Recovery of karri forest after a severe wildfire at Northcliffe, Western Australia

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Abstract

Wildfires in the forests regions of southwest Australia are predicted to increase in both frequency and severity with projected changes in climate. While karri (*Eucalyptus diversicolor*) forests are considered relatively fire tolerant, there are few published studies of karri forest response to high severity fire and their capacity to persist under future fire regimes is uncertain. In January 2015, the largest and most severe karri forest fire on record burnt extensive areas of old-growth (>250 years) karri forest near Northcliffe, Western Australia, resulting in a mosaic of burn severities that included unburnt patches through to complete crown consumption. This study quantified the effects of differing fire severity on the recruitment and survival of karri seedlings, the mortality of mature karri trees, and the composition of the understory plant community after the Northcliffe fire. Sites were surveyed in both March and July 2016 across a gradient of fire severity, recording karri seedling density and height, mature tree mortality, overstorey canopy cover and understorey community composition. In addition, soil samples were collected and analysed for nutrient and chemical properties and fungal fruiting bodies were recorded during July. Mature karri tree mortality was 87 % greater at high fire severity sites than at other sites, indicating that karri trees may have an upper limit to their fire tolerance. Karri seedling growth was positively correlated with increased fire severity, and was best explained by the increase in light availability caused by high canopy consumption, rather than by any changes in soil nutrients. Burnt sites had significantly different understorey community composition than unburnt sites, and common understorey shrub, *Trymalium odoratissimum*, was entirely absent from one extreme fire severity site. Fungal community composition also appeared to be considerably altered by extreme severity fire. These findings suggest that karri forests may have an ecological tipping point and are consistent with recent studies undertaken in different fire-adapted forest types burnt by severe fire, both in Australia and elsewhere. This study further highlights the need for long-term research into the effects of climate change and severe wildfire on forest ecosystems worldwide.

Table of contents

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Introduction

Globally, there is increasing concern over the potential impacts of changing fire regimes on the conservation of temperate forests (Flannigan *et al.* 2013). Climate change projections indicate that wildfires will likely be more frequent, extensive and severe in many temperate regions of the world (Liu 2010; Flannigan *et al.* 2013). Indeed, the occurrence of severe wildfires (i.e., resulting in significant environmental change; Keeley 2009) in eucalypt forests in southern Australia is known to have increased in recent decades (Bradstock *et al.* 2014). Recent fires of extreme severity have also impacted the forests of southeastern Australia, usually considered to be highly tolerant of fire. For example, both the extensive 'Black Saturday' wildfire of 2009 in Victoria, and large fires in Tasmania resulted in unusually high mortality of eucalypts and shifts in stand structure (Nolan *et al.* 2014; Bennett *et al.* 2016; Prior *et al.* 2016). Tree mortality also affects understorey plant community composition through changes in resource availability (Dietze & Moorcroft 2011). Consequently, elevated tree mortality can have extensive ecological impacts with the potential to cause a shift to alternative states (Millar & Stephenson 2015). There is a critical need to determine the long-term ecological effects of extreme severity fire on forests currently considered fire-adapted in order to better predict how ecosystems will be affected by the projected increase in severe fire events (Stephens *et al.* 2013).

As for many other regions in Australia, wildfires in southwest Western Australia (SWWA) are predicted to increase in both frequency and severity in coming decades (Williams *et al.* 2001; Hughes 2003; Liu 2010). Both wild and prescribed fires are key drivers of ecological processes in the tall open karri (*Eucalyptus diversicolor* F. Muell.) forests of SWWA, including initiating regeneration and recruitment of plant communities (Christensen and Abbott 1989; McCaw *et al.* 2000; Burrows 2008). In contrast to the dominant understorey species of the karri forest, there is little if any soil-stored seed bank of karri (*E. diversicolor*) and seed volume is highly dependent on canopy seed from surrounding trees (Gill 1994; Bradshaw 2015). Extensive mortality of mature karri trees due to severe fire could therefore be detrimental to their regeneration, whilst not affecting the regeneration of understorey species. How mature karri forest will respond in both the short and long term to more frequent wildfires of extreme severity is largely unknown as such fires have occurred only rarely in the past (Boer *et al.* 2009; McCaw *et al.* 2015). However, a recent karri forest wildfire of unprecedented severity and extent has provided a unique opportunity to investigate the impacts of severe fire on karri forest.

In January 2015, a wildfire burned almost 100,000 hectares of karri forest, coastal heath and dairy pasture across the Warren Bioregion of SWWA over 20 days. This fire, referred to as the "Northcliffe fire", was the largest single fire in the southwest forests since 1961 and the most severe in the karri forest in recorded history (Lachlan McCaw, Department of Parks & Wildlife, pers. comm.). The unprecedented severity of the Northcliffe fire provides the first opportunity to assess capacity of mature karri forests to recover from the type of high severity fire events that are projected to become more common. Karri forests are of high environmental, cultural and heritage importance and a valuable timber resource (Christensen 1992, Calver *et al.* 1998; Bradshaw 2015), as well as a major attraction for ecotourism activities (Carlsen & Wood 2004). Consequently, optimising management and protection of these endemic forests in the face of numerous and sometimes conflicting values/uses and projected climate change, including changing fire regimes, is critical for their sustainable use and conservation.

Severe fires can change plant community composition even in fire-adapted ecosystems (Kuenzi *et al.* 2008), and extremely severe fires have the potential to cause dramatic and even permanent composition change (Scheffer *et al.* 2001). Differences in fire severity are known to lead to significant variation in post-fire regeneration in tall open *Eucalyptus regnans* forest in eastern Australia (Ashton & Martin 1996; Vivian *et al.* 2008). After the extreme severity wildfires that occurred between 2002 and 2009 across southeastern Australia (labelled as "megafires" by Adams *et al.* 2003), a number of studies reported significant ecological impacts such as extensive and unusually high tree mortality and stand structure shifts (Nolan *et al.* 2014; Bennett *et al.* 2016). Like most eucalypts, karri trees exhibit numerous adaptations that help them cope with fire. Karri trees have thick, protective bark and a capacity to resprout from epicormic buds along the stems and branches, enabling them to persist following low to moderate severity fires (Wardell-Johnson 2000). Higher severity fires tend to promote post-fire ashbeds, which have increased available phosphorus (P) and nitrogen (N) compared to unburnt areas (Adams *et al.* 2003). While karri seedlings are known to have significantly increased growth in ashbeds (Loneragan & Loneragan 1964), the extent to which ashbeds develop after extreme fires is likely to be highly variable and seedling recruitment and survival also depend on the availability of viable seed.

Adaptations facilitating persistence after fire are also present in the understorey plant community of the karri forest. Whilst species such as *Kingia* and *Persoonia* species can prolifically re-sprout following fire, most of the dominant understorey species such as *Trymalium odoratissimum* and *Chorilaena quercifolia* are thought to recruit from the soil seed bank (Wardell-Johnson *et al.*

2007; Bradshaw 2015). Prolific germination and growth of understorey species is likely to directly affect karri seedling growth and survival by competing for nutrients and light, as has been observed in other forest systems (Saunders & Puettmann 1999). There has been little quantitative assessment of understorey regeneration in response to variable fire severity, particularly high to extreme severity fire and in mature karri forest. This lack of research means fire severity tolerance thresholds for key species and their possible interactions with karri seedlings are not well understood.

Fires severe enough to kill mature trees could cause permanent changes to the structure and functioning of a karri forest ecosystem. While it is generally understood that fire facilitates karri recruitment and regeneration, most studies have focused on the even-aged regrowth of logged coupes that were less than 30 years old (McCaw *et al.* 1994; McCaw *et al.* 2000), or on the effects of different fire-return intervals on mostly mixed karri-marri or karri-tingle forests (Wardell-Johnson *et al.* 2004). A notable exception is a recent study of wildfire impacts on mature and unlogged karri-red tingle (*Eucalptus jacksonii* Maiden) forest that was burned by wildfire in 2001 (McCaw & Middleton 2015). McCaw and Middleton (2015) concluded that the tall open eucalypt forests of SWWA rarely experience complete stand replacement after wildfire and that multi-aged stands are likely to be more widespread than previously thought. However, the maximum fire severity assessed by McCaw and Middleton (2015) was not sufficient to kill mature trees. Consequently, 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 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, and suggests that karri forest differs from other tall forests in their response to high severity fire.

The objective of this study was to investigate how differences in fire severity affect the mortality, recruitment and growth of karri and karri forest understorey. While the Northcliffe fire was unprecedented in its scale and severity, like many forest fires it was also spatially heterogeneous, resulting in a mosaic of forest areas variably impacted by the fire. This mosaic allowed an investigation of the response of old-growth karri forest to a range of fire severities for the first time. Specifically, the aim of this study was to:

(i) Quantify recruitment and survival of karri seedlings as well as the survival and re-sprouting response of mature karri trees with increasing fire severity;

(ii) Analyse if differences in seedling density and growth among fire severities corresponded with changes in light and nutrient availability; and

(iii) Investigate changes in dominance and abundance of key understorey species associated with increasing fire severity.

Karri seedling recruitment and growth were hypothesised to be highest at sites of high fire severity due to increased light availability resulting from the loss of canopy and to increased nutrient availability owing to their release from organic matter by the fire (e.g. enhanced mineralisation). It was also expected that mature karri tree mortality would be highest at high severity sites and that the composition of the regenerating understorey at high severity sites would be significantly different to unburned or low severity sites.

Material and methods

The Northcliffe wildfire

On January 28th 2015, a lightning strike ignited a fire in the O'Sullivan forest block near the town of Northcliffe, in southwest Western Australia (Figure 1). Over 20 days, the fire burnt approximately 98,650 ha of the Warren Bioregion including significant areas of mature karri forest containing trees over 250 years old. The fire burned heterogeneously, leaving some patches of forest completely defoliated with high tree mortality, and others with only light to moderate understorey scorch (Figure 2).

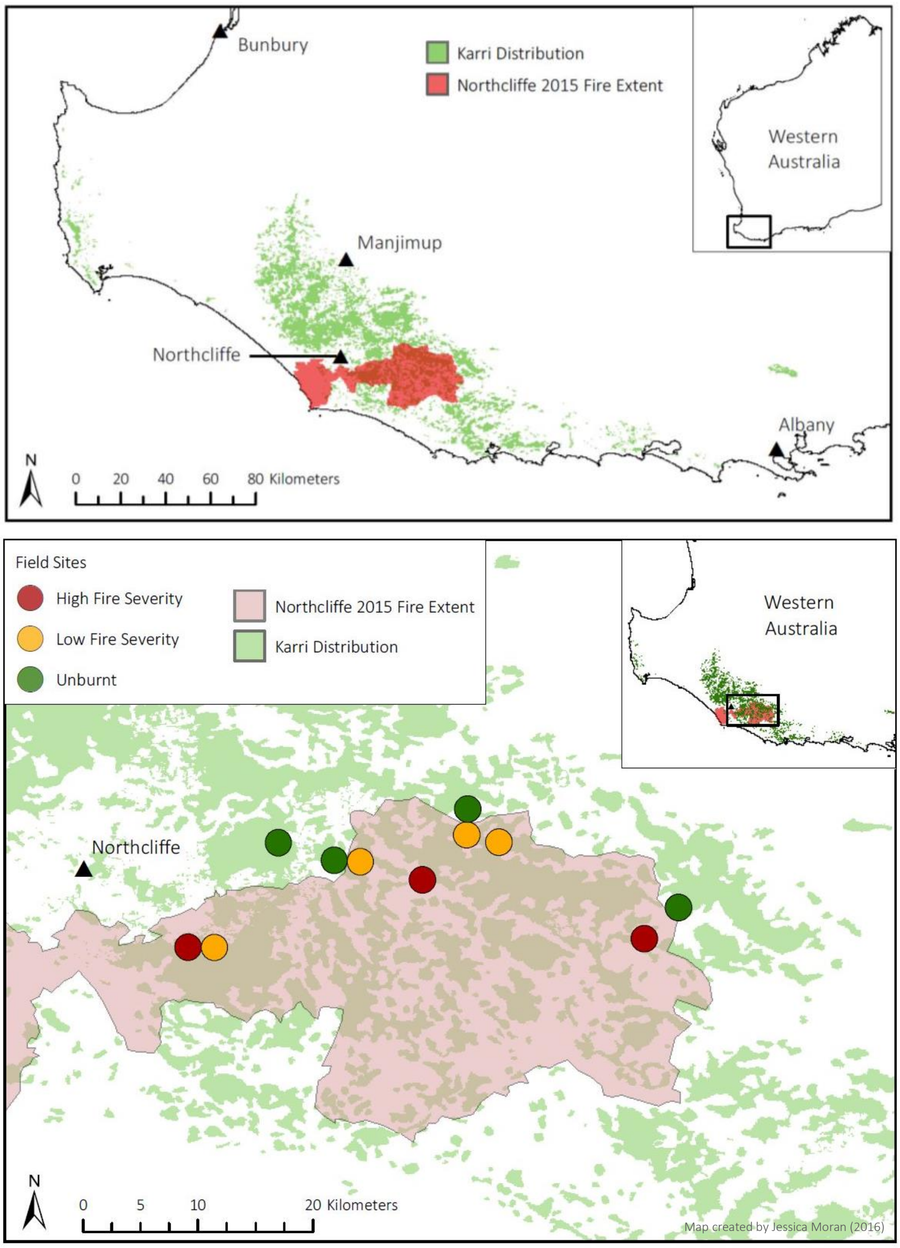

Figure 1. Map of karri (*Eucalyptus diversicolor*) distribution and study sites within the ~100,000 ha Northcliffe 2015 fire scar (Western Australia). All sites were unlogged, old-growth karri forest (trees >250 years), located on similar landform, and soil type and were determined to have had similar pre-fire understorey structure and composition. Data source: N.V.I.S. (2010) & Landgate (2015).

