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RELICTS AT RISK: IMPACTS OF THE 2016 TASMANIAN FIRES ON PENCIL PINE (*ATHROTAXIS CUPRESSOIDES*)

Aimee Bliss, Lynda Prior and David Bowman
University of Tasmania & Bushfire and Natural Hazards CRC

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Cover: Burnt Pencil Pine near Lake Mackenzie, Tasmania. Photo: Aimee Bliss

CONTENTS

ABSTRACT

Aimee Bliss, Lynda Prior and David Bowman, School of Biological Sciences, University of Tasmania, Hobart, 7001

We investigated a recent wildfire in Tasmania's Wilderness World Heritage Area that burnt long-held fire refugia. Using a field survey we documented and assessed the impact of this fire on *Athrotaxis cupressoides*, a long-lived, fire-sensitive conifer of Gondwanan origin. We used Akaike Information Criterion (AIC) based model selection and multi-model inference to relate *A. cupressoides* mortality and recruitment to micro-habitat features; rock and burnt shrub cover, as well as tree size, previous fire damage and minimum twig diameter (a proxy for fire intensity). Large proportions of *A. cupressoides* populations were killed by the fire. Mortality increased with burnt shrub cover and minimum twig diameter and decreased with rock cover, while we found a U-shaped response with DBH. Seedlings occurred predominately in unburnt areas and were negatively associated with burnt shrub cover and minimum twig diameter. Interestingly, we found thresholds of ~15% shrub cover and ~2mm minimum twig diameter, whereby mortality markedly increased and seedling presence decreased past these thresholds. Fire scar presence was positively related to mortality and influenced higher mortality rates in larger stems. Collectively, these fire impacts jeopardise the long-term future of *A. cupressoides* populations in this region. Furthermore, our results suggest that increasing fires in this region will cause range contraction of *A. cupressoides* into the most fire-proof landscape settings, potentially threatening the long-term persistence of this species. Intervention strategies, highlighted by this study, may assist in the recovery of *A. cupressoides* populations burnt in this fire and in the overall long-term conservation of this iconic species.

INTRODUCTION

During the summer of 2016, Tasmania experienced numerous wildfires ignited by dry lightning strikes (Natural Values Conservation Branch 2016; Press 2016). These fires burnt 126,800 ha across Tasmania, including 19,800 ha of the TWWHA. These fires sparked wide-spread international concern and several investigations into the management and impact of these fires were launched, including a national Senate inquiry (Commonwealth of Australia 2016; Gill 2016; Horstman 2016; Hunt 2016; Marris 2016). The fires occurred following record breaking dry and hot spring conditions, which have partially been attributed to anthropogenic climate change (Black and Karoly 2016; Karoly et al. 2016; Bureau of Meteorology 2016). Importantly, such extreme dry and warm conditions can cause this regions typically wet organic 'peat' soils to dry out, increasing its capacity to burn, enabling the spread of fire through alpine Tasmania's otherwise low fuel environments.

One palaeoendemic, fire sensitive conifer burnt by these fires was the pencil pine, *Athrotaxis cupressoides* D. Don. Approximately 85 ha of *A. cupressoides* habitat was burnt in this event (Natural Values Conservation Branch 2016; Press 2016). *A. cupressoides*, like many of Tasmania's palaeoendemic conifers, is long-lived, slow growing, has poor dispersal ability and exhibits no fire adapted traits (Enright and Hill 1995). These life history traits provide limited capacity for *A. cupressoides* to survive or recover following fire events (Fitzgerald 2011). Thus, fire can have fatal and permanent impacts on *A. cupressoides* populations demonstrated by areas of

A. cupressoides habitat that were burnt by wildfire in the last century but still show little to no regeneration (Corbett 1996; Holz et al. 2015). Thus, with increasing extreme fire events predicted in alpine Tasmania (Fox-Hughes et al. 2014; Lucas et al. 2007), it is essential to improve our understanding of fire in these systems. Currently such knowledge is limited, due to the rarity of large, severe fires in Tasmania's alpine environment and the inappropriateness of experimenting on this long-lived species of conservation importance. Large tracts of *A. cupressoides* habitat were burnt in the 1960's, but these fires were only investigated in retrospect (Holz et al. 2015). Thus, the 2016 fire offers an opportunity to address these knowledge gaps, essential to assist in the management of this iconic species. Furthermore, this research will provide important insights into fire impacts in alpine environments, regions globally at risk from climate change (Camac et al. 2013).

1.1 Aims

We undertook the first survey of *A. cupressoides* populations one year post-fire, within the region most strongly affected by the 2016 Tasmanian fires at Lake Mackenzie. From this survey, we aim to document the impact of the fire on *A. cupressoides* populations and assess the role of environmental and biological variables on (i) mortality, and (ii) recruitment of *A. cupressoides*.

