Forest Ecology and Management 459 (2020) 117850

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Fire severity impacts on tree mortality and post-fire recruitment in tall eucalypt forests of southwest Australia

Hannah Etchells[a,*], Alison J. O'Donnell[a], W. Lachlan McCaw[b], Pauline F. Grierson[a]

[a] Ecosystems Research Group, School of Biological Sciences, the University of Western Australia, Perth, Australia
[b] Department of Biodiversity, Conservation and Attractions, Brain Street, Manjimup, Western Australia, Australia

ARTICLE INFO

Keywords:
Understorey composition
Eucalyptus diversicolor
Karri forest
Soil nitrogen
Regeneration

ABSTRACT

Wildfires are predicted to increase in both frequency and severity across Mediterranean climate regions worldwide. While many Mediterranean-type ecosystems are considered broadly fire tolerant, there is little understanding of how differences in fire severity affect plant community dynamics, tree mortality and recruitment. In the tall karri (*Eucalyptus diversicolor* F. Muell) forests of southwest Australia, low to moderate severity wild and prescribed fires are relatively common. Mature karri trees survive these events and recover rapidly due to their thick bark and ability to prolifically resprout from epicormic buds. However, despite a projected increase in the frequency of high severity wildfires, the impact of such extreme fires on tree mortality and understory community composition is not well understood. We used a large and severe wildfire event in southwest Australia to assess how fire severity impacted recruitment and survival of karri seedlings, the mortality of mature karri trees, and the composition of the understory plant community. Mature karri tree mortality was 87% greater at sites burnt at high severity compared to unburnt sites and sites burnt at low severity. Understorey plant community composition of burnt sites was different to unburnt sites, driven largely by significant shifts in dominance. Notably, the usually dominant understorey shrub *Trymalium odoratissimum* was entirely absent from forests burnt at extreme high severity. These results indicate that karri forests burnt at very high severity undergo changes in stand structure that will persist for many decades, and that the structure and species composition of the understorey may also be altered significantly. This indication of a possible fire severity threshold is consistent with the findings of recent studies in other Mediterranean climates following catastrophic wildfires. This study highlights the need for further research into the effects of severe wildfire on forest ecosystems that are otherwise considered fire tolerant.

1. Introduction

Globally, there is increasing concern over the potential impacts of changing fire regimes on the conservation of temperate forests (Liu et al., 2010). Climate change projections indicate that wildfires will likely be more frequent, extensive and severe (Stephens et al., 2013) but the consequences of higher fire severity for diversity and function of many forest systems remains unquantified. Fire severity is generally quantified as the amount of above and below ground organic matter consumed (Keeley, 2009). Fire intensity is more difficult to determine as it requires on-ground measurement of fuel consumption and fire characteristics and is generally inferred from severity measures after a fire has occurred (Keeley, 2009). While severe fires can change plant community composition - even in fire-adapted ecosystems (Kuenzi et al., 2008) - projected increases in severity have the potential to cause dramatic and even permanent composition change owing to higher mortality rates (Scheffer et al., 2001) and destruction of seedbanks (Ooi et al., 2014). For example, extensive and severe fires that occurred between 2003 and 2009 in Victoria, including the ‘Black Saturday’ fires, and large fires in Tasmania in 2016 resulted in unusually high mortality of the dominant overstorey trees (*Eucalyptus* spp.) and shifts to more even-aged stand structures (Bennett et al., 2016; Fairman et al., 2016; Prior et al., 2016). However, instances of extreme fire severity have been relatively uncommon in the forests of southwest Australia since the 1960s when a program of prescribed burning at the landscape scale was introduced (Boer et al., 2009). In order to determine the long-term ecological impacts of projected increased wildfire severity and to implement adaptive management, it is critical to understand the fire severity thresholds for these fire-adapted ecosystems.

In the tall karri (*Eucalyptus diversicolor* F. Muell.) forests of

---

* Corresponding author.
E-mail address: hannah.etchells@research.uwa.edu.au (H. Etchells).

https://doi.org/10.1016/j.foreco.2019.117850
Received 30 October 2019; Received in revised form 23 December 2019; Accepted 26 December 2019

southwest Western Australia (SWWA), both wild and prescribed fires are key drivers of ecological processes, including initiating regeneration and recruitment of plant communities (Christensen and Abbott, 1989; Wardell-Johnson et al., 2007; Burrows, 2008). These forests exist entirely within the southwest Australian Biodiversity Hotspot and are of high conservation priority (Myers et al., 2000). As for many other temperate and Mediterranean regions, fire danger is increasing across SWWA, and the increase has become more evident since 2000 (Dowdy, 2018). How karri forests respond in both the short and long term to more frequent wildfires of extreme severity is largely unknown as such fires have occurred infrequently in (at least) the past 100 years (Christensen and Abbott, 1989; Burrows, 2008). One of the most severe fires that has been documented in the karri forest of SWWA occurred in 1937. Anecdotal reports of the roughly 52,000 ha 1937 fire suggests that it was intense enough to cause mortality of mature karri trees, however the severity of this fire and the response of karri in terms of mortality and recruitment was not quantified. However, in January 2015, a significant portion of the karri forest estate was impacted by the largest single wildfire in the southwest forests since 1961, and one of the most severe in the karri forest in recorded history - hereby referred to as the Northcliffe fire. The 2015 Northcliffe fire burnt under dry summer conditions and on several occasions exhibited violent pyroconvection resulting in the formation of pyrocumulonimbus clouds (Sharples et al., 2016). The extent and severity of this fire provided a valuable opportunity to assess capacity of mature karri forests to recover from the type of high severity fire events that are projected to become more frequent in the future.

Fires severe enough to kill mature trees can cause long-term changes to the structure and functioning of a karri forest ecosystem. While it is generally understood that fire facilitates recruitment and regeneration of karri, past studies of post-fire stand and understorey regeneration have focused on the even-aged regrowth of logged coupes that were < 30 years old (McCaw et al., 1994), or on the effects of different fire-return intervals on mostly mixed karri-marri (*Corymbia calophylla* Lindl.) or karri-tingle (*Eucalyptus jacksonii* Maiden) forests (McCaw et al., 2000; Wardell-Johnson, 2000; Wardell-Johnson et al., 2018). A notable exception is a recent study of wildfire impacts on mature and unlogged karri-red tingle forest that was burnt by wildfire in 2001 (McCaw and Middleton, 2015). McCaw and Middleton (2015) concluded that the tall open eucalypt forests of SWWA rarely experience high tree mortality or complete stand replacement after wildfire, and that multi-aged stands are likely to be the norm. However, they concluded that because the maximum potential fire intensity in tall eucalypt forests is an order of magnitude greater than experienced at their study sites, more intense fires would likely have a greater impact on stand structure through increased mortality. Nevertheless, the impact of high mortality rates of mature karri trees on post-fire seedling recruitment remains unknown. The existence of mostly uneven-aged stands of karri (Bradshaw and Rayner, 1997) indicates that perhaps fires severe enough to kill entire stands of mature karri forest have not occurred as frequently in SWWA as in eastern Australia, where even-aged stands are more common (Ashton, 1976).