The Northcliffe wildfire occurred during a summer of above average temperatures, below average rainfall, and an unusually high level of lightning strike incidence (closest weather stations at Northcliffe and Shannon, Bureau of Meteorology 2016). Understorey vegetation and accumulated leaf litter was therefore very dry and flammable. Prior to the fire, there were areas of the forest that had not been burnt, either by wildfire or prescribed fire, in over 30 years and had therefore accumulated high amounts of leaf litter and woody debris. Owing to localised variation in fuel loads, coupled with topographic complexity, and logging and fire history, the Northcliffe fire resulted in a patchy mosaic of fire severity.

Study sites and sampling design

Sites of differing fire severity were selected for comparison from across the karri forest impacted by the Northcliffe fire. Fire severity is quantified as the amount of above and below ground organic matter consumed and is often used as an indicator of intensity. Fire intensity is more difficult to determine as it requires on-ground measurement of temperatures and flame height (Keeley 2009) and is generally inferred from severity measures after a fire has occurred (e.g. Boer *et al.* 2009). Fire severity was initially assessed qualitatively (e.g. if canopy was burned, scorch of understorey) and then categorised from a numerical score based on their level of crown scorch (Figure 3; Lacey & Johnston 1990; McCaw & Middleton 2015). All sites were old-growth karri forest (containing several trees estimated to be older than 250 years) that had never been logged. All sites were located on similar landform, and soil type and were determined to have had similar pre-fire

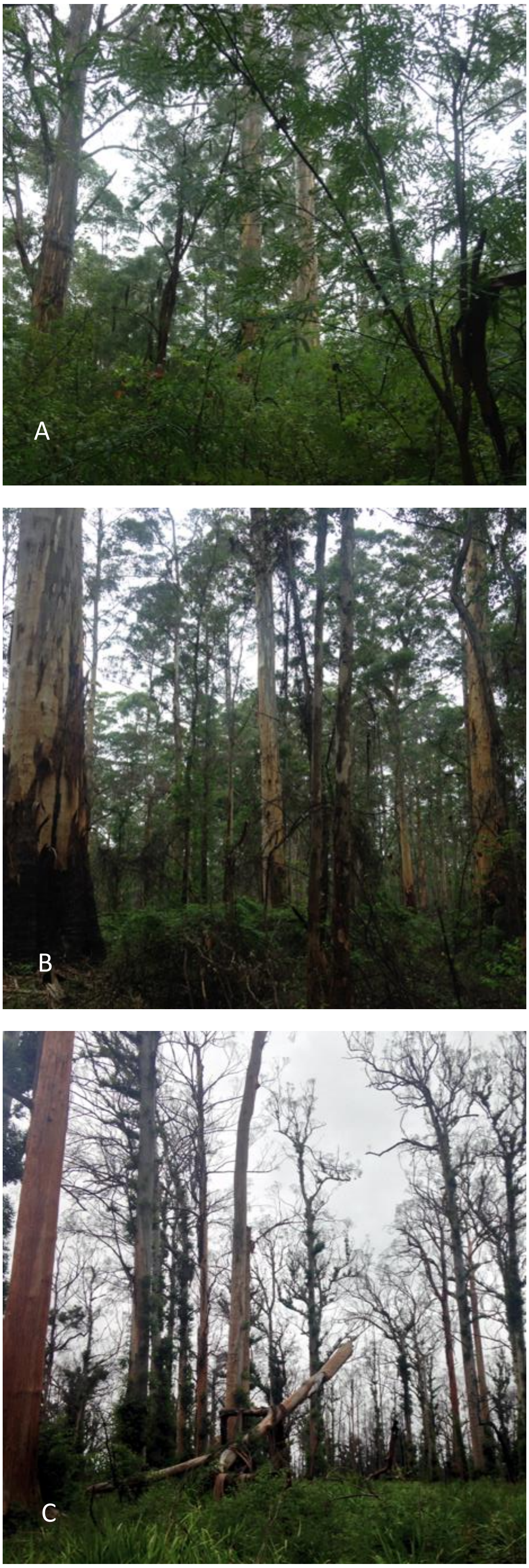

Figure 2. Karri forest vegetation regeneration after different fire severities. **A**: Unburnt for >50 years; **B**: Low severity, **C**: High severity. All photos taken 13 months after fire in Northcliffe, Western Australia. Photos: H. Etchells.

understorey structure and composition. A total of 11 sites were identified, comprised of four replicates of each of the unburnt and low severity and three replicates of high severity. Replicate sites for each fire severity class were chosen to encompass as much of the Northcliffe fire scar as possible (Figure 1). Karri forest understorey in surveyed sites and the Northcliffe area in general is largely dominated by *Trymalium odoratissimum* and *Chorilaena quercifolia*, both shrubs that can grow to over 3 m tall, or *Allocasuarina decussata*, a medium tree (up to 15 m) that is usually confined to gullies. Sites were sampled in the austral early autumn (20th-25th March 2016; ~14 months after the fire) and again in mid-winter (11th-15th July 2016; ~17 months after fire) to ensure that data encompass seasonal variability in rainfall and consequent impacts on seedling recruitment and survival.

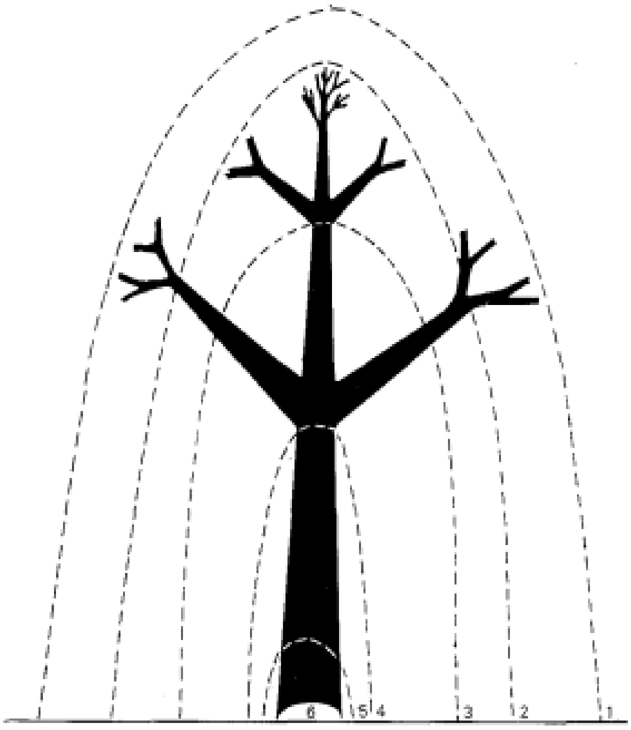

Figure 3. Conceptual diagram of the crown scorch assessment method used in this project, showing destruction of tree bud reserves with increasing fire severity (1 = no fire damage, 6 = extreme fire damage severity). Figure sourced from Lacey & Johnson (1990).

Vegetation sampling

A 30 m x 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 estimate stand basal area (m^2 ha-1) and assess recruitment and population structures. Trees were considered dead if they had complete crown loss and there was no epicormic resprouting above 10 m (Figure A2). Forest stand basal area is commonly used as a surrogate for seed production (Greene & Johnson 1994), and has also been shown to positively correlate with higher seed germination and seedling persistence in tall open *Eucalyptus* forest in eastern Australia (Vivian *et al.* 2008). Total basal area is also a useful indicator of pre-fire fuel loads that may have influenced variation in fire severity among sites.

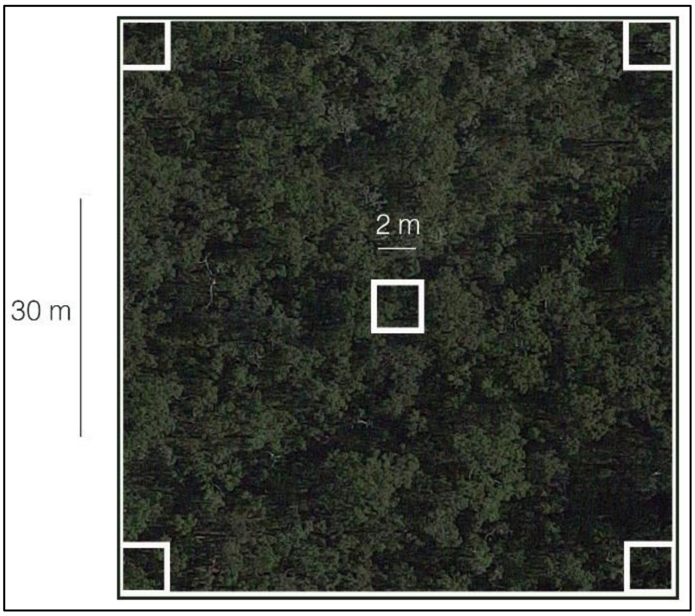

Figure 4. Diagram of 30 m x 30 m survey plot with position of five 2 m x 2 m sub plots. Placing sub plots at four corners and centre of plot aims to capture an accurate representation of whole plot heterogeneity.

In March 2016 and again in July 2016, karri seedling density and heights were estimated within five 4 m^2 subplots located within each 30 x 30 m quadrat (Figure 4). 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. Seedling density per 1 m^2 was then multiplied by mean seedling height, to give a metric of seedling growth per 1 m^2 that provided a comprehensive representative measure of the rapid vertical growth of karri seedlings at each site.

In order to account for potential competition for light and nutrients from understorey regeneration as well as changes in plant functional types among fire severity classes (e.g. see Pekin *et al.* 2009), all understorey plant species rooted within each of the 4 m^2 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 averaged across each 30 x 30 m quadrat as an estimate per hectare. In the July sampling period, fruiting bodies of all fungi (predominantly Basidiomycetes) 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.

Soil nutrient sampling and analysis

Three soil samples (0-10 cm) were collected and bulked for each 4 m^2 sub plot at each site in both March and July 2016. Soils were kept cool during transport to the laboratory, where they were then sieved (<2 mm). Moisture content of sieved soils was estimated by deducting the weight of a small sample of soil that had been dried for 24 hours in a 70 C° oven from its fresh weight (Grierson & Adams 2000). Soil pH (in water) of soils in each subplot was measured using a standard pH electrode inserted into a well-mixed vial of soil and de-ionised water in a 1:1 ratio (Thomas 1996). Labile organic phosphorus (Po) and inorganic phosphorus (Pi) of soils were extracted in 0.1 M sodium hydroxide (NaOH) for 16 hours (Bowman and Cole, 1978 as modified by 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‰. In this instance, the use and interpretation of isotope analyses is confined to providing a comparative index of the differing impacts of fire severity on organic matter combustion and transformations (Certini *et al.* 2011)

Data analyses

The interacting effects of fire severity and soil properties on seedling growth and tree mortality were examined using generalized linear models (GLMs) in R (ver. 3.1.1, R Core Team 2014) with site and sampling period as random effects. The models initially included all potentially predictive environmental variables (soil Pi, Po, % N, %C, $\delta^{13}C$, $\delta^{15}N$, pH and moisture content, canopy consumed for karri seedling growth and canopy consumed and soil moisture for mature tree mortality) and were run repeatedly, with the least significant variable removed each time, 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 (ver. 3.1.1, R Core Team 2014).