BACKGROUND

STUDY REGION

This study was conducted at the Lake Mackenzie region, on the north-eastern boundary of the Central Plateau in Tasmania, Australia (41°40''S, 146°22''E; 900-1200 m.a.s.l; Fig.1). The Central Plateau is a broad undulating highland, interspersed with over 4,000 lakes and tarns (Banks 1972; Pemberton 1986). The climate is cool maritime, experiencing mean annual rainfall of 2091 mm. Temperatures range from a mean daily maximum of 19°C in January to a mean daily minimum of -1.5°C in July, with frequent frosts and snow fall occurring in any month (Bureau of Meteorology 2017; rainfall data for Lake Mackenzie, temperatures for Liawenee). The geology of this region is dominated by Jurassic dolerite and basalt (Pemberton 1986). Soils are predominantly dolerite mineral soils, often overlaid by organic 'peat' soil (Pemberton 1986). Vegetation of the area is alpine and subalpine, occurring in mosaics of eucalypt forests (e.g. *Eucalyptus coccifera*), alpine heath (e.g. *Richea scoparia*), coniferous woodlands (*Athrotaxis cupressoides*) and bolster heath (e.g. *Abrotanella forsteroides*) (Kirkpatrick 1983; Reid et al. 2005). This region is recognized as internationally significant wilderness, demonstrated by its inclusion within the Tasmanian Wilderness World Heritage Area (TWWHA) (Fig. 1).
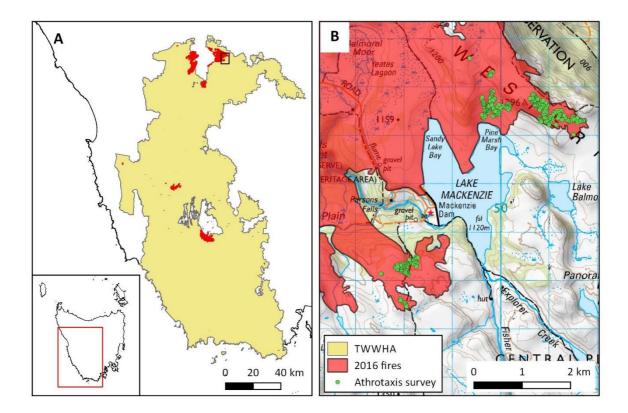

FIGURE 1 (A) BOUNDARY OF THE TASMANIA'S WILDERNESS WORLD HERITAGE AREA AND LOCATION OF THE 2016 FIRE WITHIN THIS REGION. (B) LOCATION OF A. *CUPRESSOIDES* POPULATIONS SURVEYED AT THREE SITES (LMS, LMF AND LMB) WITHIN THE 2016 MERSEY COMPLEX FIRE FOOTPRINT AT THE LAKE MACKENZIE REGION, AT THE NORTH-EAST BOUNDARY OF THE TASMANIAN WILDERNESS WORLD HERITAGE AREA.

FIRE HISTORY

Fire has a long history in the alpine region of Tasmania; historic charcoal records suggest fire has occurred in these areas for thousands of years (Stahle et al. 2016). However, these fires were probably of low intensity, evident from low levels of charcoal in lake sediments and abundance of living *A. cupressoides* with fire scars (this species is killed by high intensity fires) (Allen et al. 2017; Dodson 2001). Prior to European colonisation of Tasmania, fire occurrence was influenced by large scale climate fluctuations and local ignitions by Aboriginal people, who used 'fire-stick farming' to promote growth of palatable plant species to attract macropods (Holz et al. 2015; Press 2016; Stahle et al. 2016). Following British colonisation, and the exile of Aboriginal people, European settlers utilised the Central Plateau region throughout the 19th and 20th centuries (Corbett 1996; Cubit 1996). During this time, shepherds and trappers used fire similarly to Aborigines, igniting low intensity fires to promote pasture for livestock (Corbett 1996; Cubit 1996). As well as these low intensity fires, extreme fire events have occurred twice in the last 50 years on the Central Plateau (Press 2016). In the summer of 1960-61, following the driest spring–summer on record since the 1930s, three human-ignited fires burned approximately 60% of the Central Plateau (Holz et al. 2015). This fire killed large areas of *A. cupressoides* woodlands, affecting over one-third of its geographic extent and killing one tenth of the Central Plateau population (Holz et al. 2015; Johnson and Marsden-Smedley 2002). Following the inclusion of the Central Plateau in the TWWHA in 1982, the region remained mostly fire free until the 2016 fires (Johnson and Marsden-Smedley 2002; Press 2016).