Like most eucalypts, karri trees exhibit multiple adaptations that help them cope with fire. Karri have thick, protective bark and a capacity to resprout from epicormic buds along the stems and branches, but not from basal lignotubers, making their fire response different from many other eucalypts (Wardell-Johnson et al., 2007). This specialised form of resprouting enables them to consistently and rapidly regenerate and regrow their canopies even if they have been mostly or entirely consumed by moderate to high severity fire. However, evidence of widespread fire-caused mortality of mature karri in SWWA and more recently of other eucalypts in SE Australia (Bennett et al., 2016; Fairman et al., 2016) that are generally regarded as being fire tolerant, highlights the fact that fire-tolerance thresholds exist even for species with a strong capacity for resprouting. Adaptations facilitating persistence after fire are also present in the understorey plant community of the karri forest. While some species can re-sprout prolifically following fire, many of the dominant understorey species such as *Trymalium odoratissimum* and *Chorilaena quercifolia* are killed by fire and recruit from the soil seed bank (Christensen, 1992; Wardell-Johnson et al., 2007). We might expect understorey species to differ in their responses to extreme severity fire owing to differences in the thermal tolerances of the seedbank (Ooi et al., 2014) or to differences in nutrient availability after fire (Grierson and Adams, 2000; Pekin et al., 2009), as well as due to changing competition dynamics with the overstorey species. However, there have been few assessments of fire severity tolerance of understorey species in the karri forest, and thus their possible interactions with significant overstorey changes and karri seedling recruitment are not well understood.

This study of the Northcliffe fire seeks to compare the response of overstorey and understorey plants across a gradient of fire severity, and investigate how karri forest community dynamics will be impacted by changes of this magnitude. Like many forest fires, the Northcliffe fire was spatially heterogeneous, resulting in a mosaic of forest areas variably impacted by the fire. This mosaic allowed an investigation of the response of mature karri forest to a range of fire severities across large landscape scales. We expected karri trees to survive low severity fire, but that the extent of mortality would increase in areas burnt at higher severity. We also expected karri seedling recruitment to be higher in areas with higher levels of soil nitrogen and phosphorus, and sought to investigate how these increases were linked with fire severity. Furthermore, we aimed to assess how such an extreme fire event affects the recruitment of understorey species in this system. We expected that shifts in understorey composition would be consistent with negative impacts of fire severity on the overstorey.

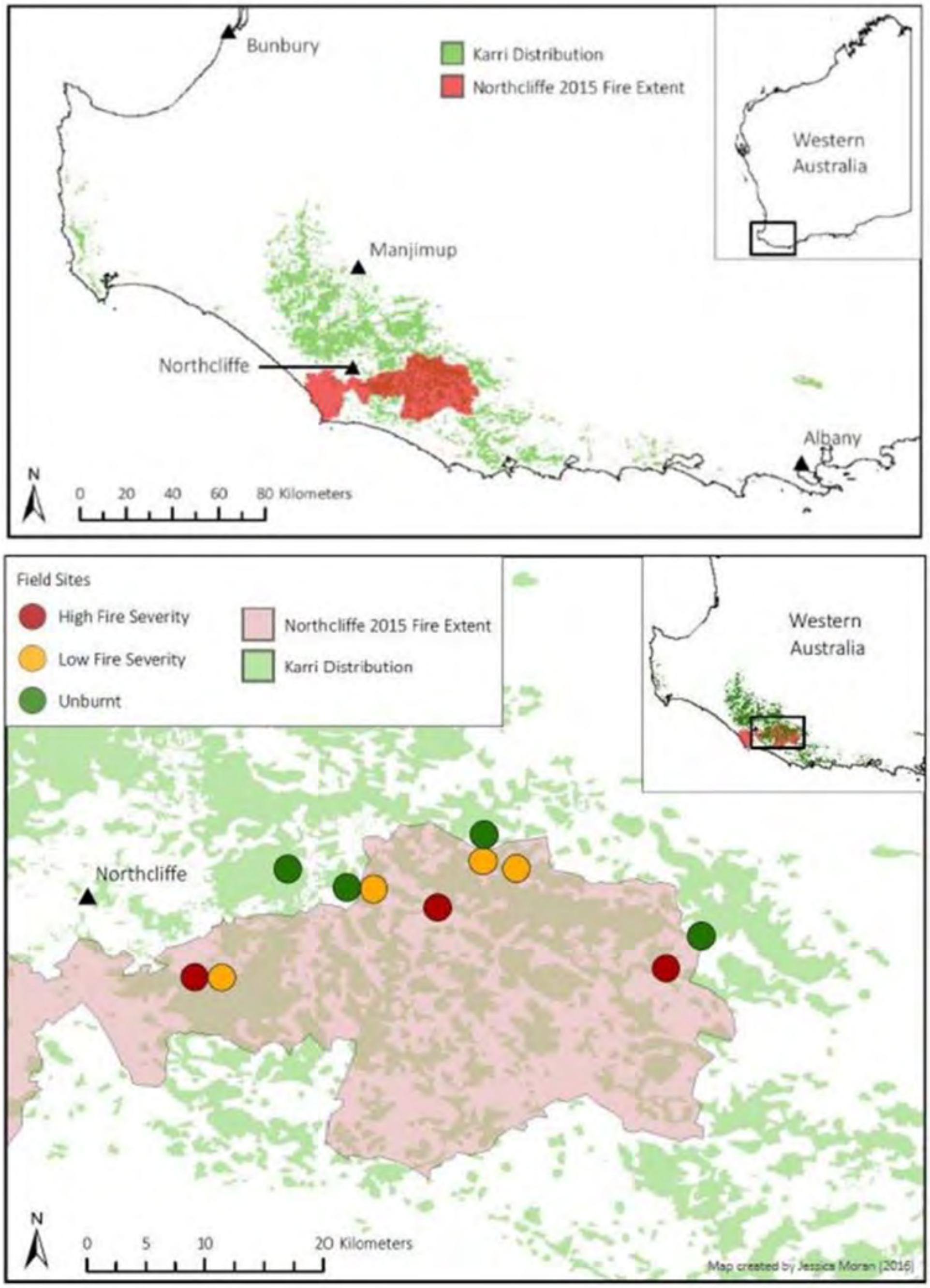
2. Materials and methods

2.1. The Northcliffe wildfire

On 28 January 2015, a lightning strike ignited a fire in the O'Sullivan forest block near the town of Northcliffe, in SWWA (Fig. 1). Over 20 days, the fire burnt 98,650 ha of the Warren Bioregion including significant areas of mature karri forest containing trees over 250 years old. The wildfire occurred during a summer of above average temperatures, below average rainfall, and an unusually high incidence of lightning ignition (Bureau of Meteorology, 2015; Department of Fire and Emergency Services, 2015). While fine-scale specific fuel loadings were not measured pre-fire, it is understood that some patches of the forest had not been burnt, either by wildfire or prescribed fire, in over 30 years and had accumulated high amounts of leaf litter and woody debris (Department of Fire and Emergency Services, 2015). Overall, understorey vegetation and accumulated leaf litter were very dry and flammable owing to the prevailing conditions, with the McArthur Forest Fire Danger Index at High or Very High for six consecutive days (Bureau of Meteorology, 2015; Department of Fire and Emergency Services, 2015). Owing to localised variation in fuel loads, coupled with topographic complexity and logging and fire histories, the Northcliffe fire burnt heterogeneously, leaving some patches of forest completely defoliated, and others with only low to moderate understorey scorch (Figs. 2 and 3).

