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Are germination cues for soil-stored seedbanks different in structurally different fire-prone communities?

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Abstract Many plant species are dependent on soil-stored seeds for their persistence in fire-prone systems. Seed germination is often stimulated by fire-related cues including heat and smoke, but the way these cues promote germination may differ between structurally distinct plant communities with historically different fire regimes. In this study we examined the effects of heat, smoke and their interactions on the germination of soil-stored seeds from shrubby woodlands and herbaceous forests in south-east Australia. The effect of these treatments on species richness, diversity and composition, and species richness and density of germinants within life-forms (grass, forb, shrub) were assessed. Soils from each community were subjected to low heat (40°C), low heat with smoke, smoke, high heat (80°C), high heat with smoke and untreated (control) before being placed in a glasshouse, where the germinants were identified and counted. Greater species richness was stimulated by high heat treatments and smoke in both communities, a trend driven by shrubs and forbs, rather than grasses. Greater species diversity was stimulated by high heat with smoke in both communities. Greater densities of grass germinants were stimulated by all treatments, except low heat, in both communities. For forbs and shrubs, the effect of treatment depended on community. Compared to the control, low

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heat with smoke (forbs) and both low heat and low heat with smoke (shrubs) increased densities in the woodland but not in the forest. There were unique species compositions, different from the control, in all treatments in the forest but not in the woodland, where composition in low heat was not different from the control. These results indicate the importance of high soil temperatures and smoke in both communities. In the absence of wildfires, recurring prescribed burns that heat the soil to low temperatures are likely to reduce plant richness, diversity, and density resulting in a change in understorey species composition and structure.

Key words: fire regimes, germination cues, herbaceous forest, shrubby woodland, soil-stored seedbank.

INTRODUCTION

Many plant species which are killed by fire are dependent on a soil-stored seedbank for their persistence in fire-prone systems (Keeley *et al.* 2012). Germination of seeds is often stimulated by fire-related cues including heat, chemicals from smoke, or a combination of the two (Bell 1999; Keeley & Fotheringham 2000). Those species in which germination is dependent on fire-related cues are likely to be susceptible to changes in fire regimes through management or climate change. Therefore determining the relative importance of different fire-related germination cues is important for the conservation and management of floristic diversity in fire-prone ecosystems.

Differences in vegetation structure result in fire regimes that vary between vegetation communities (Murphy *et al.* 2013). The intensity, frequency, and timing of fires are, in part, dependent on fuel accumulation and availability, which varies with productivity (Bradstock 2010). Although little is known about fire intensity in temperate shrubby and forest communities (Enright *et al.* 2012; Gill 2012), there is more information on frequency and timing. Shrubby woodlands on sandy soils experience relatively frequent fires (12-45 years) in the shrub layer from spring to summer (Cheal 2010; Enright *et al.* 2012). By comparison, temperate herbaceous eucalypt forests on more productive loam soils experience less frequent fires (25-100 years) that burn the ground layer, also from spring to summer (Duncan & Brown 1995; Tran & Wild 2000; Cheal 2010).

Vegetation communities with different fire regimes may be expected to have different responses to fire-related germination cues. Fire-prone shrubby systems, like heath, chaparral, fynbos and kwongan are dominated by species that are stimulated to germinate by heat shock, smoke and charred wood (Dixon *et al.* 1995; Keeley & Bond 1997; Bell 1999). Many shrubs, especially physically dormant species such as legumes, are dependent on soil temperatures of between 80°C and 100°C to break the seed coat (e.g. Fabaceae; Auld & O'Connell 1991). In herbaceous systems smoke and lower soil temperatures are important for germination (30-60 °C; Warcup 1980; Read *et al.* 2000), since high temperatures can inhibit or have no effect on germination (Clarke *et al.* 2000), although

this is not always the case (Hill & French 2003). So, changes in fire-related germination cues may differently affect the germination success of species in structurally different communities.

One of the germination cues, soil temperature, is influenced by fire type. Soil temperature is positively influenced by the consumption of ground fuels, which in turn is influenced by fuel moisture. Since prescribed burns are undertaken when fuel moisture levels are moderate, they often result in low soil temperatures (30-60°C; Walstad *et al.* 1990; Bradstock & Auld 1995; Penman & Towerton 2008). In contrast, wildfires often occur when fuels are drier, generally resulting in higher soil temperatures (Beadle 1940; Certini 2005).

The influence of soil temperatures and patterns exhibited by germination after a fire is still not clear in some Australian systems. Most studies investigating the effects of heat and smoke on plant germination have either been undertaken in shrubby woodlands (Enright & Kintrup 2001; Wills & Read 2002) or herbaceous woodlands and dry sclerophyll forests (Clarke *et al.* 2000; Read *et al.* 2000; Penman *et al.* 2008) but not in taller forests with a herbaceous understorey. Furthermore, there are no studies that have compared the effects of temperature and smoke on germination of seeds from soil in communities with contrasting herbaceous and shrubby understoreys.

A range of fire-prone plant communities occur in the Great Otways National Park, south-eastern Australia (Department of Sustainability and Environment 2012). Whilst wildfires have occurred regularly in the past, more recently prescribed burning has been used for both fuel reduction and ecological purposes (Department of Primary Industries 2013). Shrubby woodlands and herbaceous forests are floristically and structurally different communities that are targeted for these burns. Shrubby woodlands are characterised by a dense shrub stratum with an overstorey of scattered low eucalypts. In contrast, herbaceous forest is typified by forbs and grasses, scattered shrubs and an overstorey of tall dense eucalypts. We hypothesised that: 1/ germination of soil-stored seed will be more reliant on high soil temperatures in shrubby woodland than herbaceous forest because 1a/ germination of shrubs will be stimulated by high soil temperatures and 1b/ germination of herbaceous (grass, forb) species will be stimulated by both high and low soil temperatures; 2/ smoke will be similarly important for germination of species in both communities.

