1	5.7 ± 2.1	3.6 ± 1.4
Annual/biennial	All	0.8 ± 0.4	0.6 ± 0.4	0.4 ± 0.2	0.8 ± 0.5	0.6 ± 0.4	0.5 ± 0.4	0.5 ± 0.5	0.8 ± 0.8	3.6 ± 1.7	1.4 ± 1
	Forbs	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.4	0 ± 0	0 ± 0	1.1 ± 0.7	0 ± 0
	Grasses	0.6 ± 0.4	0.4 ± 0.4	0.3 ± 0.2	0.6 ± 0.4	0.4 ± 0.4	0.1 ± 0.1	0.5 ± 0.5	0.8 ± 0.8	2.5 ± 1.1	1.4 ± 1
Perennial	All	1.2 ± 0.6	1.9 ± 0.9	0.5 ± 0.4	1.4 ± 0.8	1.1 ± 0.6	2.2 ± 0.9	0 ± 0	1 ± 0.7	2.1 ± 1	2.3 ± 1.2
	Forbs	0.9 ± 0.4	1.5 ± 0.7	0.1 ± 0.1	1 ± 0.8	0.7 ± 0.4	1.3 ± 0.6	0 ± 0	0.9 ± 0.7	1.5 ± 0.8	1.1 ± 0.6
	Shrubs/subshrubs	0.3 ± 0.3	0.4 ± 0.3	0.4 ± 0.4	0.4 ± 0.4	0.4 ± 0.4	0.9 ± 0.6	0 ± 0	0.1 ± 0.1	0.5 ± 0.4	1.2 ± 0.7

Table S11.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for introduced species in the spring quadrats for plant cover.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = -0.44, *P* = 1.0	T (254) = -1.29, *P* = 0.40	T (254) = -0.23, *P* = 0.82
Annual/biennial	All	T (295) = -1.47, *P* = 0.69	T (254) = 0.49, *P* = 0.87	T (254) = 0.39, *P* = 0.70
	Forbs	T (295) = 0.48, *P* = 1.0	T (254) = < 0.01, *P* = 1.00	T (254) = 0.29, *P* = 0.77
	Grasses	T (295) = 1.22, *P* = 0.83	T (254) = 0.60, *P* = 0.82	T (254) = -0.57, *P* = 0.57
Perennial	All	T (295) = -1.47, *P* = 0.69	T (254) = -1.71, *P* = 0.20	T (254) = 0.39, *P* = 0.70
	Forbs	T (295) = -0.81, *P* = 0.97	T (254) = -0.98, *P* = 0.60	T (254) = -0.08, *P* = 0.94
	Shrubs/subshrubs	T (295) = -1.25, *P* = 0.81	T (254) = -0.75, *P* = 0.73	T (254) = 0.28, *P* = 0.78

Table S12.1 Species **richness** of **introduced species** flora in the **control** quadrats (mean species m^{-2} ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	1 ± 0.2	1 ± 0.2	1.1 ± 0.3	1.2 ± 0.3	1.2 ± 0.3	1 ± 0.2	0.3 ± 0.2	0.4 ± 0.4	0.5 ± 0.3	0.5 ± 0.3
Annual/biennial	All	0.8 ± 0.2	0.7 ± 0.1	0.9 ± 0.2	0.8 ± 0.2	0.8 ± 0.2	0.4 ± 0.1	0.3 ± 0.2	0.3 ± 0.3	0.4 ± 0.3	0.4 ± 0.3
	Forbs	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
	Grasses	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.2
Perennial	All	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
	Forbs	0.1 ± 0	0.1 ± 0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
	Shrubs/subshrubs	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1

Table S12.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for richness of introduced flora.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = 0.81, *P* = 0.97	T (254) = -0.77, *P* = 0.72	T (254) = 1.09, *P* = 0.26
Annual/biennial	All	T (295) = 4.02, *P* = < 0.01	T (254) = 0.62, *P* = 0.81	T (254) = 0.20, *P* = 0.84
	Forbs	T (295) = 0.37, *P* = 1.00	T (254) = 0.70, *P* = 0.76	T (254) = 0.12, *P* = 0.91
	Grasses	T (295) = 7.12, *P* = < 0.01	T (254) = 0.31, *P* = 0.95	T (254) = 0.19, *P* = 0.85
Perennial	All	T (295) = -2.84, *P* = 0.05	T (254) = -1.90, *P* = 0.14	T (254) = 1.63, *P* = 0.10
	Forbs	T (295) = -3.63, *P* = < 0.01	T (254) = -1.75, *P* = 0.19	T (254) = 0.99, *P* = 0.32
	Shrubs/subshrubs	T (295) = -0.91, *P* = 0.94	T (254) = -1.42, *P* = 0.33	T (254) = 1.72, *P* = 0.09

Table S13.1 Species **richness** of **introduced species** flora in the **autumn** quadrats (mean species m^{-2} ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	0.6 ± 0.4	0.3 ± 0.2	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0.5 ± 0.4	0.4 ± 0.4	0.3 ± 0.3	0.3 ± 0.3
Annual/biennial	All	0.4 ± 0.3	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
	Forbs	0.2 ± 0.2	0.1 ± 0.1	0	0	0	0	0.1 ± 0.1	0	0	0
	Grasses	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Perennial	All	0.2 ± 0.2	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.3 ± 0.3	0.1 ± 0.1	0.1 ± 0.1
	Forbs	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.3 ± 0.3	0.1 ± 0.1	0.1 ± 0.1
	Shrubs/subshrubs	0.1 ± 0.1	0	0	0	0	0	0	0	0	0

Table S13.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for richness of introduced flora.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = 1.47, *P* = 0.68	T (254) = -0.44, *P* = 0.90	T (254) = 0.14, *P* = 0.89
Annual/biennial	All	T (295) = 1.41, *P* = 0.72	T (254) = -0.74, *P* = 0.74	T (254) = 0.11, *P* = 0.91
	Forbs	T (295) = 1.52, *P* = 0.65	T (254) = -0.65, *P* = 0.79	T (254) = < 0.01, *P* = 1.00
	Grasses	T (295) = 0.36, *P* = 1.00	T (254) = -0.53, *P* = 0.86	T (254) = 0.16, *P* = 0.87
Perennial	All	T (295) = 1.00, *P* = 0.92	T (254) = < -0.01, *P* = 1.00	T (254) = 0.11, *P* = 0.91
	Forbs	T (295) = 1.12, *P* = 0.87	T (254) = < -0.01, *P* = 1.00	T (254) = 0.19, *P* = 0.85
	Shrubs/subshrubs	T (295) = < 0.01, *P* = 1.00	T (254) = < 0.01, *P* = 1.00	T (254) = < -0.01, *P* = 1.00

Table S14.1 Species **richness** of **introduced species** flora in the **spring** quadrats (mean species m^{-2} ± SE). Cell shading has been weighted per row, such that within a row the largest value(s) will have the darkest shading and the smallest value(s) will be white.

Longevity	**Lifeform class**	**Unfenced**						**Fenced**			
		-2.5	-0.5	2.5	4.5	10	18	2.5	4.5	10	18
All	All	0.4 ± 0.1	0.4 ± 0.2	0.5 ± 0.2	0.9 ± 0.4	0.9 ± 0.3	1.1 ± 0.4	0.1 ± 0.1	0.4 ± 0.2	1.7 ± 0.6	0.9 ± 0.3
Annual/biennial	All	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.7 ± 0.3	0.2 ± 0.1
	Forbs	0	0	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.2	0	0	0.4 ± 0.2	0
	Grasses	0.1 ± 0.1	0	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.2 ± 0.1
Perennial	All	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.6 ± 0.3	0.8 ± 0.2	0	0.3 ± 0.2	1 ± 0.4	0.7 ± 0.3
	Forbs	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.4 ± 0.2	0.4 ± 0.2	0	0.2 ± 0.1	0.7 ± 0.3	0.5 ± 0.2
	Shrubs/subshrubs	0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.4 ± 0.2	0	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.1

Table S14.2 Statistical differences between the first and last survey, between fenced and unfenced, and between seasons for richness of introduced flora.

Longevity	**Lifeform class**	**0.5 before vs 18 after (Unfenced; Control)**	**Control vs Spring (Fenced; 18 months)**	**Fenced vs Unfenced (Control; 18 months)**
All	All	T (295) = -2.09, *P* = 0.29	T (254) = -1.24, *P* = 0.43	T (254) = 0.38, *P* = 0.70
Annual/biennial	All	T (295) = -0.53, *P* = 0.99	T (254) = -0.18, *P* = 0.98	T (254) = 0.40, *P* = 0.69
	Forbs	T (295) = -0.94, *P* = 0.94	T (254) = < 0.01, *P* = 1.00	T (254) = 1.19, *P* = 0.24
	Grasses	T (295) = 0.24, *P* = 1.00	T (254) = -0.26, *P* = 0.96	T (254) = -0.40, *P* = 0.69
Perennial	All	T (295) = -3.00, *P* = 0.03	T (254) = -1.90, *P* = 0.14	T (254) = 0.24, *P* = 0.81
	Forbs	T (295) = -1.82, *P* = 0.45	T (254) = -1.75, *P* = 0.19	T (254) = -0.31, *P* = 0.76
	Shrubs/subshrubs	T (295) = -2.91, *P* = 0.04	T (254) = -1.42, *P* = 0.33	T (254) = 0.70, *P* = 0.48

Table S15. Statistical differences due to the effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **cover 4.5 months** after fire using generalised linear mixed models.

