

Resistance and resilience to changing climate and fire regime depend on plant functional traits

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Summary

1. Changing disturbance–climate interactions will drive shifts in plant communities: these effects are not adequately quantified by environmental niche models used to predict future species distributions. We quantified the effects of more frequent fire and lower rainfall – as projected to occur under a warming and drying climate – on population responses of shrub species in biodiverse Mediterranean-climate type shrublands near Eneabba, southwestern Australia.

2. Using experimental fires, we measured the density of all shrub species for four dominant plant functional groups (resprouter/non-sprouter × serotinous/soil seed bank) before and after fire in 33 shrubland sites, covering four post-fire rainfall years and fire intervals from 3–24 years.

3. Generalized linear mixed effects models were used to test our *a priori* hypotheses of rainfall, fire interval and plant functional type effects on post-fire survival and recruitment.

4. At shortened fire intervals, species solely dependent on seedling recruitment for persistence were more vulnerable to local extinction than were species with both seedling recruitment and vegetative regrowth. Nevertheless, seedling recruitment was essential for population maintenance of resprouting species. Serotinous species were less resilient than soil seed storage species regardless of regeneration mode. Critically, in relation to changing climate, a 20% reduction in post-fire winter rainfall (essential for seedling recruitment) is predicted to increase the minimum inter-fire interval required for self-replacement by 50%, placing many species at risk of decline.

5. Synthesis. Our results highlight the potentially deleterious biodiversity impacts of climate and fire regime change, and underscore weaknesses inherent in studies considering single impact factors in isolation. In fire-prone ecosystems characterized by a projected warming and drying climate, and increasing fire hazard, adaptive approaches to fire management may need to include heightened wildfire suppression and lengthened intervals for prescribed fire to best support the *in situ* persistence of perennial plant species and of plant biodiversity. This conclusion is at odds with the view that more managed fire may be needed to mitigate wildfire risk as climate warms.

Key-words: climate change, fire interval, plant population and community dynamics, resprouting, self-replacement, serotiny, soil seed bank, species loss

Introduction

Disturbance regime, encompassing frequency, intensity and spatial extent of disturbance, is a fundamental driver of species composition and coexistence (promoting species coexis-

tence, Roxburgh, Shea & Wilson 2004) and ecosystem fluxes (pyrogenic carbon emissions, Campbell, Harmon & Mitchell 2011). Fire is one of the most common, and best studied, causes of recurrent landscape scale disturbance, and has shaped evolution and adaptation in many taxa globally (Bond & Keeley 2005). Altered fire frequency alone is a significant component of global environmental change and has been implicated in species loss and invasions (Brooks *et al.* 2004). However, its expected interaction with climate change is

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complex. Climate change is predicted to result in decreased precipitation and increased temperatures across many fire-prone regions (Schneider *et al.* 2007). In more productive regions, where fuel is not limiting, this may result in longer fire seasons and increased fire likelihood, thus shortening fire intervals, while reduced productivity may lead to increased fuel limitation and less fire in other situations (Cary *et al.* 2006; Westerling *et al.* 2006; Moritz *et al.* 2012). The response of vegetation to increased fire frequency may also involve feedbacks that alter flammability (e.g. increase in annual grasses, Brooks *et al.* 2004). Shortened fire intervals driven by a changing climate may lead to future widespread loss of forest species and interact synergistically with climate change (Westerling *et al.* 2011), with the potential to cause ecological 'surprises' (Paine, Tegner & Johnson 1998).

Mediterranean-type climate regions are projected to be among the most 'at risk' to the future impacts of climate change worldwide: Thomas *et al.* (2004) identify shrublands as the global structural vegetation type likely to lose the largest fraction of species (29%), and Malcolm *et al.* (2006) identify southwestern Australia (SWA) and the Cape Region of South Africa as two of the most vulnerable global biodiversity hotspots, potentially losing more than 2000 plant species each over the next 100 years. The Mediterranean-type climate region of SWA is a global biodiversity hotspot (Myers *et al.* 2000; Hopper & Gioia 2004). It covers an area of 300 000 km² and contains at least 7380 plant taxa, of which > 50% are endemic (Hopper & Gioia 2004). Mean maximum temperature in the region has increased by 0.15–0.20 °C per decade over the period 1900–2007, one of the fastest rates in Australia, and annual rainfall has decreased by 20% since the 1970s (Bates *et al.* 2008). Climate change projections to 2070 based on a number of global climate models (GCMs), assuming a medium emissions scenario, project a further temperature increase of 1–3 °C across all seasons of the year, a further 10–20% reduction in rainfall (largely in winter) and a higher frequency of extreme events such as droughts. These projections infer a hotter, drier climate with more high fire danger days and shorter fire intervals (Enright *et al.* 2012).

Different plant taxa, and plant functional groups, may respond to shortened disturbance intervals and their interaction with changing climate in different ways, leading to potential shifts in plant community composition, diversity, structure and function. In particular, a key issue is how the relative resistance and resilience of taxa may be affected. Based on the community-level interpretations of Grime *et al.* (2000) and Diaz-Delgado *et al.* (2002), we define *resistance* as the capacity of extant populations to survive disturbance through persistence, and *resilience* as their capacity to recover to pre-disturbance abundance levels through recruitment. The biota of fire-prone ecosystems have many traits that enable population persistence under a given fire regime (Gill 1981). Among plants, a fundamental dichotomy exists in fire response, with some species capable of resprouting following fire, while species without this capacity rely exclusively on accumulated seed banks for regeneration. These different plant functional types (PFTs) result in populations that are

multi-aged and long-lived on the one hand, and single-aged and shorter lived on the other. Resprouter species may persist through a combination of resistance and resilience (Lamont, Enright & He 2011), but non-sprouter species have no resistance to fire. A second dimension of plant response to fire is the form of seed storage, either in a canopy (serotinous) or in a soil-stored seed bank (SSB). Seed banks have the potential to confer resilience in species responses to changing environmental conditions (Enright *et al.* 2007). However, there may be important differences in response to changing climate-fire regimes between serotinous and SSB species. Some fraction of the seed bank in SSB species may not germinate after a given fire, so that seeds from different cohorts are carried over between successive fires, lowering the risk of population decline or local extinction (Auld & Denham 2006), while all seeds of serotinous species are released by fire and germinate in the next wet season, or they perish (Enright *et al.* 2007). Thus, resilience varies by seed bank type and the conditions that prevail during germination and establishment. Populations of serotinous species may therefore be more vulnerable to extinction under continued climate warming and drying (Buma *et al.* 2013).