METHODS

Study area

The study was undertaken in the Great Otway National Park (59 000 ha) in south eastern Australia. The area experiences a Mediterranean climate, characterised by warm dry summers and cool wet winters, with a mean annual minimum of 10.5°C and a maximum of 18.2°C (Bureau of Meteorology

2012). The study concentrated on shrubby woodland and herbaceous forest (also called foothill forest), which receive mean annual rainfalls of 700 mm and 1000 mm, respectively (Bureau of Meteorology 2012). Shrubby woodland occurs on sandy soils on gently undulating topography at low elevation (180 m asl). It has an overstorey of scattered low (≤ 10 m), eucalypts (*Eucalyptus baxteri*), and an understorey of dense shrubs with grasses and forbs. The herbaceous forest occurs on clay loams on moderate slopes at higher elevation (600 m asl). It has an overstorey dominated by *E. obliqua* (≤ 25 m), and an understorey of forbs and grasses with scattered shrubs (Department of Sustainability and Environment 2007; Department of Sustainability and Environment 2012). These communities were last burned by a wildfire in 1983, and since then have been the subject of prescribed burning, which usually targets small areas (< 400 ha) to satisfy fuel reduction and ecological goals (Department of Primary Industries 2013).

Sampling design and site selection

A geographic information system (ArcGIS 10.1, ESRI 2011) was used to identify a potential sampling zone by determining all ridge-top areas of shrubby woodland and herbaceous forest within the study area that were last burned in 1983, with slope $\leq 5^\circ$ and within 100 m of the road network. Within this zone, 10 points were randomly selected in each vegetation community. Prior to sampling ground truthing was conducted to confirm the vegetation community, time of last fire and an absence of other disturbances. The 30 year post-fire period ensured the accumulation of a considerable soil seedbank (Cheal 2010). Sites were ≥ 20 m from roads to reduce their effects (e.g. runoff) and ≥ 1000 m from each other to reduce spatial autocorrelation.

Soil sampling

At each site a quadrat (20 m $\times$ 20 m) was placed parallel to the road. Within each quadrat a total of 20 soil samples were collected from a 4 m $\times$ 5 m grid of equally spaced points. Metal soil corers (7.5 cm diameter) were used to collect soil samples to 5 cm depth (Auld and O'Connell 1991; Hodgkinson et al. 1980; Read et al. 2000; Wills and Read 2007). The total volume of soil collected per vegetation community was approximately 0.044 m³, which is comparable with other studies (Enright *et al.* 1997; Wills & Read 2002). Soil samples were collected in late March 2013, after most plant species had finished flowering and fruiting (Wills & Read 2002).

Experimental procedure

Soil samples from each site were combined and dried at room temperature for a week (Enright *et al.* 1997). The samples were then sieved through 8 mm mesh to remove large pieces of litter and rocks, and then all samples from each vegetation community were mixed to remove the effect of spatial variation in the soil seedbanks (Enright & Kintrup 2001). The soil from each community was then

divided into 36 samples and placed in aluminium trays to provide for six treatments each with six replicates.

The treatments applied to the soil samples in each vegetation community included high heat (HH), low heat (LH), smoke (S), high heat with smoke (HHS), low heat with smoke (LHS) and a control (C). In the high and low heat treatments soil samples were placed in ovens at 100 °C for 45 minutes and 45 °C for 30 minutes, respectively. The aim was to reach soil temperatures of 80 °C in the high heat and 40 °C in the low heat, simulating the temperatures experienced during wildfires and prescribed burns, respectively (Raison *et al.* 1986; Bradstock & Auld 1995; Enright & Kintrup 2001). To measure the temperature of soil during heating, a sensor was buried in the soil in each replicate tray (Auld and O'Connell 1991). These sensors reached 70 – 80 °C in the high heat treatment and 30 – 40 °C in the low heat treatment.

Three different ovens were used for heating the soil samples. Two replicates of each heat treatment were allocated to each of these to ensure no bias associated with an oven effect (Morrison & Morris 2000). After heating, all soil samples were spread to a depth of 1.5 cm over a mixture of vermiculite and sterilised sand in plastic germination trays (28 cm × 34 cm; 1428 cm³). Smoke treatments were applied to all designated trays after the heated soil samples had cooled. The smoke solution was made by diluting 100 ml of Regen 2000 Smokemaster in 1 litre of water (Grayson Australia Pty. Ltd). Each smoke treated tray was given 400 ml of smoke solution to saturate the soil and simultaneously non-smoke treated trays were given 400 ml of water. Trays were allocated randomly to tables in a glass house, and tables were rotated weekly to minimise position bias. Trays were watered to maintain soil moisture for the duration of the experiment from April to August 2013 (16 weeks).

The germination and density of all seedlings were recorded weekly from week 5 to week 16, after which there were negligible numbers of new seedlings. Seedlings were firstly identified as morphospecies and representatives were transplanted for final identification. To avoid overcrowding seedlings were regularly removed. About 20 species from each vegetation community could not be identified and were given names according to their life-form (e.g. Grass sp.1).

Statistical analyses

We used both linear and generalised linear models to assess the influence of treatment (high heat, low heat, smoke, high heat with smoke, low heat with smoke, control), vegetation community (herbaceous forest and shrubby woodland), and their interaction on both vascular plant species richness and diversity. Diversity was calculated using the effective number of species derived from the Shannon diversity index, H . Values are calculated as exponential (H) and used to compare the diversity of biotic communities on a linear scale; a community with a value of 5 is half as diverse as a community with a value of 10 (Jost, 2006). We used a generalised linear model with a log link and a

Poisson distribution to analyse species richness, as these data were in the form of counts. We treated species diversity values as continuous, so in this case we used a linear model with a Gaussian distribution.

We were primarily interested in determining the existence of treatment effects, and if treatment interacted with vegetation community. Consequently, for both species richness and diversity, we built three alternative models (treatment $\times$ vegetation community, treatment + vegetation community and treatment) which we compared using information theoretic model selection. The model including vegetation community alone was not considered as it did not relate to our hypotheses. We used Akaike's information criterion corrected for small sample size (AICc) and Akaike weights to compare the level of support for our three models (Burnham & Anderson, 2002). In addition, R^2 was generated for each model, using the standard approach for linear models and the method of Nakagawa and Schielzeth (2013) for generalised linear models. For each response variable, the best model was used to generate contrasts between the control and the other treatments. When relevant, vegetation community and interaction contrasts were also displayed. Graphical displays were generated from the raw data.