Longevity & lifeform class/species	**C(F*U)**	**F(C*S)**	**S(F*U)**	**F(C*A)**	**A(F*U)**	**F(A*S)**
All natives	T(254) =-0.58, P =0.56	T(254) =2.87, P =0.01	T(254) =-2.05, P =0.04	T(254) =-3.53, P =0.01	T(254) =-1.05, P =0.29	T(254) =-0.88, P =0.65
All annual/biennial natives	T(254) =-1.36, P =0.89	T(254) =-0.92, P =0.63	T(254) =4.72, P =0.64	T(254) =2.6, P =0.02	T(254) =0.41, P =0.68	T(254) =1.75, P =0.19
Forbs	T(253) =1.09, P =0.91	T(253) =-0.97, P =0.59	T(253) =4.78, P =0.63	T(253) =0.75, P =0.74	T(253) =0.28, P =0.78	T(253) =-0.2, P =0.98
Non-grass graminoids	na	na	na	na	na	na
Drosera binata	na	na	T(21) =0.43, P =0.67	na	T(21) =< 0.01, P =1.00	T() =0.32, P =0.75
All perennial natives	T(254) =-0.56, P =0.58	T(254) =3.17, P =< 0.01	T(254) =-1.82, P =0.07	T(254) =-3.71, P =< 0.01	T(254) =-1.13, P =0.26	T(254) =-0.75, P =0.73
Ferns	T(253) =1.42, P =0.16	T(253) =4.85, P =< 0.01	T(253) =0.37, P =0.71	T(253) =-4.72, P =< 0.01	T(253) =0.01, P =0.98	T(253) =-0.24, P =0.97
Gleichenia microphylla	T(120) =1.28, P =0.20	T(120) =2.40, P =0.02	T(120) =-0.60, P =0.55	na	na	na
Forbs	T(253) =-0.48, P =0.63	T(253) =0.54, P =0.85	T(253) =0.44, P =0.66	T(253) =0.67, P =0.78	T(253) =-0.85, P =0.39	T(253) =1.24, P =0.43
Grasses	T(253) =1.66, P =0.87	T(253) =4.54, P =0.89	T(253) =-0.46, P =0.64	T(253) =< 0.01, P =1.00	T(253) =-2.61, P =1.00	T(253) =-0.45, P =0.89
Non-grass graminoids	T(253) =-0.3, P =0.76	T(253) =1.46, P =0.31	T(253) =-0.46, P =0.64	T(253) =-0.11, P =0.99	T(253) =-0.26, P =0.80	T(253) =-1.48, P =0.3
Baumea rubiginosa	T(114) =1.91, P =0.06	T(114) =0.20, P =0.98	T(114) =-0.50, P =0.62	T(114) =0.74, P =0.74	T(114) =-0.39, P =0.70	T(114) =0.74, P =0.74
Baumea tetragona	T(110) =0.88, P =0.38	T(110) =2.02, P =0.11	T(110) =-0.05, P =0.96	T(110) =-0.72, P =0.75	T(110) =-0.92, P =0.36	T(110) =1.62, P =0.24
Empodisma minus	T(49) =0.62, P =0.54	T(49) =0.37, P =0.93	T(49) =-1.14, P =0.26	T(49) =-0.66, P =0.79	T(49) =-0.16, P =0.87	T(49) =-0.91, P =0.63
Gahnia sieberiana	T(75) =-0.91, P =0.37	T(75) =1.17, P =0.25	T(75) =-0.81, P =0.42	T(75) =-1.33, P =0.39	na	T(75) =0.23, P =0.97
Shrubs/subshrubs	T(253) =-0.22, P =0.82	T(253) =0.58, P =0.83	T(253) =0.35, P =0.73	T(253) =0.28, P =0.96	T(253) =-0.51, P =0.61	T(253) =0.88, P =0.66
Acacia provincialis	T(37) =-0.68, P =0.50	T(37) =3.19, P =< 0.01	T(37) =-0.03, P =0.98	na	na	na
Hibbertia tenuis	T(93) =0.26, P =0.79	T(93) =0.75, P =0.74	T(93) =-1.33, P =0.19	T(93) =-0.13, P =0.99	T(93) =-0.45, P =0.65	T(93) =0.61, P =0.81
Leptospermum continentale	T(253) =2.21, P =0.03	T(253) =0.30, P =0.95	T(253) =1.21, P =0.23	T(253) =1.8, P =0.17	T(253) =-0.22, P =0.83	T(253) =1.57, P =0.26
Sprengelia incarnata	T(253) =0.16, P =0.87	T(253) =0.20, P =0.98	T(253) =-0.21, P =0.83	T(253) =0.59, P =0.82	T(253) =0.27, P =0.79	T(253) =0.41, P =0.91
Viminaria juncea	T(48) = -0.20, P =0.84	T(48) =0.36, P =0.93	T(48) = 0.47, P =0.64	T(48) =< -1.76, P =0.19	T(48) = 0.15, P =0.88	T(48) =-2.33, P =0.06
Trees	na	na	na	na	na	na
All introduced	T(254) =1.72, P =0.09	T(254) =0.02, P =1.00	T(254) =1.25, P =0.21	T(254) =-0.01, P =1.00	T(254) =0.12, P =0.91	T(254) =-0.03, P =1.00
All annual/biennial introduced	T(254) =1.69, P =0.09	T(254) =0.09, P =1.00	T(254) =0.67, P =0.50	T(254) =-0.13, P =0.99	T(254) =0.41, P =0.68	T(254) =-0.05, P =1.00
Forbs	T(253) =2.47, P =0.81	T(253) =2.97, P =0.95	T(253) =0.51, P =0.61	T(253) =-0.29, P =0.96	T(253) =< 0.01, P =1.00	T(253) =< -0.01, P =1.00
Leontodon taraxacoides	T(46) =-4.41, P =< 0.01	T(46) =3.97, P =< 0.01	T(46) =0.47, P =0.64	na	na	na
Lotus pedunculatus	T(253) =0.13, P =0.89	T(253) =0.33, P =0.94	T(253) =0.26, P =0.79	T(253) =-0.32, P =0.95	T(253) =< 0.01, P =1.00	T(253) =< -0.01, P =1.00
Grasses	T(253) =1.36, P =0.18	T(253) =0.15, P =0.99	T(253) =0.29, P =0.77	T(253) =-0.28, P =0.86	T(253) =0.47, P =0.64	T(253) =-0.15, P =1.00
Holcus lanatus	T(26) =0.89, P =0.38	T(26) =0.56, P =0.84	T(26) =< 0.01, P =1.00	T(26) =1.76, P =0.19	T(26) =0.32, P =0.75	T(26) =0.04, P =0.04
All perennial introduced	T(254) =0.56, P =0.58	T(254) =0.07, P =1.00	T(254) =1.01, P =0.31	T(254) =0.08, P =1.00	T(254) =-0.11, P =0.92	T(254) =0.01, P =1.00
Forbs	T(253) =-0.12, P =0.91	T(253) =2.49, P =0.97	T(253) =0.26, P =0.79	T(253) =< -0.01, P =1.00	T(253) =0.01, P =0.99	T(253) =-0.25, P =0.97
Shrubs/subshrubs	T(253) =6.43, P =0.52	T(253) =2.11, P =0.98	T(253) =0.05, P =0.96	T(253) =< -0.01, P =1.00	T(253) =< 0.01, P =0.99	T(253) =-0.21, P =0.98
Rubus anglocandicans	T(253) =0.57, P =0.57	T(253) =< 0.01, P =1.00	T(253) =0.29, P =0.77	T(253) =< 0.01, P =1.00	T(253) =< -0.01, P =1.00	T(253) =< -0.01, P =1.00

Table S16. Statistical differences due to the effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **cover 18 months** after fire using generalised linear mixed models.

Longevity & lifeform class/species	**C(F*U)**	**F(C*S)**	**S(F*U)**	**F(C*A)**	**A(F*U)**	**F(A*S)**
All natives	T(254) =-1.88, *P* =0.06	T(254) =1.98, *P* =0.19	T(254) =-3.99, *P* =< 0.01	T(254) =< -0.01, *P* =1.00	T(254) =-2.62, *P* =0.01	T(254) =1.96, *P* =0.12
All annual/biennial natives	T(254) =0.16, *P* =0.87	T(254) =-0.38, *P* =0.92	T(254) =0.26, *P* =0.80	T(254) =< 0.01, *P* =1.00	T(254) =< -0.01, *P* =1.00	T(254) =-0.38, *P* =0.92
Forbs	T(253) =0.09, *P* =0.93	T(253) =-0.42, *P* =0.90	T(253) =-0.23, *P* =0.82	T(253) =< 0.01, *P* =1.00	T(253) =< -0.01, *P* =1.00	T(253) =-0.43, *P* =0.90
Non-grass graminoids	na	na	na	na	na	na
Drosera binata	na	na	T() =-2.61, *P* =0.02	na	T() =-0.42, *P* =0.68	T(21) =< -0.01, *P* =1.00
All perennial natives	T(254) =-1.89, *P* =0.06	T(254) =2.01, *P* =0.13	T(254) =-3.96, *P* =< 0.01	T(254) =-0.05, *P* =1.00	T(254) =-2.56, *P* =0.01	T(254) =1.94, *P* =0.13
Ferns	T(253) =0.59, *P* =0.56	T(253) =5.40, *P* =< 0.01	T(253) =-2.45, *P* =0.01	T(253) =-5.01, *P* =< 0.01	T(253) =0.02, *P* =0.98	T(253) =-0.07, *P* =1.00
Gleichenia microphylla	T() =0.80, *P* =0.43	T() =3.60, *P* =< 0.01	T() =-1.25, *P* =0.22	na	na	na
Forbs	T(253) =-0.27, *P* =0.79	T(253) =-0.40, *P* =0.91	T(253) =-0.58, *P* =0.56	T(253) =0.81, *P* =0.70	T(253) =-0.76, *P* =0.45	T(253) =0.46, *P* =0.89
Grasses	T(253) =0.34, *P* =0.73	T(253) =-1.10, *P* =0.51	T(253) =-0.73, *P* =0.47	T(253) =< -0.01, *P* =1.00	T(253) =< -0.01, *P* =1.00	T(253) =-1.10, *P* =0.51
Non-grass graminoids	T(253) =-0.23, *P* =0.82	T(253) =-1.24, *P* =0.43	T(253) =-1.79, *P* =0.74	T(253) =2.67, *P* =0.02	T(253) =-2.55, *P* =0.01	T(253) =1.46, *P* =0.31
Baumea rubiginosa	T(114) =2.21, *P* =0.03	T(114) =-0., *P* =0.98	T(114) =-0.25, *P* =0.81	T(114) =2.28, *P* =0.06	T(114) =-0.47, *P* =0.64	T(114) =2.85, *P* =0.01
Baumea tetragona	T(110) =0.65, *P* =0.52	T(110) =-0., *P* =0.97	T(110) =-1.39, *P* =0.17	T(110) =-2.19, *P* =0.08	T(110) =-0.67, *P* =0.50	T(110) =2.64, *P* =0.03
Empodisma minus	T(49) =0.56, *P* =0.58	T(49) =-1.096, *P* =0.52	T(49) =-1.94, *P* =0.06	T(49) =0.15, *P* =1.00	T(49) =-2.00, *P* =0.05	T(49) =-1.18, *P* =0.47
Gahnia sieberiana	T(75) =-0.50, *P* =0.62	T(75) =-1.702, *P* =0.22	T(75) =-0.87, *P* =0.39	T(75) =-0.09, *P* =1.00	na	T(75) =1.25, *P* =0.43
Shrubs/subshrubs	T(253) =-0.88, *P* =0.38	T(253) =-1.54, *P* =0.27	T(253) =-2.06, *P* =0.04	T(253) =2.67, *P* =0.02	T(253) =-0.66, *P* =0.51	T(253) =1.41, *P* =0.34
Acacia provincialis	T() =-0.84, *P* =0.40	T() =-3.20, *P* =< 0.01	T() =0.44, *P* =0.66	na	na	na
Hibbertia tenuis	T(93) =-0.10, *P* =0.92	T(93) =-1.04, *P* =0.55	T(93) =-3.81, *P* =< 0.01	T(93) =2.17, *P* =0.08	T(93) =-1.80, *P* =0.07	T(93) =1.28, *P* =0.41
Leptospermum continentale	T(253) =1.50, *P* =0.13	T(253) =-1.67, *P* =0.22	T(253) =0.07, *P* =0.95	T(253) =3.05, *P* =0.01	T(253) =0.34, *P* =0.74	T(253) =1.61, *P* =0.24
Sprengelia incarnata	T(253) =0.08, *P* =0.93	T(253) =-0.25, *P* =0.97	T(253) =0.07, *P* =0.94	T(253) =3.00, *P* =0.01	T(253) =-0.30, *P* =0.77	T(253) =2.97, *P* =< 0.01
Viminaria juncea	T(48) =< -0.01, *P* =1.00	T(48) =-2.35, *P* =0.06	T(48) =-2.23, *P* =0.03	T(48) =0.81, *P* =0.70	T(48) =-1.76, *P* =0.09	T(48) =-2.99, *P* =0.01
Trees	na	na	na	na	na	na
All introduced	T(254) =1.29, *P* =0.20	T(254) =-1.30, *P* =0.40	T(254) =-0.23, *P* =0.82	T(254) =0.04, *P* =1.00	T(254) =-0.04, *P* =0.97	T(254) =-1.29, *P* =0.40
All annual/biennial introduced	T(254) =0.30, *P* =0.76	T(254) =-0.32, *P* =0.95	T(254) =-0.39, *P* =0.70	T(254) =0.15, *P* =0.99	T(254) =-0.06, *P* =0.95	T(254) =0.49, *P* =0.87
Forbs	T(253) =0.16, *P* =0.87	T(253) =-0.24, *P* =0.96	T(253) =-0.29, *P* =0.77	T(253) =-0.26, *P* =0.96	T(253) =< 0.01, *P* =1.00	T(253) =5.46, *P* =1.00
Leontodon taraxacoides	T(46) =0.45, *P* =0.65	T(46) =-2.13, *P* =0.04	T(46) =-1.22, *P* =0.23	na	na	na
Lotus pedunculatus	T(253) =0.52, *P* =0.60	T(253) =< -0.01, *P* =1.00	T(253) =< -0.01, *P* =1.00	T(253) =< 0.01, *P* =1.00	T(253) =< 0.01, *P* =1.00	T(253) =< -0.01, *P* =1.00
Grasses	T(253) =-0.05, *P* =0.95	T(253) =0.18, *P* =0.98	T(253) =-0.57, *P* =0.57	T(253) =0.38, *P* =0.92	T(253) =-0.10, *P* =0.92	T(253) =0.60, *P* =0.82
Holcus lanatus	T(26) =1.37, *P* =0.18	T(26) =-2.94, *P* =0.01	T(26) =< -0.01, *P* =1.00	T(26) =2.78, *P* =0.02	T(26) =0.59, *P* =0.56	T(26) =5.70, *P* =< 0.01
All perennial introduced	T(254) =1.42, *P* =0.15	T(254) =-1.65, *P* =0.23	T(254) =0.36, *P* =0.70	T(254) =-0.06, *P* =1.00	T(254) =0.11, *P* =0.91	T(254) =-1.71, *P* =0.20
Forbs	T(253) =0.56, *P* =0.57	T(253) =-0.95, *P* =0.61	T(253) =-0.08, *P* =0.94	T(253) =-0.03, *P* =1.00	T(253) =0.08, *P* =0.94	T(253) =-0.98, *P* =0.59
Shrubs/subshrubs	T(253) =0.66, *P* =0.51	T(253) =-0.75, *P* =0.73	T(253) =-0.28, *P* =0.78	T(253) =< -0.01, *P* =1.00	T(253) =< 0.01, *P* =1.00	T(253) =-0.75, *P* =0.73
Rubus anglocandicans	T(253) =0.56, *P* =0.57	T(253) =-0.48, *P* =0.88	T(253) =-0.63, *P* =0.53	T(253) =< 0.01, *P* =1.00	T(253) =< -0.01, *P* =1.00	T(253) =-0.48, *P* =0.88

Table S17. Statistical differences due to the effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **richness 4.5 months** after fire using generalised linear mixed models.