STUDY SPECIES

Athrotaxis cupressoides is a very long lived (>1000 years), slow growing, endemic Tasmanian conifer (Allen et al. 2011; Gibson et al. 1995; Ogden 1978). This species, as well as *Athrotaxis selaginoides* are the only extant species from the *Athrotaxis* genus that is 150 million years old (a hybrid of the two species, *A. laxifolia*, also exists) (Jordan et al. 2016; Leslie et al. 2012). Today, *A. cupressoides* is found in the alpine regions of central and western Tasmania, with the majority of the species concentrated on the Central Plateau (76% of *A. cupressoides* total distribution; Harris and Kitchener 2005). However, fossil evidence shows that *Athrotaxis* occurred on other Southern Hemisphere continents in the past (Carpenter et al. 2011; Del Fueyo et al. 2008; Jordan et al. 2016). Thus, given *Athrotaxis'* antiquity, and its current restricted geographical range, these species are considered 'palaeoendemic' and are important living links to Gondwanan flora (Jordan et al. 2016). *A. cupressoides* exhibits diverse physical forms, ranging from tall (30m) trees in sheltered habitats to dwarfed (< 5m) trees in exposed sites. This species is extremely frost tolerant, but shade intolerant and sensitive to all but the lowest intensity fires. (Cullen and Kirkpatrick 1988b; Farjon and Filer 2013; Holz et al. 2015). *A. cupressoides* has two methods of reproduction; sexual and clonal. Sexual reproduction occurs via wind-dispersed seed, with seed production occurring in episodic masting cycles every 5 - 6 years (Cullen and Kirkpatrick 1988a). However, clonal reproduction is more common, whereby *A. cupressoides* regenerates vegetatively via root suckers (Worth et al. 2016).

METHODS

FIELD SURVEYS

Field observations of fire damage to *A. cupressoides*, physical site attributes and seedling presence were undertaken in autumn of 2017, 12-13 months after the 2016 fire using a multi-scale sampling design. Three study sites, were selected within the fire-boundary of the January 2016 Mersey Complex Fire, on the Central Plateau: Lake Mackenzie South (LMS), Lake Mackenzie Front (LMF) and Lake Mackenzie Back (LMB). These sites were chosen to encompass the majority of *A. cupressoides* populations burnt in this fire event that were accessible. At each site a systematic sweep of the entire population of *A. cupressoides* was conducted, using adjacent 10m radius circular plots. Plots were centred on target trees, the largest tree within 20 metres of the population boundary. Subsequent plots were then centred on the next large tree >10 m outside of the initial plot boundary. Targeting larger trees ensured an adequate sample of all size classes to detect the influence of tree size in our analysis. Using this method we sampled >80% of the trees at each site. Within each plot up to 10 trees and their stems were recorded. At the stem level, stems were identified as 'alive' or 'dead' determined by the presence or absence of green canopy foliage. Additionally, diameter at breast height (DBH) and presence or absence of fire scars was recorded for each stem. Around the base of each tree, within a two meter radius circular plot divided into four quarters, percentage ground cover (sphagnum, soil, rock, water), percentage burnt shrub cover (hereafter shrub cover) and presence or absence of *A. cupressoides* 'seedlings' were recorded. Seedlings encompassed both true sexually produced seedlings (evident from cotyledon presence) and clonal root suckers. However, it was deemed impractical to differentiate between seedling types in our survey. In these plots, minimum twig diameter was also recorded for each quarter, from the average diameter of the five smallest twigs on burnt shrubs in that quarter measured with calipers. This measurement is a well-established post-hoc method for estimating fire intensity, based on the assumption that hotter fires consume greater twig biomass, thus the hotter the fire the greater the mean minimum twig diameter (Moreno and Oechel 1989; Whight and Bradstock 2000).

DATA ANALYSIS

We analysed relationships between environmental and biological variables and stem mortality in *A. cupressoides*. Through *a priori* knowledge of fire mechanisms and preliminary data exploration, we derived a candidate set of potential explanatory variables for stem mortality. These included percent rock cover, percent shrub cover, DBH and minimum twig diameter. Relationships between variables and stem mortality were analysed using binomial generalised linear mixed models with stem mortality as the response variable (0 = alive, 1 = dead) and plot as a random effect. We used AIC based model selection and complete subsets regression on a candidate set of models, with all possible combinations of potential explanatory variables, without interactions. The importance of each explanatory variable ($w+$) was calculated as the summed Akaike weight (w_i) of all models containing that variable (Burnham and Anderson 2002). Variables were deemed important if $w+$ was greater than 0.73 (Murphy *et al.* 2010). 'Important' variables were then used to construct a 'base' model.