Multivariate statistical analysis was used to determine if understorey community composition differed among the fire severity classes. Community data were $\log_{10}$ transformed to control for biases caused by many 0 values, and Bray-Curtis similarity measures were calculated. To assess significant differences in community composition among sites, analysis of similarity (ANOSIM) was used. Similarity percentages (SIMPER) was used to determine the relative contributions of each plant species to similarities between sites and environmental factors. Soil nutrient data were included as factors and analysed using BEST to determine which of these best explain differences in species cover. Bray-Curtis similarity measures were calculated for presence/absence data for fungal fruiting bodies at each site and analysis of similarity (ANOSIM) was used to assess significant differences among sites. All multivariate statistical analyses were undertaken in Primer V6 (Clarke & Gorley 2006).

Results

Karri seedling growth and tree mortality

No karri seedlings were present at any unburnt sites in March 2016, and only one seedling was found at a single unburnt site in July 2016. In contrast, all burned sites had seedlings at densities higher than 0.2 per m^2 (Table 1). 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 1).

Table 1. Mean (±S.E.) karri seedling growth metrics in old-growth karri forest sites of different fire severity (Unburnt (n=4), Low (n=4), High (n=3)) in March 2016 and July 2016 following the Northcliffe 2015 fire.

	Burn class	Mean karri seedling height (cm) per 4 m²	S.E.	Mean karri seedling density per 4 m²	S.E.	Mean karri seedling growth per 4 m²	S.E.
March 2016	Unburnt	0.00	0.00	0.00	0.00	0.00	0.00
	Low	21.03	5.42	0.20	0.05	3.88	1.00
	High	32.64	5.96	0.55	0.20	18.12	8.53
July 2016	Unburnt	1.00	1.00	0.01	0.01	0.05	0.05
	Low	11.33	1.93	0.21	0.04	2.44	0.66
	High	31.87	11.94	0.70	0.38	28.02	20.79

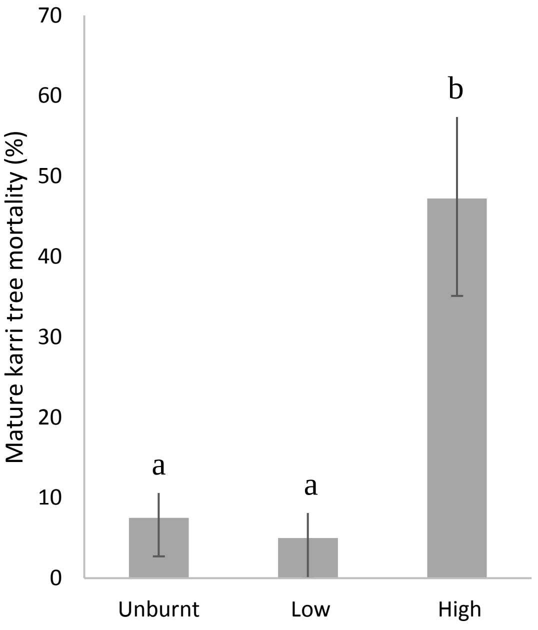

Figure 5. Mean (n = 3 or 4) mature karri tree mortality per site (%) at different fire severities following the 2015 wildfire near Northcliffe, Western Australia.

Karri tree mortality was ~87 % higher at high severity sites than both low and unburnt sites ($p<0.05$), but there was no significant difference between unburnt and low burnt sites ($p>0.05$, Figure 5). A generalised linear model showed that the variable best explaining differences in karri tree mortality was burn class ($p=0.09$).

Overall, Karri seedling growth was positively correlated with greater percent canopy loss (Figure 6). Light availability (represented by canopy loss) best explained karri seedling growth, as shown by a generalised linear model ($p<0.01$). One site ("Extreme High"), was noted as being burnt at an exceptionally high fire severity; this extreme severity site recorded the greatest canopy loss (27% greater than other high burnt sites, Figure 6), highest karri tree mortality (43% higher than other high burnt sites, Figure 5) and highest karri seedling growth (more than twice that of other high burnt sites).

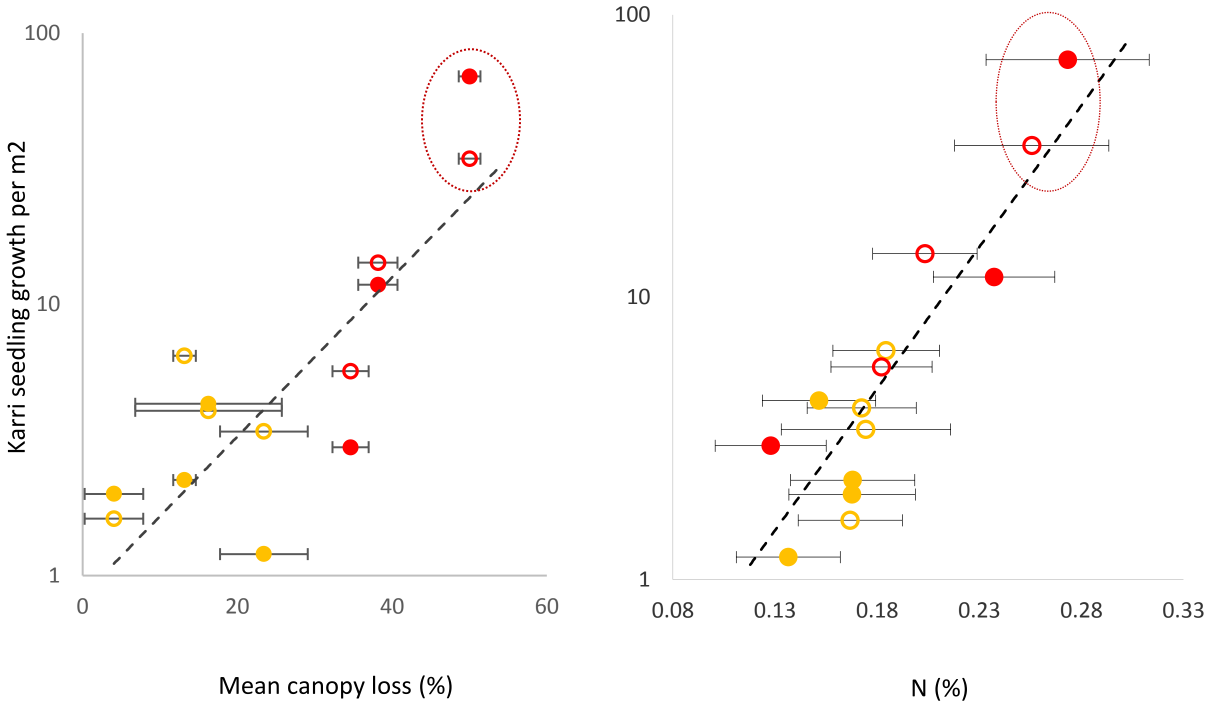

Figure 6. Karri seedling growth (density x height) per m^2 and mean (±SE) % canopy loss (n=5) for sites of low fire severity (yellow points) and high fire severity (red points) following the 2015 Northcliffe fire. Open circles represent sites sampled in March 2016; closed circles represent the same sites sampled again in July 2016. The Extreme High severity site is circled in red.

Neither burn severity nor karri seedling density were significantly correlated with labile P fractions, %C, pH, or stable isotope signatures (Table 2). However, karri seedling density increased with soil %N; this relationship was highly variable (p=0.09) and not clearly related to fire severity (Figure 6).

Table 2. Soil nutrient and chemical properties sampled from old-growth karri forest sites of different fire severity (Unburnt, Low and High) in March 2016 and July 2016 following the 2015 Northcliffe fire. CV = coefficient of variation.

	March 2016						**July 2016**					
	Unburnt		**Low**		**High**		**Unburnt**		**Low**		**High**	
	Mean	**CV (%)**	**Mean**	**CV (%)**	**Mean**	**CV (%)**	**Mean**	**CV (%)**	**Mean**	**CV (%)**	**Mean**	**CV (%)**
OH-Pi µg /g	9.53	155.62	9.94	133.32	5.39	114.85	7.17	117.41	6.07	51.28	3.46	35.90
OH-Po µg /g	26.44	11.70	24.70	5.79	21.14	38.71	31.47	40.28	27.06	22.70	21.79	9.22
δ^{15}N [‰ AIR]	2.33	27.41	3.20	19.00	3.28	10.65	3.39	14.78	4.27	20.49	3.75	8.21
δ^{13}C [‰ VPDB]	-28.84	0.61	-28.73	0.84	-28.60	0.55	-28.74	2.66	-28.46	0.78	-28.22	0.52
N [wt%]	0.18	40.46	0.18	46.82	0.21	4.18	0.16	9.67	0.16	17.70	0.21	35.57
C [wt%]	6.51	35.86	4.93	44.92	5.82	13.81	6.18	16.78	4.52	10.56	5.68	24.41
C/N	38.56	11.82	29.84	43.87	28.42	18.38	38.16	23.58	32.45	14.66	28.00	14.58
% soil moisture (w/w)	11.48	20.82	13.18	33.65	11.59	38.29	16.59	15.30	19.02	20.42	19.68	14.49
pH	6.71	5.90	7.63	5.64	7.55	1.40	7.00	3.62	7.41	1.23	7.56	4.67

Understorey diversity and community composition

A total of 47 plant species were identified across all sites and both seasons (Table A1). Species rank abundance curves sorted by burn category indicated that, proportionally, abundant species were most dominant in unburnt sites compared to burnt sites. Observed species richness (S) was on average 26 % higher in low and high severity sites than unburnt sites (Table A1). One Priority 4 threatened species, *Thomasia quercifolia*, was only present at burnt sites, and had on average 98 % greater cover at high severity sites than at low severity sites. Only one species – *Clematis pubescens* – was present at all sites. *Trymalium odoratissimum* was the most abundant 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. *Trymalium odoratissimum* was, however, entirely absent from the Extreme High severity site. This dominant understorey species was present at this site before the fire, as confirmed by abundant *T. odoratissimum* stumps and root systems – nearly entirely consumed by fire – across the entire plot (Figure A1).

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). SIMPER analysis revealed the species' contributing most to overall dissimilarity between unburnt sites and burnt sites were *T. odoratissimum* and *C. quercifolia*. *Pteridium esculentum* and *Logania serpyllifolia* contributed most to the differences between low severity and high severity sites. BEST analysis revealed that the environmental factor best explaining differences between sites were organic P and C. An MDS plot with environmental factors as vector overlay showed that the separation between burnt sites and unburnt sites was driven by an increased C/N ratio and a decrease in pH (Figure 7).