Longevity & lifeform class/species	**C(F*U)**	**F(C*S)**	**S(F*U)**	**F(C*A)**	**A(F*U)**	**F(A*S)**
All natives	T(254) =-1.48, *P* =0.14	T(254) =-0.10, *P* =1.00	T(254) =-1.24, *P* =0.21	T(254) =2.81, *P* =0.01	T(254) =-0.26, *P* =0.79	T(254) =2.87, *P* =0.01
All annual/biennial natives	T(254) =-0.33, *P* =0.74	T(254) =-2.18, *P* =0.08	T(254) =2.91, *P* =0.77	T(254) =3.08, *P* =0.01	T(254) =-0.38, *P* =0.70	T(254) =1.03, *P* =0.56
Forbs	T(254) =0.30, *P* =0.77	T(254) =-2.11, *P* =0.09	T(254) =0.84, *P* =0.4	T(254) =1.66, *P* =0.22	T(254) =0.51, *P* =0.61	T(254) =-0.38, *P* =0.92
Non-grass graminoids	na	na	na	na	na	na
All perennial natives	T(254) =-1.5, *P* =0.13	T(254) =0.37, *P* =0.93	T(254) =-1.41, *P* =0.16	T(254) =2.33, *P* =0.05	T(254) =-0.20, *P* =0.84	T(254) =2.84, *P* =0.01
Ferns	na	na	na	na	na	na
Forbs	T(254) =< 0.01, *P* =1.00	T(254) =1.34, *P* =0.38	T(254) =-0.28, *P* =0.78	T(254) =2.63, *P* =0.02	T(254) =< 0.01, *P* =1	T(254) =4.10, *P* =< 0.01
Grasses	T(254) =0.64, *P* =0.52	T(254) =-2.00, *P* =0.12	T(254) =-2.18, *P* =0.03	T(254) =-0.01, *P* =1.00	T(254) =< 0.01, *P* =1	T(254) =-1.98, *P* =0.12
Non-grass graminoids	T(254) =0.86, *P* =0.39	T(254) =-1.88, *P* =0.15	T(254) =-1.87, *P* =0.06	T(254) =4.36, *P* =< 0.01	T(254) =< -0.01, *P* =1	T(254) =2.73, *P* =0.02
Shrubs/subshrubs	T(254) =-1.46, *P* =0.15	T(254) =0.94, *P* =0.62	T(254) =-0.07, *P* =0.94	T(254) =0.84, *P* =0.67	T(254) =0.58, *P* =0.56	T(254) =1.83, *P* =0.16
Tree	na	na	na	na	na	na
All Introduced	T(254) =1.84, *P* =0.07	T(254) =0.21, *P* =0.98	T(254) =1.13, *P* =0.26	T(254) =< 0.01, *P* =1.00	T(254) =-0.07, *P* =0.95	T(254) =0.21, *P* =0.98
All annual/biennial introduced	T(254) =2.12, *P* =0.04	T(254) =0.65, *P* =0.80	T(254) =1.33, *P* =0.18	T(254) =-0.37, *P* =0.93	T(254) =0.11, *P* =0.91	T(254) =0.25, *P* =0.97
Forbs	T(254) =0.81, *P* =0.42	T(254) =0.80, *P* =0.71	T(254) =1.46, *P* =0.14	T(254) =-0.65, *P* =0.79	T(254) =< -0.01, *P* =1	T(254) =0.11, *P* =0.99
Grasses	T(254) =2.36, *P* =0.02	T(254) =0.26, *P* =0.96	T(254) =0.67, *P* =0.51	T(254) =< 0.01, *P* =1.00	T(254) =0.16, *P* =0.87	T(254) =0.26, *P* =0.96
All perennial Introduced	T(254) =0.98, *P* =0.33	T(254) =-0.30, *P* =0.95	T(254) =0.56, *P* =0.58	T(254) =0.37, *P* =0.93	T(254) =-0.23, *P* =0.82	T(254) =0.09, *P* =1.00
Forbs	T(254) =-0.11, *P* =0.91	T(254) =-0.16, *P* =0.99	T(254) =0.82, *P* =0.41	T(254) =0.62, *P* =0.81	T(254) =-0.38, *P* =0.7	T(254) =0.48, *P* =0.88
Shrubs/subshrubs	T(254) =1.72, *P* =0.09	T(254) =-0.38, *P* =0.92	T(254) =0.07, *P* =0.95	T(254) =-0.01, *P* =1.00	T(254) =< -0.01, *P* =1.00	T(254) =-0.38, *P* =0.92

Table S18. Statistical differences due to the effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on plant **richness 18 months** after fire using generalised linear mixed models.

Longevity & lifeform class/species	**C(F*U)**	**F(C*S)**	**S(F*U)**	**F(C*A)**	**A(F*U)**	**F(A*S)**
All natives	T(254) =-1.26, *P* =0.21	T(254) =-1.05, *P* =0.55	T(254) =-0.34, *P* =0.74	T(254) =1.59, *P* =0.25	T(254) =-0.72, *P* =0.47	T(254) =0.66, *P* =0.79
All annual/biennial natives	T(254) =0.44, *P* =0.66	T(254) =-1.00, *P* =0.60	T(254) =0.67, *P* =0.51	T(254) =< -0.01, *P* =1.00	T(254) =< -0.01, *P* =1.00	T(254) =-0.97, *P* =0.60
Forbs	T(254) =0.30, *P* =0.77	T(254) =-1.30, *P* =0.40	T(254) =-0.63, *P* =0.53	T(254) =< -0.01, *P* =1.00	T(254) =< -0.01, *P* =1.00	T(254) =-1.30, *P* =0.40
Non-grass graminoids	na	na	na	na	na	na
All perennial natives	T(254) =-1.43, *P* =0.15	T(254) =-0.91, *P* =0.63	T(254) =-0.50, *P* =0.62	T(254) =1.69, *P* =0.25	T(254) =-0.76, *P* =0.45	T(254) =0.90, *P* =0.64
Ferns	na	na	na	na	na	na
Forbs	T(254) =< -0.01, *P* =1.00	T(254) =-0.84, *P* =0.68	T(254) =-1.91, *P* =0.06	T(254) =1.97, *P* =0.20	T(254) =< -0.01, *P* =0.81	T(254) =1.29, *P* =0.40
Grasses	T(254) =1.28, *P* =0.20	T(254) =-2.81, *P* =0.02	T(254) =-1.34, *P* =0.18	T(254) =< -0.01, *P* =1.00	T(254) =< 0.01, *P* =1.00	T(254) =-2.81, *P* =0.02
Non-grass graminoids	T(254) =-1.16, *P* =0.25	T(254) =-2.06, *P* =0.10	T(254) =-0.81, *P* =0.42	T(254) =2.42, *P* =0.42	T(254) =-1.12, *P* =0.26	T(254) =0.54, *P* =0.85
Shrubs/subshrubs	T(254) =-1.42, *P* =0.16	T(254) =-0.41, *P* =0.91	T(254) =-0.33, *P* =0.74	T(254) =1.68, *P* =0.32	T(254) =0.26, *P* =0.80	T(254) =1.40, *P* =0.35
Tree	na	na	na	na	na	na
All introduced	T(254) =1.09, *P* =0.26	T(254) =0.77, *P* =0.72	T(254) =-0.38, *P* =0.70	T(254) =-0.44, *P* =0.30	T(254) =0.14, *P* =0.89	T(254) =-1.24, *P* =0.43
All annual/biennial introduced	T(254) =0.2, *P* =0.84	T(254) =0.62, *P* =0.81	T(254) =-0.40, *P* =0.69	T(254) =-0.74, *P* =0.20	T(254) =0.11, *P* =0.91	T(254) =-0.18, *P* =0.98
Forbs	T(254) =0.12, *P* =0.91	T(254) =0.70, *P* =0.76	T(254) =-1.19, *P* =0.24	T(254) =-0.65, *P* =< 0.01	T(254) =< -0.01, *P* =1.00	T(254) =< 0.01, *P* =1.00
Grasses	T(254) =0.19, *P* =0.85	T(254) =0.31, *P* =0.95	T(254) =-0.40, *P* =0.69	T(254) =-0.53, *P* =0.20	T(254) =0.16, *P* =0.87	T(254) =-0.26, *P* =0.96
All perennial introduced	T(254) =1.63, *P* =0.10	T(254) =-1.90, *P* =0.14	T(254) =-0.24, *P* =0.81	T(254) =< -0.01, *P* =1.20	T(254) =0.11, *P* =0.91	T(254) =-1.90, *P* =0.14
Forbs	T(254) =0.99, *P* =0.32	T(254) =-1.75, *P* =0.19	T(254) =-0.31, *P* =0.76	T(254) =< -0.01, *P* =1.20	T(254) =0.19, *P* =0.85	T(254) =-1.75, *P* =0.19
Shrubs/subshrubs	T(254) =1.72, *P* =0.09	T(254) =-1.42, *P* =0.33	T(254) =-0.70, *P* =0.48	T(254) =< 0.01, *P* =1.00	T(254) =< -0.01, *P* =1.00	T(254) =-1.42, *P* =0.33

Table S19. Effect of season (C = “unburnt control”, A = “autumn burn”, S = “spring burn”) and fencing (F = “fenced”, U = “unfenced”) on *H. tenuis* plant counts (Mean species ± SE) across each survey date (TSF = “time since fire” in months) using generalised linear mixed models.

TSF	FC	FA	FS	UC	UA	US	Significantly different (*p* value)
-2.5	na	na	na	0.58 ± 0.17	0.29 ± 0.23	0.43 ± 0.19	Unfenced(Autumn - Control; T (103) = -1.04, *P* = 0.56) Unfenced(Autumn - Spring; T (103) = -0.48, *P* = 0.88) Unfenced(Control - Spring; T (103) = 0.61, *P* = 0.82) Unfenced(Autumn - Control; T (103) = -1.47, *P* = 0.31)
-0.5	na	na	na	0.62 ± 0.17	0.18 ± 0.25	0.38 ± 0.19	Unfenced(Autumn - Spring; T (103) = -0.65, *P* = 0.79) Unfenced(Control - Spring; T (103) = 0.96, *P* = 0.61) Unfenced(Autumn - Control; T (204) = -0.63, *P* = 0.80)
2.5	2.00 ± 1.46	1.75 ± 0.73	1.08 ± 0.59	0.60 ± 0.44	0.60 ± 0.44	0.67 ± 0.69	Unfenced(Autumn - Spring; T (204) = -0.61, *P* = 0.81) Unfenced(Control - Spring; T (204) = -0.08, *P* = 1.00) Fenced(Autumn - Control; T (204) = -0.15, *P* = 0.99) Fenced(Autumn - Spring; T (204) = 0.71, *P* = 0.76) Fenced(Control - Spring; T (204) = 0.58, *P* = 0.83) Autumn(Fenced vs Unfenced; T (204) = -1.57, *P* = 0.12) Control(Fenced vs Unfenced; T (204) = -0.92, *P* = 0.36) Spring(Fenced vs Unfenced; T (204) = -0.46, *P* = 0.65)
4.5	2.00 ± 1.46	3.25 ± 0.73	2.43 ± 0.62	0.45 ± 0.44	1.50 ± 0.84	1.33 ± 0.75	Unfenced(Autumn - Control; T (204) = 1.10, *P* = 0.51) Unfenced(Autumn - Spring; T (204) = 0.15, *P* = 0.99) Unfenced(Control - Spring; T (204) = -1.00, *P* = 0.57) Fenced(Autumn - Control; T (204) = 0.77, *P* = 0.72) Fenced(Autumn - Spring; T (204) = 0.85, *P* = 0.67) Fenced(Control - Spring; T (204) = -0.27, *P* = 0.96) Autumn(Fenced vs Unfenced; T (204) = -1.57, *P* = 0.12) Control(Fenced vs Unfenced; T (204) = -1.02, *P* = 0.31) Spring(Fenced vs Unfenced; T (204) = -1.13, *P* = 0.26)
10	1.50 ± 1.46	4.75 ± 0.73	3.00 ± 0.59	0.45 ± 0.44	1.67 ± 0.84	1.00 ± 0.69	Unfenced(Autumn - Control; T (204) = 1.28, *P* = 0.41) Unfenced(Autumn - Spring; T (204) = 0.61, *P* = 0.81) Unfenced(Control - Spring; T (204) = -0.67, *P* = 0.78) Fenced(Autumn - Control; T (204) = 2.00, *P* = 0.12) Fenced(Autumn - Spring; T (204) = 1.86, *P* = 0.15) Fenced(Control - Spring; T (204) = -0.95, *P* = 0.61) Autumn(Fenced vs Unfenced; T (204) = -2.77, *P* = 0.01)

							Control(Fenced vs Unfenced; T (204) = -0.69, *P* = 0.49) Spring(Fenced vs Unfenced; T (204) = -2.20, *P* = 0.03)
18	0.60 ± 0.44	5.25 ± 0.73	2.83 ± 0.59	0.41 ± 0.44	1.67 ± 0.84	0.67 ± 0.69	Unfenced(Autumn - Control; T (204) = 1.33, *P* = 0.38) Unfenced(Autumn - Spring; T (204) = 0.92, *P* = 0.63) Unfenced(Control - Spring; T (204) = -0.32, *P* = 0.95) Fenced(Autumn - Control; T (204) = 3.23, *P* = <0.01) Fenced(Autumn - Spring; T (204) = 2.57, *P* = 0.03) Fenced(Control - Spring; T (204) = -1.8, *P* = 0.17) Autumn(Fenced vs Unfenced; T (204) = -3.22, *P* = <0.01) Control(Fenced vs Unfenced; T (204) = 0.27, *P* = 0.79) Spring(Fenced vs Unfenced; T (204) = -2.39, *P* = 0.02)

Table S20. Frequency of introduced species recorded from fenced or unfenced quadrats.