Inspection of the raw data showed a U-shaped response of DBH for stem mortality, as has been reported in some other tree species (Prior *et al.* 2009). To test whether there was statistical support for such a response, we added the term DBH^2 (accounts for quadratic shape) to the base model and compared the two models. A model was considered superior if it reduced AIC by > 2 (Burnham and Anderson 2002). We were also interested in whether scars from previous fires affected survival during the 2016 fire. We tested this by adding 'fire scar' to the base model and comparing model AICs. Additionally, inter-correlations were found between fire scars and DBH of stems. To confirm which variable was driving stem mortality, we separately analysed the effects of (i) fire scars using only small and medium stems; and (ii) the effect of tree size in larger stems, using only medium and large stems with fire scars. Finally, to detect any residual effect of site that was not explained by our selected variables, we added this term to the base model and compared AIC values.

We also analysed relationships between environmental and biological variables and presence of *A. cupressoides* seedlings, using the same analytical approach outlined above. Potential explanatory variables included in our candidate model set, included percent shrub cover, percent unburnt soil, minimum twig diameter and tree size (DBH). We included unburnt soil as a variable for this analysis, based on field observations of seedling occurrence in unburnt patches. Relationships between variables and seedling presence were analysed using binomial generalised linear mixed models with seedling presence as the response variable (0 = absent, 1 = present) and plot as a random effect. All data was analysed in R (R Core Team 2015).

RESULTS

MORTALITY

Overall, the 2016 fire had a substantial effect on *A. cupressoides* populations at Lake Mackenzie. Of the 1215 trees and 3118 stems measured that were alive before the fire, two thirds were killed. Environmental and biological variables showed strong influences on stem mortality of *A. cupressoides* at Lake Mackenzie within areas burnt. The variables shrub cover, minimum twig diameter and DBH were all important predictors of stem mortality ($w+= 1$), while rock cover was less important ($w+ = 0.73$).

Stem mortality showed a strong positive relationship with percentage shrub cover and minimum twig diameter ($w+ = 1$; Fig. 2), a proxy for fire intensity. Interestingly, clear thresholds where stem mortality markedly increased, were evident for both shrub cover and minimum twig diameter. Stem mortality increased considerably, almost doubling when shrub cover was greater than ~15% (Fig. 2). Similarly, stem mortality was much greater (~3x) at minimum twig diameters greater than 2mm (Fig. 2). In comparison, changes in stem mortality above these thresholds were small for both variables. However, stem mortality showed a clear linear increase at minimum twig diameters greater than 2mm, not evident for shrub cover past the ~15% threshold (Fig. 2). At minimum twig diameters greater than 9mm all stems were killed (Fig. 2). Stem mortality at minimum twig diameters less than 2mm was quite low, with one quarter of stems dead (Fig. 2).
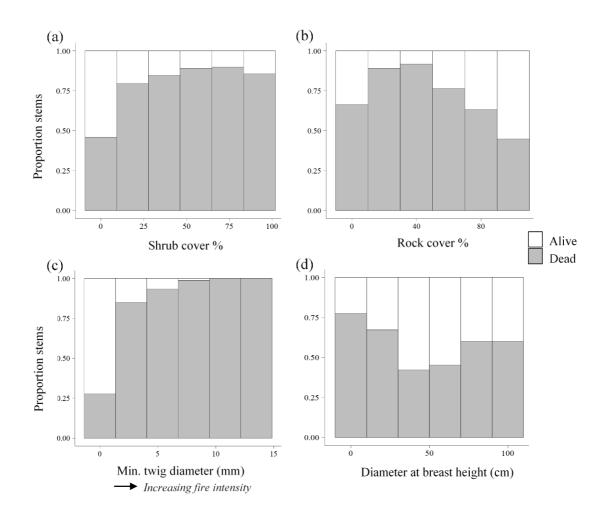
FIGURE 2 RELATIONSHIPS BETWEEN VARIABLES AND PROPORTION OF *A. CUPRESSOIDES* STEMS KILLED IN THE 2016 FIRES. VARIABLES ARE *(A)* PERCENTAGE SHRUB COVER *(B)* PERCENTAGE ROCK COVER *(C)* MINIMUM TWIG DIAMETER (MM) *(D)* DIAMETER AT BREAST HEIGHT (CM).