2.2. Site description, study plots and sampling

Sites of differing fire severity were selected for comparison from across the 98,650 ha karri forest impacted by the Northcliffe fire. The gradient of fire severity was determined using a remotely-sensed spectral index from Landsat satellite images (difference Normalised Burn Ratio, dNBR, see Fig. 2 and Table 1), and then confirmed on-ground using a traditional crown-scorch assessment method (Lacey and Johnston, 1990; McCaw and Middleton, 2015, see Table 1). A total of 11 sites were identified, comprised of four plots of each of the unburnt



Map created by Jessica Moran (2016)

Fig. 1. Map of karri (*Eucalyptus diversicolor*) distribution and study sites within the ~100,000 ha Northcliffe 2015 fire scar in southwest Western Australia. Data source: Landgate, 2015; N.V.I.S, 2010.

and low severity and three plots of high severity. The decision to merge low and moderate severity sites into one category (low severity) was made during on-ground crown scorch assessment, because many of the sites in this range contained equal numbers of trees that would fall into either category, making them difficult to accurately separate (Table 1). One of the high severity sites had complete overstorey canopy consumption, a low percentage of mature trees with epicormic resprouting and evidence of large understorey shrubs having been entirely consumed, leaving only roots and small charred stumps at ground level. This site is herein referred to as the extreme severity site. The extreme severity site was very close to the original lightning ignition point, and due to its unprecedented level of fire severity, we were not able to find a comparable replicate for this category. While there were other areas within the fire scar that were classified as extreme high severity, none were suitable as replicate for this study as they occurred either in other vegetation types or in logged karri forest. Thus, while we have attempted to categorise sites into fire severity classes, they in fact encompass a gradient of impacts across the Northcliffe fire scar (Figs. 2 and 3).

All sites were old-growth karri forest (containing several trees estimated to be older than 250 years) that had never been logged, were located on similar landform, and soil type and were determined to have had similar pre-fire understorey structure and composition. Karri forest understorey at the surveyed sites and across the Northcliffe area in general is largely dominated by the large shrubs (> 3 m) *Trymalium odorissimum*, *Acacia pentadenia* and *Chorilaena quercifolia*. We sampled sites in the dry austral early autumn in March 2016 (13 months after fire) and again in the wet winter in July 2016 (17 months after fire) to

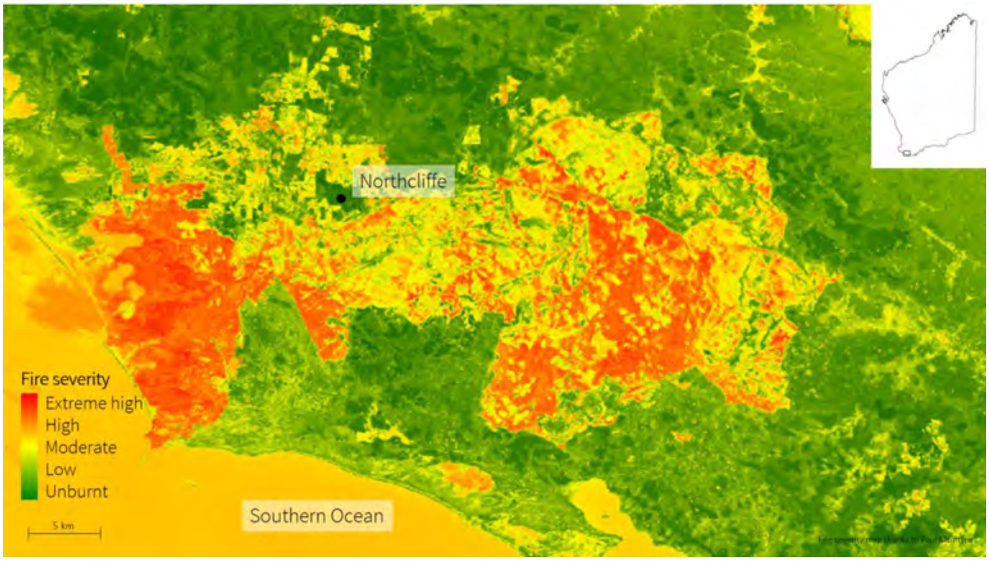


Fig. 2. Map showing fire severity within the ~100,000 ha Northcliffe 2015 fire scar in southwest Western Australia. Severity determined using a remotely-sensed spectral index from satellite images (difference Normalised Burn Ratio, Roy et al., 2006).

encompass seasonal variability in seedling recruitment and survival.

A 30 m × 30 m (900 m^2) plot was established at each site. Within each plot, all trees (live and dead) > 1.0 cm in diameter at breast height (1.3 m above ground, DBH in mm) were counted and their diameter recorded to determine stand basal area (m^2 ha^{-1}) and assess recruitment and population structures. Trees with no evidence of sprouting from the crown or the stem above 10 m height were classified as dead on the basis that they had lost any ability to continue normal growth and development, and no longer retained the growth form of a mature tree. Canopy cover was estimated using photographs taken from 1.3 m above the ground with a 29 mm (wide-angle) lens pointed directly up, then processed in ImageJ2 (Rueden et al., 2017) to calculate percent of image covered by canopy. Canopy loss was determined by calculating the cover difference between burnt sites and the mean cover of unburnt sites.

At each sampling time, karri seedling density and heights were measured within five 4 m^2 subplots located within each 30 × 30 m plot. Seedling densities were summed over the five subplots at each site and converted to density per m^2. Seedling height for the five subplots was averaged at each site and then multiplied by seedling density to give a metric of seedling growth. All understorey plant species rooted within each of the subplots were identified to species level and percentage cover and species diversity (Species richness, Shannon-Weiner, & Pielou's evenness) for each subplot was estimated. Understorey cover was then averaged across each site.

In the winter sampling 17 months after fire, above-ground fruiting bodies of fungi found within each site were collected opportunistically and their presence recorded and photographed. Unique species were given an identifying specimen number but were not further classified taxonomically.