Species†	**Class**	**Fenced**	**Unfenced**
Only detected in unfenced quadrats			
Aira cupaniana Guss	AG	0	1
Briza minor L.	AG	0	15
Trifolium spp	AFo	0	2
Vulpia bromoides (L.) Gray	AG	0	7
Detected in either fenced or unfenced quadrats			
Cirsium vulgare (Savi) Ten.	PFo	5	9
Genista monspessulana (L.) L.A.S.Johnson	PS	3	11
Holcus lanatus L.	AG	18	43
Lotus pedunculatus Schkuhr	AFo	1	22
Rubus anglocandicans A.Newton	PS	4	26
Senecio pterophorus DC.	PFo	1	4
Solanum nigrum L.	PFo	7	1
Soliva sessilis Ruiz & Pavs	AFo	8	8
Taraxacum officinale	PFo	11	18

‡Class represents the Longevity and lifeform class of each species, such that: P = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids.

Table S21. Frequency of introduced species recorded from in unburnt controls, spring burnt and autumn burnt quadrats.

Species†	**Class**	**Control**	**Spring**	**Autumn**
Only detected in control unburnt quadrats				
Briza minor L.	AG	15	0	0
Vulpia bromoides (L.) Gray	AG	7	0	0
Anthoxanthum odoratum L.	PG	0*	0	0
Arctotheca calendula Levyns	AFo	0*	0	0
Lysimachia arvensis U.Manns & Anderb	AFo	0*	0	0
Only detected in Spring burnt quadrats				
Trifolium spp	AFo	0	2	0
Aira cupaniana Guss	AG	0	1	0
Solanum nigrum L.	PFo	0	8	0
All other species				
Cirsium vulgare (Savi) Ten.	PFo	4	7	3
Genista monspessulana (L.) L.A.S.Johnson	PS	9	5	0
Holcus lanatus L.	AG	40	13	8
Lotus pedunculatus Schkuhr	AFo	20	3	0
Rubus anglocandicans A.Newton	PS	20	10	0
Senecio pterophorus DC.	PFo	0	1	4
Soliva sessilis Ruiz & Pavs	AFo	9	6	1
Taraxacum officinale	PFo	15	11	3

‡Class represents the Longevity and lifeform class of each species, such that: P = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids. *Species occurred in at least one quadrat before it was burnt.

Table S22. Presence and absence summary data of **native** species extracted from government “Ramble” flora surveys in *Swamps of the Fleurieu Peninsula* Ecological Communities, all of which are recorded as being long unburnt. n = 25 swamp surveys

Species	**Number of occurrences**
Acacia melanoxylon	7
Acacia myrtifolia	1
Acacia provincialis	11
Acacia retinodes	1
Acacia verniciflua	1
Acacia verticillata ssp. *ovoidea*	15
Acaena echinata	1
Acaena novae-zelandiae	3
Acrotriche serrulata	1
Aira sp.	1
Allocasuarina muelleriana ssp. muelleriana	1
Allocasuarina robusta	3
Allocasuarina striata	3
Banksia marginata	3
Baumea gunnii	1
Baumea juncea	10
Baumea laxa	1
Baumea rubiginosa	23
Baumea tetragona	23
Billardiera cymosa	1
Blechnum minus	25
Blechnum nudum	2
Blechnum wattsii	1
Carex appressa	12
Carex bichenoviana	3
Carex fascicularis	2
Carex gaudichaudiana	2
Carex tereticaulis	2
Cassytha glabella	2
Cassytha melantha	2
Centella cordifolia	14
Centrolepis fascicularis	6
Cryptostylis subulata	1
Cycnogeton alcockiae	1
Cycnogeton procerum	1
Cyperus sanguinolentus	1
Cyperus tenellus	2
Daviesia brevifolia	1
Daviesia leptophylla	1
Daviesia ulicifolia	1
Dianella revoluta	2
Dillwynia hispida	3
Drosera auriculata	2
Drosera binata	7
Drosera hookeri	1
Drosera pygmaea	6
Drosera whittakeri	4
Eleocharis acuta	3
Eleocharis gracilis	4
Eleocharis sphacelata	1
Empodisma minus	19
Epacris impressa	1
Epilobium pallidiflorum	13
Eucalyptus baxteri	2
Eucalyptus cosmophylla	6
Eucalyptus dalrympleana	1
Eucalyptus fasciculosa	1
Eucalyptus ovata	11
Euchiton collinus	1
Ficinia nodosa	1
Gahnia sieberiana	23
Gahnia trifida	6
Gleichenia microphylla	20
Glyceria australis	3
Gonocarpus mezianus	3
Gonocarpus micranthus ssp. *micranthus*	13
Gonocarpus tetragynus	1
Goodenia albiflora	1
Goodenia blackiana	3
Goodenia ovata	13
Gratiola peruviana	18
Grevillea lavandulacea ssp. *lavandulacea*	1
Grevillea sp.	1
Haeckeria cassiniiformis	1
Hakea carinata	4
Hakea rostrata	2
Hibbertia empetrifolia ssp. *radians*	2
Hibbertia exutiacies	2
Hibbertia riparia	4
Hibbertia sericea var. *sericea*	1
Hibbertia tenuis	2
Hydrocotyle verticillata	1
Hypolepis rugosula	9
Isolepis inundata	9
Isopogon ceratophyllus	3
Ixodia achillaeoides ssp. *alata*	1
Juncus bufonius	7
Juncus caespiticius	1
Juncus pallidus	20
Juncus pauciflorus	4

Juncus planifolius	22
Juncus sarophorus	9
Juncus subsecundus	1
L. continentale x L. lanigerum	13
Lepidosperma longitudinale	18
Lepidosperma semiteres	2
Lepidosperma viscidum	1
Leptocarpus tenax	7
Leptospermum continentale	22
Leptospermum lanigerum	14
Leptospermum myrsinoides	2
Lilaeopsis polyantha	1
Lindsaea linearis	4
Lobelia anceps	5
Lomandra multiflora ssp. *dura*	2
Lycopodiella lateralis	1
Lycopus australis	3
Lythrum hyssopifolia	11
Lythrum salicaria	1
Marianthus bignoniaceus	1
Melaleuca decussata	9
Melaleuca squamea	13
Microlaena stipoides var. *stipoides*	1
Myriophyllum amphibium	13
Myriophyllum simulans	4
Olearia glandulosa	1
Olearia ramulosa	2
Olearia teretifolia	1
Ornduffia umbricola var. *umbricola*	4
Oxalis acetosella	1
Patersonia occidentalis	13
Persicaria decipiens	6
Persoonia juniperina	1
Phragmites australis	16
Pimelea linifolia ssp. *linifolia*	1
Pimelea octophylla	1
Platylobium obtusangulum	3
Poa sp.	7
Potamogeton ochreatus	1
Pteridium aquilinum	1
Pteridium esculentum ssp. *esculentum*	15
Pterostylis nutans	1
Pultenaea daphnoides	3
Pultenaea dentata	7
Pultenaea involucrata	2
Pultenaea viscidula	1
Rytidosperma racemosum var. racemosum	1
Schenkia australis	1
Schizaea bifida	1
Schoenus apogon	1
Schoenus carsei	1
Schoenus maschalinus	11
Senecio glomeratus ssp. *glomeratus*	5
Senecio minimus	2
Sprengelia incarnata	4
Spyridium parvifolium	1
Spyridium thymifolium	3
Stackhousia sp.	1
Stenanthera conostephioides	1
Stylidium graminifolium	2
Tetrarrhena sp.	1
Thysanotus patersonii	1
Triglochin alcockiae	1
Triglochin procerum	1
Triglochin striata	1
Typha domingensis	2
Utricularia dichotoma	4
Villarsia umbricola	5
Viminaria juncea	18
Viola eminens	2
Viola hederacea	3
Xanthorrhoea semiplana ssp. *semiplana*	3
Xyris operculata	5

Table S23. Presence and absence summary data of **introduced** species extracted from government "Ramble" flora surveys in *Swamps of the Fleurieu Peninsula* Ecological Communities, all of which are recorded as being long unburnt. n = 25 swamp surveys

Species	**Number of occurrences**
Acetosella vulgaris	1
Adiantum aethiopicum	1
Anthoxanthum odoratum	4
Arctotheca calendula	3
Asparagus asparagoides	1
Bartsia sp.	1
Briza maxima	2
Callitriche stagnalis	7
Cirsium vulgare	13
Conyza sumatrensis	1
Cotula coronopifolia	1
Galium sp.	1
Genista monspessulana	3
Geranium sp.	5
Holcus lanatus	25
Hypericum japonicum	5
Hypochaeris radicata	8
Isolepis levynsiana	5
Juncus articulatus	5
Juncus effusus	11
Lagurus ovatus	1
Leontodon saxatilis	6
Leontodon taraxacoides	7
Lotus subbiflorus	4
Lotus pedunculatus	25
Malva parviflora	1
Pennisetum clandestinum	1
Pinus radiata	9
Plantago major	10
Rorippa nasturtium-aquaticum	1
Rosa canina	3
Rubus fruticosus aggregate	23
Rumex crispus	2
Senecio pterophorus	13
Solanum nigrum	10
Sonchus asper	2
Sonchus oleraceus	1
Taraxacum sp.	1
Trifolium campestre	7
Ulex europaeus	13
Vellereophyton dealbatum	3
Zantedeschia aethiopica	2

Table S24. The fire response, growing and flowering periods of **native** species detected during the study. Information sourced from an unpublished Department for Environment and Water database, the Electronic Flora of South Australia at flora.sa.gov.au, expert advice, and observations during the experiment.

Species	**Class**	**Fire Response**	**Seed storage/resprouting mechanism**	**Peak Flowering Period**
Acacia myrtifolia C. L. Willdenow	PS	Sr	Persistent Soil	July — Oct.^{S}
Acacia provincialis A.Camus	PS	Sr	Persistent Soil	Dec. — Feb.
Acacia verticillata C. L. Willdenow (*nt*)	PS	Sr	Persistent Soil	Aug. — Novs^{S}
Baumea juncea (R.Br.) Palla	PGm	R	Rhizome	Sep. — Apr.^{SA}
Baumea rubiginosa (Spreng.) Boeckeler (*ra*)	PGm	R	Rhizome	Throughout^{SA}
Baumea tetragona (Labill.) S.T.Blake (*nt*)	PGm	R	Rhizome	Throughout^{SA}
Blechnum minus (R.Br.) Ettingsh (*nt*)	PGm	R	Rhizome	NA
Centrolepis fascicularis Labill. (*vu*)	AGm	S	Persistent Soil	Novs — Feb.^{S}
Cyperus tenellus L.f.	AGm	S	Transient Soil	Sep. — Jan.^{S}
Drosera binata Labill. (r *vu*)	AFo	**Rs**	Persistent Soil	Dec. — Apr.^{A}
Drosera pygmaea DC (*nt*)	AFo	**Rs**	Persistent Soil	Sep. — Jan.^{S}
Eucalyptus ovata Labill. (*vu*)	PT	R	Epicormic & Lignotuber	Throughout^{SA}
Euchiton collinus Cass	PFo	S	Transient Soil	Oct. — Dec.^{S}
Gahnia sieberiana Kunth (*nt*)	PGm	R	Basal	Throughout^{SA}
Gleichenia microphylla R.Br. (r *ra*)	PF	R	Rhizome	NA
Gonocarpus micranthus Thunb. (r *vu*)	PFo	Sr	Persistent Soil	Dec. — Feb.
Goodenia ovata Sm.	PS	Sr	Persistent Soil	Throughout.^{SA}
Gratiola peruviana L.	PFo	S	Persistent Soil	Novs — May.^{SA}
Hibbertia tenuis Toelken & R.J.Bates (CR e *cr*)	PS	S	Persistent Soil	Throughout.^{SA}
Isolepis inundata R.Br.	AGm	**Rs**	Rhizome	Oct. — Apr.^{SA}
Juncus planifolius R.Br. (*nt*)	PGm	**Rs**	Rhizome	Dec. — Feb.
Leptospermum continentale Joy Thomps.	PS	Rs	Basal	Oct. — Jan.^{S}
Leucopogon hirsutus Sond. (*r*)	PS	S	Persistent Soil	Aug. — Oct.^{S}
Lobelia anceps L.f.	PFo	S	Persistent Soil	Novs — Jul.^{SA}
Lythrum hyssopifolia L.	AFo	S	Persistent Soil	Oct. — Feb.^{S}
Melaleuca decussata R.Br. (*nt*)	PS	Rs	Canopy	Sep. — Feb.^{S}
Melaleuca squamea Labill. (r *ra*)	PS	Rs	Canopy	Sep. — Novs^{S}