Our objectives in this study were to quantify the minimum fire-free period necessary to maintain populations of different PFTs based on fire-adapted traits for perennial woody species of biodiverse Mediterranean-type shrublands in SWA, and to address two related questions: (i) How do resistance and resilience of plant taxa vary by functional type and fire frequency?; and (ii) Do fire-climate interactions affect the persistence of these PFTs? In addressing these objectives, we aim to identify those PFTs most vulnerable to population declines, or local extinction, when subjected to shortened fire intervals and a drier climate. Our results show how disturbance and climate change can interact to filter particular combinations of fire-adapted traits and therefore inform adaptive management for biodiversity conservation in fire-prone regions.

Materials and methods

STUDY SETTING

The study was conducted in biodiverse Mediterranean-type shrublands (kwongan) of the Geraldton Sandplain region of SWA, 250–350 km north of Perth (Fig. 1). The region is warm-dry Mediterranean, with mean annual rainfall of 494 mm, 80% of which falls in the winter period from May to September (Eneabba climate station No. 008225, Australian Bureau of Meteorology). Mean daily maximum temperature ranges from 19.6 °C in July to 36.2 °C in February.

The shrublands are fire prone, with mean fire intervals estimated to range over 17–28 years across several shrubland types during the last 37 years (Enright *et al.* 2012). Vegetation is characterized by a broad range of perennial woody species as well as tussock and rhizomatous monocot taxa (Cyperaceae, Restionaceae, some Poaceae) growing in sandy soils of varying depth and age (Enright *et al.* 2012). Two distinct soil types, sand over limestone and heavily leached acidic sands, were included in the study. Time since last fire (TSF) was determined for natural shrubland vegetation across the study region from Jurien

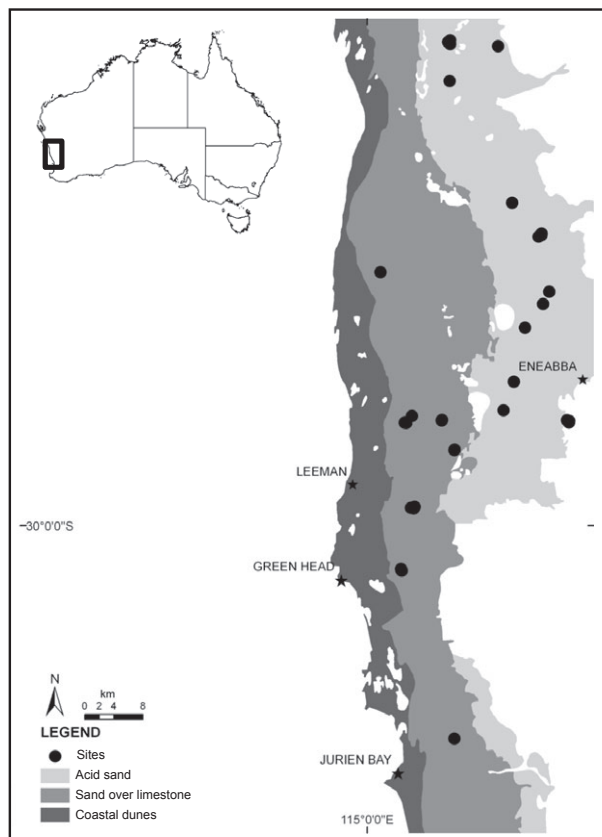


Fig. 1. Location of experimental fire sites on the Geraldton Sandplain, SW Australia.

Bay in the south to Mt Adams Road in the north (Fig. 1) using fire history maps derived from satellite imagery. Selected sites ($n = 33$) ranged in TSF from 3 to 24 years, with a bias towards sites < 10 years since last fire in order to focus on impacts of shortened fire intervals. These sites of varied time since fire were burned experimentally to create fire interval treatments of varying length (see below). The sample included shrubland sites on both shallow sands over limestone ($n = 17$) and acid ($n = 16$) sandy soils (see Table S1 in Supporting Information for plot details).

DATA COLLECTION

A 40×40 m plot was established at each site and eight replicate 4×4 m subplots located within each based on a restricted random distribution such that subplot boundaries were no closer than 2 m.

Table 1. Annual, winter (May–November), and summer (December–March) rainfall totals (mm) in the year prior to autumn (April–May) experimental fires, showing % deviation from the long-term mean for Eneabba (BoM; 1965–2011)

Year	Annual precipitation	Deviation (%)	Winter precipitation	Deviation (%)	Summer precipitation	Deviation (%)	N plots	Fire intervals sampled (years)
2005	465	–5	426	5	NA	NA	NA	NA
2006	346	–30	226	–45	43	1	4	4,8
2007	398	–19	351	–14	41	–3	13	3,5,6,7,9,11,14,16
2008	492	0	344	–16	126	298	10	4,6,7,12,14,15
2009	413	–16	393	–3	6.5	–85	6	3,5,7,8,9,24

See Supporting Information for plot-level details.

The identity and density of all woody species were recorded in each subplot. From 4 to 13 plots were sampled in autumn (March–April) of each year from 2006 to 2009, and then burned later in the same autumn (April–May) by state government fire management staff. Applying fire treatments over multiple years ensured that a range of pre- and post-fire rainfall conditions were sampled (see below, Table 1). Where fires did not propagate due to unsuitable weather or lack of fuel continuity, subplots were burned (including a 2 m buffer) using a truck-mounted flamethrower (see Fontaine *et al.* 2012 for details of fire behaviour and fuel measurements).

Plots burned in 2006–08 were remeasured for density of all woody species 3 years after fire, and plots burned in 2009 were remeasured 2 years after fire. Mortality of new recruits is highest in the first year (and may exceed 50%, Enright & Lamont 1989), declining to a mean of around 1–3% by the time individuals are 8 years old (Enright *et al.* 1998). At 2–3 years, new recruits have survived through several summers and have a high probability of reaching reproductive maturity (most by ages 2–6 years, Burrows 2008; Enright *et al.* 2012). Among resprouters, most mortality is associated with the fire event and post-fire resprouts older than 1 year are likely to persist through the inter-fire interval (annual mortality $< 1\%$, Enright & Lamont 1992), returning to reproductive stage within 2–3 years (Enright *et al.* 2011). Rainfall in the winter and summer preceding, and following, experimental fires ranged from average (within 5% of mean rainfall) to very dry (30–45% below average) (Table 1). Experimental fires were lit under weather conditions ranging from Moderate to Very High fire danger according to the McArthur Forest Fire Danger Index, but with no significant relationship between measures of fire intensity/severity and either weather conditions or fuel age (see Fontaine *et al.* 2012 and references therein for details).