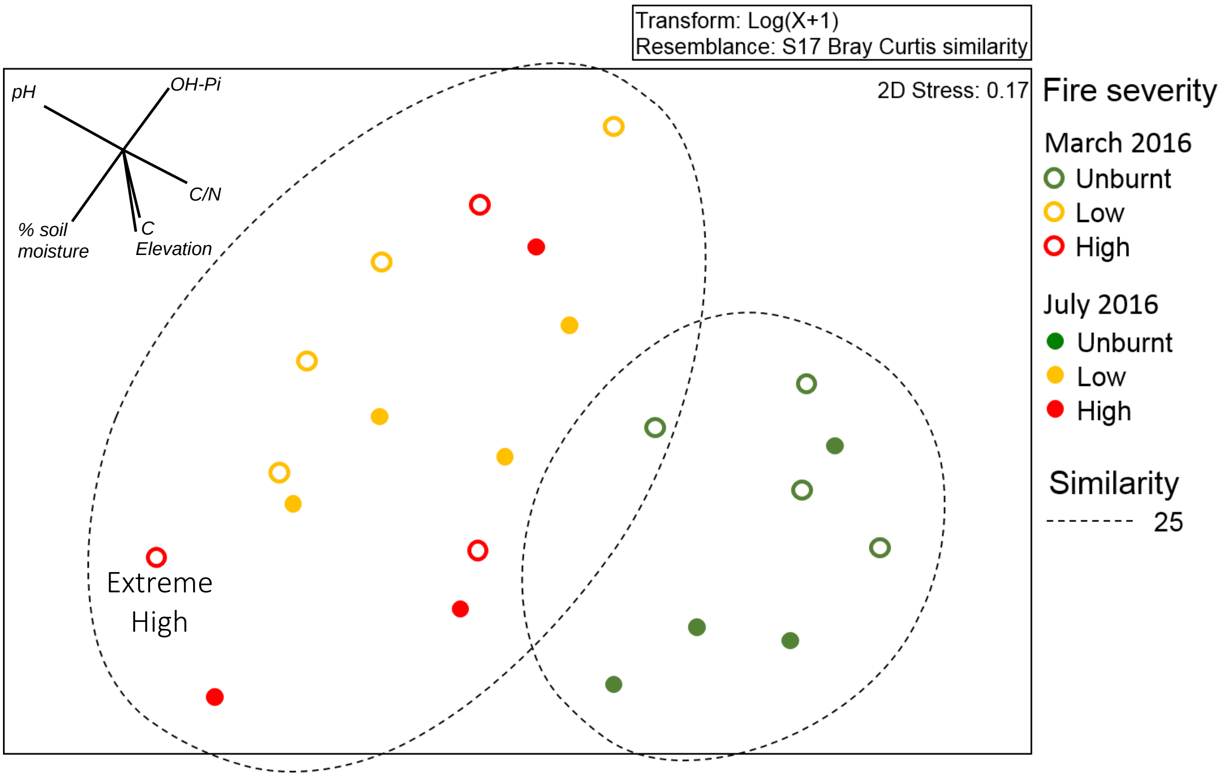

Figure 7. Non-metric multidimensional scaling ordination using cover data labelled by fire severity, with environmental factors as vector overlay. Each data point represents a mean (n=5) of a single site surveyed in either March 2016 (open circles) or July 2016 (closed circles), following the February 2015 wildfire near Northcliffe, Western Australia. Extreme High severity site indicated in bottom left of figure. Data are log(x+1) transformed with Bray-Curtis similarity resemblance applied.

In July 2016, 48 unique fungal fruiting bodies were identified across all sites. An MDS plot showed that fungal community composition was different between unburnt and burnt sites, and entirely different at the Extreme High severity site (Figure A3). ANOSIM confirmed the significance of these differences (P<0.01).

Discussion

The Extreme High fire severity associated with the Northcliffe fire resulted in extensive mortality of mature trees. Karri tree mortality was highest at high severity sites, indicating that this species' ability to regenerate following fire by epicormically resprouting has an upper limit. This threshold for potential recovery of individual trees reflects observations of high tree mortality in other tall open *Eucalyptus* forests in eastern Australia subject to extreme fire severity (Nolan *et al.* 2014; Bennett *et al.* 2016). However, despite greater karri mortality at high severity sites, there were no significant differences in karri seedling growth between sites burned at high and low severity. Very severe fire therefore has the ability to change the stand structure of karri forest by killing mature trees without a proportional increase in karri seedling growth. Largely even-aged regenerating stands are known to be less fire-tolerant than multi-aged stands because karri are not able to effectively regenerate following complete defoliation until they are between 12-20 years old (McCaw 1986). Severe fires could therefore cause a transition to a simplified stand structure and a more open forest, which might increase sensitivity to future fires. Consequently, if wildfires increase in frequency and severity, karri forest stand structure and plant community composition could potentially shift, leading to a cascade of other as yet unknown ecological impacts.

The hypothesis that karri seedling recruitment and growth would be highest at sites of high fire severity was supported. Higher seedling density and growth was likely driven by an increase in light availability due to loss of canopy with increasing fire severity. The lack of karri seedlings at unburnt sites also suggests that low light availability limits seedling recruitment when sites are undisturbed. The Extreme High severity site had far higher seedling growth than any other site, despite very high tree mortality and complete canopy removal. Fire-stimulated seedfall usually occurs in the days following canopy scorch (Christensen 1971; Bradshaw 2015), but the Extreme High severity site had no canopy at all remaining. Because there is very little soil-stored seed bank of karri seeds (Gill 1994; Bradshaw 2015), the seedling recruitment at this site is likely to be from karri trees outside of the survey site. However, the Extreme High severity site was surrounded by similarly burnt forest and only one or two karri trees within 100 m of the site had any portion of their scorched canopies intact. It is therefore possible that all the karri seedlings at this site are the recruits of only a few trees, and that seeds were able to disperse from up to 100 m away - by wind, or potentially by seed-harvesting invertebrates (Ashton 1979; Wallace & Trueman 1995). This remaining seed tree density is similar to the minimum of four seed trees per ha that are retained following karri harvesting in order to ensure future recruitment (Bradshaw 1999). If fires of this severity or higher occur in the future, more extensive stands of karri may suffer complete canopy destruction, effectively removing sources of seeds and leading to recruitment limitation. This study indicates that seeds may be able to recruit from trees up to 100 m away (the closest observed to impacted sites), but highlights the need for research to determine the impact on recruitment and seed dispersal following mass tree mortality caused by extremely severe fire.

Fire is known to play 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 & Loneragan 1964; O'Connell *et al.* 1988) there were no significant differences in soil nutrient characteristics (on a site basis) related to fire severity in this study. Consequently, the density of karri seedlings and their growth were not strongly correlated to soil nutrient or other chemical properties. Seedling growth nevertheless increased with soil N availability; this observation is largely driven by the large increases in soil N at the Extreme High severity site that showed greatest tree mortality and virtually complete combustion of the understorey. This finding suggests that there is possibly a temperature or combustion threshold before N becomes mobilised and available for plant uptake (as discussed in Certini 2005), and that understorey removal may decrease resource competition.

However, it is also possible that an influx of nutrients caused by fire was not detectable in this study due to the timing of sampling after 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 over the preceding 14 months, as has been recorded following fire in tall open forests in eastern Australia (Weston & Attiwill 1996). Soil nutrients can also be highly heterogeneous in their distribution; future studies focussed on quantifying the spatial and temporal dynamics of organic matter transformations after fire may help elucidate the dependence or otherwise of karri seedlings on fire-released nutrient fluxes.

Based on these findings, the Northcliffe fire has the potential to cause large shifts in understorey community composition at sites burnt with high fire severity. If fires are highly patchy in severity this will also result in increasing beta diversity (i.e. species turnover among sites). While the regenerating understorey at high severity sites was not significantly different in community composition to those that experienced lower severity fire, burnt sites were significantly different from unburnt sites in both species richness and in the relative dominance of key shrubs. *Thomasia quercifolia,* a priority 4 species (Hearn et al. 2006), was only abundant in high severity sites. Little is known of the fire response of *T. quercifolia* but these results indicate that its rarity may be due to it being an obligate seeder that requires high severity fire to break seed dormancy. Interestingly, there was a complete absence of the otherwise most abundant understorey species, *Trymalium odoratissimum*, at the Extreme High severity site. This absence is notable because at unburnt sites it comprises nearly half of the total understorey cover. Burnt stumps identified as *T. odoratissimum* were common across the Extreme High severity site, indicating its presence prior to the fire. The lack of regeneration of this key understorey species could be because the fire burnt at such high temperatures that the soil-stored seedbank was killed. Extremely severe fire has been shown to be capable of destroying seedbank of species that are normally fire-tolerant, and can kill the seedbank of even fire-facultative seeders (Moreno & Oechel 1991; Hanley *et al.* 2003). The temperature and fire severity thresholds of *T. odoratissimum* and other karri forest understorey species are unknown and worthy of further investigation.

Trymalium species are also known to form an obligate symbiosis with ectomycorrhizal fungi, and very hot fire 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, preliminary collection of fungal fruiting bodies suggests that a drastic shift in fungal community composition took place at the Extreme High severity site (Figure A3). While these assessments are quite preliminary, observations of fungal fruiting bodies across the fire severity gradient is consistent with observations in eastern Australian forests that fire can cause large fungal community composition changes (Johnson 1995). A recent study in logged karri forest has also indicated that fungal community composition following severe fire may take decades to return to pre-fire composition (Robinson *et al.* 2008). Further investigation into the effects of the Northcliffe fire on soil microbiology and fungal composition of old-growth forest would improve understanding of the impacts of severe fire on karri forest.

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 & Rowley 1998), and comprises a significant proportion of the understorey biomass. If *T. odoratissimum* is now locally extinct in karri stands burned with high fire severity, ecosystem functioning of these stand 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 & Carpenter 2007). 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 driven by climate change 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 the Extreme High severity site will provide a unique example of how karri forest community composition and stand dynamics may be affected by the projected increase in severe wildfires.

Overall, this study demonstrates that high severity fire has substantial effects on the mortality, recruitment and growth of karri and karri forest understorey. If severe fire events occur more frequently in the Anthropocene (Lewis & Maslin 2015), karri forest structure and composition could be considerably altered. The Extreme High severity site monitored during this study provides indication that karri forest has a fire severity threshold, beyond which trees cannot recover and 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 (Scheffer *et al.* 2001). The results of this study indicate that karri forest is not perpetually fire tolerant, and highlights the urgent need for comprehensive research into fire severity thresholds. These findings are consistent with recent studies undertaken in different forest types burnt by severe fire both in Australia and elsewhere (eg: Collins & Roller 2013; Nolan *et al.* 2014; Cai & Yung 2016; Bennett *et al.* 2016; Prior *et al.* 2016), and further emphasise the need for long-term research into the effects of climate change and severe wildfire on forest ecosystems worldwide (Anderegg *et al.* 2013; Sharples 2016).

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Appendix 1

RESEARCH PROPOSAL

Recovery of karri forest after an extreme wildfire at Northcliffe, Western Australia

Hannah Etchells 21379349
Honours in Botany, School of Plant Biology
The University of Western Australia 2016

Supervisors: Dr Pauline Grierson, Dr Alison O'Donnell (School of Plant Biology, The University of Western Australia) & Dr Lachlan McCaw (WA Department of Parks and Wildlife).

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Table of Contents

Introductory statement

Wild and prescribed fires are an intrinsic feature of the karri (*Eucalyptus diversicolor* F. Muell.) forests of southwest Western Australia (SWWA), initiating regeneration and recruitment of vegetation communities (Abbott & Burrows 2003; Hopper *et al.* 2003). As for many other regions of the world, there is increasing concern over potential risks of changing fire regimes associated with climate change to the conservation of karri forests. Fires are projected to increase in severity and frequency due to decreased rainfall, higher temperatures and increased lightning occurrence (Girardin *et al.* 2013; Liu *et al.* 2013). Karri are known to regenerate following fire by epicormic resprouting and increased seedling recruitment (Ashton & Attiwill 1994; Wardell-Johnson 2000). However, our understanding of karri forest response to wildfire is based primarily on studies of low and moderate severity fires, or on even-aged karri re-growth post-logging (Christensen & Abbott 1989; McCaw *et al.* 1994; McCaw *et al.* 2000). Given the projected likelihood of more frequent and higher severity wildfires in SWWA in the future, there is an urgent need to develop a comprehensive understanding of how high severity fires affect the recruitment, survival and growth of karri and the diversity of the associated understorey (Williams *et al.* 2001; Hughes 2003). This information is crucial in order to inform management and conservation and to determine how karri forest will persist into the future (Wardell-Johnson *et al.* 2007; Boer et al. 2009; Dean & Wardell-Johnson 2010; McCaw & Middleton 2015).

This research project will examine the ecological response of karri forests to differing wildfire severity in SWWA. The recovery of mature karri trees and seedling recruitment and survival will be investigated at sites impacted by the 2015 Northcliffe fire – the largest and most severe karri forest fire on record (Lachlan McCaw, Department of Parks & Wildlife, pers. comm.). Analysis of regeneration at both patch and landscape scales will enable assessment of small- and large-scale heterogeneity of the effects of fire on karri forest communities in order to develop a more comprehensive understanding of how karri forest responds to severe wildfire.