Microlaena stipoides (Labill.) R.Br.	PG	R	Persistent Soil	Novs — Dec.^{S}
Patersonia occidentalis R.Br. (*ra*)	PGm	R	Persistent Soil	Oct. — Dec.^{S}
Poa labillardieri Steud. (*nt*)	PG	S	Persistent Soil	Oct. — Feb.^{S}
Pteridium esculentum (G.Forst.) Cockayne	PF	R	Rhizome	NA
Schoenus apogon Roem. & Schult.	AGm	Rs	Rhizome	Oct. — Jan.^{S}
Schoenus maschalinus Roem. & Schult. (*vu*)	AGm	**Rs**	Rhizome	Oct. — Feb.^{S}
Senecio glomeratus Desf. ex Poir. (*vu*)	AFo	S	Persistent Soil	Novs — Feb.^{S}
Spiranthes australis (R.Br.) Lindl.	PFo	R	A-Tuber	Dec. — Mar.^{A}
Sprengelia incarnata Sm. (r *vu*)	PS	Sr	Persistent Soil	Aug. — Feb.^{SA}
Stylidium armeria (Labill.)	PFo	Rs	Persistent Soil	Oct. — Jan.^{S}
Thelymitra cyanea (Lindl.) Benth. (e *en*)	PFo	R	A-Tuber	Novs — Mar.^{SA}
Utricularia dichotoma Labill. (vu)	PFo	R	Basal	Oct. — Apr.^{SA}
Viminaria juncea (Schrad. & J.C.Wendl.) Hoffmanns. (r *vu*)	PS	S	Persistent Soil	Novs — Feb.^{S}
Viola eminens K.R.Thiele & Prober (*vu*)	PFo	Sr	Persistent Soil	Oct. — Jan.^{S}
Xyris operculata Labill. (r *vu*)	PGm	R	Basal	Dec. — Feb.

‡Class represents the Longevity and lifeform class of each species, such that: *P* = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids. †Brackets represents the species conservation status, such that: CE = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (EPBC Act 1999), Lowercase = State rating (Barker *et al.* 2020), Italics = Regional rating (Gillam & Urban 2014); Fire response is given as R = primarily resprouts, S = primarily recovers from seeds, Rs = primarily resprouts but known to recover from seed, Sr = primarily recovers from seed but has been known to resprout; Seed storage or resprouting mechanism lists the primary response post fire as observed in the field or as identified in government fire response databases (J. Trezise pers. obs., 2020; Abley 2014; Kenny *et al.* 2014); species in **Bold** have had their recovery changed from R to Rs, based on field observations, likewise both species of Drosera were changed from transient to persistent based on results. Peak flowering period gives the primary flowering time for the species as per the State Herbarium of South Australia (Barker *et al.* 2020) with those disrupted by a spring fire denoted with ^{S} and autumn with ^{A}.

Table S25. The fire response, growing and flowering periods of **introduced** species detected during the study. Information sourced from an unpublished Department for Environment and Water database, the Electronic Flora of South Australia at flora.sa.gov.au, expert advice, and observations during the experiment.

Species	**Class**	**Fire Response**	**Seed storage/resprouting mechanism**	**Peak Flowering Period**
Aira cupaniana Guss	AG	S	Persistent Soil	Sep. — Dec.^{S}
Anthoxanthum odoratum L.	PG	Rs	Transient Soil	Aug. — Dec.^{S}
Arctotheca calendula Levyns	AFo	S	Transient Soil	Aug. — Oct.^{S}
Briza minor L.	AG	S	Transient Soil	Aug. — Dec.^{S}
Cirsium vulgare (Savi) Ten.	PFo	S	Transient Soil	Novs — Feb.^{S}
Genista monspessulana (L.) L.A.S.Johnson	PS	S	Persistent Soil	Aug. — Feb.^{S}
Holcus lanatus L.	AG	S	Transient Soil	Aug. — Dec.^{S}
Lotus pedunculatus Schkuhr	AFo	S	Persistent Soil	Novs — Feb.^{S}
Lysimachia arvensis U.Manns & Anderb	AFo	S	Persistent Soil	Aug. — Novs^{S}
Rubus anglocandicans A.Newton	PS	R	Basal	Novs — Feb.^{S}
Senecio pterophorus DC.	PFo	S	Transient Soil	Novs — Mar.^{SA}
Solanum nigrum L.	PFo	S	Persistent Soil	Throughout^{SA}
Soliva sessilis Ruiz & Pavs	AFo	S	Persistent Soil	Oct. — Novs^{S}
Taraxacum officinale	PFo	S	Transient Soil	Throughout^{SA}
Trifolium spp	AFo	S	Persistent Soil	Sep. — Dec.^{S}
Vulpia bromoides (L.) Gray	AG	S	Transient Soil	Sep. — Jan.^{S}

[‡] Class represents the Longevity and lifeform class of each species, such that: *P* = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids; Fire response is given as R = primarily resprouts, S = primarily recovers from seeds, Rs = primarily resprouts but known to recover from seed, Sr = primarily recovers from seed but has been known to resprout; Seed storage or resprouting mechanism lists the primary response post fire as observed in the field or as identified in government fire response databases (Abley 2014; Kenny *et al.* 2014; Trezise pers. obs.) Peak flower period gives the primary flowering time for the species as per the State Herbarium of South Australia (Barker *et al.* 2020) with those disrupted by a spring fire denoted with ^{S} and autumn with ^{A}.

Appendix 5. Publications

The following shows Chapter 3, which is the only published chapter related to this thesis. All other chapters are in publication style but have not yet been submitted. Chapter 3 was published in Austral Ecology and can be found online at https://doi.org/10.1111/aec.12957

Trezise J. E., Facelli J., Paton D. P. & Davies R. (2021) The effect of heat and smoke on the soil seed banks of heathlands on permanent freshwater swamps. *Austral Ecology* **46**, 39-51.

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The effect of heat and smoke on the soil seed banks of heathlands on permanent freshwater swamps

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Abstract In South Australia, *Swamps of the Fleurieu Peninsula* are critically endangered due to past vegetation clearance and changes in hydrology, but still contain a high diversity of threatened plant species. This vegetation community provides habitat for 82 threatened ground-stratum plant species, including the nationally critically endangered subshrub *Hibbertia tenuis* which is endemic to these swamps. With infrequent burning, native ferns and taller shrubs outcompete these species. We conducted glasshouse trials to determine the potential of fire to regenerate threatened and other swamp plant species. Soil samples from eight swamps were used in germination trials with half of each sample treated with heat plus smoke, and half left untreated. Samples were spread onto trays ($n = 188$), and seedling emergence was recorded for twelve months. Emergence was dominated by native species (2649 seedlings m^{-2}) compared to exotics (675 seedlings m^{-2}). In total, 48 native and 25 introduced species germinated, with 21% of germinated native species absent from the above-ground vegetation. The dominant native fern *Gleichenia microphylla* did not emerge from any soil samples, indicating that recovery likely lags behind that of ground-strata species, giving them time to establish and set seed before being outcompeted. Thirty-four rare or threatened species germinated, including five species absent from above-ground vegetation. Of all native species that emerged, only five were confined to heat plus smoke treatments, suggesting most species will regenerate without fire if overstorey competition is reduced. However, seedling emergence of native shrubs/subshrubs more than doubled with the fire treatment. Of particular importance, *H. tenuis* showed an 18-fold increase in germination when treated with heat plus smoke. This study supports the utility of ecological burns as a management tool to regenerate threatened plant species in long-undisturbed peaty heathlands on permanent swamps.

Key words: competition, fire, seedling emergence, soil seed bank, swamps.

INTRODUCTION

Alteration of natural fire regimes is one of many factors threatening biodiversity in Mediterranean ecosystems (Bond & Van Wilgen 1996; Keith *et al.* 2002; Underwood *et al.* 2009). With the exception of areas deliberately burnt to reduce fuel loads, native vegetation near to agricultural and residential areas is often very infrequently burnt, as managers concentrate more on fire suppression rather than the ecological requirements of biota (Gill & Williams 1996). This is problematic in fire-adapted vegetation, as altering fire regimes changes ecosystem structure (Menges & Hawkes 1998; Peterson & Reich 2001; Brockway *et al.* 2002), which can negatively impact biodiversity (Leach & Givnish 1996; Ottewell *et al.* 2011). While most research focuses on adverse effects of high-frequency burning (Bradstock *et al.* 1995; Bradstock *et al.* 1997), more recent studies document the loss of species diversity due to exclusion of fire (Keith & Bradstock 1994; Keith *et al.* 2002; Davies *et al.* 2013). This applies particularly to small remnants of native vegetation in heavily cleared agricultural and urban landscapes that frequently support high concentrations of threatened flora (Lawson *et al.* 2010; Davies *et al.* 2013; Taylor 2019).

In long-unburnt vegetation, overstorey species can outcompete ground-stratum species via both above-ground and below-ground processes (Davies *et al.* 2010), while also restricting seedling establishment (Keith & Bradstock 1994; Keeley & Fotheringham 2000; Amarasekare & Possingham 2001). Herbaceous understorey species are particularly affected (Sparks *et al.* 1998; Bond & Keeley 2005). Burning not only provides important cues for germination (Kenny 2000; Williams *et al.* 2003; Downes *et al.* 2014) but may also be essential for seedling survival by reducing competition and creating favourable growing conditions (Ooi *et al.* 2004; Bond & Keeley 2005). Some species may persist in the soil seed bank after exclusion from the above-ground vegetation

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(Looney & Gibson 1995; Milberg 1995; Hopfensperger 2007). These seed banks are subject to decay as seeds lose viability over time with seed bank half-lives differing between species (e.g. Auld *et al.* 2000; Ooi *et al.* 2007). In the absence of conditions required for seedling recruitment, many mature plants will senesce, and seed production will eventually cease, resulting in declining abundance of viable seed in the soil seed bank. Moreover, when specific conditions (e.g. disturbance) are required to trigger germination, local extinctions may occur if the time between such disturbance events is greater than the lifespan of the species in both the above-ground vegetation and soil seed bank (Enright *et al.* 1996; Bradstock & Kenny 2003).

Seeds of fire-adapted plants often require heat and/or smoke to trigger germination (Bell *et al.* 1993; Staden *et al.* 2000). Heat may break physical dormancies, for example through high temperatures opening impermeable seed coatings (Tieu *et al.* 2001), while smoke is an important chemical cue (Staden *et al.* 2000). Fire may also promote recruitment by providing favourable growing conditions such as increased light penetration by removing dense overstorey (Vaughton 1998; Keeley & Fotheringham 2000). Some fire-adapted species will still germinate at low abundances in the absence of fire to enable limited recruitment into small gaps (e.g. DeSimone & Zedler 1999; Ooi *et al.* 2006), but resulting seedlings often suffer high mortality due to competition (e.g. Van Der Meer *et al.* 1999; Zhu *et al.* 2003). As such, germination into small gaps is often insufficient to sustain populations (e.g. Skoglund 1992; Morgan 1997).

The *Swamps of the Fleurieu Peninsula* Ecological Community is confined to the Fleurieu Peninsula of South Australia (Fig. 1) and is listed as critically endangered under the Australian *Environment Protection and Biodiversity Conservation Act* 1999 (EPBC Act; Threatened Species Scientific Committee 2013). These permanent freshwater swamps have been extensively cleared and drained since European settlement and now only 2% remain in relatively unmodified condition (Harding 2005). Prior to European settlement, these ecosystems were burnt from lightening strikes or from aboriginal burning (Bickford & Gell 2005) but are now threatened by inappropriate fire regimes with fires likely being too infrequent (Duffield & Hill 2002; Quarmby 2011; Threatened Species Scientific Committee 2013). These long-unburnt swamps have become dominated by dense coral fern *Gleichenia microphylla*, which outcompetes most ground-stratum species (Conservation Council of South Australia, unpublished database, 2018).

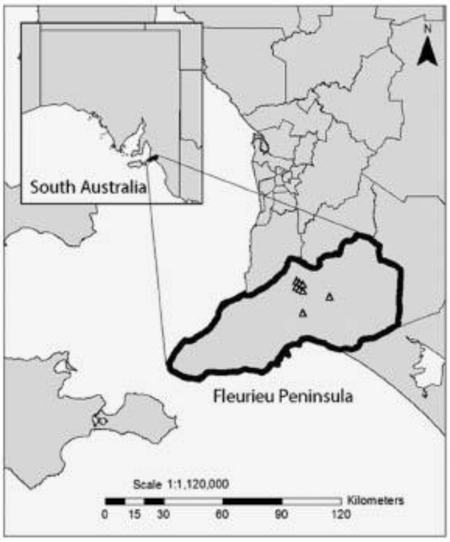

Fig. 1. Study boundary in the Fleurieu Peninsula, South Australia. The eight swamps are represented by hollow black triangles (△) which are classified as permanent swamps. Map created using ArcGIS package (version 10.3.1) using spatial data from the Department of Planning, Transport and Infrastructure (1996).