DATA STRUCTURE

A total of 153 woody species in 16 plant families was recorded in 264, 4×4 m subplots across the 33 experimental fire sites (Table 2, Table S2 and archived data set, Enright *et al.* 2014). Species were assigned as resprouting or killed in response to fire, and with a serotinous or soil-stored (SSB) seed bank. All non-serotinous, woody species showed fire-cued germination apart from a few species characterized by post-fire flowering and dispersal of non-dormant seeds upon ripening (e.g. *Xanthorrhoea* spp.), but none of these were present in our samples. Data on species traits were obtained from our past work on this system (Enright *et al.* 2007), other published information (Sweedman & Merritt 2006) or personal observations during this study (see Table S2 for complete species list and trait set). All four PFTs were represented by more than one plant family, with number of species ranging from 12 (fire-killed + serotinous) to 63 (resprouter + SSB). Our fundamental unit of analysis was the ratio of change

Table 2. The distribution of plant species among PFTs and fire intervals, numbers of replicate sites per fire interval, and number of individual species-in-subplot records (samples) by PFT and fire interval

Regeneration mode	Seed store	Families	Species	Samples
Non-sprouter	Serotinous	2	12	480
	Soil	9	41	1171
Resprouter	Serotinous	3	37	1121
	Soil	13	63	1549
Totals		16	153	4321

Fire interval	Replicates	Species	Samples
3	2	37	218
4	4	94	479
5	5	103	713
6	5	83	601
7	3	82	430
8	2	69	271
9	3	65	396
11	1	34	146
12	1	37	150
14	4	88	583
15	1	24	103
16	1	28	126
24	1	25	105
Total	33	153	4321

in abundance (count of individuals) for each species, within each 16 m² subplot, from pre- to post-fire fire. A total of 4321 change records were obtained, ranging from 480 for fire-killed+serotinous, to 1549 for resprouter + SSB PFTs. All fire intervals < 10 years were represented by more than one plot (Table 2). The number of species recorded at each fire interval ranged from 25 (24-year interval) to 103 (5-year interval), while the number of change records per fire interval ranged from 103 to 713, with an average of 131 records per plot.

STATISTICAL ANALYSES

To test our *a priori* hypotheses relating to fire interval, climate and PFT, we first organized data, then evaluated and checked candidate models and finally extracted parameter estimates from the best-supported model. Relative changes in abundance from pre- to post-fire were represented as response ratios, that is, post-fire density minus pre-fire density divided by the sum of pre- and post-fire, to give a value ranging from -1 (species loss) to 1 (species gain), with 0 indicating no change in density.

Rainfall in the year before fire may influence size of the seed store (in resprouters and non-sprouters) and energy reserves (in resprouters) that are present at the time of burning (Enright *et al.* 2011), while rainfall in the first winter following fire influences seed germination and early seedling establishment, and summer rainfall plays a key role in determining over-summer survival in the first year following fire (Enright & Lamont 1992). Thus, rainfall in the summer (December–March) and winter (May–November) before and after fire were used as covariates in the candidate models, along with substrate type (sand over limestone versus acid sands) and fire type (propagated, did not propagate). Herbivory, measured as counts of kangaroo scats in subplots, was also included as a covariate since small burn area can result in high levels of post-fire seedling mortality and regrowth damage from browsing animals (Tyler 1995).

We constructed a set of additive candidate models (see Table S3) representing our *a priori* hypotheses of climate, fire interval and PFT effects with generalized linear mixed effects models with a normal distribution implemented in R (R Development Core Team 2010) using the lme4 package (Bates & Maechler 2010). Fixed effects included fire interval (range 3–24 years), indicator variables for plant functional traits (resprouter/non-sprouter, canopy/soil seed storage) and continuous measures of rainfall (relativized to percentage of 30-year mean rainfall to improve model fit; range 66–100), as well as covariates (Table S3). We included dependency within plots (i.e. for subplots), and among species, in our statistical model using a random effect. We examined data to test for spatial dependency (i.e. that spatially proximate subplots would have greater similarity) using Sorensen's distance but found no relationship (Fig. S1). Using AIC as our model selection criterion, covariates for fire type, substrate and herbivory were examined in the full additive model, with no evidence found to retain them in the model. Next, we examined all possible two-way interactions of climate, fire interval and PFT and considered linear effects of fire interval and rainfall as well as a pseudo-threshold fire interval using the square root of fire interval (see Table S3 for the full model set). The pseudo-threshold was chosen to represent reported threshold effects of fire interval (Fontaine *et al.* 2012), but also to avoid excessive parameters (as in a logistic growth equation). Model selection followed the suggestions of Zuur *et al.* (2009) using AIC fit with restricted maximum likelihood to compare models with identical random effect structures. Final model fits and model selection were carried out using fits based on full log likelihood. Plots of residuals and quartiles were used to assess model fit and behaviour; no problems were detected (Fig. S2). The best-supported model and parameter estimates were then compared against the expectations of the research questions. Given the structure of the top model for the entire data set, we then applied the same global model to seedlings and vegetative resprouts of resprouter species to better understand fire-climate impacts on resprouter species dynamics.

Results

STATISTICAL MODEL

Regression using linear mixed-effect models yielded a best-supported model (Akaike model weight of 0.97; Table S3) containing indicator terms for resprouting and seed storage type (serotinous, SSB), a threshold effect of fire interval (square root of years since fire) and winter rain after fire, as well as interactions between winter rain and resprouting and fire interval with resprouting and seed storage (Fig. 2, Tables 3 and S3). No effect of substrate type (limestone versus acid sand), ignition type, herbivory, or other measures of rainfall were supported by the data (Tables 2 and S3).

FIRE INTERVAL EFFECTS

Non-sprouter (fire-killed) species showed low resilience to short interval fires regardless of seed-based traits, with serotinous species the worst affected (Fig. 2a,b). The density of serotinous species 2–3 years post-fire was almost always less than pre-fire levels at sites with previous fire interval < 15 years (Fig. 2a). Soil seed bank species showed greater resilience, with pre-fire abundance levels regularly reached for fire intervals of 5–6 years or more (Fig. 2b). Resprouter