To determine if the effect of treatment and vegetation community differed among plants of different form, we allocated each species to a life-form category; grass, forb, or shrub. We used species richness and the density of germinants (the number of germinants within each tray) within each life-form as two new response variables. For each response variable, and for each life-form separately, we built three alternative models (treatment $\times$ vegetation community, treatment + vegetation community and treatment) and used AICc and Akaike weights to compare them, as described above. Because both response variables were counts, we used a generalised linear model with a log link and a Poisson distribution in both cases.

The analyses described above were conducted in R 3.3.1 (R Core Team, 2016). Linear models and generalised linear models were run using the `lm` and `glm` functions of the stats package (R Core Team, 2016). AICc and Akaike weights were calculated using MuMIn (Barton, 2014), and R^2 for generalised linear models was calculated using piecewiseSEM (Lefcheck, 2016). Overdispersion in Poisson models was checked by comparing the ratio of the residual deviance to the residual degrees of freedom, which should equal 1 if distributional assumptions are met. In the analysis of forb density we detected substantial overdispersion; the dispersion parameter of the global model was 1.83. To solve this problem we re-ran the models using a negative binomial distribution (`glm.nb` function in the MASS package - Venables & Ripley, 2002), which reduced the dispersion parameter in the global model to 1.20. Assumptions of normality and equal variances were checked using histograms of residuals and fitted values plots, and no major violations were detected.

We used PERMANOVA (including post-hoc pairwise tests) to examine the effects of treatment and its interaction with vegetation community on species composition (PRIMER, Clarke & Warwick 2001). PERMANOVA was applied to a Bray-Curtis similarity matrix derived from standardised

(division by the maximum) and transformed ($\log x+1$) counts of each species. The same similarity matrix was used to generate a multidimensional scaling (MDS) ordination, providing a graphical representation of how the treatments influenced species composition. Similarity percentage (SIMPER) analyses were used to determine the species that contributed most to the differences among treatments in each community.

RESULTS

Effect of treatment on species richness and diversity

Totals of 42 and 55 species germinated in the soil seedbanks of shrubby woodland and herbaceous forest, respectively. Forb and shrub species, followed by grass species dominated the soil seedbank in both communities (Fig. 1). Four grass, 2 forb and 6 shrub species were the most abundant germinants (≥ 6 germinants) in shrubby woodland, compared with 2 grass, 22 forb and 12 shrub species in herbaceous forest (Appendix S1).

Raw data reflecting the effect of treatment on species richness and diversity are presented in Appendix S2. The response of species richness to treatment was generally similar in the herbaceous forest and shrubby woodland (weight of additive model 1.0; Table 1). Compared with the control, and averaged across the two communities, high heat with smoke, high heat, and smoke caused detectable 53%, 37% and 27% increases in species richness, respectively (Fig. 2a, b).

The result was similar for species diversity (weight of additive model 0.91; Table 1), but in this case high heat with smoke was the only treatment to clearly result in greater diversity (21%) relative to the control (Table 1). While modelling indicated a consistent effect of treatment on species diversity in the two vegetation communities, the raw data suggests that the effect of high heat with smoke may have been somewhat greater in the herbaceous forest than the shrubby woodland (Fig. 2c, d; Appendix S2b).

Effect of treatment on species richness and density within life-forms

Raw data reflecting the effect of treatment on species richness and density within life-forms are presented in Appendices S3 and S4. Species richness within all three life-forms (grass, forbs and shrubs) responded to treatment similarly in herbaceous forest and shrubby woodland, with additive or treatment only models being substantially better than models including the treatment by vegetation community interaction (Table 2). For grass, none of the treatments caused richness to increase beyond the control value, while for forbs, high heat with smoke caused a detectable 37% increase. Shrub richness was affected by treatment more than grass and forbs; relative to the control, shrub

richness was increased by high heat with smoke, high heat, and smoke by 107%, 74% and 47% respectively.

The response of germinant density to treatment differed substantially between grass on one hand and forbs and shrubs on the other. For grass, treatment had a similar effect on density in both vegetation communities (weight of additive model 0.82; Table 3). Compared with the control, all treatments except for low heat resulted in greater density. The largest effects were associated with high heat with smoke and high heat; relative to the control these treatments increased density by 311% and 240% respectively (Fig. 3). For forbs and shrubs, the effect of treatment on density depended on vegetation community (weight of the interactive models were 0.80 and 1.0 respectively, Table 3). The different patterns of treatment effect in the two communities were mainly due to the positive influence of low heat with smoke (forbs) and both low heat with smoke and low heat (shrubs) on density in the shrubby woodland but not in the herbaceous forest (Table 3). For herbaceous forest forbs, smoke, high heat with smoke and high heat increased density by 22%, 18% and 17% respectively, relative to the control, while in the shrubby woodland low heat with smoke, high heat with smoke and smoke increased density by 273%, 136% and 109%, respectively (Table 3, Fig. 3). For herbaceous forest shrubs, high heat with smoke, high heat, and smoke increased density by 212%, 159% and 138% respectively. In the shrubby woodland all treatments resulted in greater density than the control, including 258% and 67% increases following the application of low heat with smoke and low heat, respectively (Table 3, Fig. 3).

Effect of treatment on species composition

PERMANOVA revealed a significant two way interaction between treatment and community, indicating that species compositions were differently affected by treatments in the shrubby woodland and herbaceous forest ($P < 0.001$; Table 4). In the shrubby woodland there were significant differences in species composition among all pairs of treatments except control and low heat, low heat and low heat with smoke, low heat and smoke, low heat with smoke and smoke, low heat and high heat, and low heat and high heat with smoke (Appendix S5; Fig. 4a). These results indicate that although species compositions in most treatments differed from the control, they shared similarities with the low heat treatment, where composition was quite variable among the six replicates. In herbaceous forest, species composition differed statistically between all pairs of treatments (Appendix S5; Fig 4b).