2.3. Soil sampling and nutrient analysis

We assessed the impacts of fire severity on organic matter combustion and nutrient transformations in surface soils. Three soil samples (0–10 cm) were collected from each subplot and bulked by site for each sample time (13 months and 17 months after fire). Soils were kept cool (< 20 °C) and transported to the laboratory. Soils were sieved (< 2 mm). Gravimetric moisture content was estimated by deducting the weight of a small sample of soil that had been dried for 24 h in a 70C° oven from its fresh weight (Grierson and Adams, 2000). Soil pH was measured in soil mixed with de-ionised water in a 1:1 ratio (Thomas, 1996). Labile organic phosphorus (Po) and inorganic phosphorus (Pi) were extracted in 0.1 M sodium hydroxide (NaOH) for 16 h (Grierson and Adams, 2000) and analysed using a modified ascorbic acid method (Murphy and Riley, 1962). Total C and N (%) contents and stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of soils were obtained using a continuous flow system consisting of a Delta V Plus mass spectrometer connected to a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan/Germany) at the West Australian Biogeochemistry Centre at The University of Western Australia (www.wabc.uwa.edu.au). All stable isotope analyses are reported in permil (‰) after multi-point normalisation to international scales (Skrzypek, 2013), with combined analytical uncertainty of < 0.10‰.

2.4. Data analyses

The interacting effects of fire severity (as % canopy consumed) and soil properties on seedling growth were examined using generalised linear models (GLMs) in R (R Core Team, 2014) with site and sampling period as random effects. The models initially included all potentially predictive environmental variables (% canopy consumed, soil Pi, Po, % N, %C, $\delta^{13}C$, $\delta^{15}N$, pH and moisture content for karri seedling growth and only % canopy consumed and soil moisture for mature tree mortality). The best models were chosen by backwards stepwise selection until only significant variables remained. Differences in karri seedling growth, mature karri tree mortality and soil properties among fire severity classes were tested using ANOVA in R (R Core Team, 2014).

Multivariate analyses were used to explore if and how understorey community composition differed with fire severity in Primer V6 (Clarke and Gorley, 2006a, 2006b). Community data were log10(x + 1) transformed to control for biases caused by many 0 values, and Bray-Curtis similarity measures were calculated. Analysis of similarity (ANOSIM) was used to assess significant differences in community composition among sites. Similarity percentages (SIMPER) were used to determine the relative contributions of each plant species to similarities between sites and environmental factors. Soil properties and nutrient were included as factors and analysed using BEST to determine to what extent any of these variables explained differences in species cover among sites. Bray-Curtis similarity measures were also calculated for presence/absence data for fungal fruiting bodies at each site and ANOSIM was used to assess significant differences among sites. Species richness was calculated for each site and one-way ANOVAs were used to test for differences among fire severity categories.

Fig. 3. Karri forest vegetation regeneration after different fire severities. A: Unburnt for > 50 years; B: Low severity; C: High severity. All photos taken 13 months after fire in Northcliffe, Western Australia. Photos: H. Etchells.

3. Results

3.1. Karri tree mortality and seedling growth

Significant differences in tree mortality were observed among fire severity categories (Table 2). Mean (± s.e.) karri tree mortality at high severity sites (47% ± 38.0) was significantly greater than low severity (5% ± 13.0) and unburnt sites (7.5% ± 12.9, $p < 0.05$), while tree mortality was similar among unburnt and low severity sites ($p > 0.05$, Table 2).

No karri seedlings were present at any of the unburnt sites in March 2016, and only one seedling was found at a single unburnt site in July 2016. In contrast, all burnt sites had seedlings at densities higher than 0.2 m^{-2} (Table 2). Karri seedling growth was significantly higher at burnt sites compared to unburnt sites ($p < 0.05$), but there was no significant difference between low severity and high severity sites owing to the high variation among plots (Table 2). Fire severity as represented by % canopy loss was the only factor that explained karri seedling growth, where karri seedling growth increased with percent canopy loss ($R^2 = 0.62$, $p < 0.01$, Fig. 4a). Karri seedling density was also higher in sites with higher soil % N, but this relationship was highly variable and while broadly correlated to fire severity appeared to be driven by one or two sites ($R^2 = 0.87$, $p = 0.09$, Fig. 4b). Differences in karri seedling density among sites were not explained by P availability, %C, pH, or stable isotope signatures.

The extreme high site, which was burnt at an exceptionally high fire severity stood out from the other high-severity sites as having the highest karri tree mortality (43% higher than other high severity sites), greatest canopy loss (27% greater than other high severity sites, Fig. 4), and highest karri seedling growth (more than twice that of other high severity sites). It also showed the highest increase in seedling density in the 4 month period between sampling times (i.e., 13 to 17 months post-fire, 21.43%).

3.2. Soil nutrients

There were no statistically significant differences in soil chemical properties (labile P fractions, %C, pH, or stable isotope signatures %N) among sites of different fire severities or between sampling seasons due to high variability within sites (Table 3). However, in the 4 months between sampling periods (13 to 17 months post-fire), there was a decrease in the variability of soil Pi, particularly at high severity sites. During the same period, there was also an increase in variability of soil Po at unburnt and low severity sites, but a decrease at high severity sites.

3.3. Understorey diversity and community composition

A total of 47 vascular plant species were identified across all sites and both seasons. Only one species – the climber *Clematis pubescens* – was present at all sites. *Trymalium odoratissimum* was the most abundant understorey species in 10 of 11 sites, making up 7–10% of the average regenerating understorey seedling cover at burnt sites and 43% of the average mature understorey cover at unburnt sites. *T. odoratissimum* was, however, entirely absent from the extreme high severity site. The presence of stumps and root systems of *T. oderatissimum* – nearly entirely consumed by fire – across the entire site confirm that this species was present at the site before the fire. An MDS plot and ANOSIM revealed a significant difference in community composition between unburnt and burnt sites ($P < 0.01$), but no significant difference between low and high severity ($P > 0.05$) (Fig. 5). SIMPER analysis revealed the species contributing most to overall dissimilarity between unburnt sites and burnt sites were the large shrubs *T. odoratissimum* and *C. quercifolia*. Observed species richness (S) was on average 26% higher in burnt sites (low and high severity) than unburnt sites (Fig. 6).

Table 1
Assessment criteria used to group sites into fire severities based on the difference Normalised Burn Ratio (dNBR) and on-ground crown-scorch assessment method from Lacey and Johnston (1990) and McCaw and Middleton (2015).

Difference Normalised Burn Ratio (dNBR)	On-ground crown scorch assessment criteria of 30 m × 30 m plot	Fire severity
−0.1 to + 0.1	All trees in plot unburnt	**Unburnt**
0.1 to 0.27	> 50% of trees in plot with crown recovering from shoots on fine terminal branches.	**Low**
0.27 to 0.44	> 50% of trees in plot crown recovering from epicormic shoots on intermediate branches without extensive resprouting from the stem.	**Moderate**
0.44 to 0.66	> 50% of trees in plot with crown dead with epicormic shoots on the stem only	**High**
> 0.66	> 50% of trees in plot with complete crown consumption, no epicormic resprouting, trees completely dead.	**Extreme high**

Table 2
Variation in mean (n = 3 or 4) and standard error (s.e.) karri seedling recruitment, growth (density × height) and mature tree mortality 13 months and 17 months after the Northcliffe January 2015 fire. Superscript letters denote statistically significant differences ($p < 0.05$) between groups.