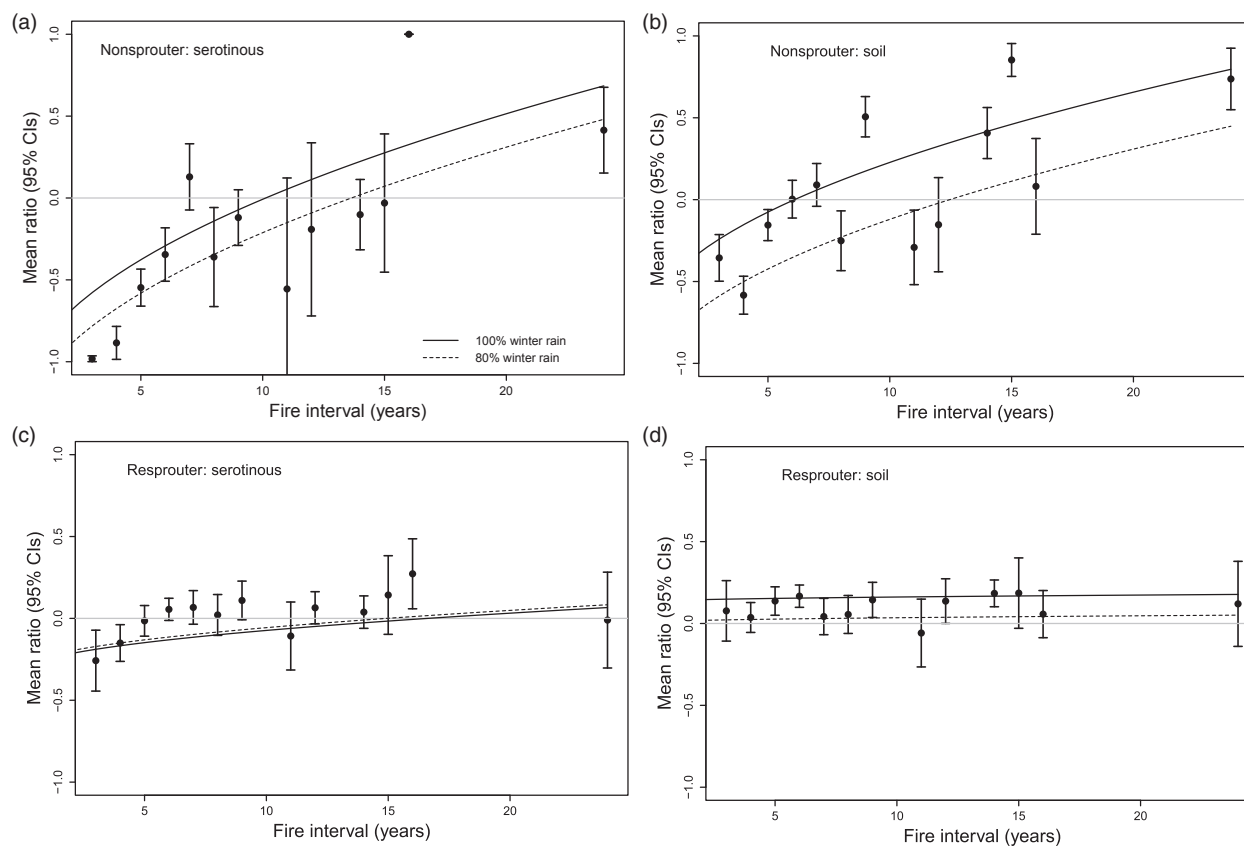


Fig. 2. Mean ($\pm 95\%$ confidence interval) woody plant species abundance changes in fire-prone shrublands near Eneabba, Western Australia in relation to fire interval (post-fire relative to pre-fire) for (a) non-sprouter + serotinous, (b) non-sprouter + soil, (c) resprouter + serotinous and (d) resprouter + soil. Fitted lines are from the best-supported model and correspond to years of 100% (solid) and 80% (dotted) mean winter rainfall in the first year after fire (the mean for the duration of the study was 85%). Grey horizontal line at 0 represents no change in abundance from before to after experimental fires.

Table 3. Effects of fire interval, climate, and PFT on pre-post-fire changes of abundance in Western Australia shrublands using hierarchical linear mixed effect models. Parameter estimates taken from top model based on ΔAIC and bolded t -values reflecting statistical significance at the 0.05 level

Term	Estimate	SE	t -Value
Main effects			
Intercept	-0.5	0.3	1.6
Fire interval (square root)	0.01	0.04	0.2
Serotinous	0.3	0.2	1.2
Non-sprouting	-2.0	0.2	9.6
Winter rain (following fire)	0.01	0.003	1.7
Interactions			
Fire interval \times Non-sprouting	0.32	0.03	11.1
Fire interval \times Serotinous	0.07	0.03	2.5
Non-sprouting \times Winter rain	0.01	0.002	4.4
Serotinous \times Winter rain	-0.01	0.002	3.0

species – whose post-fire abundance is due to the persistence of pre-fire individuals plus the establishment of new seedlings – showed strong resistance to the effects of a single experimentally shortened fire interval (Fig. 2c,d). Serotinous resprouters (Fig. 2c) showed some reduction in abundances at

the shortest fire intervals, while soil seed bank species changed little for any of the fire intervals tested, and their pre- and post-fire abundance levels were consistently above zero (Fig. 2d). Although fire-killed species showed low resilience at short fire intervals, they had a much greater capacity for population increase at longer fire intervals than did resprouter species, a mean ratio of 0.5 representing a tripling in density (Fig. 2a,b).

Separating resprouting (resistance) and seedling recruitment (resilience) responses for resprouter species showed that seedling recruitment after fire is essential for population maintenance in the resprouter functional group types described here (Fig. 3c,d, Table 4). Resprouter seedlings demonstrated remarkably similar parameter estimates to the global model (Table 4). Serotinous resprouter species showed uniform resprouter persistence (resistance) in relation to fire interval at levels just below those required for self-replacement (Fig. 3a, Table 4), but rapidly rising recruitment (resilience) as fire interval increased. Resprouters with soil seed storage (Fig. 3b, d) showed reduced resistance at long fire intervals, while seedling recruitment increased with increasing fire interval, leading to an overall stable population response by species in relation to fire interval (Fig. 2d).