SIMPER analyses indicated that the differences in species compositions between treatments in each community were the result of comparatively small additive contributions of quite a few species rather than a few dominant ones. However, there were trends in the occurrence of life-forms that explained the first 20% of dissimilarities between the treatments that differed significantly from the control (Appendix S6). Shrubs were more abundant in high heat than control: Shrub sp. 4, *Pimelea*

linifolia, Shrub sp.12 in shrubby woodland; Shrub sp. 1, *Spyridium parvifolium*, *Pultenaea daphnoides* and *Lepidosperma* sp. 1 in herbaceous forest. Shrubs were also more abundant in high heat with smoke than control: *Dillwynia glaberrima*, and Shrub sp. 12 in shrubby woodland; Shrub sp. 3, *Pultenaea daphnoides*, *Prostanthera lasiophylla*, and *Geranium* sp. 1 in the herbaceous forest. In the shrubby woodland shrubs were more abundant in control than smoke, eg., Shrub sp. 12 and 7. In contrast, herbaceous forest shrubs were more abundant in smoke than control, eg., *Prostanthera lasianthos*, *Spyridium parvifolium* and *Pultenaea forsythiana*. Forbs contributed to differences between low heat treatments (low heat, low heat and smoke) and the control, where they tended to be more abundant in low heat treatments. For example, in the herbaceous forest *Senecio glomeratus* and *Oxalis exilis* were more abundant in low heat and *Hydrocotyle foveolata* was more abundant in low heat with smoke, while in the shrubby woodland *Xanthosia dissecta* was more abundant in low heat and smoke. However, differences between the low heat treatments and the control in the shrubby woodland were most strongly influenced by Shrub sp. 12, which was more abundant in both the low heat treatments (Appendix S6).

DISCUSSION

Structurally different plant communities likely evolved with different fire regimes. Since fire regimes influence soil temperatures, plants that regenerate from the soil-stored seed bank may be responsive to different germination cues in these different communities. Examining this thesis is important, given the susceptibility of these species to changes in fire regimes through management or climate change. We hypothesised that germination of soil-stored seed would be 1/ more reliant on high soil temperatures in shrubby woodland than herbaceous forest and that 2/ smoke would be similarly important for germination in both communities. We found that the high heat, high heat with smoke and smoke treatments has similar effects on richness, diversity, density and composition in both communities. These results do not support our first hypothesis but are consistent with our second. The types of fires that these communities are subjected to will influence soil temperatures, which will have consequences for the richness, diversity and composition of species dependent on the soil seed bank for germination.

Effects of treatments on richness, diversity, density and composition

Species richness was increased by both high heat treatments (high heat, high heat with smoke) and smoke, while diversity was only increased by high heat with smoke. Further, we found that these effects were similar in both vegetation communities. The trend in richness was driven by shrubs and forbs, which constituted between 36% (woodland) to 38% (forest) and 40% (woodland) to 51% (forest), of all species, respectively (excluding tree species). While shrubs are a dominant structural

component of the shrubby woodland, forbs and grasses are more prominent in the herbaceous forest. Grass richness, which constituted between 7% (forest) to 14% (woodland) of all species, was independent of treatment. The results of other studies are mixed. Relative to untreated controls, high heat did not increase species richness in herbaceous forest (Hill & French 2003), and neither high heat nor smoke increased richness in shrubby woodland (Enright *et al.* 1997). In contrast, other studies from shrubby woodland show that both high heat (Wills & Read 2002) and smoke (Enright & Kinrup 2001) increase richness. The effect of fire-related germination cues on species diversity is less well studied. In shrubby woodland neither heat, smoke or ash had a detectable effect on plant diversity (Enright *et al.* 1997). With the exception of our study, we are unaware of diversity results for herbaceous forest systems.

Greater densities of grass, forb and shrub species were similarly stimulated by both high heat treatments and smoke in both communities. Densities of forb and shrub species were also variously stimulated by low heat treatments (low heat, low heat with smoke) in the shrubby woodland. This latter trend was driven by a small number of species, including Shrub sp. 12 and *Xanthosia dissecta*, which responded positively to low heat. While these results are relatively consistent with those in other shrubby woodland studies (Enright *et al.* 1997; Enright & Kinrup 2001; Wills & Read 2002), results in herbaceous forests vary from agreement (Warcup 1980; Clarke *et al.* 2000; Read *et al.* 2000; Penman *et al.* 2008), to a negative effect of high heat on herb densities (Clarke *et al.* 2000), a positive effect of low heat on herb densities (Warcup 1980) or no treatment effect (Hill & French 2003). The implication is that the densities of germinants in relation to fire related cues are easier to predict in shrubby woodlands than herbaceous forests.

There were unique species compositions in all treatments in both communities, except for low heat and control in the shrubby woodland. This suggests that heat and smoke work independently or in interaction to influence species composition. Although other comparable studies have not looked at the interactive effects of heat and smoke on species composition, the independent effects of high and low heat have been reported in herbaceous forest (Hill & French 2003) and shrubby woodland (Enright & Kinrup 2001) and also smoke in shrubby woodland (Wills & Read 2002). The relative importance of low heat in the shrubby woodland studied by Enright & Kinrup (2001) compared with our study, may indicate regional variation in germination cues.

Species respond to different germination cues. High heat is well known for its ability to fracture the seed coats of species with physically dormant seeds, thereby facilitating germination of species like *Dillwynia glaberrima* and *Pultenaea daphnoides* (Auld & O'Connell 1991). Smoke, which stimulated the germination of *Poranthera microphylla* and *Isopogon ceratophylla*, is a universal signal that fire has occurred and conditions are suitable for germination, especially after rain (Brown & van Staden 1997). Other species, like *Spyridium parvifolium*, *Pimelea axiflora*, and *Schoenus apogon* hedge their bets by germinating in response to both high heat and smoke, separately, while

species, like *Comesperoma* sp. 1 were dependent on their less frequently reported combined effects (Keith 1997; Thomas *et al.* 2007; Penman *et al.* 2008). Species capable of germinating in response to a range of cues (e.g. heat and smoke separately) are more likely to have greater success than those with more specific requirements (e.g. heat and smoke together).