	Fire severity	Seedling height (cm) per m^2	s.e.	Seedling density per m^2	s.e.	Seedling growth per m^2	s.e.	Mature tree mortality (%)	s.e.
13 mo.	Unburnt	0.00^{a}	0.00	0.00^{a}	0.00	0.00^{a}	0.00	5.00^{a}	13.01
	Low	21.03^{b}	5.42	0.20^{b}	0.05	4.21^{b}	1.00	7.50^{a}	12.92
	High	32.64^{c}	5.96	0.55^{c}	0.20	17.95^{c}	8.53	47.22^{b}	38.08
17 mo.	Unburnt	1.00^{a}	1.00	0.01^{a}	0.01	0.01^{a}	0.05	5.00^{a}	13.01
	Low	11.33^{d}	1.93	0.21^{b}	0.04	2.38^{d}	0.66	7.50^{a}	12.92
	High	31.87^{bc}	11.94	0.70^{d}	0.38	22.31^{c}	20.79	47.22^{b}	38.08

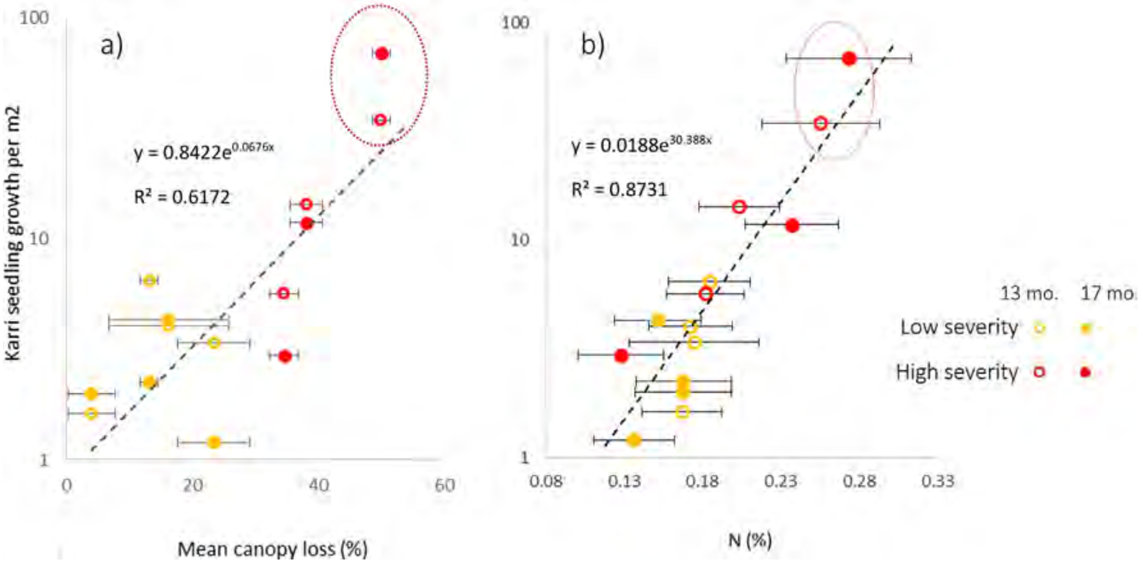


Fig. 4. Relationship between karri seedling growth (density × height) per m^2 and **a)** Mean canopy loss (%); and **b)** total soil nitrogen (N, %), following the 2015 Northcliffe fire. The extreme severity site is circled in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Soil nutrient and chemical properties of old-growth karri forest sites of different fire severity (Unburnt, Low and High) 13 months (March 2016) and 17 months (July 2016) after the January 2015 Northcliffe fire. CV = coefficient of variation.

			OH-Pi µg /g	OH-Po µg /g	C/N	% soil moisture (w/w)	pH	δ15N [‰ AIR]	δ13C [‰ VPDB]	N [wt%]	C [wt%]
13 mo.	Unburnt	**Mean**	**9.53**	**26.44**	**38.56**	**11.48**	**6.71**	**2.33**	**−28.84**	**0.18**	**6.51**
		CV (%)	155.62	11.7	11.82	20.82	5.9	27.41	0.61	40.46	35.86
	Low	**Mean**	**9.94**	**24.7**	**29.84**	**13.18**	**7.63**	**3.2**	**−28.73**	**0.18**	**4.93**
		CV (%)	133.32	5.79	43.87	33.65	5.64	19	0.84	46.82	44.92
	High	**Mean**	**5.39**	**21.14**	**28.42**	**11.59**	**7.55**	**3.28**	**−28.6**	**0.21**	**5.82**
		CV (%)	114.85	38.71	18.38	38.29	1.4	10.65	0.55	4.18	13.81
17 mo.	Unburnt	**Mean**	**7.17**	**31.47**	**38.16**	**16.59**	**7**	**3.39**	**−28.74**	**0.16**	**6.18**
		CV (%)	117.41	40.28	23.58	15.3	3.62	14.78	2.66	9.67	16.78
	Low	**Mean**	**6.07**	**27.06**	**32.45**	**19.02**	**7.41**	**4.27**	**−28.46**	**0.16**	**4.52**
		CV (%)	51.28	22.7	14.66	20.42	1.23	20.49	0.78	17.7	10.56
	High	**Mean**	**3.46**	**21.79**	**28**	**19.68**	**7.56**	**3.75**	**−28.22**	**0.21**	**5.68**
		CV (%)	35.9	9.22	14.58	14.49	4.67	8.21	0.52	35.57	24.41

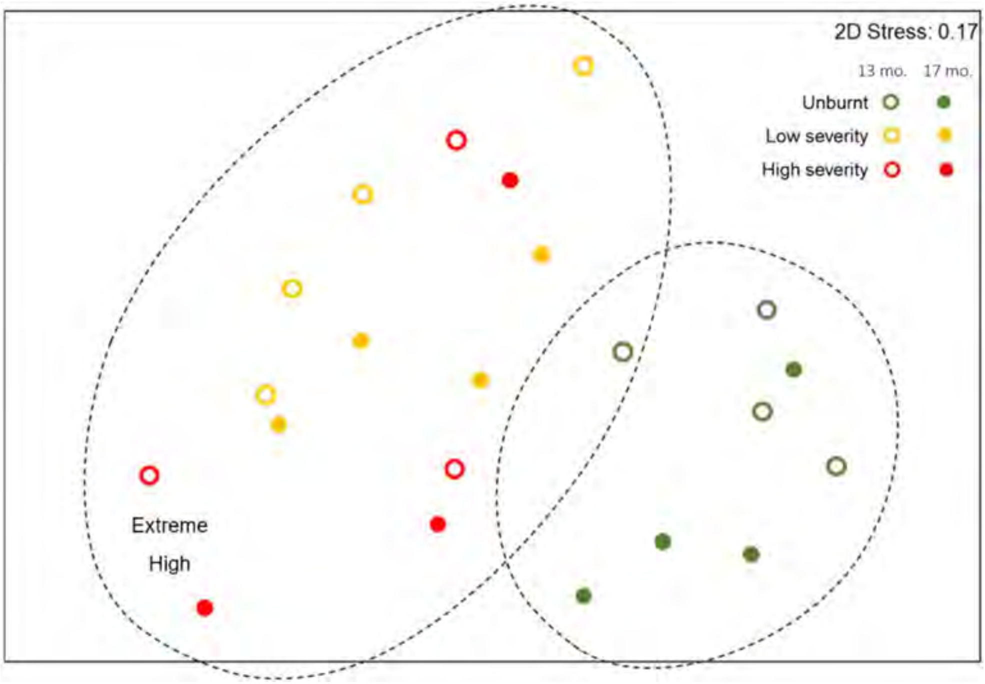


Fig. 5. Non-metric multidimensional scaling (MDS) ordination of understorey plant community composition, with environmental factors as vector overlay. Data collected 13 and 17 months following the Northcliffe fire. Each data point represents a single site. Data were log(x + 1) transformed and a Bray-Curtis similarity resemblance was applied. Dashed line indicates 25% similarity.