Rock cover was negatively, albeit weakly related to stem mortality ($w+$ =0.73). This negative relationship was only apparent when rock cover was greater than 50% (Fig. 2). Indeed, at rock cover less than 50% stem mortality showed a positive relationship with rock cover (Fig. 2). Stem size (DBH) was strongly related to stem mortality ($w+$= 1). Our analysis supported a U-shaped relationship of DBH with stem mortality. Hence, small and large stems had higher proportions killed than medium sized stems, with lowest mortality when DBH was 50cm (Fig. 2). We also found that fire scar presence, indicative of prior exposure to fire, was positively related to stem mortality (Fig. 3). Fire scar prevalence also increased with stem size, with all stems with a DBH greater than 90cm having fire scars (Fig. 3). To investigate possible bias in our assessment of the effect of fire scars and stem size due to the inter-correlations of these variables, further analysis was conducted. In small and medium stem classes, which contained stems with and without fire scars, modelling showed increased mortality in stems with fire scars. Constraining the analysis to only medium and large stems with fire scars showed no increase in mortality with stem size. These lines of evidence suggest that the positive relationship we found between fire scar presence and stem mortality is driving the upturn in stem mortality in large stems.
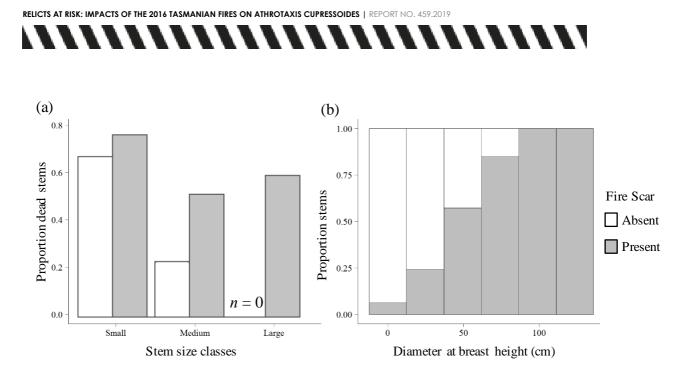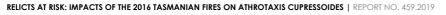
FIGURE 3 RELATIONSHIPS BETWEEN FIRE SCARS AND A. CUPRESSOIDES STEMS. (A) PROPORTION OF STEMS DEAD WITH OR WITHOUT FIRE SCARS ACROSS THREE STEM SIZE CLASSES. SMALL = DBH < 40CM, MEDIUM = DBH > 40 < 80CM, LARGE = DBH > 80CM. (B) PROPORTION OF STEMS WITH AND WITHOUT FIRE SCARS DEPENDING ON STEM SIZE (DBH CM).

RECRUITMENT AND REGENERATION

A. cupressoides seedlings were found at all sites surveyed within the 2016 fire boundary. Seedling presence overall was low (~10%), but widespread, occurring at multiple plots (Table 1). The variables, shrub cover, unburnt soil, minimum twig diameter and tree size (DBH) were all important predictors of seedling presence ($w+ = 1$). We found negative relationships between seedling presence, shrub cover and minimum twig diameter and positive relationships between unburnt soil and DBH (Fig. 4). Seedlings were only present at very low levels of shrub cover (<15%) and minimum twig diameters (<2mm) (Fig. 4). High seedling presence (>50%) occurred when unburnt soil was greater than 80% (Fig. 4). There was a linear increase in seedling presence as trees increased in size, with highest seedling presence occurring when trees DBH was greater than 175 cm (Fig. 4).

TABLE 1 SEEDLING PRESENCE ACROSS SITES AT LAKE MACKENZIE. REPRESENTED AT TWO SCALES (I) AROUND THE BASE OF A TREE (2M^R) (II) WITHIN 10M^R PLOTS.

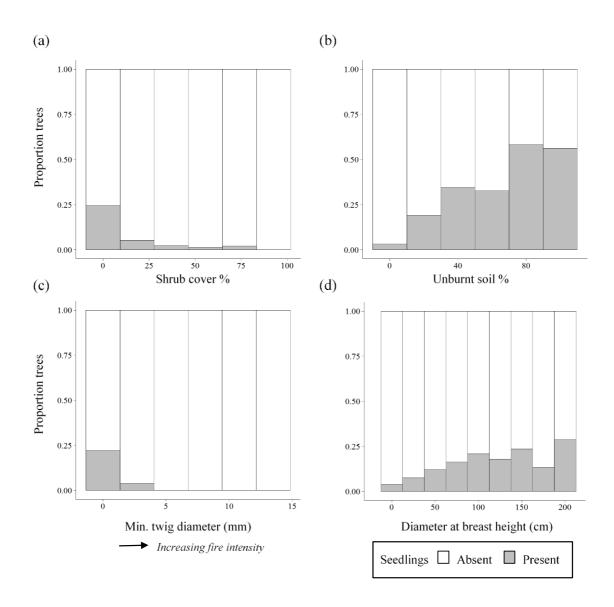| Proportion seedlings present	Sites			
	LMS	LMF	LMB	Overall
Trees	0.06	0.14	0.03	0.09
Plots	0.17	0.2	0.05	0.14

FIGURE 4 RELATIONSHIPS BETWEEN VARIABLES AND SEEDLING PRESENCE AROUND A. *CUPRESSOIDES* TREES AT LAKE MACKENZIE. VARIABLES ARE *(A)* SHRUB COVER % *(B)* UNBURNT SOIL % *(C)* MINIMUM TWIG DIAMETER (MM) *(D)* DIAMETER AT BREAST HEIGHT (CM).