Although we controlled for soil temperature in our experiments, the textural differences in the soils underlying our two vegetation communities may differently influence their *in situ* soil temperatures during fires. Sandy soils, characteristic of shrubby woodlands have lower water holding capacity than the clay loams of the herbaceous forest (Busse *et al.* 2010). Since lower soil moisture content leads to higher soil temperatures (Campbell *et al.* 1995; Enniful & Torvi 2008; Busse *et al.* 2010), we might expect comparatively higher soil temperatures in shrubby woodland than the herbaceous forest during a fire, which may in turn contribute to their respective species compositions.

Ecological implications

High heat is important for forb and shrub germination. Fires capable of heating the soil to at least 70 °C are likely to stimulate the germination of greater numbers of species and at higher densities than those that heat the soil to 40 °C (Enright & Kinrup 2001). Higher soil temperatures are more likely in wildfires than prescribed burns (Bradstock & Auld 1995; Penman & Towerton 2008), which are ignited only during benign weather and fuel conditions (Walstad *et al.* 1990; Certini 2005). Variation in weather and fuel conditions during wildfires will invariably lead to a patchwork of different severities and thus soil temperatures (Beadle 1940; Rab 1996; Certini 2005). This will provide opportunities for the germination of species responsive to a range of cues.

The longer term persistence of species that fail to germinate in less severely burnt patches will depend on the time to the next high severity fire, the longevity and viability of above ground plants and their soil-stored seeds (Noble & Slatyer 1980; Bradstock & Kenny 2003). The intention of prescribed burning programs to exclude wildfire for long periods is a concern. In our study area there have been no wildfires since 1983 (i.e. 34 years). This is beyond the average return interval for shrubby woodlands in south-east Australia (Enright *et al.* 2012). The application of prescribed fire, while not guaranteed to exclude wildfire, may substantially alter the spatial heat signature of the fire regime, which, as the data show, may have important implications for plant community composition and the persistence of individual species, especially shrubs and forbs. By comparison, species which are partly or totally dependent on smoke to germinate may continue to germinate in patchily burned areas and in the adjacent unburnt areas (Penman *et al.* 2011). However, their establishment success may be limited by above ground competition, which is more disadvantageous for shrubs than herbs, since the latter can take advantage of smaller gaps (Clarke *et al.* 2000).

The ecological implications for fire-prone systems that have shifted from wildfires to prescribed burns are potentially significant. Low soil temperatures during prescribed burns may

reduce the germination success of many shrub and forb species and in the absence of wildfires, lead to their reduced densities (Penman *et al.* 2011) because they are either killed by prescribed fires or senesce and are not replaced. Lower densities of shrubs and forbs may further reduce flammability, in both communities, thereby creating a negative flammability feedback loop. As a consequence, we predict that fire regimes dominated by prescribed burning have the potential to change the floristic composition and structure of shrubby woodlands and herbaceous forests.

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SUPPORTING INFORMATION

Appendix S1. Densities (mean, standard error) of seedlings after treatments (C control, LH low heat, LHS low heat with smoke, S smoke, HH high heat, HHS high heat with smoke) in shrubby woodland and herbaceous forest (number/1428cm³) for species with ≥ 6 germinants.

Appendix S2. The value of (a) species richness and (b) species diversity associated with each replicate tray in shrubby woodland and herbaceous forest. Species diversity values represent the effective number of species, calculated as the exponent of Shannon's diversity index. Treatment abbreviations are LH low heat, LHS low heat with smoke, S smoke, HH high heat and HHS high heat with smoke.

Appendix S3. The value of species richness associated with each replicate tray in shrubby woodland and herbaceous forest. Data are presented separately for (a) grass, (b) forbs and (c) shrubs. Treatment abbreviations are LH low heat, LHS low heat with smoke, S smoke, HH high heat and HHS high heat with smoke.

Appendix S4. The number of germinants associated with each replicate tray (one tray = 1428 cm³ of soil) in shrubby woodland and herbaceous forest. Data are presented separately for (a) grass, (b) forbs and (c) shrubs. Treatment abbreviations are LH low heat, LHS low heat with smoke, S smoke, HH high heat and HHS high heat with smoke.

Appendix S5. Results of PERMANOVA post hoc pair wise tests.

Appendix S6. Results of similarity percentage (SIMPER) analyses used to determine the species that contributed most to the differences between treatments.

Table 1. Responses of plant species richness and diversity to treatment (control, high heat, high heat with smoke, low heat, low heat with smoke, smoke) and vegetation community (herbaceous forest and shrubby woodland). Models are ranked by AICc, and estimates and 95% CIs are presented for the best model. For each contrast, estimates represent differences between vegetation types and between the control and other levels of treatment. Positive estimates indicate a higher value of the response

590 variable in the first listed level. See methods for details of R^2 calculation for generalised linear
 591 models.