Background

The karri forests of southwest Australia

This research project is focused on the tall open karri forests of southern Western Australia. Karri forest occurs in a mosaic throughout the Warren Bioregion within the SWWA biodiversity hotspot (Christensen 1992; Myers *et al.* 2000; Figure 1). Karri trees can reach up 90 m and are some of the world's tallest and most productive eucalypt stands (Dean & Wardell-Johnson 2010). There are numerous understorey vegetation types across the range of the karri forest, distinguishable most noticeably by their dominant species (Inions *et al.* 1990). In the warmer north-western areas of the karri forest distribution, the understorey is dominated by *Bossiaea laidlawiana,* whereas the wetter, cooler southern regions have an understorey dominated by *Trymalium floribundum* and *Chorilaena quercifolia. Allocasuarina decussata*-dominated understorey is generally confined to gullies and low-lying areas across karri distribution. Species composition varies on a finer scale within each of these broad understorey types depending on depth and type of underlying substrate, elevation and rainfall (Inions *et al.* 1990). The karri forest understorey cannot therefore be considered as one homogeneous vegetation type. Karri forests are of high cultural and heritage importance and a valuable timber resource (Christensen 1992, Calver *et al.* 1998; Bradshaw 2015). Karri forests are also a major attraction for WA's ecotourism industry (Carlsen & Wood 2004). Consequently, optimising management and protection of these complex forests in the face of numerous and sometimes conflicting values/uses and projected climate change, including changing fire regimes, is critical for their sustainable use and conservation.

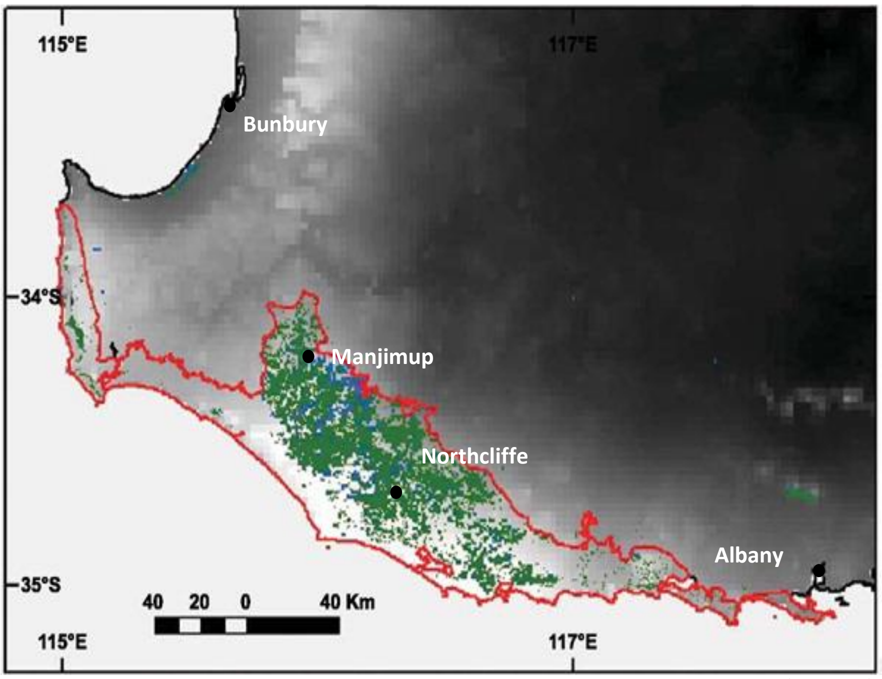

Figure 1. Distribution of karri forest in southwest Western Australia (SWWA). Green indicates current range; blue indicates pre-European range; red line indicates the Warren Bioregion. Background shading indicates mean annual rainfall: darker areas are lower rainfall; lighter areas are higher rainfall. Map sourced from Dean & Wardell-Johnson (2010).

Defining forest fire regimes

The intensity and severity of any fire have a large impact on the ecological consequences of that fire (Rice 1993). Fire intensity refers to the heat output measure from fire, while fire severity refers to the degree of environmental change caused by fire (Keeley 2009). Fire severity is often quantified as the amount of above and belowground organic matter consumed. In contrast, fire intensity is more difficult to determine as it requires on-ground measurement. Consequently, intensity data have been largely restricted to highly monitored, low intensity prescribed burns (McCaw 2013), with little quantifiable measures for wildfires due to their sudden and uncontrollable nature. Instead, fire severity can be used as a measure of intensity (Keeley 2009). High intensity and severity wildfires occur in SWWA on a periodic basis, usually following particularly dry and hot summers (Bradstock *et al.* 2013). Such weather and subsequent fire conditions are projected to become more common (Hughes 2003), with largely unknown potential impacts of forest structure and composition.

Fire – both lit by humans and via lighting strikes – has been a regular occurrence across SWWA for millennia (Hopper *et al.* 2003). As such, fires have played a large role in shaping plant community structure, composition and species richness (Gill 1975). For at least 40,000 years, Aboriginal people in SWWA used regular controlled fires for natural resource management (Gammage 2011). In the two hundred years since European invasion, however, fire regimes have been altered in frequency and intensity due to loss of traditional burning regimes, in an attempt to avoid large wildfires and protect human life and property. In the early days of European occupancy fires were completely suppressed wherever possible (Hopper *et al.* 2003). As experience and understanding of Australian climatic conditions and the important ecological role of fire in many ecosystems increased, fire was increasingly used to manage fuel loads, promote regeneration and to maintain key ecosystem processes such as nutrient cycling (Bradstock *et al.* 2013; McCaw 2013).

Prescribed burning, where low intensity fires are deliberately lit, is now a regular part of environmental management SWWA. Such fires are intended to both reduce the intensity of wildfires by removing accumulated organic matter, and to promote biodiversity using mosaic burning techniques to increase environmental heterogeneity (McCaw *et al.* 1996). In contrast to wildfires, prescribed burns in SWWA are usually of low to moderate severity, to ensure controllability (Burrows 2008; but see Boer *et al.* 2009). Prescribed burns are used in the karri forest to both control fuel build-up and to encourage karri recruitment and regeneration of understorey species (Burrows 2008). However, there is some debate as to the effectiveness of low intensity prescribed burns for the recruitment of karri forest; whilst prescribed burns can stimulate seed germination they do not necessarily result in sapling persistence and maturation (McCaw *et al.* 2000). Little is known about karri forest response to very high intensity fires due to their infrequency, but this information is crucial to comprehensively understanding karri forest regeneration under changing climatic conditions.

Fire impacts on karri forests

Fires are a naturally occurring and regular disturbance in the karri forest of southwest Australia. However, there has been remarkably little assessment of how the karri forest, and particularly the ecologically dominant species *Eucalyptus diversicolor*, responds to fires of differing severity. Differences in fire severity are known to lead to significant variation in post-fire regeneration in tall open *Eucalyptus* forest in eastern Australia (Ashton & Martin 1996; Vivian *et al.* 2008). It is generally understood that fire facilitates karri recruitment and regeneration, but most studies on this topic have either been focused on even-aged logged regrowth younger than 30 years (McCaw *et al.* 1994; McCaw *et al.* 2000), or on the effects of different fire return intervals (Wardell-Johnson *et al.* 2004). A notable exception is a recent study of wildfire in mature, unlogged mixed karri-red tingle (*Eucalptus jacksonii* Maiden) forest burned in 2001 (McCaw & Middleton 2015). This study examined the response of canopy and key understorey trees and seedling recruitment and persistence over eight years following high severity fire, concluding that the tall open eucalypt forests of SWWA rarely experience complete stand replacement and that multi-aged stands are common. However, the study of McCaw & Middleton (2015) focused solely on sites that had experienced complete canopy crown scorch but did not include any sites where fire severity was sufficient to kill mature trees. Consequently, the effects of substantial mature karri tree mortality on regenerating forest stands remains unknown.

Fire severity is likely to play an important role in the recovery and recruitment of karri post-fire (Bradshaw & Rayner 1997; McCaw *et al.* 2000; McCaw & Middleton 2015). However, in contrast to the tall forests of eastern Australia (e.g. Vivian *et al.* 2008; Bradstock 2009; Sharples *et al.* 2016), there has been remarkably little study of recruitment and regeneration of karri after high-severity wildfire, possibly because there have been few events of very large size and impact on record. Old and even-aged stands in the tall open forests of eastern Australia are proposed to be due to past fire events that burned with such high severity that entire stand of mature trees were killed (Ashton & Attiwill 1994). However, karri forests are usually uneven-aged and, even after severe fire, rarely experience complete stand mortality and subsequent replacement (McCaw & Middleton 2015; Bradshaw 2015). The existence of uneven-aged stands indicates that fires severe enough to kill entire stands of mature trees have perhaps not occurred as frequently in SWWA as in eastern Australia, and that the forest types differ in their response to high severity fire. Given climate projections for SWWA indicate that summers will become hotter and drier with higher lightning strike rates (Williams *et al.* 2001; Hughes 2003) it is likely the frequency and severity of wildfires across the region will also increase. It is therefore critical to develop a comprehensive understanding of how fire severity affects the mortality, recruitment and growth of karri in order to inform management and conservation and to improve understanding of how the karri forest will respond to potential changes in the fire regime with changes in climate.

Regeneration and adaptations of the karri forest to fire

Karri trees exhibit numerous adaptations that help them cope with and benefit from fire. Fire facilitates karri recruitment and regeneration by reducing competition for light, nutrients and water, stimulating seed fall, creating a nutrient-rich ash bed for seedling germination and eliminating seed predators and seedling pathogens (Wardell-Johnson 2000; Clarke *et al.* 2015). Karri trees also have thick, protective bark that enables persistence following low to moderate-severity fires from epicormic re-sprouting from crowns and trunks (Wardell-Johnson 2000). Adaptations facilitating persistence after fire are also present in the understorey plant community of the karri forest. Whilst certain understorey plants such as *Kingia* and *Persoonia* species can prolifically re-sprout following fire, most of the dominant understorey species are thought to recruit from the soil seed bank (Wardell-Johnson *et al.* 2007; Bradshaw 2015).

In contrast to understorey species, karri seed is largely held within the crowns of mature trees and is released from seed capsules in late summer or autumn of the fourth year following flowering, with germination occurring after autumn rainfall (Bradshaw 2015). Fire also stimulates seed fall, and post-fire soil nutrient influx and changed environmental conditions lead to significantly higher levels of seed germination than in unburnt areas (Bradshaw 2015). However, unlike understorey species, it is generally understood that there is only a small stored seed bank of karri seeds, and that volume of seed is highly dependent on canopy seed from surrounding trees (Bradshaw 2015). Mass mortality of mature karri trees due to severe fire or logging could therefore be detrimental to their regeneration, whilst not affecting the regeneration of understorey species that have a large stored soil seed bank. Fires severe enough to kill mature trees could consequently cause permanent changes to the community structure and function of a karri forest ecosystem.

The effects of fire on soil nutrients

Seedling recruitment and survival in the karri forest after fire is also likely to be impacted by changes in soil nutrient availability. Fire is known to play 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 leaf litter and woody debris (Adams *et al.* 2003). In the karri forest, with regular fire (5-6 year return intervals), levels of available N and P have been shown to be the most highly variable affected nutrients (O'Connell 1988). Karri forest usually grows on young reddish-brown loam with an underlying substrate of clay, but can also be found on red or yellow podzols in areas of sufficiently high rainfall (McArthur & Clifton 1975; Bradshaw 2015). These soils have higher levels of phosphorus (P) and nitrogen (N) than other SWWA vegetation types, largely influenced by decomposition of leaf litter from the high biomass understorey species (O'Connell & Menage 1982).