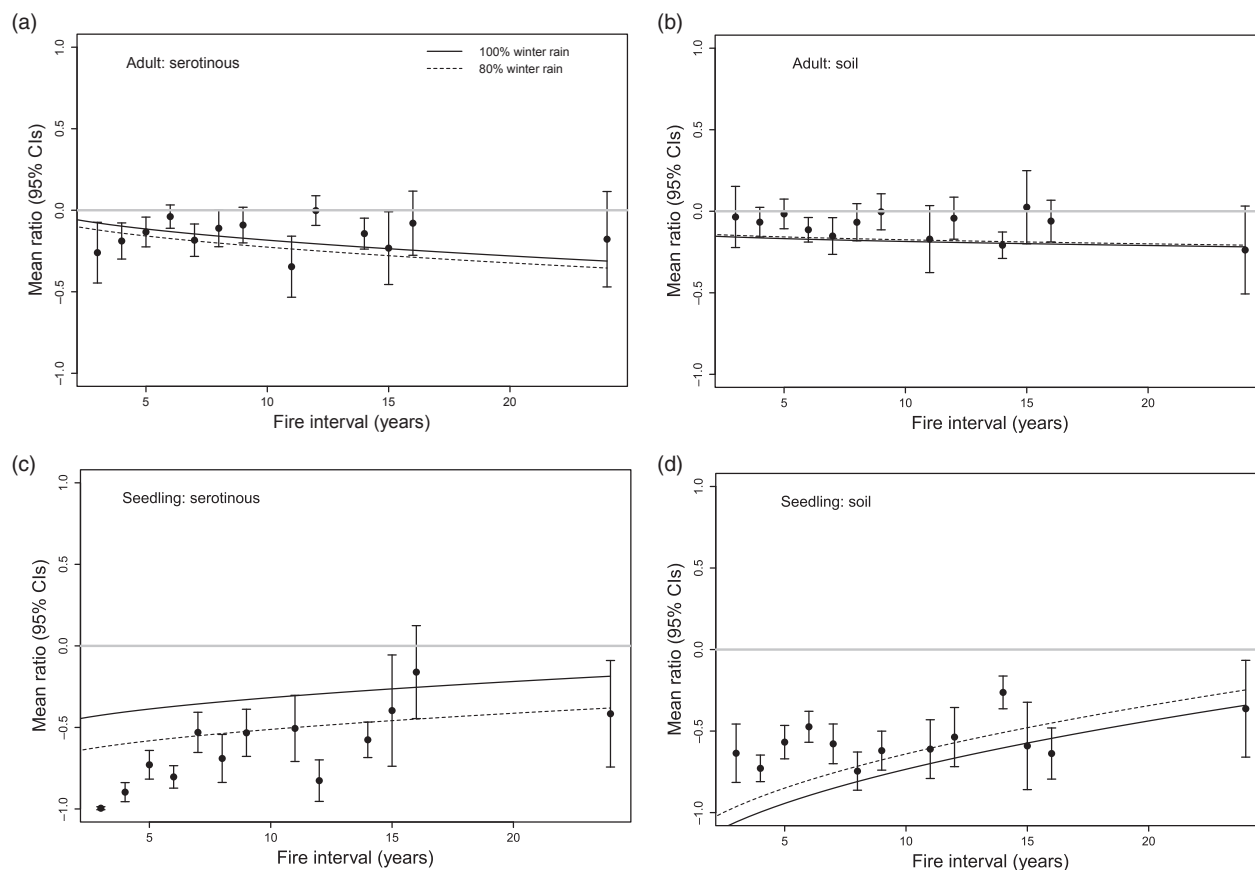


Fig. 3. Mean ($\pm 95\%$ confidence interval) change in abundance (post-fire relative to pre-fire) for resprouting a) serotinous and b) SSB plants (resistance) and seedling c) serotinous and d) SSB plants (resilience) in the two (serotinous, SSB) resprouter plant functional types in fire-prone shrublands near Eneabba, Western Australia. Fitted lines are from the best-supported model and correspond to years of 100% (solid) and 80% (dotted) mean winter rainfall in the first year after fire (the mean for the duration of the study was 85%). Grey horizontal line at 0 represents no change in abundance from before to after experimental fires.

Table 4. Effects of fire interval, climate, and PFT on pre-post-fire changes of abundance in seedlings and adults of resprouting woody species from Western Australian shrublands using hierarchical linear mixed effect models. Parameter estimates taken from global model for combined data set based on Δ AIC and bolded *t*-values reflecting statistical significance at the 0.05 level

Term	Estimate	SE	<i>t</i> -Value
Seedlings			
Main effects			
Intercept	-1.5	0.3	5.5
Fire interval (square root)	0.08	0.04	1.9
Serotinous	0.6	0.3	2.2
Winter rain (following fire)	0.01	0.003	3.0
Interactions			
Fire interval \times Serotinous	0.2	0.03	4.4
Serotinous \times Winter rain	-0.01	0.003	5.1
Adults			
Main effects			
Intercept	-0.2	0.3	0.6
Fire interval (square root)	-0.1	0.04	1.9
Serotinous	0.1	0.2	0.4
Winter rain (following fire)	0.002	0.003	0.7
Interactions			
Fire interval \times Serotinous	0.1	0.03	1.7
Serotinous \times Winter rain	-0.003	0.003	1.0

CLIMATE EFFECTS

A clear effect of rainfall in the winter after fire was evident. Non-sprouting species showed reduced resilience in drier than average winters, whereas resprouting species showed little change (Fig. 2), other than for recruitment (resilience) in soil seed storage resprouters where dry years after fire adversely affected recruitment (Fig. 3). Under average conditions, results suggested that the most sensitive PFT, serotinous non-sprouters, would self-replace at fire intervals > 10 years, but at 80% of average winter rain this threshold fire interval increased by 50% to around 15 years (Fig. 2a). The most resistant – resilient PFT, SSB resprouters, showed self-replacement at all fire intervals and for both 100% and 80% post-fire winter rainfall, but population change was estimated to be lower (closer to zero) in dry years (Fig. 2d).

PLANT FUNCTIONAL TYPE INTERACTION EFFECTS

Interactive responses were present among PFTs and fire interval (Fig. 2, Table 3). Non-sprouting species showed much higher sensitivity (lower resilience) to shortened fire intervals than species possessing resprouting capacity (higher resistance) (Fig. 2).

Discussion

We present clear evidence that PFT, disturbance frequency (fire interval), post-fire rainfall and their interactions, strongly influence woody species persistence in fire-prone Mediterranean-type shrublands of SW Australia. Taxa in particularly sensitive groups (e.g. fire-killed, serotinous species) are almost certainly at greater risk of local extinction than predicted from studies of fire regime change (Enright, Lamont & Marsula 1996; Westerling *et al.* 2011) or climate-related effects (Fitzpatrick *et al.* 2008) alone. Studies of the potential impacts of global environmental change on the distribution and abundance of plant and animal species are becoming commonplace, but most use empirical evidence or models that predict future states based on a single factor, for example, the bioclimatic envelope approach for predicting future species distributions based on global-circulation-model (GCM) scenarios (Thuiller *et al.* 2005; Fitzpatrick *et al.* 2008). Pearson & Dawson (2003) and Yates *et al.* (2009) have highlighted the shortcomings of the bioclimatic envelope approach that ignores biotic interactions, phenological and demographic changes, habitat fragmentation, evolutionary change and dispersal ability, among other possible interacting factors. Here, we used field-based experiments to test the potential effects of shortened fire intervals – projected to occur in Mediterranean-type vegetation regions as climate warms and dries (Enright *et al.* 2012) – and their interaction with rainfall variation, on the resistance and resilience of woody species in biodiverse shrublands.

