Lack of reliable post-fire recovery mechanisms makes the iconic Tasmanian conifer *Athrotaxis cupressoides* susceptible to population decline

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Abstract

Athrotaxis cupressoides is an iconic Tasmanian palaeoendemic conifer that is vulnerable to fire. A survey of three populations burnt by severe fire in 2016, conducted one year post-fire, found 33% of stems were still alive, with many surviving stems suffering some canopy scorch. We re-surveyed these populations to quantify delayed mortality, resprouting and presence of juveniles, and to determine whether fire impacts can be reliably assessed after one year. We applied three measures of fire severity: canopy scorched, canopy consumed, and the minimum burnt twig diameter of neighbouring shrubs. We found overall stem survival in 2020 was 31%, and that 97% of stems that were dead 4 years post-fire had died within the first year. Our best predictor of stem mortality was percent canopy scorched. Overall, 1.8% of burnt stems resprouted, but severely burnt stems did not resprout. Juveniles were present around 9.9% of burnt trees in 2017, and only 1.8% in 2020. From this and other work, we conclude that *A. cupressoides* stems are not unusually fire sensitive, but rather, that the species' vulnerability to severe fire results from its lack of reliable recovery mechanisms. This study shows that fire-caused mortality can be reliably assessed 12 months after a fire, and possibly earlier. Interventions such as sowing seed or transplanting seedlings could be necessary to re-establish fire-killed populations.

Introduction

Palaeoendemics are ancient, geographically restricted plant and animal clades that typically persist in small refugia, and have probably been selected against in most places (Jordan *et al.* 2016). Australia's island state of Tasmania is rich in palaeoendemic plants. Here, these species are concentrated in open vegetation at, or slightly above, the tree line, in constantly moist areas with equable temperatures and few or no fires (Jordan *et al.* 2016). Vulnerability to fire could therefore be a key feature of the ecology of these palaeoendemics. Thus, understanding their responses to fire is essential in predicting how their populations will fare as climate change leads to more frequent and more severe fire, as well as in developing ways of mitigating its impact.

One important Tasmanian palaeoendemic species is the iconic conifer *Athrotaxis cupressoides* D. Don (pencil pine), which is found in montane areas in central and western Tasmania. The species has a limited capacity to disperse by seed, and sexual regeneration appears less common than clonal growth via production of ramets (Worth *et al.* 2016b). The vulnerability of *A. cupressoides* to fire is demonstrated by the fact that extensive fires during the dry summer of 1960/61 are estimated to have eliminated it from about 10% of its entire range (Corbett 1996; Johnson and Marsden-Smedley 2002; Holz *et al.* 2015). A large-scale geographic survey of *A. cupressoides* populations across Tasmania found that burnt areas had fewer live trees and fewer juveniles than areas with no evidence of fire (Bowman *et al.* 2019). However, detailed studies of responses closely following severe fire have only recently been reported (also by Bowman *et al.* 2019).

Early assessment of fire damage is important for planning and carrying out the remediation, rehabilitation or restoration of vulnerable plant populations. It is also necessary in understanding regeneration dynamics, and to differentiate seed germination and/or ramet initiation from juvenile survival. However, overseas studies have found that substantial fire-induced mortality of conifer trees can continue for three or more years post fire (Stephens and Finney 2002; McHugh and Kolb 2003). Indeed, delayed mortality in the few years after a fire can exceed the initial mortality during the first growing season post fire (Thies *et al.* 2006). This delayed mortality makes the early evaluation of fire effects potentially problematic. The importance of delayed mortality for fire-affected *A. cupressoides* populations is not known.