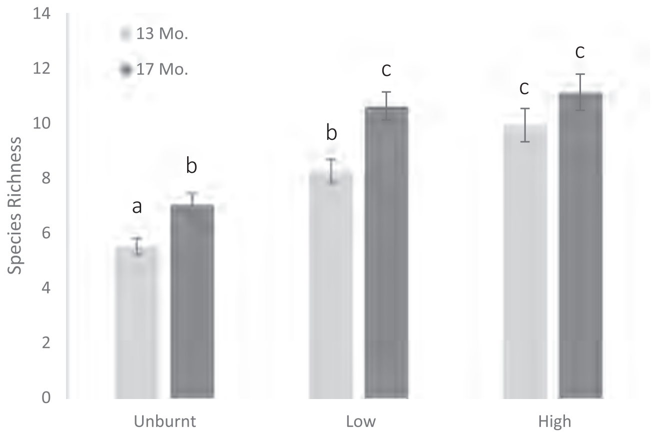


Fig. 6. Mean (n = 3 or 4) plant species richness at sites with different fire severity, 13 months and 17 months following the Northcliffe 2015 fire. Superscript letters denote statistically significant differences ($p < 0.05$) between groups.

4. Discussion

Extensive mortality of mature trees occurred in areas of the Northcliffe fire that experienced very high fire severity. The high mortality rates recorded at high severity sites (~30–65%) in this study have rarely been observed in mature karri forest, however anecdotal evidence suggests that there was widespread mortality of mature karri trees in the aftermath of the 1937 wildfire. These widespread mortality events indicate that there is potentially an upper severity threshold to this species' ability to survive and regenerate by epicormic resprouting following fire. This finding is consistent with high tree mortality recently observed in tall open eucalypt forests of eastern Australia after catastrophic wildfire (Benyon and Lane, 2013; Bennett et al., 2016). There are potentially long-term consequences of the high mortality rate of mature trees and the subsequent structural dominance of young trees for forests burnt with high severity. Young karri trees are not able to effectively regenerate following complete defoliation until they are between 12 and 20 years old (McCaw, 1986). Consequently, stands now dominated by young trees will be vulnerable to subsequent fires for a period of several decades, and surviving mature trees are likely to have stem injuries and dead branches in the crown that may readily ignite resulting in further damage to the tree. Therefore, future fire management planning for areas burnt by the Northcliffe fire will need to consider the timing and weather conditions under which future planned fire is introduced in order to protect consolidated patches of young regenerating forest.

Higher seedling density and growth at high severity sites was likely driven by an increase in light availability due to loss of canopy with increasing fire severity. There was also a positive correlation between % soil N and karri seedling growth, and despite this trend not being statistically significant, it is an indication that multiple interacting factors are impacting this ecosystem, making it difficult to determine cause and effect. The lack of karri seedlings at unburnt sites also suggests that the combination of low light availability and lower soil N limits seedling recruitment when sites are undisturbed, indicating that this system is reliant on canopy gaps caused by disturbances – such as fire – for recruitment. Notably, the extreme high severity site was the only site that saw a large increase in karri seedling growth from 13 months to 17 months post-fire. The combination of unusually high mature tree mortality and prolific seedling growth could lead to a denser and more even-aged area of forest, similar to stands regenerated after timber harvesting (McCaw et al., 2002). Therefore, areas with high levels of seedling recruitment should be monitored and appropriately managed if necessary to mitigate the fire risk caused by elevated fuel loadings.

While wildfire can result in significant shifts in karri forest understorey community composition due to its capacity to remove fire-sensitive species, this impact is highly dependent on severity. Burnt sites were significantly different from unburnt sites in both species richness and in the relative dominance of key shrubs. Notably, there was a complete absence of the otherwise abundant understorey species, *Trymalium odoratissimum*, at the extreme high severity site even though abundant prior to the fire. This absence is remarkable because at unburnt, low severity and both of the other high severity sites, *T. odoratissimum* comprises nearly half of the total understorey cover. The temperature and fire severity thresholds of *T. odoratissimum* and other karri forest understorey species are unknown. However, extreme fire severity has been shown to destroy the seedbank of species that are normally fire-tolerant, and can kill the seedbank of even fire-facultative seeders (Moreno and Oechel, 1991; Hanley et al., 2003). *Trymalium* species are also known to form an obligate symbiosis with ectomycorrhizal fungi, and very intense fires can kill mycorrhiza (Warcup, 1980; Pattinson et al., 1999). It is possible that germination and/or persistence of *T. odoratissimum* was inhibited by loss of its symbiotic partners. Indeed, a pilot study collection of fungal fruiting bodies suggests that a drastic shift in fungal community composition took place at the extreme high severity site (Supplementary Figure S1). While these assessments are preliminary, observations of fungal fruiting bodies across the fire severity gradient are consistent with observations in eastern Australian forests that fire can cause large fungal community composition changes (Johnson, 1995). Furthermore, high severity fire in logged karri forest is known to have significant impacts on fungal community composition that persist beyond five years (Robinson et al., 2008).

Mortality of the soil seedbank of key understorey species and/or on fungal and microbial symbionts is likely to have a strong influence on both short- and long-term community structure and can also affect overstorey recruitment and persistence (Tyler, 1995). *Trymalium odoratissimum* is recognised as an important habitat for several bird species (Russell and Rowley, 1998), and comprises a significant proportion of karri understorey biomass. If *T. odoratissimum* becomes locally extinct in karri stands burnt with extreme high fire severity, ecosystem functioning of these stands will likely be altered. Ecological theory dictates that communities that experience lower levels of disturbance can return to pre-disturbance composition sooner and more effectively than those that experienced higher levels of disturbance (Scheffer et al., 2001; Ives and Carpenter, 2007). Extreme high severity sites would therefore be expected to take longer to return to their pre-fire composition than low severity sites. However, after extreme disturbance, some communities reach a “tipping point”, and it becomes unlikely they will have the capacity return to their pre-disturbance composition (Chapin et al., 2004). Severe fire events are projected to become more common in the future, so determining tipping points of ecosystems is critical in order to effectively conserve them (Adams, 2013). The extreme high severity site, with its loss of its dominant understorey species, has potentially suffered such a disturbance, and could have reached a tipping point from which it will not return to its pre-fire composition. Future monitoring of this site will provide a valuable example of how karri forest community composition and stand dynamics may be affected by the projected increase in severe wildfires.