Eighty-four plant species listed as threatened at the national, state or regional level, have been recorded within these swamps and their margins. All but two of which are ground-stratum species (Table S3.1 in Appendix S3) and likely to be adversely affected by coral fern overabundance. One of these, the Yundi guinea flower (*Hibbertia tenuis*), a short-lived perennial subshrub, is listed as critically endangered under the EPBC Act 1999 and is endemic to these swamps (Quarmby 2011). Prior to this study, only 20 individuals were known to occur, all confined to two swamps (Quarmby 2011) where they were restricted to human-cleared trails through dense coral fern (J. Trezise pers. obs.). Fire reduces the dominance of coral fern, leading to a transient period of increased plant richness (Walker & Boneta 1995; Clarkson 1997), particularly of herbs and grasses (Timmins 1992; Johnson 2001). Species richness can decline as time since fire increases (Bond & Van Wilgen 1996), and this successional pattern has been observed in a wide range of ecosystems (e.g. Ross *et al.* 2002; Peterson & Reich 2008; Bohlman *et al.* 2016). The present study aimed to determine the emergence response of *H. tenuis* and other plant species of the Fleurieu Peninsula swamps to fire associated cues of smoke and heat. While previous studies have found that smoke enhances seedling emergence of other *Hibbertia* species (Dixon *et al.* 1995; Hidayati *et al.* 2012), the effect of fire on *H. tenuis* and other threatened flora is poorly understood. We used an *ex situ* seedling emergence approach using soil samples taken from Fleurieu Peninsula swamps including two swamps containing *H. tenuis* and six with suitable habitat for the species.

These samples were exposed to heat and smoke treatments in glasshouse trials aimed to simulate the effect of fire and to determine whether these stimulated the germination of seeds held within the soil seed bank. Smoke and heat treatments enhance germination for many species in fire-prone ecosystems (Morris 2000; Read *et al.* 2000; Reyes & Trabaud 2009) and have been used in seedling emergence studies to replicate the effects of fire on soil seed banks (Cochrane *et al.* 2007; Auld & Ooi 2008; Rawson *et al.* 2013). In addition to recording the emergence of native swamp species, we also recorded the emergence of introduced species to gain an insight into whether ecological burns were likely to enhance emergence of weeds from pre-existing seed banks.

METHODS

This study was undertaken in eight Fleurieu Peninsula swamps of the Yundi and Nangkita areas on the Fleurieu Peninsula, South Australia (Fig. 1). The region has a Mediterranean climate that averages 756 mm of rain per annum (Myponga – Bureau of Meteorology 2019). These heathy, permanently saturated swamps occur on grey clay soils with high gravel and peat content. Vegetation is predominantly a remnant peat bog ecological community (as defined by Harding 2005), dominated by *G. microphylla* (average 44% cover) and intermixed with prickly tea-tree *Leptospermum continentale*, native broom *Viminaria juncea*, and other native shrubs and sedges.

All eight swamps were located within a two kilometre radius of historical records of *H. tenuis* (Quarmby 2011; Barker *et al.* 2020). Swamps either contained *H. tenuis* or at least suitable habitat for the species. These swamps were unlikely to have been burnt for at least 59 years based on historic imagery dating back to 1958 (Department for Environment & Water 2020), and have probably not been burnt for at least 86 years using additional information held within government fire records dating back to 1931 (Department for Environment & Water 2016).

Eight 1 × 1 m^2 quadrats were randomly allocated, using the ArcGIS package version 10.3.1 (Esri 2014), in each swamp totalling 64 quadrats. Two of these swamps contained *H. tenuis*, and additional quadrats were erected around every observed individual, totalling 30 quadrats. For each quadrat, per cent cover of each species was estimated with the point intercept method, using a 1 × 1 m^2 grid divided into a hundred 10 × 10 cm^2 cells. Percentage cover for each species was estimated by pushing a 2 m long pin into the north-eastern corner of every cell and recording the percentage of times that species was intercepted by the pin tip. Additional species found within the quadrat, but not intercepted by the pin were given a cover value of 0.1%, meaning that cover for each species could range from 0.1% to 100%.

To quantify the germinable contents of the soil seed bank and assess responses to the fire treatment, we used an *ex situ* seedling emergence approach (e.g. Cochrane *et al.* 2007; Davies *et al.* 2013; Rawson *et al.* 2013). This approach measures the numbers of seedlings that emerge during the monitoring period, but will not detect all seeds present in the soil seed bank (Ter Heerdt *et al.* 1996) and species that may require special germination treatments or take more than a year to emerge. This method was favoured over direct extraction as it is more time efficient (enabling more sampling), avoids bias towards larger seeds (Ter Heerdt *et al.* 1996; Ferrandis *et al.* 1999; Gonzalez & Ghermandi 2012) and differentiates between viable and unviable seed (Hidayati *et al.* 2012).

In August 2017, a 30 cm diameter auger was used to take cores from the centre of each quadrat. Cores were taken to a depth of 5 cm since this is where the majority of seed occurs (Auld & O'Connell 1991; Auld & Denham 2006; Wills & Read 2007). Large debris (e.g. rhizomes) was removed from the cores which were then thoroughly mixed and separated into two paired samples. Mixed samples were then spread into growing trays (33 × 14 × 5 cm^3 with drainage holes) on top of a 1 cm deep layer of sterile drainage sand.

One tray from each pair was treated with heat plus smoke to simulate fire, the other sample being used as a control. Heat was administrated by pouring 200 mL of boiling water evenly on top of the treated samples, compared with 200 mL of water at room-temperature for the control samples. This high temperature (~100°C) is comparable to natural temperatures experienced on and just below soil surfaces during fire (Bradstock *et al.* 1994; Bradstock & Auld 1995; Williams *et al.* 2003) and heat shock commonly has been shown to promote seed germination (Enright *et al.* 1997; Wills & Read 2002; Liyanage & Ooi 2015). This approach was used instead of oven heat treatment because the samples were wet and prolonged exposure to wet-heat can kill seeds (Turner & Dixon 2009). Furthermore, drying samples could be considered an extra treatment as wetting and drying periods are often important mechanisms for breaking seed dormancies (Merritt *et al.* 2007). After water application, treated soil trays were subject to smoke in a smoke tent for 15 min. The smoke was generated by burning wheat hay in a 200 L barrel drum, following Rawson *et al.* (2013). Aerosol smoke was used since it is the most effective methods to stimulate germination in fire dependant seeds (Page 2009) and has been widely used in similar studies (e.g. Read *et al.* 2000; Reyes & Trabaud 2009; Thomas *et al.* 2010).

Soil trays were then randomly placed in a greenhouse and were rotated fortnightly around the glasshouse to limit any influence of position. Water was withheld for the first 48 h, after which trays were automatically watered at intervals adjusted to ensure soils were always waterlogged. Several additional trays filled with drainage sand were randomly placed among the experimental trays to test for airborne seed contamination. Trays were monitored for 12 months, with seedlings recorded and removed immediately after reaching sufficient size for reliable identification. Species that failed to flower in this period were grown on

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in separate pots to confirm initial identification. When individuals died before flowering or fruiting, they were identified by comparing with other individuals that survived to a point where they could be identified. Seedlings of threatened species were grown and then translocated onto private land and all others were discarded. Nomenclature followed the Electronic Flora of South Australia (Barker *et al.* 2020). Where possible, a herbarium voucher specimen was collected and pressed for each species, and these will be submitted to the South Australian Herbarium.

We compared the species richness and abundances of key species that emerged in the treated and untreated samples using the R statistical package version 3.5.1 (R Core Team 2019) and the generalised linear mixed model (GLMM) package glmmADMB from version 0.6.5 (Bolker *et al.* 2012). We also used the adonis2 function from the vegan package from version 2.5-2 (Oksanen & Blanchet 2019) to assess the difference between species composition in the treated and untreated samples. Treatment was considered a fixed factor, while swamp and quadrat were treated as random factors. Swamp variance did not significantly contribute to our models and therefore we did not compare between them. Furthermore, these swamps were the only sites available and so although they were not selected randomly, they were treated as such in our models. Distribution and dispersion of the data for each species informed the link functions used for each model, such that dispersion tests directed the use of either a Poisson or Negative Binomial distribution. Statistics for individual species and lifeform groups were calculated subject to emergence occurring in either a treated or untreated tray of each pair, such that tray pairs without emergence were excluded from calculations to avoid zero inflation. Mean numbers of seedlings per treatment for each species were extrapolated from the surface area of trays ($0.046\ m^2$) to the surface area of quadrats ($1\ m^2$). Species richness values are given per tray and have not been extrapolated as they do not scale in a linear fashion. GLMMs were also used to compare numbers of species in each lifeform class between treatments.

RESULTS

The heat plus smoke treatment resulted in significantly larger numbers of seedlings of native shrubs/subshrubs (64 seedlings m^{-2}) emerging than from untreated soil (27 m^{-2}; χ^2 (1) = 11.1, $P = <0.01$; Table 1). Among these, significantly more *H. tenuis* emerged from treated soil (5 m^{-2}) than from untreated soil (<1 m^{-2}; χ^2 (1) = 16.0, $P = <0.01$; Table 1) as was the case for *Goodenia ovata* (30 m^{-2} treated *v.* 9 m^{-2} untreated; χ^2 (1) = 5.6, $P = <0.01$; Table 1).

However, for all native species together, density of seedlings emerging from heat- and smoke-treated soil (1274 m^{-2}) did not differ significantly when compared with the numbers emerging from untreated soil (1350 m^{-2}; χ^2 (1) = 0.11, $P = 0.74$; Table 1). Significant differences were also found for some introduced species. Four times less seedlings of introduced perennial forbs emerged from treated soil (1 m^{-2}) compared with untreated soil (4 m^{-2}; χ^2 (1) = 5.45, $P = 0.02$; Table 1), while the introduced annual forb *Lysimachia arvensis* had almost half as many seedlings in treated soil (6 m^{-2} treated *v.* 12 m^{-2} untreated; χ^2 (1) = 1.58, $P = 0.02$; Table 1). The treatment also appeared to suppress emergence of introduced *Rubus anglocandicans* (4 m^{-2} treated *v.* 8 m^{-2} untreated; χ^2 (1) = 3.49, $P = 0.06$; Table 1).

Richness of native species emerging for heat- and smoke-treated soil (mean: 5.6 species $tray^{-1}$) did not differ significantly from untreated soil (mean: 5.4 species $tray^{-1}$; χ^2 (1) = 0.48, $P = 0.49$; Table 3). Richness of introduced species was also similar between the treated (mean: 1.8 species $tray^{-1}$) and untreated soil (mean: 1.9 species $tray^{-1}$; χ^2 (1) = 0.21, $P = 0.64$; Table 3). Species composition did not differ statistically between the treated and untreated samples ($F_{1,81} = 0.72$, $P = 0.63$), but they did contain different species. Of the 48 native species that emerged in the trays, five species (*Acacia verticillata*, *Epilobium billardierianum*, *Eragrostis tenellula*, *Eucalyptus ovata* and *Olearia glandulosa*) emerged only in trays treated with heat plus smoke, while four native species (the perennial forbs *Asperula conferta* and *Lagenifera huegelii*, the fern *Blechnum minus*, and the rush *Juncus caespiticius*) emerged only in untreated trays. Of the 25 introduced species, four were only present in heat plus smoke-treated trays while five were only present in untreated trays.

Thirty-four plant species listed as threatened or rare at the national, state or regional level, emerged (Table 2). Nineteen seedlings of the critically endangered species *H. tenuis* were recorded, including from a swamp (from the random samples) where it was previously unknown. Ten native species and eight introduced species that emerged were not found in the above-ground vegetation including five species of conservation concern (Table 2), including *O. glandulosa*, a shrub listed as vulnerable at the state level and two regionally threatened species, *Pultenaea dentata* and *Hypericum japonicum*. We recorded 54 perennial and 17 annual native species in the above-ground vegetation, compared to 32 perennial and 16 annual species in the germinable soil seed bank (Table 1). For perennial ferns/clubmosses, only one species of fern *B. minus* emerged from the soil seed bank, despite six species of fern and two species of clubmoss being recorded from the above-ground vegetation (Appendix S2).