Pausas *et al.* (2004) explored evidence for filtering of species trait sets in fire-prone shrubland ecosystems in relation to fire regimes and prospective climate change impacts based on key PFTs defined by ability to resprout (resprouters/non-sprouters) and presence of a persistent seed bank (present/absent). However, their analyses did not separate seed bank types as a potential factor influencing persistence, and drew no clear conclusions concerning potential climate change impacts. Our study focuses on key seed storage trait differences among species of fire-prone ecosystems (serotinous versus soil stored), analyses rainfall variation effects and draws well-supported conclusions concerning the adverse impacts of shortened fire interval and reduced rainfall on woody species resistance – resilience.

Our results highlight the synergistic effects of recruitment conditions after fire (reduced seedling establishment rates when dry years follow fires) and fire interval (shorter fire intervals allowing less time for seed accumulation). Seed stores reflect the length of the fire interval over which each stand has developed (representing periods of 3–24 years in our experiments), and post-fire recruitment rates reflect the abiotic conditions (especially rainfall) in the first 2–3 years following fire. Fire interval (which corresponds to plant age for fire-killed species and new post-fire recruits of resprouter species) and seed store are important, and become critical when below average rainfall follows fire, as is increasingly likely under projected climate change scenarios (Burgman & Lamont 1992; Fitzpatrick *et al.* 2008; Yates *et al.* 2009; Westerling *et al.* 2011).

PLANT TRAITS AND PFT RESPONSES

Seed banks have great potential for conferring increased flexibility on species in their response to changing environmental conditions. For most plant species, populations comprise a mixture of individuals recruited in different years, so that individuals have been filtered by different sets of recruitment conditions, influencing the genetic make-up of those populations (Finch-Savage & Leubner-Metzger 2006). It has been argued that seed banks of continuously recruiting species buffer against rapid changes in the genetic composition of populations that would otherwise be deleterious if changes in growing conditions were only temporary (Ellstrand & Elam 1993). In the case of climate and fire regime change, genetic diversity in the seed bank may provide the opportunity for rapid *in situ* selection to more permanent changes in growing conditions via strong filtering selection during the seedling stage (Mandák *et al.* 2006).

Our study shows that there may be important differences in response to changing climate-fire regimes among species with differing seed bank traits, especially for fire-killed species. For soil storage species, some fraction of the seed bank may not germinate after a given fire, so that seeds from different cohorts are carried over, and the risk of rapid local extinction is reduced (Auld & Denham 2006). However, in serotinous species, all seeds are dispersed after fire and germinate as soon as suitable temperature and moisture conditions are met, or they perish (Lamont *et al.* 1991). Thus, resilience depends in part on seed bank type, with serotinous species less able to respond to the directional change in environmental conditions expected under global climate change (Buma *et al.* 2013). This may explain the pattern of species richness in serotinous species – highest in SW Australia and South Africa, the two Mediterranean-climate regions of the world with the most reliable winter rainfall (Cowling *et al.* 2005) and strongest evidence of long-term climatic stability (Meadows & Sugden 1993), i.e. most consistently favourable post-fire recruitment conditions.

An established approach in the conservation management of fire-prone vegetation is to determine tolerable fire regimes for species that are sensitive to fire interval (Bradstock & Kenny 2003). Fire-killed serotinous species are often identified as among the most sensitive of PFTs due to their reliance on a seed bank that does not persist beyond the senescence of parents (Enright *et al.* 1998; Bradstock & Kenny 2003). While risk of population decline due to senescence under lengthened fire intervals is possible, decline has more often been identified in relation to immaturity risk associated with shortened fire intervals (Keeley *et al.* 2012). Minimum tolerable fire interval has variously been estimated as longest time to reach maturity (Bradstock & Kenny 2003), age at which 50% of individuals first set seeds, or a rule of thumb multiplier (often in the range 2–4 × youngest age at which plants set seeds: Burrows 2008). Our results provide estimates of minimum tolerable fire interval (Fig. 2), and its variation in relation to climate, which are unrelated to the juvenile period approach. They show that while estimates may be comparable

under average conditions, declining rainfall (as projected for Mediterranean-climate type regions) is likely to markedly increase the minimum tolerable fire interval, especially for serotinous non-sprouters.

In our study, minimum estimated time to self-replacement in serotinous, fire-killed species under average rainfall is predicted to occur at a fire interval of about 10 years (Fig. 2a), a value that agrees closely with demographic model estimates for the fire-killed species, *Banksia hookeriana*, in this region (Enright, Lamont & Marsula 1996). However, for rainfall reduced to 80% of the 30-year mean, estimated minimum time for self-replacement increases by 50% to around 15 years. These are likely to be underestimates of minimum time for self-replacement since stands were assessed 2–3 years after fire and further mortality will occur over subsequent inter-fire years. These results suggest that minimum tolerable fire interval estimates based on the juvenile period approach may not be conservative enough when fire and climate change impacts on resilience are considered together. While highly predictable winter rainfall (Cowling *et al.* 2005) may have favoured the accumulation and persistence of serotinous species in SW Australia and South Africa, the projected interactive effects of climate and fire regime change may now threaten this suite of species more than previously anticipated.

Among fire-killed species with soil seed storage, a similar overall pattern of response to fire interval and rainfall change is revealed, with a reduction to 80% of average rainfall increasing the estimated minimum time to self-replacement from 7 to 13 years. Soil stored seeds may require either a heat 'shock' (hard-seededness: Auld & Denham 2006) or chemical triggers in smoke (Flematti *et al.* 2011) to break dormancy, promoting germination in the first winter after fire. There may also be a difference in resilience between germination cueing strategies, since germination may be more spatially variable, and decline more quickly with soil depth for heat than for smoke (Odion & Davis 2000; Auld & Denham 2006). Dry soil is a good insulator and fires at short intervals associated with low fuel loads may not provide sufficient heat for seeds buried at depths of more than a few millimetres. In contrast, post-fire rain may carry the smoke signal deeper into the profile regardless of fire-interval or fuel-load effects on fire intensity and combustion properties. Thus, higher post-fire germination rates for smoke-triggered species may deplete soil seed stores more fully than is the case for heat-triggered species. However, supporting evidence is lacking.