Fire plays a key role in determining nutrient availability in many Australian ecosystems, both directly by changing properties of the soil itself, and by nutrient cycling through consumption of canopy and woody debris (Adams et al., 2003). While several studies have demonstrated increased availability of both N and P in karri forest soils after fire (Loneragan and Loneragan, 1964), we did not observe significant differences in overall soil nutrient availability related to fire severity, largely due to large variation within sites. This lack of a fire-driven increase in nutrients is explained at least in part by the timing of sampling, which was more than one year after the fire. Both karri seedlings and understorey species are capable of rapidly utilising sudden nutrient influxes after germination and during early development (O'Connell, 1988). Any initial flush of nutrients caused by fire may therefore have already been taken up by the regenerating understorey and live trees, immobilised by microbes and soil interactions or lost from soils through leaching (Weston and Attiwill, 1996). Nevertheless, much higher soil nitrogen was still observable at the site burnt at greatest severity (the extreme high severity site) even 17 months after the fire. Further studies focused on quantifying the spatial and temporal dynamics of organic matter and nutrient transformations in soils after fire of variable severity and soil heating may help elucidate the dependence or otherwise of karri seedlings on fire-released nutrient fluxes.

Overall, this study demonstrates that high severity fire has substantial effects on the mortality, recruitment and growth of karri and associated understorey plant species. If, as projected, severe fire events become more frequent, karri forest structure and composition could be considerably altered. The extreme high severity site monitored during this study provides indication that karri forest may have a fire severity threshold, beyond which trees recovery is compromised and the understorey is considerably altered. Ecological communities that experience switches to alternative states are also likely to experience large and potentially irreversible changes in ecosystem function (Kuenzi et al., 2008). However, a limitation of this study is that sites have so far only been monitored for 17 months, not sufficiently long enough to confirm that recolonization of the understorey may occur from wind-blown or animal-dispersed seed. Nevertheless, the findings are consistent with recent studies undertaken in different forest types burnt by severe fire both in Australia and elsewhere (Collins and Roller, 2013; Bennett et al., 2016; Prior et al., 2016), and further emphasise the need for long-term research into the ecological tolerances of fire prone forest ecosystems worldwide, and how these may interact with a warmer and drier climate.

Funding

This research was funded by The University of Western Australia, the Department of Biodiversity, Conservation and Attractions (Western Australia) and the Mary Janet Lindsay of Yanchep Memorial Fund Scholarship.

CRediT authorship contribution statement

Hannah Etchells: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Alison J. O’Donnell:** Supervision, Methodology, Writing - original draft, Writing - review & editing. **W. Lachlan McCaw:** Supervision, Writing - review & editing, Resources, Funding acquisition. **Pauline F. Grierson:** Supervision, Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

I acknowledge the Pibelmen Noongar and Menang Noongar people, the traditional custodians of the land where this study took place. Thanks to Jen Middleton, Cameron Etchells and other volunteers for fieldwork assistance, Dr Jordan Iles and Kate Bowler for laboratory guidance, Jessica Moran and Dr Paul Macintyre for help with GIS and mapping, and the useful advice of anonymous reviewers.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117850.

References

Adams, M.A., 2013. Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. For. Ecol. Manage. 294 (2013), 250–261.

Adams, M.A., Grierson, P.F., Burrows, C., Abbott, I., Burrows, N., 2003. Fires, soils and plant nutrition in south-west Western Australian forests: a focus on spatial and temporal variability. In: Fire in Ecosystems of South-west Western Australia: Impacts and Management. Symposium Proceedings, Blackhuys Publishers, Western Australia, 2003, vol. 1, pp. 189–203.

Ashton, D.H., 1976. The development of even-aged stands of *Eucalyptus regnans* F. Muell.

in central Victoria. Austral. J. Bot. 24 (3), 397–414.

Bureau of Meteorology (Western Australia Regional Office), 2015. Meteorological Aspects of the Waroona, Lower Hotham and O'Sullivan Fires January/February 2015.

Bennett, L.T., Bruce, M.J., MacHunter, J., Kohout, M., Tanase, M.A., Aponte, C., 2016. Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire. For. Ecol. Manage. 380, 107–117.

Benyon, R.G., Lane, P.N., 2013. Ground and satellite-based assessments of wet eucalypt forest survival and regeneration for predicting long-term hydrological responses to a large wildfire. For. Ecol. Manage. 294, 197–207.

Bradshaw, F., Rayner, M.E., 1997. Age structure of the karri forest: 2. Projections of future forest structure and implications for management. Austral. Forest. 60, 188–195.

Boer, M.M., Sadler, R.J., Wittkuhn, R.S., McCaw, L., Grierson, P.F., 2009. Long-term impacts of prescribed burning on regional extent and incidence of wildfires—evidence from 50 years of active fire management in SW Australian forests. For. Ecol. Manage. 259, 132–142.

Burrows, N.D., 2008. Linking fire ecology and fire management in south-west Australian forest landscapes. For. Ecol. Manage. 255, 2394–2406.

Chapin III, F.S., Callaghan, T.V., Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G., Zimov, S.A., 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? AMBIO: J. Human Environ. 33 (6), 361–365.

Christensen, P., Abbott, I., 1989. Impact of fire in the eucalypt forest ecosystem of southern Western Australia: a critical review. Austral. Forest. 52, 103–121.

Christensen, P., 1992. The Karri Forest – Its Conservation Significance and Management. Department of Conservation and Land Management, Como, Western Australia.

Clarke, K.R., Gorley, R.N., 2006a. PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.

Clarke, K.R., Gorley, R.N., 2006b. PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth, pp. 192.

Collins, B.M., Roller, G.B., 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecol. 28, 1801–1813.

Dowdy, A.J., 2018. Climatological variability of fire weather in Australia. J. Appl. Meteorol. Climatol. 57 (2), 221–234.

Fairman, T.A., Nitschke, C.R., Bennett, L.T., 2016. Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. Int. J. Wildland Fire 25 (8), 831–848.

Grierson, P.F., Adams, M.A., 2000. Plant species affect acid phosphatase, ergosterol and microbial P in a Jarrah (Eucalyptus marginata Donn ex Sm.) forest in south-western Australia. Soil Biol. Biochem. 32 (13), 1817–1827.

Hanley, M., Unna, J., Darvill, B., 2003. Seed size and germination response: a relationship for fire-following plant species exposed to thermal shock. Oecologia 134 (1), 18–22.

Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. Science 317, 58–62.

Johnson, C.N., 1995. Interactions between fire, mycophagous mammals, and dispersal of ectomycorrhizal fungi in Eucalyptus forests. Oecologia 104 (4), 467–475.

Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. Int. J. Wildland Fire 18, 116–126.

Kuenzi, A.M., Fulé, P.Z., Sieg, C.H., 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. For. Ecol. Manage. 255 (3), 855–865.

Lacey, C.J., Johnston, R.D., 1990. Woody clumps and clumpwoods. Austral. J. Bot. 38 (3), 299–334.

Landgate, 2015. Northcliffe fire scar extent. https://www0.landgate.wa.gov.au/.

Liu, Y., Stanturf, J., Goodrick, S., 2010. Trends in global wildfire potential in a changing climate. For. Ecol. Manage. 259 (4), 685–697.

Loneragan, O., Loneragan, J.F., 1964. Ashbed and nutrients in the growth of seedlings of karri (Eucalyptus diversicolor F.v.M.). J. Royal Soc. Western Austral. 47, 75–80.

Major Incident Review of the Lower Hotham and O'Sullivan fires. Department of Fire and Emergency Services, 2015. Available https://www.dfes.wa.gov.au/publications/MajorIncidentReports/DFES-MIR-LowerHothamandOSullivanFinalReport.pdf.

McCaw, W.L., Neal, J.E., Smith, R.H., 2002. Stand characteristics and fuel accumulation in a sequence of even-aged Karri (*Eucalyptus diversicolor*) stands in south-west Western Australia. For. Ecol. Manage. 158 (1–3), 263–271.

McCaw, W.L., Middleton, T., 2015. Recovery of tall open eucalypt forest in south-western Australia following complete crown scorch. Fire Ecol. 11, 95–107.

McCaw, W.L., 1986. Behaviour and short term effects of two fires in regenerated karri (Eucalyptus diversicolor) forest. Technical Report-Western Australian Department of Conservation and Land Management (Australia) 9.

McCaw, W.L., Smith, R.H., Neal, J.E., 1994. Stem damage and crown recovery following high intensity fire in a 16-year-old stand of *Eucalyptus diversicolor* and *Eucalyptus muellerana*. Austral. Forest. 57, 76–81.

McCaw, W.L., Smith, R.H., Neal, J.E., 2000. Post-fire recruitment of red tingle (*Eucalyptus jacksonii*) and karri (*Eucalyptus diversicolor*) following low-moderate intensity prescribed fires near Walpole, south-western Australia. CALM Sci. 3, 87–94.

Moreno, J.M., Oechel, W.C., 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. Ecology 72 (6), 1993–2004.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772), 853.

N.V.I.S., 2010. National Vegetation Information System (NVIS) Version 4.2 - Australia - Key Layer for the Sources of Present (Extant) Vegetation Data. http://www.environment.gov.au/fed/catalog/search/resource/downloadData.page?uuid=%7B1C47096A-C3DF-4F5D-A692-576BFFE72E51%7D.

O'Connell, A.M., 1988. Nutrient dynamics in decomposing litter in karri (Eucalyptus diversicolor F. Muell.) forests of south-western Australia. J. Ecol. 76, 1186–1203.

Ooi, M.K., Denham, A.J., Santana, V.M., Auld, T.D., 2014. Temperature thresholds of physically dormant seeds and plant functional response to fire: variation among species and relative impact of climate change. Ecol. Evol. 4 (5), 656–671.

Pattinson, G.S., Hammill, K.A., Sutton, B.G., McGee, P.A., 1999. Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. Mycol. Res. 103 (04), 491–496.

Pekin, B.K., Boer, M.M., Macfarlane, C., Grierson, P.F., 2009. Impacts of increased fire frequency and aridity on eucalypt forest structure, biomass and composition in southwest Australia. For. Ecol. Manage. 258, 2136–2142.

Prior, L.D., Williamson, G.J., Bowman, D.M.J.S., 2016. Impact of high-severity fire in a Tasmanian dry eucalypt forest. Austral. J. Bot. 64, 193–205.

R. Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org/.

Robinson, R.M., Mellican, A.E., Smith, R.H., 2008. Epigeous macrofungal succession in the first five years following a wildfire in karri (*Eucalyptus diversicolor*) regrowth forest in Western Australia. Austral. Ecol. 33 (6), 807–820.

Roy, D.P., Boschetti, L., Trigg, S.N., 2006. Remote sensing of fire severity: assessing the performance of the normalized burn ratio. IEEE Geosci. Remote Sens. Lett. 3 (1), 112–116.

Rueden, C.T.; Schindelin, J., Hiner, M.C. et al., 2017. ImageJ2: ImageJ for the next generation of scientific image data. BMC Bioinf. 18:529, PMID 29187165, doi:10.1186/s12859-017-1934-z.

Russell, E., Rowley, I., 1998. The effects of fire on a population of Red-winged Fairy-wrens Malurus elegans in Karri forest in southwestern Australia. Pac. Conserv. Biol. 4 (3), 197–208.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413 (6856), 591–596.

Sharples, J.J., Cary, G.J., Fox-Hughes, P., Mooney, S., Evans, J.P., Fletcher, M.S., Fromm, M., Grierson, P.F., McRae, R., Baker, P., 2016. Natural hazards in Australia: extreme bushfire. Clim. Change 1–15.

Skrzypek, G., 2013. Normalization procedures and reference material selection in stable HCNOS isotope analyses: an overview. Anal. Bioanal. Chem. 405 (9), 2815–2823.

Stephens, S.L., Agee, J.K., Fulé, P.Z., North, M.P., Romme, W.H., Swetnam, T.W., Turner, M.G., 2013. Managing forests and fire in changing climates. Science 342, 41–42.

Thomas, G.W., 1996. Methods of Soil Analysis Pt 3 – Chemical Methods (Chapter 16), Ed. DL Sparks.

Tyler, C.M., 1995. Factors contributing to post-fire seedling establishment in chaparral: direct and indirect effects of fire. J. Ecol. 1009–1020.

Warcup, J.H., 1980. Ectomycorrhizal associations of Australian indigenous plants. New Phytol. 85 (4), 531–535.

Wardell-Johnson, G.W., 2000. Responses of forest eucalypts to moderate and high intensity fire in the Tingle Mosaic, south-western Australia: comparisons between locally endemic and regionally distributed species. Austral. Ecol. 25, 409–421.

Wardell-Johnson, G.W., Williams, M., Mellican, A., Annells, A., 2007. Floristic patterns and disturbance history in karri (*Eucalyptus diversicolor*) forest, south-western Australia: 2. Origin, growth form and fire response. Acta Oecologica-Int. J. Ecol. 3, 137–150.

Wardell-Johnson, G., Luxton, S., Craig, K., Brown, V., Evans, N., Kennedy, S., 2018. Implications of floristic patterns, and changes in stand structure following a large-scale, intense fire across forested ecosystems in south-western Australia's high-rainfall zone. Pac. Conserv. Biol. 23 (4), 399–412.

Weston, C.J., Attiwill, P.M., 1996. Clearfelling and burning effects on nitrogen mineralization and leaching in soils of old-age *Eucalyptus regnans* forests. Forest Ecol. Manag. 89, 13–24.