DISCUSSION

The results from this study illustrate that high intensity wildfire in Tasmania's alpine environments have significant detrimental effects on *A. cupressoides* populations. The 2016 wildfires at Lake Mackenzie caused high mortality and adverse demographic effects that jeopardise the future viability of *A. cupressoides* populations in this region. Additionally, we found that fire impacts were heterogeneous, whereby local variations in percentage shrub cover, rock cover and fire intensity (indicated by minimum twig diameter) influenced *A. cupressoides* mortality and recruitment. We identified thresholds of shrub cover (~15%) and minimum twig diameter (2mm), whereby mortality markedly increased, and seedling presence decreased past these levels. Interestingly, our results also suggest that low intensity fires have occurred in this landscape during the lifetimes of existing mature trees. Furthermore, we detected a legacy effect of past fires, whereby stems that had been burnt before (evident from presence of a fire scar) were more likely to be killed by a subsequent fire. This study provides important insights to inform the conservation and management of this species and contributes to our understanding of *A. cupressoides* fire ecology.

POPULATION IMPACTS

Mortality of *A. cupressoides* following the 2016 fire was high, with two-thirds of trees and stems within the burnt area killed. Importantly, we found a U-shaped demographic effect of the fires, whereby small and large stems had higher mortality rates than medium sized stems. Higher mortality in small stems concurs with numerous studies across multiple geographies, tree species and forest types (Botequim *et al.* 2017; Brando *et al.* 2012; Granzow-de la Cerda *et al.* 2012; Keyser *et al.* 2006; Lee *et al.* 2010; Maringer *et al.* 2016). The overall U-shaped mortality-size relationship we detected, albeit less common in the literature, was found in old-growth Scots pine forest in northern Sweden (Linder *et al.* 1998) and in eucalyptus dominated savanna woodland in northern Australia (Prior *et al.* 2009). Overall, our study highlights that medium sized *A. cupressoides* are the most resilient to fire.

One year post-fire we observed *A. cupressoides* seedling presence at low levels, but widespread throughout our study area. Most of the seedlings were present in unburnt or very minimally burnt patches. The lack of seedlings in burnt areas questions suggestions that new stands of *A. cupressoides* are initiated after fire (Cullen and Kirkpatrick 1988a). Our results show that *A. cupressoides* can clearly germinate in this area (albeit only in unburnt patches), which was also found by other studies in the region (Holz *et al.* 2015). Thus, our results support conclusions drawn by Cullen and Kirkpatrick (1988a) that regeneration failure in this region, manifested as a lack of small trees, is likely due to herbivory rather than *A. cupressoides* inability to propagate. Interestingly, I found that seedlings were positively associated with larger trees. Potentially, this relationship occurs because larger trees have greater resources to expend on reproduction. For instance, they have larger root beds to produce clonal shoots and more abundant aerial seed banks to produce seed. Globally, positive trends have been found between plant size and energy allocated to reproduction (Wenk and Falster 2015). For instance, old-growth Mountain Ash eucalypts produce massive seed crops comparatively to younger trees (Lindenmayer 2016). Therefore, it is likely that the increased mortality in larger trees within *A. cupressoides* populations I surveyed, will have a knock-on demographic effect via reduced seed sources.

Together, our results suggest that populations of *A. cupressoides* within the area burnt in the 2016 fires, although not completely eradicated by the fire, are no longer viable. The demographic effect of the fire, whereby high proportions of small trees were killed, appears permanent as seedlings will most likely be removed through herbivory. Furthermore, the resilience of these populations to future fires will decrease as there are now few small trees to grow into resilient medium sized trees. Additionally, numerous large trees were killed by the fire, reducing overall recruitment in these populations. Trees that were burnt in this fire but survived will develop fire scars, making them more vulnerable to fires in the future. Thus, without intervention these populations will be unlikely to persist in the long term and can be considered in 'extinction debt' (Kuussaari *et al.* 2009). This concept explains the phenomenon whereby local extinction is inevitable but it may take a considerable amount of time to occur; exacerbated by the long generation times of *A. cupressoides* (Kuussaari *et al.* 2009).