Species able to regrow vegetatively after fire are generally more tolerant of changing fire – climate regimes than are fire-killed species since their persistence is determined by a combination of resistance and resilience (Lamont, Enright & He 2011), and this is supported in the results presented here. Both serotinous and SSB resprouter functional groups show approximately stable populations across a broad range of fire intervals, but with serotinous species more adversely impacted by short fire intervals (< 10 years) and SSB species by lower than average post-fire rainfall (Fig. 2). When the response of resprouters is assessed separately for resistance (vegetative regrowth of pre-fire individuals) versus resilience (post-fire

seedling recruitment), it is evident that vulnerability to population decline is driven primarily by conditions that adversely affect seed store size and seedling recruitment (Fig. 3). While shortened fire intervals will reduce time available for seed bank accumulation, a drying climate will affect both rates of seed production (and accumulation) and post-fire seedling recruitment levels. Using a subset of the data (for resprouting individuals) reported here, Enright *et al.* (2011) described reduced persistence of resprouting plants through fire at both very short (< 5 years) and very long (24–42 years) fire intervals. That pattern is evident here for serotinous (Fig. 3a) but not for SSB species which show decline only at long intervals (Fig. 3b), again suggesting a potentially higher vulnerability to decline for serotinous resprouters than for resprouter species with soil seed storage.

LONG-TERM IMPLICATIONS

While our results show reduced resilience over a single shortened fire interval, especially when combined with reduced post-fire rainfall, the longer term implications (e.g. after repeated short-interval fires) are of even greater concern, with many fire-killed species likely to spiral rapidly towards local extinction. Resprouting (especially for serotinous) species may also become threatened as recruitment increasingly falls short of levels required for parent replacement. In addition, changes caused by altered competitive interactions may lead to less readily predictable changes in the density of some other species, as shown for sandstone heaths and woodlands in the Sydney region by Morrison *et al.* (2006) and Keith *et al.* (2007).

The findings presented here are based on a large and robust data set encompassing many species. They have important implications both for changing wildfire regimes associated with climate change, and for the managed use of fire for biodiversity conservation and asset protection. Based on shorter fire intervals on the one hand (a fire regime consequence of climate change, Moritz *et al.* 2012), and less favourable conditions for recruitment after fire on the other (a plant demographic consequence of climate change), we propose that future fire management of these, and other, biodiverse Mediterranean-type shrublands will require an adaptive response from managers if current levels of biodiversity are to be maintained. Such responses include the possible lengthening of planned fire intervals where a drying climate is likely to reduce post-fire recruitment levels, and planned fires only undertaken when a set of defined plant demographic and climate conditions are met. For example, biodiversity values may best be safeguarded if (i) assessment of seed stores for key woody species suggests a high availability of seed for recruitment after fire – in serotinous species total seed store can be readily assessed at any time of the year, and in SSB species a seasonally varying set of species can be assessed for their current seed crop, and (ii) rainfall is projected to be average or above average in the post-fire recruitment period based on seasonal forecasts. A set of rapid appraisal guidelines that will best safeguard the multiple

land-use values of fire-prone ecosystems and are simple for land managers to evaluate and deliver could readily be developed and tested.

Conclusions

We analysed the impacts of shortened fire interval and pre- and post-fire interannual rainfall variation on persistence and recruitment of woody species in relation to key PFTs in woody species of biodiverse, fire-prone shrublands in SW Australia. Reduced rainfall in the first winter after fire (critical for establishment and survival of seedlings) markedly increased the minimum fire interval required to ensure self-replacement of fire-killed species. Serotinous, fire-killed species were the plant functional group most vulnerable to local extinction and the least resilient to altered fire – climate regimes under a drying climate. Soil seed storing (SSB), fire-killed species were less vulnerable than serotinous species, most likely due to carry-over of some dormant soil-stored seeds from one fire cycle to the next. Resprouting species showed a combination of resistance and resilience that made them more tolerant of changing fire-climate regimes than fire-killed species, but within this group serotinous species were more vulnerable than SSB species. These trends were revealed in relation to experimental fires over a single fire interval, with repeated burning at shortened intervals likely to accelerate rates of species decline and loss. Our study underscores the weaknesses inherent in previous work that only considers one component of global change (e.g. fire-interval change, climate change) and the complexity of management challenges as global environmental changes proceed. In the fire-prone ecosystems considered here, adaptive approaches to fire management may include heightened wildfire suppression, lengthened fire intervals for prescribed fire and increased pre-fire monitoring (measuring seed stores, drought conditions) to best predict potential fire impacts.

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Data accessibility

Data available from the Dryad Digital Repository: (Enright *et al.* 2014).
Data files:
Enright.etal_PrimaryDataset_PlantResponses,
PFT_PlotScaleData_JEcol
PFT_datasetJEcol_2_ResproutersSeedAdult

References

- Auld, T.D. & Denham, A.J. (2006) How much seed remains in the soil after a fire? *Plant Ecology*, **187**, 15–24.
- Bates, D. & Maechler, M. (2010) lme4: Linear mixed-effects models using S4 classes. <http://CRAN.R-project.org/package=lme4>.
- Bates, B.C., Hope, P., Ryan, B., Smith, I. & Charles, S. (2008) Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climatic Change*, **89**, 339–354.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global herbivore: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, **20**, 387–394.
- Bradstock, R. & Kenny, B. (2003) An application of plant functional types to fire management in a conservation reserve in southeastern Australia. *Journal of Vegetation Science*, **14**, 345–354.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677–688.
- Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B. & Johnstone, J.F. (2013) The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, **63**, 866–876.
- Burgman, M.A. & Lamont, B.B. (1992) A stochastic model for the viability of *Banksia cuneata* populations: environmental, demographic, and genetic effects. *Journal of Applied Ecology*, **29**, 719–727.
- Burrows, N. (2008) Linking fire ecology and fire management in south-west Australian forest landscapes. *Forest Ecology and Management*, **255**, 2394–2406.
- Campbell, J.L., Harmon, M.E. & Mitchell, S.R. (2011) Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Frontiers in Ecology and the Environment*, **10**, 83–90.
- Cary, G.J., Keane, R.E., Gardner, R.H., Lavorel, S., Flannigan, M.D., Davies, I.D., Li, C., Lenihan, J.M., Rupp, T.S. & Mouillot, F. (2006) Comparison of the sensitivity of landscape-fire-succession models to variation in terrain, fuel pattern, climate and weather. *Landscape Ecology*, **21**, 121–137.
- Cowling, R.M., Ojeda, F., Lamont, B.B., Rundel, P.W. & Lechmere-Oertel, R. (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone Mediterranean-climate ecosystems. *Global Ecology and Biogeography*, **14**, 509–519.
- Diaz-Delgado, R., Lloret, F., Pons, X. & Terradas, J. (2002) Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. *Ecology*, **83**, 2293–2303.
- Ellstrand, N.C. & Elam, D.R. (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics*, **24**, 217–242.
- Enright, N.J. & Lamont, B.B. (1989) Seed banks, fire season, safe sites and seedling recruitment in 5 co-occurring *Banksia* species. *Journal of Ecology*, **77**, 1111–1122.
- Enright, N.J. & Lamont, B.B. (1992) Recruitment variability in the resprouting shrub *Banksia attenuata* and non-sprouting congeners in the northern sandplain heaths of southwestern Australia. *Acta Oecologica*, **13**, 727–741.
- Enright, N., Lamont, B.B. & Marsula, R. (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *Journal of Ecology*, **84**, 9–17.
- Enright, N.J., Marsula, R., Lamont, B.B. & Wissel, C. (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *Journal of Ecology*, **86**, 946–959.
- Enright, N., Mosner, E., Miller, B., Johnson, N. & Lamont, B.B. (2007) Soil vs. canopy seed storage and plant species coexistence in species-rich Australian shrublands. *Ecology*, **88**, 2292–2304.
- Enright, N.J., Fontaine, J.B., Westcott, V.C., Lade, J. & Miller, B.P. (2011) Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecology*, **212**, 2071–2084.
- Enright, N.J., Clarke, M., Keith, D. & Miller, B.P. (2012) Australian sclerophyllous shrubby ecosystems: heathlands, heathy woodlands and mallee woodlands. *Flammable Australia: Fire Regimes and Biodiversity in a Changing World* (eds R. Bradstock, A. Gill & R. Williams), pp. 215–234. CSIRO Publishing, Melbourne.
- Enright, N.J., Fontaine, J.B., Lamont, B.B., Miller, B.P. & Westcott, V.C. (2014) Data from: resistance and resilience to changing climate and fire regime depend on plant functional traits. *Dryad Digital Repository*, doi:10.5061/dryad.7n139.
- Finch-Savage, W.E. & Leubner-Metzger, G. (2006) Seed dormancy and the control of germination. *New Phytologist*, **171**, 501–523.