A total of 8748 seedlings of native plants and 2224 seedlings of introduced plants emerged in the trays, equivalent to 3324 ± 328 (mean ± SE) seedlings emerging per square metre. Averaged across both treatments, the densities of germinating native seed (2649 ± 245 seedlings m^{-2}; 48 species) were significantly greater than for introduced species

Table 1. Abundance and species richness for lifeform classes in above-ground vegetation compared with emergence from the soil seed bank. Comparisons between numbers of seedlings which emerged from heat plus smoke-treated samples (HS) and from control samples (C), using GLMs

		Above-ground vegetation		Germinable soil seed bank						
Life-history classes	Lifeform class/species	% Cover	Richness	% Total	Richness	HS (seedlings m^{-2})	C (seedlings m^{-2})	$P^{\dagger}$	χ^2	$n^{\ddagger}$
Natives		94.0	71	80.3	48	1273.9 ± 251.2	1349.6 ± 256.7	0.740	0.110	92
Annuals/ biennials	All	1.3	17	39.2	16	608.6 ± 91.1	682.1 ± 109.2	0.762	0.092	86
	Forbs	<0.1	8	1	6	20.2 ± 9.4	9.6 ± 3.9	0.178	1.812	20
	Grasses	<0.1	1	<0.1	1	0.6 ± 0.4	0.3 ± 0.3	na	na	1
	Non-grass graminoids	1.1	8	38.3 38.27%	9	587.9 ± 81.2	672.1 ± 105.0	0.704	0.144	88
	Juncus bufonius	0		8.5		138.2 ± 49.4	236.2 ± 44.6	0.012	5.840	59
Perennial	All	92.7	54	41.1	32	665.3 ± 160.2	667.5 ± 147.6	0.964	0.002	92
	Ferns & clubmosses	45.3	6	<0.1	1	0	0.1 ± 0.1	na	na	3
	Gleichenia microphylla	43.7		0		0	0	na	na	0
	Forbs	1.1	20	6.9	12	153.8 ± 52.3	76.5 ± 17.4	0.155	2.026	61
	Grasses	0.8	3	4.3	1	84.6 ± 33.3	58.4 ± 20.5	0.513	0.428	22
	Non-grass graminoids	21.1	11	26.3	8	363.0 ± 58.1	506.0 ± 101.9	0.056	3.642	84
	Carex appressa	<0.1		0.6		2.7 ± 1.4	16.6 ± 11.7	0.057	3.615	8
	Shrubs/subshrubs	24.3	12	3.4	9	63.8 ± 16.3	26.5 ± 7.6	<0.01	11.082	45
	Goodenia ovata	0		1.2		29.5 ± 14.9	9.3 ± 6.6	<0.01	5.626	6
	Hibbertia tenuis	8.9		0.2		5.4 ± 2.5	0.3 ± 0.3	<0.01	16.000	8
	Leptospermum continentale	5.5		0.3		4.8 ± 2.4	5.7 ± 2.1	0.610	0.257	13
	Trees	<0.1	2	<0.1	1	0.1 ± 0.1	0.1 ± 0.1	na	na	2
Introduced species		6.0	28	19.7	26	332.3 ± 126.3	337.7 ± 128.3	0.827	0.048	71
Annuals/ biennials	All	4.4	14	13.5	15	241.4 ± 59.9	215.8 ± 49.4	0.422	0.646	67
	Forbs	0.7	8	9.5	8	174.6 ± 38.0	161.9 ± 34.9	0.442	0.592	60
	**Lysimachia arvensis*	<0.1		0.6		6.3 ± 3.1	11.7 ± 5.2	<0.05	5.484	12
	**Lotus pedunculatus*	0.4		8.3		146.0 ± 36.6	128.8 ± 33.6	0.095	5.484	43
	Grasses	3.7	5	3.6	5	66.8 ± 21.9	53.9 ± 14.5	1.000	0.000	39
	**Briza minor*	1.1		0.1		0.1 ± 0.1	na	na	na	3
	Non-grass graminoids	<0.1	1	0.4	2	0.3 ± 0.3	0.3 ± 0.3	na	na	4
Perennial	All	1.6	14	6.2	11	90.9 ± 66.4	121.9 ± 78.9	0.059	3.558	33
	Forbs	0.8	7	0.3	6	0.9 ± 0.5	3.6 ± 1.5	<0.05	5.445	10
	Grasses	<0.1	1	<0.1	1	0.3 ± 0.3	0	na	na	1
	Non-grass graminoids	<0.1	1	<0.1	1	4.2 ± 2.9	8.4 ± 6.4	na	na	1
	Shrubs/subshrubs/ twiners	0.7	3	5.9	3	85.5 ± 62.7	109.9 ± 71.0	0.214	1.544	28
	**Genista monspessulana*	<0.1		5.6		81.3 ± 62.7	110.5 ± 70.7	0.757	0.094	9
	**Rubus anglocandicans*	0.6		0.4		4.2 ± 1.4	7.8 ± 2.1	0.062	3.490	23
	Trees	<0.1	1	0	0	0	0	na	na	0

na, not applicable.

[†] Comparison of log-transformed data; only data from quadrats where the target lifeform class/species emerged in at least on tray were included in analysis.

[‡] Number of quadrats in which lifeform class/species emerged in at least one of the two paired trays.

(675 ± 159 seedlings m^{-2}; 25 species; χ^2 (369) = 15.6, i>P = <0.01). Emergence was low for most species with more than half of the emerging species producing <20 seedlings across all trays. Furthermore, no seedlings emerged in the blank control trays, indicating absence of contamination.

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Table 2. Frequency of rare and threatened plant species recorded from quadrats.

Family	Species (conservation status)	Life-history classes	Number of quadrats where species recorded (N = 94)			
			HS	C	A	S
Only recorded from the germinable soil seed bank						
RUBIACEAE	*Asperula conferta* (*ra*)	PFo	0	1	0	1
GUTTIFERAE	*Hypericum japonicum* (r *vu*)	AFo	2	1	0	2
COMPOSITAE	*Olearia glandulosa* (v *en*)	PS	1	0	0	1
LEGUMINOSAE	*Pultenaea dentata* (r *en*)	PS	1	1	0	1
MENYANTHACEAE	*Villarsia umbricola* (*ra*)	PFo	1	1	0	2
Only recorded from the above-ground vegetation						
BLECHNACEAE	*Blechnum wattsii* (r *vu*)	PFe	0	0	1	0
ONAGRACEAE	*Epilobium pallidiflorum* (*ra*)	PFo	0	0	1	0
GLEICHENIACEAE	*Gleichenia microphylla* (r *ra*)	PFe	0	0	37	0
MYRTACEAE	*Leptospermum lanigerum* (*ra*)	PS	0	0	1	0
LYCOPODIACEAE	*Lycopodiella lateralis* (r *cr*)	PFe	0	0	1	0
LYCOPODIACEAE	*Lycopodiella serpentina* (e *cr*)	PFe	0	0	1	0
MYRTACEAE	*Melaleuca squamea* (r *ra*)	PS	0	0	1	0
SCHIZAEACEAE	*Schizaea bifida* (v *en*)	PFe	0	0	1	0
COMPOSITAE	*Senecio glomeratus* (*vu*)	AFo	0	0	1	0
ORCHIDACEAE	*Thelymitra cyanea* (e *en*)	PFo	0	0	1	0
ORCHIDACEAE	*Thelymitra holmesii* (v *en*)	PFo	0	0	1	0
LENTIBULARIACEAE	*Utricularia dichotoma* (*vu*)	PFo	0	0	1	0
LENTIBULARIACEAE	*Utricularia tenella* (*ra*)	PFo	0	0	1	0
XYRIDACEAE	*Xyris operculata* (r *ra*)	PGm	0	0	1	0
Recorded from both the germinable soil seed bank and the above-ground vegetation						
CYPERACEAE	*Baumea rubiginosa* (*ra*)	PGm	14	16	23	23
UMBELLIFERAE	*Centella cordifolia* (*ra*)	PFo	6	7	1	11
CENTROLEPIDACEAE	*Centrolepis fascicularis* (*vu*)	AGm	22	22	1	34
DROSERACEAE	*Drosera binata* (r *vu*)	AFo	5	1	1	5
RESTIONACEAE	*Empodisma minus* (*ra*)	PGm	27	22	6	35
MYRTACEAE	*Eucalyptus ovata* (*vu*)	PT	2	0	1	2
HALORAGACEAE	*Gonocarpus micranthus* (r *vu*)	PFo	20	17	1	31
DILLENIACEAE	*Hibbertia tenuis* (CR e *cr*)	PS	6	1	17	7
UMBELLIFERAE	*Lilaeopsis polyantha* (*vu*)	PFo	2	1	1	2
HALORAGACEAE	*Myriophyllum amphibium* (r *vu*)	PFo	3	3	1	6
IRIDACEAE	*Patersonia occidentalis* (*ra*)	PGm	2	3	8	5
CYPERACEAE	*Schoenus maschalinus* (*vu*)	AGm	26	23	2	39
EPACRIDACEAE	*Sprengelia incarnata* (r *vu*)	PS	5	5	4	6
LEGUMINOSAE	*Viminaria juncea* (r *vu*)	PS	13	10	7	21
VIOLACEAE	*Viola eminens* (*vu*)	PFo	7	4	5	11

Two comparisons are presented: (i) seed emergence following heat plus smoke treatment (HS), compared with no treatment (C); and (ii) present in the above-ground vegetation (A) prior to sampling soil and emerging in at least one of the two paired sample trays (S).

Conservation status is given as: CE = Critically endangered, E = Endangered, V = Vulnerable, R = Rare; Upper case = National rating (EPBC Act), Lowercase = State rating 754 (Barker et al. 2005), Italics = Regional rating (Gillam & Urban 2014).

Life-history class is given as: P = Perennial, A = Annual/biennial, T = Tree, S = Shrub/subshrub, 755 Fo = Forb, Fe = Fern/clubmoss, G = Grass, Gm = Non-grass graminoids.

Discussion

In our study of the critically endangered *Swamps of the Fleurieu Peninsula* Ecological Community, we germinated 48 native species from the soil seed bank, 21% of which were absent from the above-ground vegetation. We also germinated 25 introduced species. While the seed banks of such swamps have not been previously studied, comparisons can be made with similarly designed studies investigating soil seed banks of ephemeral swamp and dry heath communities in areas of comparable rainfall in southern Australia. Although Nicol *et al.* (2003) recorded fewer (19) native species germinating from the soil seed bank of shallow ephemeral lagoons, seed densities were considerably greater (22 000–78 000 m^{-2}, emergenced monitored for 154 days) than what we recorded (2996–3652 m^{-2}, 365 days). Similarly, germinable seed densities recorded from soils under dry heath communities were also greater (4227–12 527 m^{-2}, 150 days: Enright & Kintrup 2001). The comparatively low density of seedlings emerging from the seed

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Table 3. Effect of heat and smoke treatment (HS, C = untreated control) on richness of seedling emergence from the soil seed bank; comparison of numbers of species emerging for each life-history/lifeform class

		Mean (±SE) number of species per tray		Significance[†]	
Life-history class	Lifeform class	HS	C	χ^2	*P*
Native species	All	5.6 ± 0.5	5.4 ± 0.3	0.482	0.488
Annual and biennial	All	2.6 ± 0.3	2.5 ± 0.2	0.112	0.738
	Forbs	0.8 ± 0.4	0.5 ± 0.2	1.982	0.159
	Grasses	na	na	na	na
	Non-grass graminoid	2.4 ± 0.3	2.4 ± 0.2	0.000	1
Perennial	All	3.4 ± 0.4	3.2 ± 0.2	0.398	0.528
	Ferns	na	na	na	na
	Forbs	1.2 ± 0.2	1.0 ± 0.1	0.368	0.544
	Grasses	0.7 ± 0.3	0.8 ± 0.2	0.087	0.768
	Non-grass graminoid	1.9 ± 0.3	1.9 ± 0.1	0.004	0.950
	Shrubs/subshrubs	1.03 ± 0.3	0.8 ± 0.1	1.556	0.249
	Trees	na	na	na	na
Introduced species	All	1.8 ± 0.3	1.9 ± 0.2	0.214	0.644
Annual and biennial	All	1.6 ± 0.3	1.5 ± 0.2	0.038	0.845
	Forbs	1.2 ± 0.3	1.2 ± 0.2	0.066	0.974
	Grass	0.9 ± 0.3	0.9 ± 0.2	0.013	0.908
	Non-grass graminoid	0.5 ± 0.6	1.0 ± 0.5	0.680	0.410
Perennial	All	0.7 ± 0.2	1.0 ± 0.2	2.059	0.151
	Ferns	0	0	na	na
	Forbs	0.5 ± 0.3	0.9 ± 0.2	1.513	0.219
	Grasses	na	na	na	na
	Non-grass graminoid	0.7 ± 0.9	0.3 ± 0.3	0.339	0.560
	Shrubs/subshrubs	0.6 ± 0.2	0.82 ± 0.2	1.261	0.261
	Trees	0	0	na	na

na, not applicable/insufficient data for analysis.

Analysis is made using GLM models with negative binomial distributions.