Our findings have broad implications for *A. cupressoides*. Large fire events in our study region, coincide with extreme climate conditions, demonstrated by the 2016 fires and large fires in the 1960's, both which were preceded by atypical dry and warm springs (Bureau of Meteorology 2016; Holz *et al.* 2015). Thus, with warming and drying trends predicted to continue in this region (Fox-Hughes *et al.* 2014; Lucas *et al.* 2007), it is likely that long held fire refugia will be overwhelmed and *A. cupressoides* range will contract. Indeed, if populations burnt in the 2016 fires become locally extinct it will result in a contraction of *A. cupressoides* northern range. Perhaps, large physical barriers that impede fire, such as extensive scree slopes and lakes, may enable *A. cupressoides* and other fire sensitive species to persist in this landscape. However, the long-term viability of smaller populations is questionable, as the already low genetic diversity of this species will likely further decline as populations shrink (Worth *et al.* 2016). Indeed, Worth *et al.* (2016) show that past fires have caused genetic decline and bottlenecks in some *A. cupressoides* populations. Thus, increased fires in this region may threaten the long-term persistence of *A. cupressoides*.

INFLUENCES OF MORTALITY AND RECRUITMENT

Our study found a positive relationship between shrub cover and mortality. This is not surprising as shrubs contribute to fuel loads and fuel continuity, essential to the spread of fire (Collins and Stephens 2010; Lutz *et al.* 2017; Scott *et al.* 2014). Other studies have found similar relationships, where shrub cover contributed to tree mortality (e.g. Yosemite National Park, USA; Collins and Stephens 2010), or positively influenced fire severity (e.g. 2000 California fires; Crotteau *et al.* 2013). Shrub cover is thought to increase mortality of trees in close proximity through the large and rapid release of heat that rises through tree canopies when shrubs combust, damaging leaves (Smith *et al.* 2016). Additionally, shrubs lengthen localised burning times of fires, which can contribute to cambial heating and higher levels of damage to low foliage (Lutz *et al.* 2017; Smith *et al.* 2016). Shrub cover was also negatively correlated to seedling presence in our sites. Potentially this is due to longer fire propagation time when shrubs are present that may reduce soil biomass and burn seeds and seedlings (Lutz *et al.* 2017). Interestingly, we detected a threshold of shrub cover, whereby mortality greatly increased and seedling presence decreased. This novel finding has important management implications; it could be used to assess vulnerability of other *A. cupressoides* stands and highlights a target for shrub reduction if such an intervention was undertaken. Our findings are of consequence for these ecosystems, as it has been proposed that high-severity fire events can perpetuate the spread of re-sprouting shrubs, that in turn create positive feedbacks promoting more mortality- inducing fires (Collins and Stephens 2010; Holz *et al.* 2015; Nagel and Taylor 2005). This relationship has been observed in montane forests in Yosemite National Park, USA (Collins and Stephens 2010), and in *Nothofagus pumilio* forests in northern Patagonia (Paritsis *et al.* 2015).

Our research shows that at high levels, rock cover provides some protection from fires, reducing mortality. Very rocky areas, scree slopes and 'block streams' are often cited as fire-protected sites associated with *A. cupressoides* presence (Cullen and Kirkpatrick 1988b). Similar associations between site rockiness and presence of fire-sensitive species have been found in South Africa and in Argentina (Cousins *et al.* 2016; Landesmann *et al.* 2015; White *et al.* 2016). The presumed underlying mechanism for lower mortality at rocky sites during fire events is that rocky outcrops act as fire breaks, impeding fire spread (Clarke *et al.* 2014; Krawchuk *et al.* 2016). In Our study, such fire protective mechanisms appear apparent only at high levels of rockiness. Indeed, at low levels of rock cover, mortality showed a positive relationship with rockiness. Findings from other studies suggest that rock cover may exacerbate fire impacts, by increasing evaporative demands and the duration of surface heating when burnt (Szarzynski 2000; Villalba and Veblen 1997; Stoof *et al.* 2011). Further investigation is needed to confirm these effects in our study environment.

Across our study area, we found that stem mortality increased with minimum twig diameter (a proxy for fire intensity). Similar relationships have been found in other studies, including in Amazon rainforests in Brazil (Brando *et al.* 2012), *Pinus patula* plantations in South Africa (Bird and Scholes 2005) and in ponderosa pine and Douglas-fir forests in western USA (Youngblood *et al.* 2009). Fire intensity represents the energy released during various phases of a fire (Keeley 2009). Changes in weather and landscape features result in spatially variable fire intensities (Collins and Stephens 2010; Hammill and Bradstock 2006). Experimental studies have found that fire intensity corresponds to depth of stem tissue damage, thus increasing mortality (Bova and Dickinson 2005). Interestingly, we found a threshold of minimum twig diameters of 2mm, whereby *A. cupressoides* mortality markedly increased at minimum twig diameters greater than this. This result shows that *A. cupressoides* can survive fires, but only of very low intensity. Future research, using laboratory burning experiments to quantify the fire intensity at 2mm minimum twig diameter of common shrubs at our study region (e.g. *Richea scoparia* and *Orites acicularis*), would be useful. This would provide managers with a fire intensity measure to inform potential fuel reduction burns in alpine regions of Tasmania, or targets for fire suppression.