Models and contrasts	ΔAIC_c	Akaike weight	Estimate (95% CI)	P	R^2 (%)
Species richness					
Treatment + vegetation	0	1.00			90.3
Forest vs. Woodland			0.81 (0.69, 0.95)	<0.001	
High heat vs. Control			0.31 (0.10, 0.53)	<0.01	
High heat with smoke vs. Control			0.43 (0.22, 0.64)	<0.001	
Low heat vs. Control			0.05 (-0.17, 0.28)	0.65	
Low heat with smoke vs. Control			0.13 (-0.09, 0.35)	0.26	
Smoke vs. Control			0.24 (0.03, 0.46)	0.03	
Treatment $\times$ vegetation	11.7	0.00			91.1
Treatment	163.3	0.00			11.5
Species diversity					
Treatment + vegetation	0	0.91			41.5
Forest vs. Woodland			1.62 (1.03, 2.20)	<0.001	
High heat vs. Control			0.89 (-0.12, 1.90)	0.09	
High heat with smoke vs. Control			1.35 (0.34, 2.36)	0.01	
Low heat vs. Control			0.22 (-0.79, 1.23)	0.67	
Low heat with smoke vs. Control			-0.33 (-1.34, 0.68)	0.51	
Smoke vs. Control			-0.19 (-1.20, 0.82)	0.71	
Treatment $\times$ vegetation	4.7	0.09			48.6
Treatment	24.4	0.00			14.9

598

599 **Table 2.** Responses of grass, forb and shrub species richness to treatment (control, high heat, high
600 heat with smoke, low heat, low heat with smoke, smoke) and vegetation community (herbaceous
601 forest and shrubby woodland). Models are ranked by AICc, and estimates and 95% CIs are presented
602 for the best model. For each contrast, estimates represent differences between vegetation types and
603 between the control and other levels of treatment. Positive estimates indicate a higher value of the
604 response variable in the first listed level. See methods for details of R^2 calculation for generalised
605 linear models.

Models and contrasts	$\Delta AICc$	Akaike weight	Estimate (95% CI)	P	R^2 (%)
Grass					
Treatment + vegetation	0	0.56			23.0
Forest vs. Woodland			-0.30 (-0.64, 0.04)	0.09	
High heat vs. Control			-0.04 (-0.63, 0.54)	0.88	
High heat with smoke vs. Control			0.08 (-0.48, 0.66)	0.77	
Low heat vs. Control			-0.36 (-1.02, 0.27)	0.26	
Low heat with smoke vs. Control			0.08 (-0.48, 0.66)	0.77	
Smoke vs. Control			0.08 (-0.48, 0.66)	0.77	
Treatment	0.5	0.44			11.4
Treatment $\times$ vegetation	12.6	0.00			26.8
Forb					
Treatment + vegetation	0	1.00			94.4
Forest vs. Woodland			1.91 (1.68, 2.16)	<0.001	
High heat vs. Control			0.22 (-0.07, 0.52)	0.14	
High heat with smoke vs. Control			0.31 (0.02, 0.60)	0.04	
Low heat vs. Control			0.16 (-0.14, 0.46)	0.29	
Low heat with smoke vs. Control			0.09 (-0.21, 0.40)	0.54	
Smoke vs. Control			0.20 (-0.09, 0.50)	0.18	
Treatment $\times$ vegetation	12.3	0.00			94.7
Treatment	353.2	0.00			1.4
Shrub					

Treatment	0	0.73		53.0
High heat vs. Control			0.56 (0.19, 0.94)	<0.01
High heat with smoke vs. Control			0.73 (0.37, 1.10)	<0.001
Low heat vs. Control			-0.02 (-0.45, 0.40)	0.91
Low heat with smoke vs. Control			0.21 (-0.19, 0.61)	0.31
Smoke vs. Control			0.38 (0.00, 0.78)	0.05
Treatment + vegetation	2.0	0.27		54.0
Treatment × vegetation	9.7	0.00		64.9

Table 3. Responses of grass, forb and shrub species density to treatment (control, high heat, high heat with smoke, low heat, low heat with smoke, smoke) and vegetation community (herbaceous forest and shrubby woodland). Models are ranked by AICc, and estimates and 95% CIs are presented for the best model. For non-interaction contrast, estimates represent differences between vegetation types and between the control and other levels of treatment. Positive estimates indicate a higher value of the response variable in the first listed level. See methods for details of R^2 calculation for generalised linear models.

Models and contrasts	$\Delta AICc$	Akaike weight	Estimate (95% CI)	P	R^2 (%)
Grass					
Treatment + vegetation	0	0.82			88.5
Forest vs. Woodland			1.28 (1.14, 1.41)	<0.001	
High heat vs. Control			1.22 (0.99, 1.46)	<0.001	
High heat with smoke vs. Control			1.41 (1.19, 1.65)	<0.001	
Low heat vs. Control			0.12 (-0.16, 0.41)	0.39	
Low heat with smoke vs. Control			0.62 (0.37, 0.88)	<0.001	
Smoke vs. Control			0.69 (0.44, 0.95)	<0.001	
Treatment × vegetation	3.1	0.18			89.8
Treatment	408.3	0.00			37.8
Forb					
Treatment × vegetation	0	0.80			97.4

Treatment contrasts: Forest

High heat vs. Control	0.16 (-0.01, 0.33)	0.06
High heat with smoke vs. Control	0.16 (0.00, 0.33)	0.05
Low heat vs. Control	-0.20 (-0.37, -0.02)	0.03
Low heat with smoke vs. Control	0.10 (-0.07, 0.27)	0.24
Smoke vs. Control	0.20 (0.04, 0.37)	0.02

Treatment contrasts: Woodland

High heat vs. Control	0.49 (-0.28, 1.30)	0.22
High heat with smoke vs. Control	0.86 (0.15, 1.64)	0.02
Low heat vs. Control	0.44 (-0.34, 1.25)	0.28
Low heat with smoke vs. Control	1.32 (0.65, 2.06)	<0.001
Smoke vs. Control	0.74 (0.00, 1.52)	0.05

Interaction contrasts

High heat:Forest	-0.33 (-1.14, 0.43)	0.40
High heat with smoke:Forest	-0.70 (-1.47, 0.01)	0.06
Low heat:Forest	-0.63 (-1.45, 0.15)	0.12
Low heat with smoke:Forest	-1.22 (-1.96, -0.55)	<0.001
Smoke:Forest	-0.54 (-1.32, 0.19)	0.16

Treatment + vegetation	2.8	0.20	96.7
Treatment	237.1	0.00	0.9

Shrub

Treatment × vegetation	0	1.00	87.8
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Treatment contrasts: Forest