Karri trees require mineral soil to germinate and survive as seedlings, which requires the removal of leaf litter. Leaf litter can have an allelopathic effect on seedlings, as well as preventing physical contact with the soil (Bradshaw *et al.* 2015), so fires that consume litter also promote germination. Fires also create ashbeds, which form when large quantities of organic matter are burned in a relatively small area (Chambers & Attiwill 1994). Seedling growth rate under field conditions is known to be higher in ashbeds than on most other substrates (Breidahl *et al.* 1995). Karri seedlings are known to have significantly increased growth in ashbeds due to an increase in P and N from leaf litter burning and soil heating (Loneragan & Loneragan 1964). Karri germination usually occurs mostly on the edges of the ashbed, where ash is less hydrophobic than in the centre (Bradshaw 2015). High severity fire consumes higher levels of organic matter than lower severity fires, so leads to more and P-rich ashbeds (Adams *et al.* 2003). Unusually high severity fires could therefore lead to unusually high karri germination and seedling growth, provided that adequate soil seed bank existed. Understanding how the germination and growth of karri may be affected by an increase in nutrient-rich ashbeds (due to the projected increase in high severity fires in SWWA) will lead to a better understanding of how karri forest recruitment and community dynamics may change with changes in climate.

The Northcliffe Wildfire

On January 28th 2015, a lightning strike ignited a fire in O'Sullivan forest block near the town of Northcliffe, Western Australia (Figure 1). Over 19 days, the fire burnt around 98,650 ha of the Warren Bioregion including significant areas of mature karri forest containing trees over 250 years old. The Northcliffe wildfire was the largest single fire in the southwest forests since 1961 (some twenty times larger) and the most severe in the karri forest in recorded history (Lachlan McCaw, Department of Parks & Wildlife, pers. comm.). The fire burned heterogeneously, leaving some patches of forest completely defoliated with high tree mortality, and others with only light to moderate understorey scorch (Figure 2).

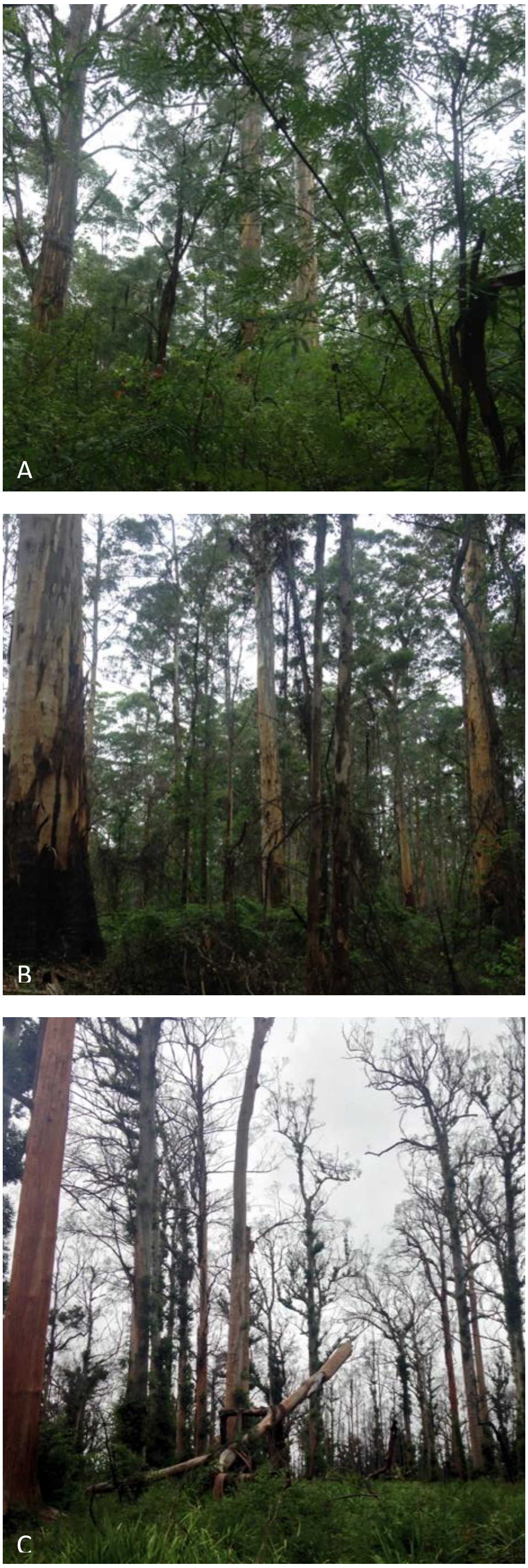

Figure 2. Karri forest vegetation regeneration after different burn severities. A: Unburnt; B: Low severity, C: High severity. All photos taken 13 months after fire in Northcliffe, Western Australia. Photos: H. Etchells.

The Northcliffe wildfire occurred at the end of a summer of above average temperatures, below average rainfall, and an unusually high level of lightning strike incidence (closest weather stations at Northcliffe and Shannon, Bureau of Meteorology 2016). Understorey vegetation and accumulated leaf litter was therefore very dry and flammable. There were areas of the forest that had not been burnt in over 30 years and had therefore accumulated high amounts of leaf litter and woody debris. Due to such heterogeneity in fuel load, as well as heterogeneity in topography, adjacent vegetation type and logging and fire history, impacts of the Northcliffe fire on the forest were not uniform. This resulted in a patchy mosaic of forest where mature trees were killed (high severity) through to small areas that remained relatively untouched or where only the understorey was burnt (low severity) (Figure 1). Consequently, the Northcliffe 2015 fire provides a unique opportunity to compare and monitor karri forest response to different severities of wildfire, including areas of unusually high severity. It also offers an opportunity to investigate factors that may be contributing to karri forest regeneration at a small scale (m) as well as a landscape (km) scale.

Aims and Objectives

This research project aims to develop a comprehensive understanding of how fire severity affects the mortality, recruitment and growth of karri in order to inform management and conservation and to determine how the karri forest will respond to changes in fire regime with changes in climate. Specifically, I will:

(i) Quantify differences in recruitment and survival of karri seedlings with differing fire severity;

(ii) Compare the survival and re-sprouting response of mature karri trees at high and low fire severity; and

(iii) Assess relationships between soil nutrients and seedling recruitment.

I hypothesise that karri seedling recruitment will be highest at sites of high burn severity due to greater nutrient influxes caused by greater consumption of organic matter by fire. However, I also hypothesise that if any sites have very high karri tree mortality (greater than 50% of trees in the site), they will have lower karri seedling recruitment despite high fire severity, due to lack of soil-stored karri seed bank. I also expect that regenerating understorey at high severity sites will be more dominated by ephemeral species and disturbance specialists than at low severity sites; that this effect will be more apparent after winter rains; and that it correlates with a decline in karri seedling persistence at those sites.

Significance and Outcomes

This research will provide significant and much-needed knowledge of the ecological responses of the karri forest to high-severity wildfire. The outcomes of this study will directly benefit conservation of the karri forest in southwest Western Australia by informing fire management decisions regarding the requirements of karri and the karri forest plant community for successful recruitment and regeneration. This project will also improve understanding of how the karri forest is likely respond to increased severity fire events caused by projected changes in climate.

Furthermore, this study will establish permanent field sites and a baseline dataset, which will underpin future investigations of the long-term recovery of karri forests following wildfire.

Methodology

Study sites

The study will be focused on sites encompassing the extent of the Northcliffe burn area. Sites of differing burn severity will be selected for comparison based on their level of crown scorch (Figure 3; Lacey & Johnston 1990; McCaw & Middleton 2015). Three severity classes will be examined – unburnt, low severity and high severity – with four replicates of each (12 sites in total). Replicate sites for each fire severity class will be chosen as evenly spaced as possible across the entire Northcliffe fire scar, in order to account for topographic and geographic variability (Figure 4).

All sites will be in old-growth karri forest (trees older than 250 years) that have not been logged and that are thought to have had similar pre-fire understorey. Karri forest understorey in surveyed sites and the Northcliffe area in general is largely dominated by *Trymalium floribundum* and *Chorilaena quercifolia*, both dense shrubs that can grow to over 3 m tall, or *Allocasuarina decussata*, a medium tree (up to 15 m) that is usually confined to gullies. Sites were sampled in early autumn (20th-25th March) and will be sampled again in late winter (July or August TBC) to ensure that data encompass seasonal variability in rainfall, and consequent impacts on nutrient transformations and seedling survival.

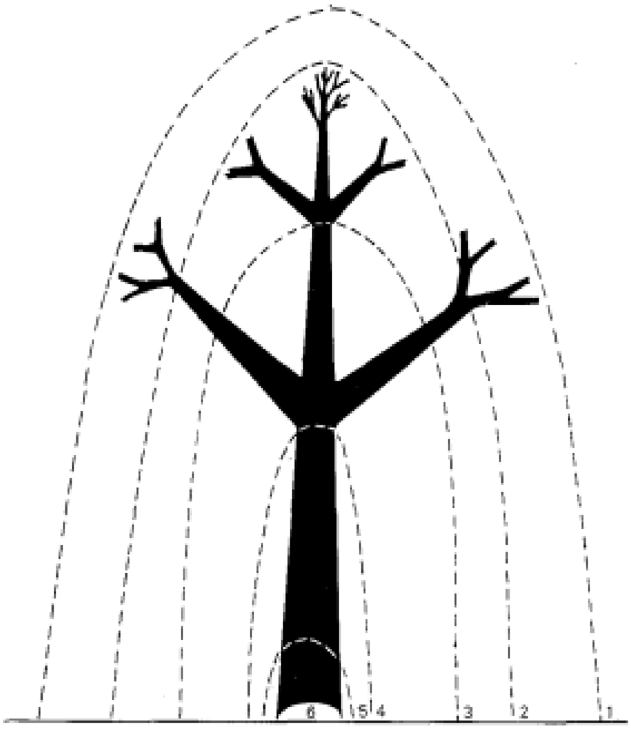

Figure 3. Conceptual diagram of the crown scorch assessment method used in this project, showing destruction of tree bud reserves with increasing fire severity (1 = no fire damage, 6 = extreme fire damage severity). Figure sourced from Lacey & Johnson (1990).

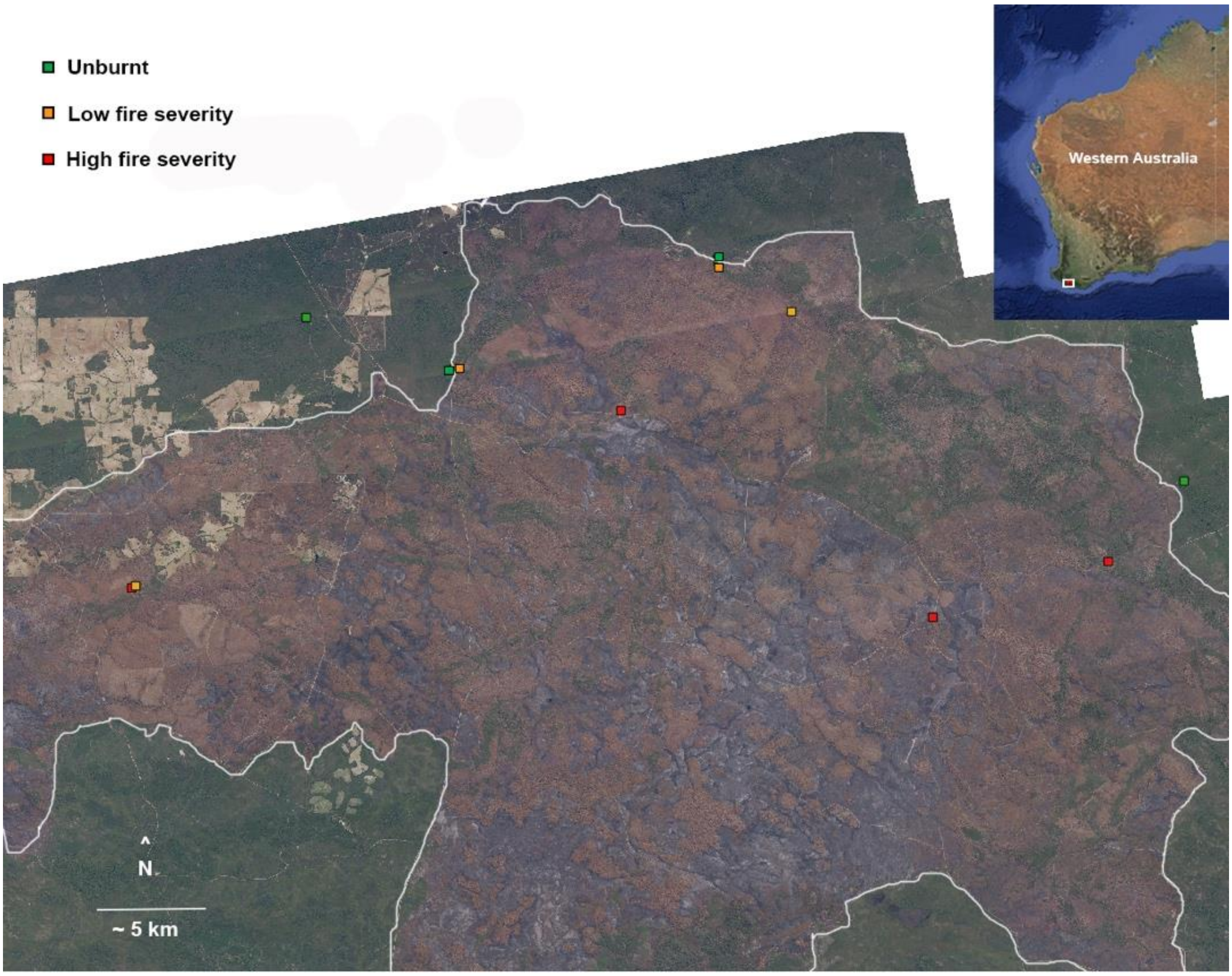

Figure 4. Extent of the Northcliffe 2015 fire (perimeter shown in white), with study sites of different fire severity indicated by coloured squares. Aerial photograph source: Department of Parks & Wildlife (2015).