INSIGHTS INTO PAST FIRE REGIMES

Results from our study allude to historical fire patterns in this region. We found numerous stems with fire scars, indicating that fire has been present in this region and trees survived. This, in combination with our finding that *A. cupressoides* survives low intensity fires, suggests that historically low intensity fires were present in this region. This is in agreement with other researchers' conclusions about fire in *Athrotaxis* habitat (Allen *et al.* 2017; Holz *et al.* 2015). Additionally, diameter and age relationships have been found in *A. cupressoides*, whereby stem diameter increases approximately 1 mm per year (Cullen and Kirkpatrick 1988a). Thus, from the positive relationship we detected between stem size and fire scar frequency it can be deduced that fire scars are more common in older stems. This suggests that fires have been frequent and patchy in this region, whereby the longer a tree/stem lives the more likely it is to be exposed to a fire. This concurs with historic charcoal records that show continuous charcoal input, indicative of frequent fires in this region for the last 1000 years (Stahle *et al.* 2016). Fire scars present important and underutilised research opportunities to reconstruct past fire regimes.

MANAGEMENT IMPLICATIONS

To conserve *A. cupressoides,* our study highlights that where possible, high intensity fires should be supressed in *A. cupressoides* stands due to the high rate of mortality that can occur. As well as improving fire-fighting response, a reduction in fire damage could be achieved through interventions that increase soil moisture content (e.g. irrigating as has been proposed to protect sequoias in the USA; Robbins 2014), increase fire breaks (man-made rocky outcrops), or reduce shrub cover (e.g. via manual removal, as has been successfully implemented in USA forests; Jerman *et al.* 2004). Of course, due to the potential of such interventions to compromise wilderness values of *A. cupressoides* habitat, they must be implemented with careful planning and consideration. Our findings show that low intensity fires could potentially be used as management tools in this environment, but only if such fires reduced shrub cover. We recommend immediate intervention to protect seedlings found within the burnt areas from herbivory, by means of installation of herbivory-exclusion fences around seedlings, to facilitate recruitment in these populations. Additionally, permanent plots in this area should be established to monitor the long-term effects of this fire event. The apparent permanent impact of these fires, together with the likelihood of increasing fire events in *A. cupressoides* habitat, suggest that it is time to seriously investigate and trial methods to establish insurance populations, within or outside *A. cupressoides'* current range.

CONCLUSION

Overall, our study shows that the 2016 Tasmanian wildfire at Lake Mackenzie has had demonstrable detrimental effects on *A. cupressoides* populations within the fire perimeter. The accumulative impacts of the fire with time, will likely cause these populations to become locally extinct. Thus, it is likely that with predicted increases in extreme fire events in this region (Fox-Hughes *et al.* 2014), long-held fire refugia will be overwhelmed and the range of *A. cupressoides* will contract into the most fire protected topographical settings in the landscape. However, whether such populations can maintain viable genetic diversity is questionable. Thus, increasing wildfire in these regions may endanger the long-term viability of *A. cupressoides*.

However, we also found variation in mortality rates within the area burnt. This heterogeneity was strongly influenced by minimum twig diameter, shrub cover and tree/stem size and weakly influenced by rock cover. We detected widespread, albeit low levels of seedlings across our sites. Furthermore, we found that *A. cupressoides* can survive low intensity fires and evidence for historical fire regimes characterised by frequent, low-intensity, patchy fires in this environment. These findings can be used to inform potential management strategies and interventions to help assist the long-term conservation of *A. cupressoides* and potentially, assist in the recovery of burnt *A. cupressoides* populations at Lake Mackenzie.

The 2016 Tasmanian wildfires are part of a global trend of increasing extreme fire events. These events are united by their underlying cause; warmer and drier conditions driven by anthropogenic climate change (Westerling *et al.* 2006). Without climate change mitigation, fire sensitive species face an uncertain future. Alpine regions, hubs for fire-sensitive vegetation, are especially vulnerable (Engler *et al.* 2011; Hughes 2003). Thus, to reduce biodiversity loss in these ecosystems it is imperative that we document and learn from fire events in these systems. Studying these unprecedented events increases our understanding of the fire ecology of fire sensitive species and the fire refugia they habit. Furthermore, such research provides important ecological insights for land-managers, information that is essential to devise successful interventions to conserve fire-sensitive species in an increasingly flammable world.

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