High heat vs. Control	0.95 (0.57, 1.36)	<0.001
High heat with smoke vs. Control	1.14 (0.76, 1.54)	<0.001
Low heat vs. Control	-0.31 (-0.83, 0.21)	0.24
Low heat with smoke vs. Control	-0.06 (-0.55, 0.42)	0.81
Smoke vs. Control	0.87 (0.48, 1.28)	<0.001

Treatment contrasts: Woodland

High heat vs. Control	0.99 (0.66, 1.34)	<0.001
High heat with smoke vs. Control	1.51 (1.19, 1.84)	<0.001
Low heat vs. Control	0.51 (0.15, 0.89)	<0.01
Low heat with smoke vs. Control	1.27 (0.95, 1.62)	<0.001
Smoke vs. Control	1.26 (0.94, 1.60)	<0.001

Interaction contrasts

High heat:Forest			-0.04 (-0.56, 0.49)	0.89
High heat with smoke:Forest			-0.37 (-0.87, 0.14)	0.15
Low heat:Forest			-0.82 (-1.46, -0.19)	0.01
Low heat with smoke:Forest			-1.34 (-1.93, -0.75)	<0.001
Smoke:Forest			-0.39 (-0.91, 0.13)	0.14
Treatment + vegetation	27.1	0.00		78.7
Treatment	167.9	0.00		46.9

Table 4. PERMANOVA results showing the effect of treatment (control, low heat, low heat with smoke, smoke, high heat, high heat with smoke), community (shrubby woodland, herbaceous forest) and their interaction on germinant composition. P-values are based on 999 permutations.

Source	df	SS	MS	Pseudo-F	P (perm)
Treatment	5	11482.0	2296.3	3.0	0.001
Community	1	1.29×10^5	1.29×10^5	170.1	0.001
Treatment $\times$ community	5	14853.0	2970.5	3.9	0.001
Residual	60	45745.0	762.4		
Total	71	2.01E5			

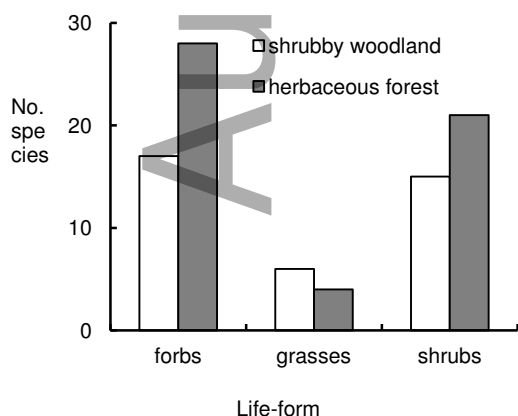


Figure 1. The number of species in each life-form in shrubby woodland and herbaceous forest.

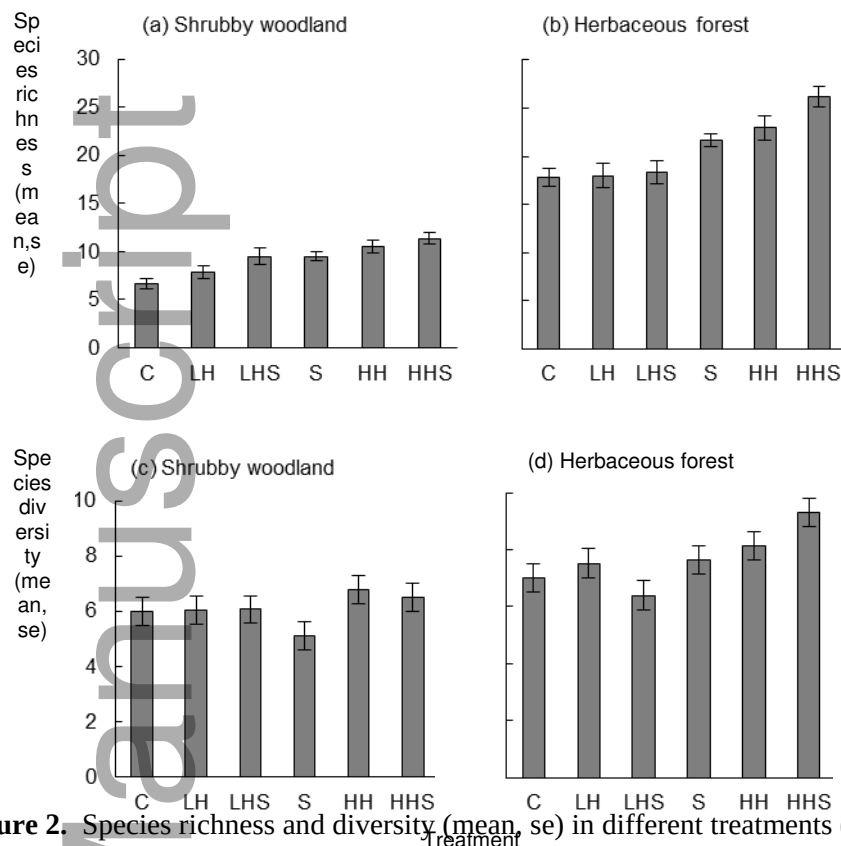


Figure 2. Species richness and diversity (mean, se) in different treatments (C control, LH low heat, LHS low heat with smoke, S smoke, HH high heat, HHS high heat with smoke) in shrubby woodland and herbaceous forest. Diversity is the exponential of the Shannon diversity index (see Methods).