Vegetation sampling

A 30 m x 30 m (900 m^2) plot will be established at each site. Within each plot, all trees > 1.0 cm in diameter at breast height (1.3 m above ground, DBH in mm) will be counted and their diameter at recorded to estimate stand basal area (m^2 ha-1) and assess recruitment and population structures. Forest stand basal area is commonly used as a surrogate for seed production (Greene & Johnson 1994), and has been shown to positively correlate with higher seed germination and seedling persistence in tall open *Eucalyptus* forest in eastern Australia (Vivian *et al.* 2008). Predicting seed bank load prior to fire is crucial if comparisons of post-fire seedling recruitment are to be made. Estimation of living and dead basal area will also provide an indicator of any variation in fuel loads among sites that may have influenced variation in fire severity among sites.

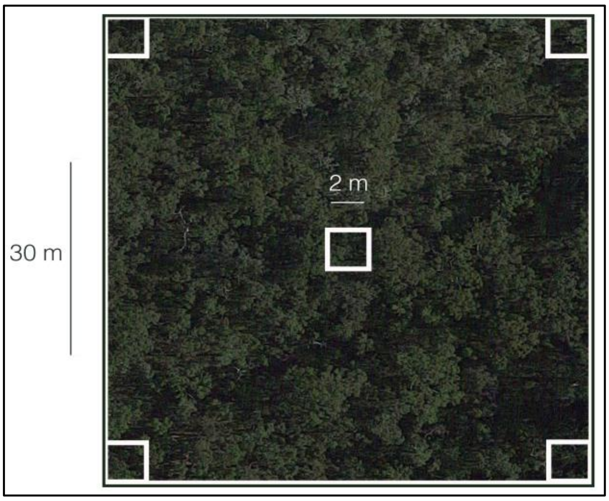

Figure 5. Diagram of 30 m x 30 m survey plot with position of five 2 m x 2 m sub plots. Placing sub plots at four corners and centre of plot aims to capture an accurate representation of whole plot heterogeneity.

Karri seedling density will be estimated within five 4 m^2 quadrats located within each 30 x 30 m plot (Figure 5) In order to account for potential seedling competition for light and nutrients as well as changes in plant functional types (e.g. see Pekin *et al.* 2009), all understorey plant species rooted within each of the 4 m^2 quadrats will be identified to species level in accordance with WA State herbarium, and percentage cover (Braun-Blanquet method) and species diversity (Species richness, Shannon-Weiner, & Pielou's evenness) for each quadrat will be estimated. Seedling density and understorey cover will be averaged across each 30 x 30 m plot and converted to a per hectare equivalent.

Soil nutrient sampling and analysis

In order to determine any potential influences of changing soil properties on seedling recruitment and understorey composition, and to characterise each plot, soil samples will be collected in each 4m^2 sub plot. Three samples per sub plot from the top 0-10 cm of soil will be collected, bulked and then sieved (2mm). Total C/N and soil carbon isotope signatures will be measured using techniques outlined in Pekin *et al.* (2000). $^{13}C/^{15}N$ will be measured at the West Australian Biogeochemistry Centre (UWA). Other soil characteristics such as pH, different indices of phosphorus availability (Bray Pi, OH-Pi and OH-Po) and nitrogen will be measured as described in Grierson & Adams (2000) and Pekin *et al.* (2009).

Data analyses

Multivariate statistical analysis will be used to determine if understorey community composition differs among the fire severity classes. Community data will likely need to be log10 transformed to control for biases caused by many 0 values, and Bray-Curtis similarity measures will be calculated. To assess significant differences in community composition among sites, analysis of similarity (ANOSIM) will be used. Similarity percentages (SIMPER) will be used to determine the relative contributions of each plant species to similarities between sites and environmental factors. Soil nutrient data will be included as factors an analysed using BEST to determine which of these best explain differences in species cover and karri seedling density. All multivariate statistical analysis will be undertaken in Primer (ver. 6). The interacting effects of fire severity and soil properties on seedling density and tree mortality will be examined using two-way analysis of variance (ANOVA) in R (ver. 3.1.1).

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Budget

Funding for this project (Table 1) will be primarily provided through support from the WA Department of Parks and Wildlife with additional support from the School of Plant Biology. No expenditure is required for the acquisition of any new equipment, or external analyses of samples, as all of the required equipment is currently available within the School of Plant Biology (the Ecosystems Research Group and the West Australian Biogeochemistry Centre) located at The University of Western Australia. Costs incurred are primarily associated with field trips (travel and accommodation), plus a small amount of consumables and the individual costs of soil analyses.

Table 1. Proposed budget for karri fire recovery Honours research project (Etchells 2016).

Task	Component	Amount	Justification
Field Work	Four wheel drive access to sites (3 trips @ $0.65/km)	$1625	Three field trips (preliminary, autumn, winter-spring) to measure four replicate sites per fire severity.
	Food (5 nights/2 trips @ $30/d for 4 people)	$1200	
	Accommodation (5 nights/2 trips @ $20/d for 4 people)	$800	
	Field sampling equipment		
	Plastic and paper bags, marker pens, flagging tape, litter and soil bags, pegs	$500	
Laboratory	***Soil Analysis***		4 severity classes x 4 sites (replicates) x 2 seasons x 5 replicates. Focus will be on top 10 cm of soil.
	Total C/ N and $^{13}\text{C}/^{15}\text{N}$ (160 samples @ $10 each)	$1600	
	Soil pH (160 @ $0.50)	$80	Estimates shown for analytical costs for stable isotopes and nutrients are subsidised (50%) by the West Australian Biogeochemistry Centre at UWA.
	Bray Pi (160 @ $0.50)	$80	
	OH-Pi and Po (160 @ $0.50)	$80	
	NH4 and NO3 (160 @ $3 each)	$480	
	Consumables		
	Vials, filter paper	$200	
	Senior First Aid training	$150	It is recommended that all university field trip participants have senior first aid training.
	Final printing and binding of thesis	$100	
Total		**$6,895**	

Timetable

To ensure the current project is completed in the 10-month time frame a timetable has been developed to ensure each component is accounted for (Table 2). Each task has been considered with respect to time to complete and due date.

Table 2. Proposed timetable for karri fire recovery Honours research project (Etchells 2016).

	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.
Autumn field trip		Δ								
Late winter field trip						Δ	Δ			
Data Analysis				Δ	Δ			Δ		
Soil Analysis			Δ	Δ			Δ	Δ		
Project Outline	Δ	Δ								
Research Proposal / Seminar		Δ	Δ							
Research Article						Δ	Δ	Δ	Δ	Δ
Research Seminar								Δ	Δ	

Appendix 2

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Increasing plant species diversity and extreme species turnover accompany declining soil fertility along a long-term chronosequence in a biodiversity hotspot

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Summary

1. Long-term soil chronosequences provide natural soil fertility gradients that can be used to explore linkages between soils and plant community composition and diversity. Well-studied forested soil chronosequences have revealed that local (α) plant diversity increases with greater soil age and declining fertility, but corresponding changes in species turnover and beta (β) diversity have not been explored, particularly in extremely species-rich regions.

2. We quantified changes in plant species diversity and community composition, and identified the edaphic drivers of these changes, along a >2-million year retrogressive dune chronosequence in the south-west Australia biodiversity hotspot.

3. We found greater plant species diversity across all growth forms as soil development proceeded and concentrations of soil nutrients, particularly phosphorus (P), diminished to extremely low levels (surface soil total P concentrations of 6 mg P kg^{-1}). Despite the high plant α diversity on older nutrient-impoverished soils, species turnover across the chronosequence was exceptionally high when all growth forms were considered (mean of 1% of species shared between the youngest and oldest soils), and there was complete turnover of woody species along the chronosequence. Such extreme species turnover across the chronosequence reflected large changes in soil chemical properties. In addition, β diversity within individual chronosequence stages increased with declining soil fertility. Shrubs remained the dominant and most speciose growth form throughout the chronosequence.

4. *Synthesis.* The large increase in plant α diversity and the extreme species turnover associated with declining soil fertility highlight the central role of soil properties in driving plant community assembly during long-term ecosystem development, previously only reported from comparatively species-poor regions. Our finding that plant β diversity increased with declining soil fertility points to a novel mechanism whereby extremely low soil fertility, rather than high productivity, promotes high β diversity. These results suggest that the interaction of an exceptionally diverse plant species pool and nutrient-impoverished soils provides the basis for the maintenance of such high β diversity at extremely low soil fertility.

Key-words: beta diversity, determinants of plant community diversity and structure, ecosystem development, non-mycorrhizal plant species, nutrient-impoverished soil, pedogenesis, phosphorus, retrogression, species richness

Introduction

Primary succession is associated with the initial stages of soil and ecosystem development and results in an increase in plant species diversity as plants gradually colonize a site (Odum 1969; Grime 2001). Many of the early successional species (i.e. 'ruderal' species sensu Grime 2001) that colonize recently exposed substrates grow quickly, are short-lived and rapidly produce many, readily dispersed seeds, making these early stages of succession amenable to study (Connell & Slatyer 1977). Direct observational studies of soil and ecosystem development in the longer term, however, are impossible