- Fitzpatrick, M.C., Gove, A.D., Sanders, N.J. & Dunn, R.R. (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Global Change Biology*, **14**, 1337–1352.
- Flematti, G.R., Merritt, D.J., Piggott, M.J., Trengove, R.D., Smith, S.M., Dixon, K.W. & Ghisalberti, E.L. (2011) Burning vegetation produces cyanohydrins that liberate cyanide and stimulate seed germination. *Nature Communications*, **2**, 360.
- Fontaine, J.B., Enright, N.J., Lade, J., Miller, B.P. & Westcott, V.C. (2012) Fire behaviour in southwestern Australian shrublands: evaluating the influence of fuel age and fire weather. *International Journal of Wildland Fire*, **21**, 385–395.
- Gill, M.A. (1981) Adaptive responses of Australian vascular plant species to fire. *Fire and the Australian Biota* (eds M.A. Gill, R.H. Groves & I.R. Noble), pp. 273–310. Australian Academy of Science, Canberra.
- Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., Askew, A.P., Corker, D. & Kieley, J.P. (2000) The response of two contrasting limestone grasslands to simulated climate change. *Science*, **289**, 762–765.
- Hopper, S.D. & Gioia, P. (2004) The southwestern Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology and Systematics*, **35**, 623–650.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G. & Rundel, P.W. (2012) *Fire in Mediterranean Ecosystems*. Cambridge University Press, Cambridge UK.
- Keith, D.A., Holman, L., Rodoreda, S., Lemmon, J. & Bedward, M. (2007) Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology*, **95**, 1324–1337.
- Lamont, B.B., Enright, N.J. & He, T. (2011) Fitness and evolution of resprouters in relation to fire. *Plant Ecology*, **212**, 1945–1958.
- Lamont, B.B., Le Maitre, D., Cowling, R. & Enright, N. (1991) Canopy seed storage in woody plants. *The Botanical Review*, **57**, 277–317.
- Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L. & Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, **20**, 538–548.
- Mandák, B.K., Bímová, K., Mahelka, V. & Plačková, I. (2006) How much genetic variation is stored in the seed bank? *Molecular Ecology*, **15**, 2653–2663.
- Meadows, M.E. & Sugden, J.M. (1993) The late Quaternary palaeoecology of a floristic kingdom: the southwestern Cape South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **101**, 271–281.
- Moritz, M.A., Parisien, M.A., Battlori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J. & Hayhoe, K. (2012) Climate change and disruptions to global fire activity. *Ecosphere*, **3**, art49.
- Morrison, D.A., Gary, G.J., Pengelly, S.M., Ross, D.G., Mullins, B.J., Thomas, C.R. & Anderson, T.S. (2006) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. *Australian Journal of Ecology*, **20**, 239–247.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Odion, D.C. & Davis, F.W. (2000) Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecological Monographs*, **70**, 149–169.
- Paine, R.T., Tegner, M.J. & Johnson, E.A. (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535–545.
- Pausas, J.G., Bradstock, R.A., Keith, D.A. & Keeley, J.E. (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, **85**, 1085–1100.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing 2.12.0*. R Foundation for Statistical Computing, Vienna, Austria.
- Roxburgh, S.H., Shea, K. & Wilson, J.B. (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology*, **85**, 359–371.
- Schneider, S.H., Semenov, S., Patwardhan, A., Burton, I., Magadza, C.H.D., Oppenheimer, M., Pittock, A.B., Rahman, A., Smith, J.B., Suarez, A. & Yamin, F. (2007) Assessing key vulnerabilities and the risk from climate change. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds M.L. Parry, O.F. Canziani, J.P. Palutikof, van der Linden P.J. & C.E. Hanson), pp. 779–810. Cambridge University Press, Cambridge.
- Sweedman, L. & Merritt, D. (2006) *Australian Seeds: A Guide to Their Collection, Identification and Biology*. CSIRO Publishing, Melbourne.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A. & Hannah, L. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.
- Tyler, C.M. (1995) Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology*, **83**, 1009–1020.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*, **313**, 940–943.
- Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H. & Ryan, M.G. (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences*, **108**, 13165–13170.
- Yates, C.J., McNeill, A., Elith, J. & Midgley, G.F. (2009) Assessing the impacts of climate change and land transformation on *Banksia* in the South West Australian Floristic Region. *Diversity and Distributions*, **16**, 187–201.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Vegetation plots sampled for post- versus pre-fire woody plant species densities.

Table S2. List of species (genera and families) sampled in experimental vegetation plots.

Table S3. Model set of *a priori* models examining additive and interactive effects of fire interval, climate, and plant functional type.

Figure S1. Sorensen similarity relative to pairwise distance (m) among subplots within sites.

Figure S2. Model diagnostics of the top model.