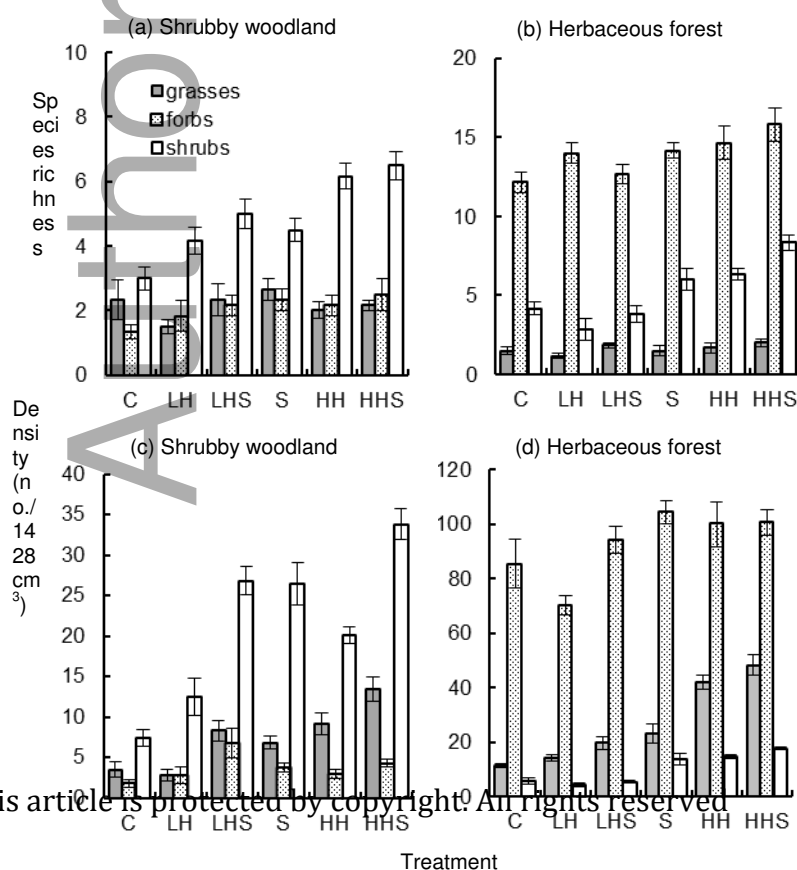


Figure 3. Richness and density (mean, se) of species in each life-form (grass, forb, shrub) in treatments (C control, LH low heat, LHS low heat with smoke, S smoke, HH high heat, HHS high heat with smoke) in shrubby woodland and herbaceous forest.

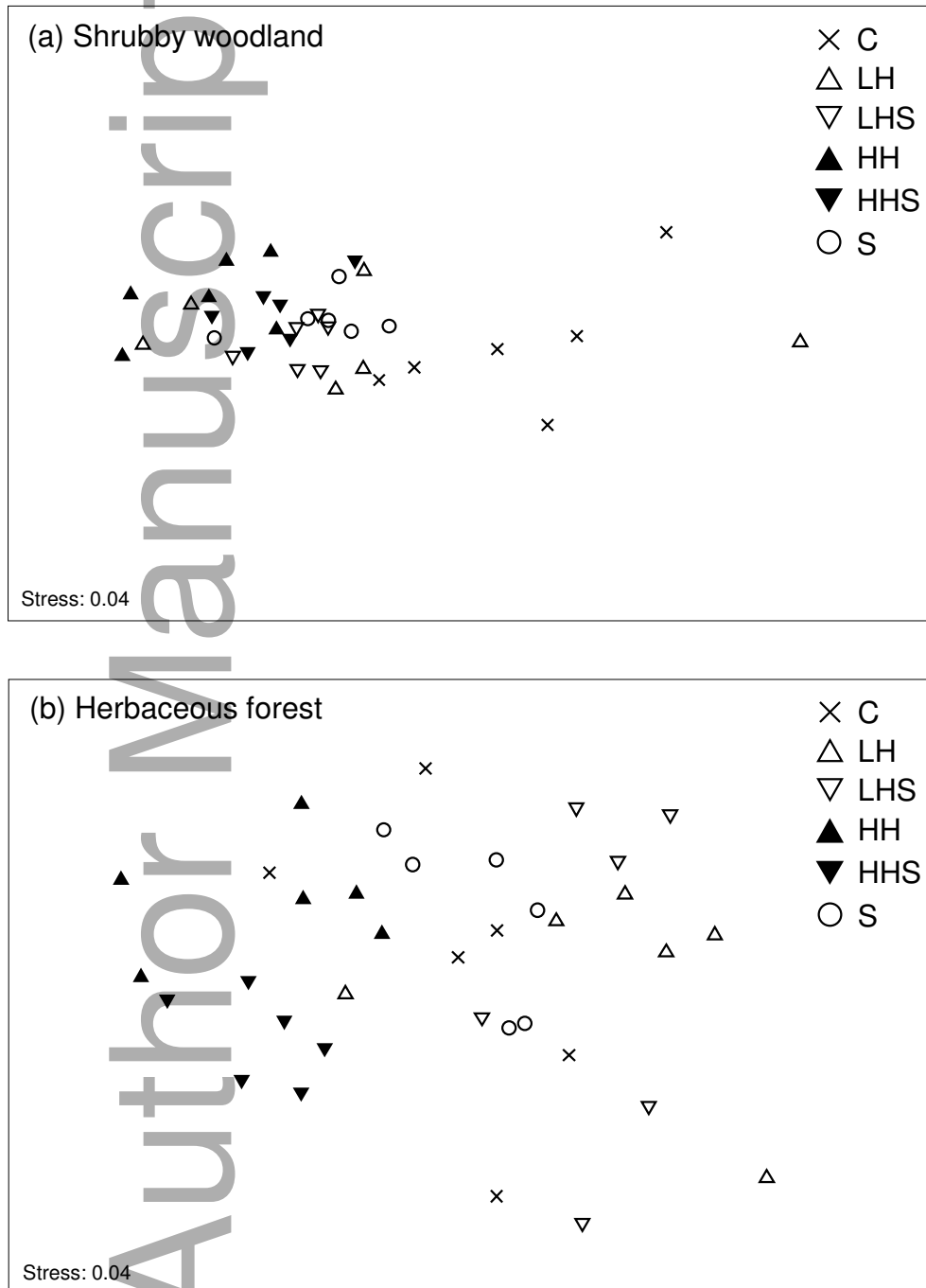


Figure 4. Species compositions in different treatments (C control, LH low heat, LHS low heat with smoke, S smoke, HH high heat, HHS high heat with smoke) in (a) shrubby woodland and (b) herbaceous forest, resulting from multidimensional scaling.

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