[†] Comparison of log-transformed data; native and introduced species calculated separately, ns = $P \geq 0.05$.

bank in long-unburnt Fleurieu Peninsula swamps may be evidence of a diminishing seed input, resulting from the long absence of fire. A persistent soil seed bank requires seed production to balance seed loss. Production of seeds diminishes as vegetation senesces over time, while soil-borne seeds suffer attrition through decay or predation (Watson & Riha 2011; Hidayati *et al.* 2012; Roberts 2012) with seed viability often following a negative exponential curve (Chambers & MacMahon 1994; Conn *et al.* 2006).

Another factor that may have affected our results was our deliberate bias towards sampling swamp margin habitats containing or likely to contain *H. tenuis*. Thus, wetter microhabitats which possibly contained a greater abundance of seed were not sampled, maybe giving a measure lower than for the swamps as a whole. A separate *in situ* experiment, which monitors the recovery of these swamps after prescribed fire, is being conducted to determine whether low seed abundance is limiting post-fire regeneration and to determine whether other factors may be contributing to this low *ex situ* seedling emergence. Nevertheless, this sampling bias did not affect the other results of the current experiment, quadrats being only assigned to areas of similar vegetation, ensuring sample variation did not significantly influence our models.

Short-lived species comprised the majority of the native soil seed bank in ephemeral gilgai wetlands (Davies *et al.* 2018) and senescent mallee–heath communities (Davies *et al.* 2013). In comparison, twice as many perennial natives emerged from the germinable soil seed bank of heath-dominated permanent Fleurieu Peninsula swamps, with approximately equal abundances of seed for each life-history class. This is indicative of the large number of perennial ground-stratum species occurring in such swamps and likely reflects their reproductive strategy of relying on a persistent soil seed bank to survive when outcompeted by dense overstorey species. As in some previous studies (McGraw 1987; Enright *et al.* 1997), the germinable soil seed bank was dominated by both annual and perennial graminoids, predominantly sedges (Cyperaceae) and rushes (Juncaceae) with these comprising 48% and 32% of all seedlings respectively. This abundant and readily germinating soil seed bank could represent an adaption to facilitate rapid recolonisation (Bell 2001) and can be attributed to the long-lived nature of their seed banks (Bakker *et al.* 1996; Leck & Schütz 2005). In contrast, 19 forb, fern and graminoid species which were poorly represented in the above-ground vegetation (<0.01% cover) did not emerge from the soil seed

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bank (Table 3; Appendix S2). Such species may be vulnerable to local extinction in swamps that are left long undisturbed, particularly if seed longevity is less than the inter disturbance period. The paucity of seed of many native species in the germinable soil seed bank (Tables S1.1 and S1.2 in Appendix S1) is consistent with other studies (e.g. Auld 1995; Davies *et al.* 2013) and may result from limited-term seed viability (Auld 1995; Davies 2005) or high rates of seed losses to granivores (Shen *et al.* 2007). Further studies are required to assess how the viability of seeds in the soil seed bank of the Fleurieu Peninsula swamps may deteriorate over time.

In the long-unburnt swamps, *G. microphylla* formed a cover dense enough to exclude most ground-stratum species. Competition from dense overstoreys in long-undisturbed vegetation can lead to a loss of species from both the above-ground vegetation as well as the soil seed bank (Bossuyt *et al.* 2006; Davies *et al.* 2013). However, the loss of species from the above-ground vegetation is not necessarily mirrored in the soil seed bank (Amiaud & Touzard 2004) and where species persist in the soil seed bank there is the potential for regeneration burns to at least partially restore above-ground plant diversity (Davies *et al.* 2013). This applied to the heathy swamps we studied, with ten (21%) of the 48 native species emerging from the sampled soil seed bank being absent from the above-ground vegetation, including five rare or threatened species. This is comparable with other south eastern Australian dry heathlands where 25–32% of species in the soil seed bank were absent from the above-ground vegetation (Wills & Read 2002, 2007).

In landscapes historically prone to fire, senescence and subsequent declines in species diversity are associated with long fire-free intervals (Cheal 2010; Shackelford *et al.* 2015). Fire intervals of approximately 45 years generally support diversity in mallee–heath, heathy dry forests and sandy heathlands (Cheal 2010; Gosper *et al.* 2011; Gosper *et al.* 2012); however, to our knowledge, no studies have assessed maximum recommended fire intervals for heathy swamps. Obligate seeders which require disturbance to break seed dormancy are particularly vulnerable to long-term fire exclusion (Orscheg & Enright 2011). *Pultenaea dentata* and *O. glandulosa*, two obligate seeding species which were absent from the above-ground vegetation, emerged from the soil seed banks taken from the Fleurieu Peninsula swamps. This was despite these swamps being unburnt for at least 59 years. Likewise, *H. tenuis* emerged from soil samples obtained from one swamp where it was also absent in the above-ground vegetation. This indicates the longevity of the soil seed banks of these species and the potential to establish new populations of obligate species by regenerative burning.

Although there was no significant difference in the numbers of native species that emerged from the heat plus smoke and untreated soils, significantly more seedlings of native shrubs and subshrubs emerged. This seems to apply particularly to the dwarf shrub *G. ovata*, a species which also germinates in response to physical disturbance (e.g. bulldozing, J. Trezise pers. obs., 2018). Two other regionally threatened species found to benefit from fire are the shrub *V. juncea* (Auld & O'Connell 1991; Liyanage & Ooi 2015) and the perennial herb *Gonocarpus micranthus* (Timmins 1992; Johnson 2001), although both species can also emerge in the absence of fire. In contrast, two regionally 'near-threatened' species, the fern *B. minus* and the annual rush *J. caespiticius*, only germinated from untreated soil. However, one must be cautious extrapolating results of *ex situ* studies to the *in situ* situation, given that the procedure of taking, mixing and spreading the cores of topsoil over the trays may have in itself stimulated some seeds to germinate (e.g. by providing exposure to light; Davies 2005). Pre-treatments such as specific temperature stratification regimes, which occur naturally, may be required to stimulate germination in smoke-treated seed (Hidayati *et al.* 2000). Furthermore, having independent treatments consisting of smoke or heat may have produced different results.

Of greatest importance was the 18-fold increase in emergence of the nationally critically endangered *H. tenuis* in response to the heat plus smoke treatment. This indicates the potential for recovery of this species using ecological burns to both stimulate germination and also to reduce competition by the fern *G. microphylla*, which readily outcompetes *H. tenuis*. Previous recovery actions aimed at increasing the population size of *H. tenuis* by the translocation of tubestock grown from cuttings in unmodified stands of *G. microphylla* (Quarmby 2011), have had limited success with the translocated plants being outcompeted and dying within three years (J. Trezise pers. obs., 2018). Where the species persists in long-unburnt vegetation, it is confined to recently disturbed areas (e.g. tracks), indicating that fire enhances but is not critical for emergence. Despite *G. microphylla* being dominant in the swamps (average 44% cover), we recorded no plants of this native fern emerging from soil-borne spores. This agrees with previous studies that found the main fire recovery mechanism for *Gleichenia* species is resprouting from rhizomes (Walker & Boneta 1995; Clarkson 1997; McQueen & Forester 2000). Previous burns of *Gleichenia*-dominated wet heath have found fire reduces the biomass for this species for several years (R. Davies pers. obs., 2018). This is probably due to senescent *G. microphylla* developing adequately dense and dry above-ground fuel to support a burn capable of suppressing its recovery. We suggest that recovery of

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G. microphylla likely lags behind that of ground-strata species, and this gives time for ground-strata species to establish and set seed before being outcompeted.

Our study found a relatively high proportion (90%) of native species emerged in the absence of heat plus smoke, similar to proportions found from soils under senescent mallee–heath (82%; Davies *et al.* 2013). However, emergence rates from untreated soil were lower (36–50%) for seemingly less senescent dry heaths (Enright *et al.* 1997; Auld & Denham 2006; Wills & Read 2007). Relatively high emergence rates in untreated soils may be attributable to the age of the germinable soil seed bank (Davies *et al.* 2013). Morrison *et al.* (1992) found reduced levels of dormancy in older seed, attributing this to factors such as the breakdown of impervious seed coats over time and the leaching of chemicals that inhibit germination (Baskin & Baskin 1998). These processes may be particularly pertinent in permanently waterlogged soils. Although the emergence of seedlings from untreated soil suggests some capacity for plants to establish if the competition with other species was removed (e.g. by slashing), the likelihood that these would establish and set seed before the slashed plants had recovered is low. Slashing also lacks important fire-related cues (e.g. heat and smoke). So, fire not only reduces competition by removing biomass but also promotes higher germination rates which is preferable to slashing. Season of burn, intensity and other characteristics of fire will influence the magnitude of the emergence response of the plants (Miller *et al.* 2019).

Despite the observed benefits of fire as a tool to regenerate wet heath, burning can also cause increases in abundance of introduced species that exploit disturbance (Milberg & Lamont 1995; Fisher *et al.* 2009; Keeley & Brennan 2012). The Fleurieu Peninsula swamps are small and embedded within an agricultural landscape and so vulnerable to incursions of weeds following disturbances like fire. That 32 introduced species emerged from the soil seed banks was not surprising. This included several introduced species that were absent from the above-ground vegetation. While most were small short-lived forbs, one such species of concern was the highly invasive perennial grass, *Eragrostis curvula*, which appeared to be promoted by burning, emerging only from heat plus smoke-treated soil. A further highly invasive species in these swamps is European blackberry (*R. anglocandicans*). While the main post-fire strategy for this species is resprouting from perennial root stocks, seed dispersal is an important strategy used by the species to invade new areas (e.g. via animal dispersal; Davies 1998). While previous studies (research cited in Davies 2000) have found that the abundance of some introduced species may instead be inhibited by fire, we found this only applied in our study to three species which were abundant (≥7 seedlings) in the soil seed bank (the forbs *L. arvensis* and *Leontodon saxatilis*, and annual grass *Vulpia bromoides*), none of which are highly competitive. Davies (2000) describes the use of fire to specifically control weeds as being fraught with problems, due to the differing responses of different species to the same treatment, and the ability of weeds to rapidly recover in response to increased nutrients and reduced competition, even where their abundance may have been initially significantly reduced. Thus, while ecological burns of heathy swamps are essential to maintain native plant diversity, they need to be followed up with ongoing, targeted weed management to prevent escalated invasion by such species.

Peat retention needs careful consideration in any fire management in swamps. Many Fleurieu Peninsula swamps contain a substantial peat layer, and fire is globally recognised as a threat to peatlands and is exacerbated by climate change (Usup *et al.* 2004; Pemberton 2005; Whinam & Hope 2005). Peat accumulation represents a large fraction of global carbon stores (Page *et al.* 2002; Dise 2009; Page & Hooijer 2016), and so although burning can increase the above-ground plant diversity of swamps which contain peat, care is required to minimise combustion of peat. Furthermore, fire can shift ecosystems which support the development of peat, to an alternative state that does not (Frost 1995; Kettridge *et al.* 2015; Turetsky *et al.* 2015). For these reasons, application of fire needs to be conducted in a manner which enables succession but minimises peat combustion and the chance of community shift. These risks can be mitigated by prescribing fire in conditions dry enough to adequately consume above-ground competition, but also wet enough to prevent fire spreading into peat deposits (Prior *et al.* 2020). In southern Australia, these conditions often occur in autumn, but not all seasons are the same and so the moisture content of peat needs to be monitored to confirm this.

In summary, our results suggest that ecological burns may help regenerate populations of threatened plant species in heathlands on permanent swamps, as long as employed periodically at intervals less than the term of their seed viability in the soil seed bank. Prescribed burns offer a range of services likely to facilitate the regeneration of threatened ground-stratum natives in swamp habitats, including promoting seedling emergence, providing gaps in the overstorey, suppressing competition from dominant species, and providing these plants with opportunities to replenish their seed banks.

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AUTHOR CONTRIBUTIONS

James Edward Trezise: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); visualization (lead); writing-original draft (lead); writing-review & editing (equal). **David Paton:** Resources (equal); software (equal); supervision (equal); writing-review & editing (equal). **José M. Facelli:** Resources (equal); software (equal); supervision (supporting); writing-review & editing (equal). **Rick Davies:** Conceptualization (equal); methodology (equal); project administration (supporting); supervision (lead); writing-original draft (supporting); writing-review & editing (lead).

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Number of quadrats at which each native and introduced species was recorded in this study; attributes of these species; whether recorded from above-ground vegetation, germinable soil seed bank or both; and whether germinated from heat plus smoke treated soil, untreated soil, or both.

Appendix S2. Analysis is made for the above-ground vegetation (AGV) and the soil seed bank (SSB): (1) Total percent cover in the AGV of each native species or life-history/lifeform classes is assessed across all quadrats; and (2) A comparison is made between the total seed germinating from the SSB following heat plus smoke treatment (HS) compared with the control (C).

Appendix S3. Threatened plant species occurring in, or at the margins of, permanent freshwater swamps or springs in the Adelaide and Mount Lofty Ranges Region of South Australia.


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