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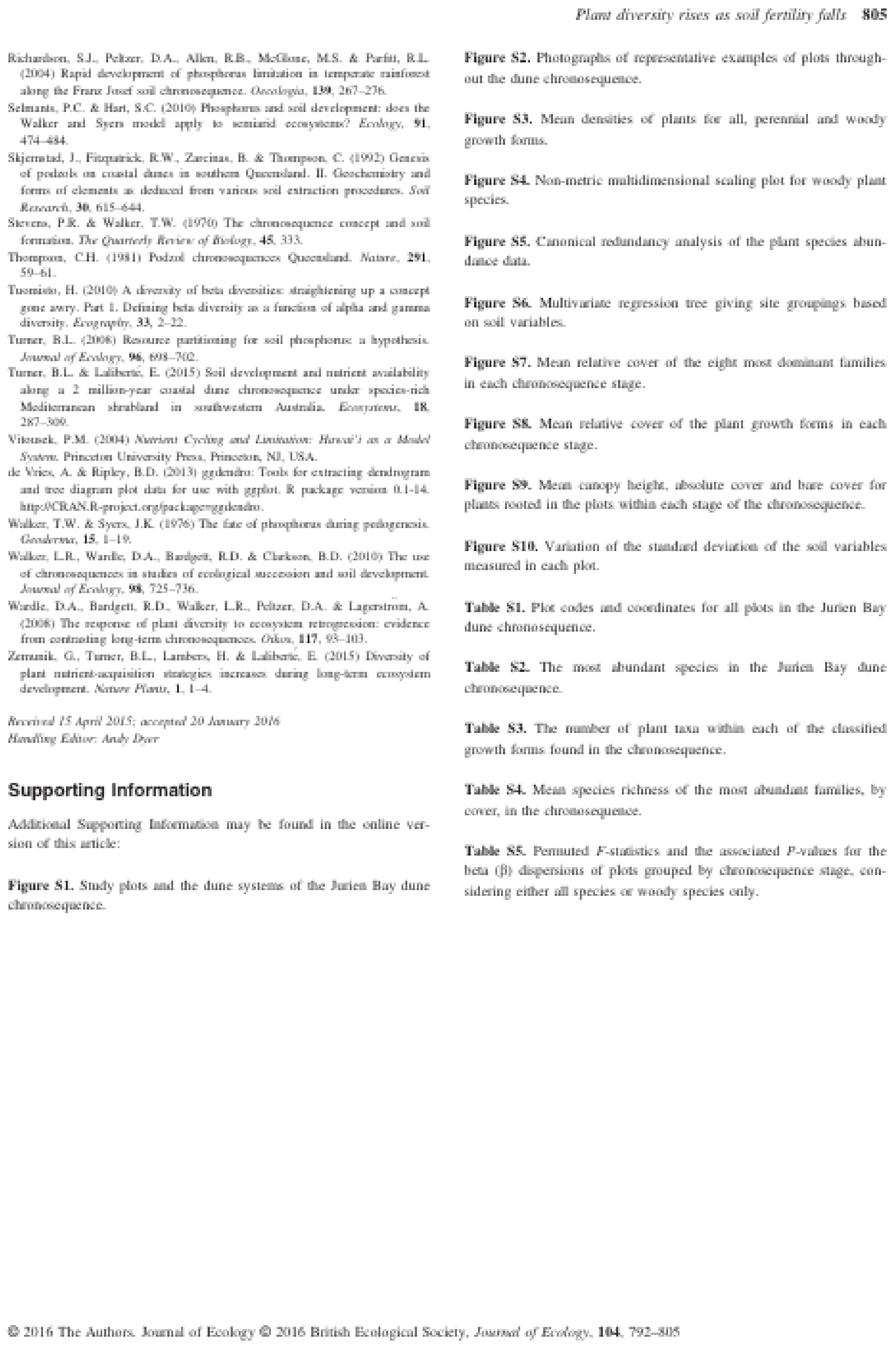
Figure A. First page of an article published in recent edition of *Journal of Ecology*, used as the style and referencing guide. (Zemunik, G., Turner, B.L., Lambers, H. and Laliberté, E., 2016. Increasing plant species diversity and extreme species turnover accompany declining soil fertility along a long-term chronosequence in a biodiversity hotspot. *Journal of Ecology.).*



Plant diversity rises as soil fertility falls **805**

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Supporting Information

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

Figure S1. Study plots and the dune systems of the Jurien Bay dune chronosequence.

Figure S2. Photographs of representative examples of plots throughout the dune chronosequence.

Figure S3. Mean densities of plants for all, perennial and woody growth forms.

Figure S4. Non-metric multidimensional scaling plot for woody plant species.

Figure S5. Canonical redundancy analysis of the plant species abundance data.

Figure S6. Multivariate regression tree giving site groupings based on soil variables.

Figure S7. Mean relative cover of the eight most dominant families in each chronosequence stage.

Figure S8. Mean relative cover of the plant growth forms in each chronosequence stage.

Figure S9. Mean canopy height, absolute cover and bare cover for plants rooted in the plots within each stage of the chronosequence.

Figure S10. Variation of the standard deviation of the soil variables measured in each plot.

Table S1. Plot codes and coordinates for all plots in the Jurien Bay dune chronosequence.

Table S2. The most abundant species in the Jurien Bay dune chronosequence.

Table S3. The number of plant taxa within each of the classified growth forms found in the chronosequence.

Table S4. Mean species richness of the most abundant families, by cover, in the chronosequence.

Table S5. Permuted *F*-statistics and the associated *P*-values for the beta (β) dispersions of plots grouped by chronosequence stage, considering either all species or woody species only.

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Figure B. Last page of an article published in recent edition of *Journal of Ecology*, used as the style and referencing guide. (Zemunik, G., Turner, B.L., Lambers, H. and Laliberté, E., 2016. Increasing plant species diversity and extreme species turnover accompany declining soil fertility along a long-term chronosequence in a biodiversity hotspot. *Journal of Ecology.)*.

Appendix 3

Table A1. Diversity and evenness indices (S, H’ and J’) for each plot in Northcliffe study area.

Plot	Date sampled	S	H’ ($\log_e$)	J'
Low fire severity 1	July 2016	24	0.697945	2.218108
High fire severity 1	July 2016	22	0.692946	2.141926
Low fire severity 2	July 2016	20	0.600307	1.79836
High fire severity 1	March 2016	18	0.604972	1.748593
High fire severity 2	July 2016	18	0.58843	1.700781
Unburnt 4	July 2016	17	0.681909	1.931993
Low fire severity 4	July 2016	17	0.606157	1.717373
Low fire severity 4	March 2016	15	0.543549	1.471958
High fire severity 2	March 2016	15	0.591407	1.60156
Unburnt 3	July 2016	15	0.372882	1.009784
High fire severity 3	July 2016	15	0.417346	1.130195
Low fire severity 2	March 2016	14	0.710851	1.875978
Low fire severity 3	July 2016	14	0.714824	1.886462
Unburnt 2	March 2016	12	0.376184	0.934782
Low fire severity 3	March 2016	12	0.620421	1.541688
High fire severity 3	March 2016	12	0.476045	1.182927
Unburnt 1	July 2016	12	0.498546	1.238839
Unburnt 4	March 2016	11	0.659474	1.58135
Low fire severity 1	March 2016	11	0.760495	1.823588
Unburnt 2	July 2016	11	0.564797	1.354325
Unburnt 3	March 2016	10	0.355043	0.817517
Unburnt 1	March 2016	8	0.515715	1.072399

Figure A1. Burnt stump remains of *Trymalium odoratissimum* at Extreme High severity site.

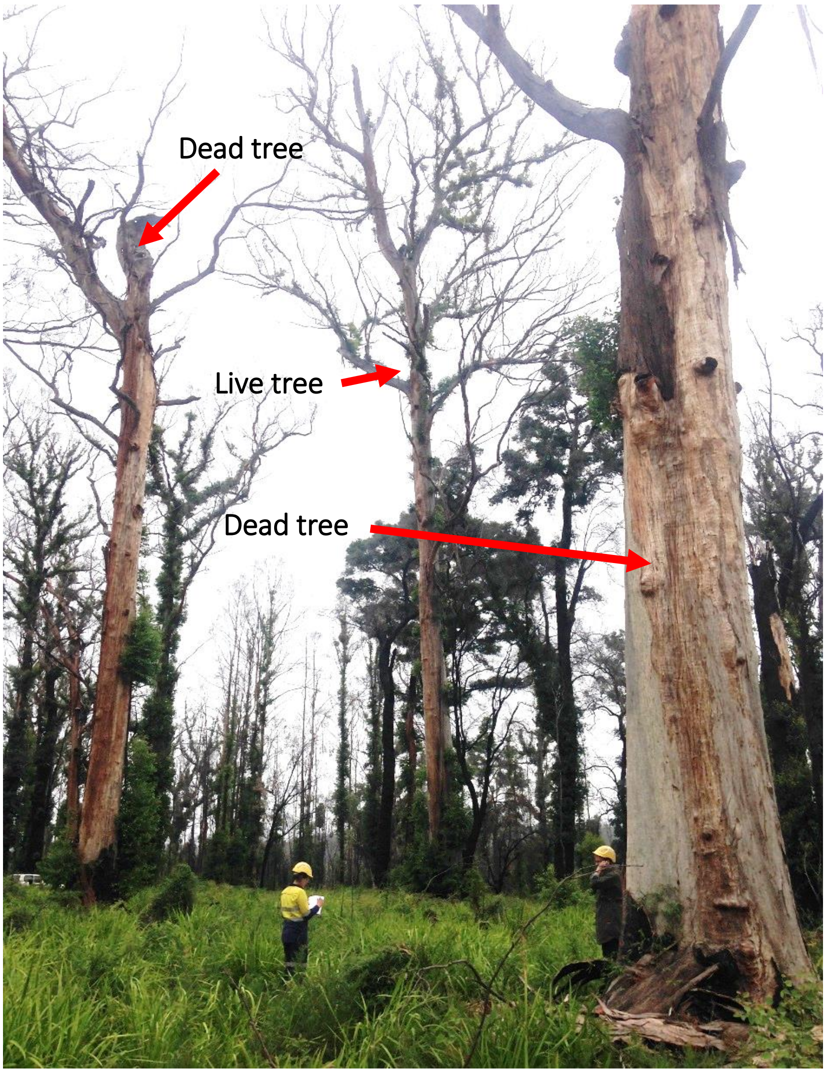

Figure A2. An example of trees considered dead vs alive based on crown loss and height of epicormic resprouting.

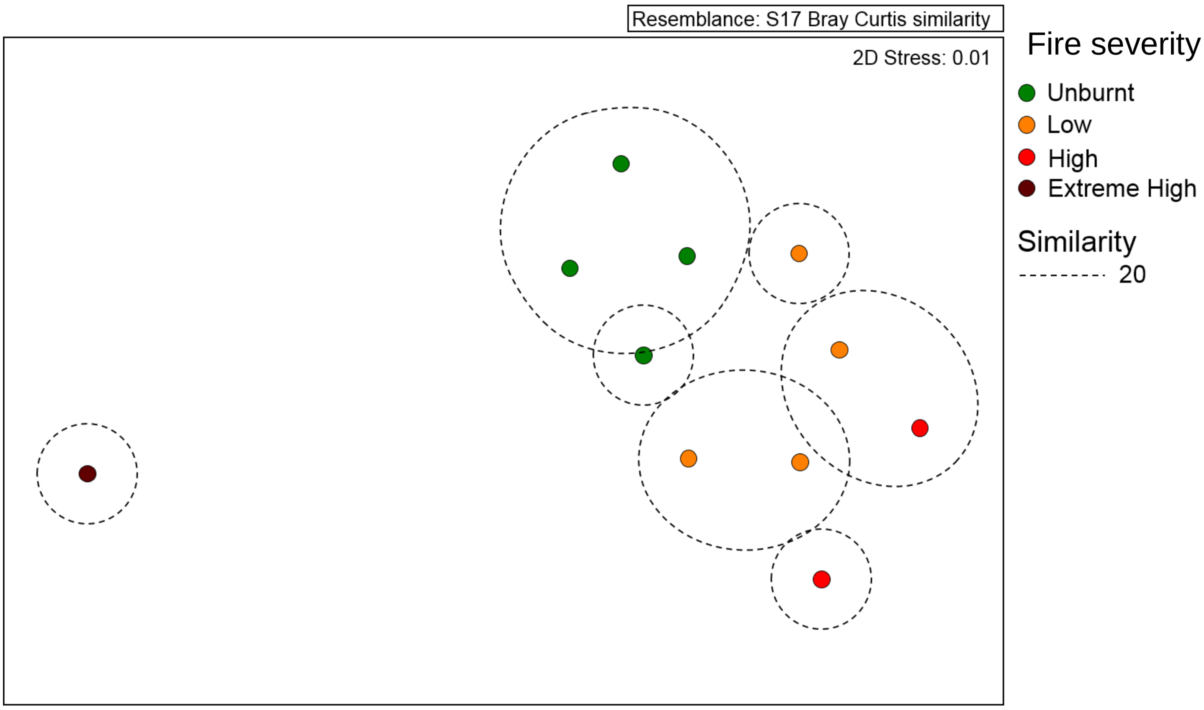

Figure A3. Non-metric multidimensional scaling ordination using fungal presence/absence data labelled by fire severity. Each data point represents a single site surveyed in July 2016, following the February 2015 wildfire near Northcliffe, Western Australia. Extreme High severity site indicated in bottom left of figure. Data have Bray-Curtis similarity resemblance applied.