Between January and March 2016, following an exceptionally dry spring, dry lightning storms ignited multiple fires in the Tasmanian Wilderness World Heritage Area. Amongst the areas burnt was almost 14,000 ha of subalpine vegetation at Lake Mackenzie, including 141 ha of *A. cupressoides* forest (Bowman *et al.* 2019; Bowman *et al. in press*). A survey of the fire-affected *A. cupressoides* populations in 2017 found that 68% of stems were killed by the fire, and juveniles were present around only 9% of burnt trees (Bliss 2017; Bowman *et al.* 2019). Many of the trees that were still alive were severely damaged, with most of the canopy scorched and dead. Crown damage is an important predictor of tree responses to fire (Peterson 1985; McHugh and Kolb 2003; Kobziar *et al.* 2006; Thies *et al.* 2006; Catry *et al.* 2010; Kane *et al.* 2017). The percentage of canopy scorched by the fire, and the percentage consumed, were also recorded in 2017 (Bliss 2017), but were not reported by Bowman *et al.* (2019) because it was uncertain how these measurements would relate to the species' ultimate post-fire responses. However, an opportunity arose to reassess these *A. cupressoides* populations in 2020, and quantify any delayed post-fire mortality that had occurred between 2017 and 2020. We were also able to relate the status of the stems in 2020 to the canopy damage evident three years earlier.

Here, we aimed to evaluate the reliability of assessments of fire impacts on *A. cupressoides* populations made one year post-fire. In particular, we quantified delayed mortality occurring between one and four years post-fire, and attempted to determine whether the ultimate fate of stems could be predicted from measurements of canopy damage made one year post-fire. In addition, we quantified resprouting and juvenile presence four years after the fire. Finally, we contextualise our results by comparing them with a large study of survival of major tree species in relation to canopy damage in the Western USA (Kane *et al.* 2017).

Methods

Study region

This study was conducted near Lake Mackenzie, on the north-eastern boundary of the Central Plateau in Tasmania, Australia (41.67°S, 146.37°E; 900-1200 m a.s.l; Fig.1). The Central Plateau is a broad undulating highland, with over 4,000 lakes and tarns (Banks 1972; Pemberton 1986). 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, with alpine heath (e.g. *Richea scoparia*), coniferous woodlands (*A. cupressoides*) and bolster heath (e.g. *Abrotanella forsteroides*) forming a mosaic with eucalypt forests (e.g. *Eucalyptus coccifera*), (Kirkpatrick 1983; Reid *et al.* 2005). This region is recognised as internationally significant wilderness, demonstrated by its inclusion within the Tasmanian Wilderness World Heritage Area (TWWHA) (Fig. 1).

The climate is cool maritime, with frequent frosts and snow, which can occur in any month (Bureau of Meteorology 2020). Mean annual precipitation (MAP) at the study location at Lake Mackenzie is 2091 mm, and temperatures range from a mean daily maximum of 19.1°C in January to a mean daily minimum of -1.6°C in July (at Liawenee; Bureau of Meteorology 2020). The rainfall station at Lake Mackenzie was open only from 1969-1992, so we used data from both the nearest open rainfall station (Western Creek, 12 km away, but only 417 m a.s.l.) and the nearest high-elevation station (Liawenee, 31 km away and 1057 m a.s.l., so at the same elevation as our study area). Both receive substantially less precipitation than Lake Mackenzie (MAP is 1166 and 923 mm respectively for Western Creek and Liawenee) (Bureau of Meteorology 2020), but monthly precipitation for both was well correlated with that at Lake Mackenzie (r was 0.86 and 0.85, respectively, for 1974-1992) (Appendix 1). Rainfall was exceptionally low in the months before the fire in January 2016 (Appendix 1). In the four years between the fire and the remeasurements reported here, total rainfall was 99% of the respective long-term averages at both Western Creek and at Liawenee, but in late 2019, the 3-month running average rainfall was less than half the long-term average (Appendix 1, based on data from Bureau of Meteorology 2020).

Fire history

Historic charcoal records suggest fire has occurred in alpine areas of Tasmania 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. selaginoides* with fire scars (this congeneric of our study species is killed by high intensity fires) (Allen *et al.* 2017; Dodson 2001; Holz *et al.* 2020). 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; Jones *et al.* 2019). 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 60 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).

The 2016 fires resulted from a series of dry lightning storms in January and February 2016, which followed an exceptionally dry winter and spring (Appendix 1). The fires burnt ~125,000 ha of vegetation across Tasmania, including over 20,000 ha of the Tasmanian Wilderness World Heritage Area (AFAC 2016). Most of the area burnt was of fire-adapted vegetation types such as treeless sedgeland and eucalypt forests. However, areas of subalpine vegetation were also burnt by high severity fires because fuels were so dry. Amongst the most serious biological damage was the burning of 141 ha of *A. cupressoides* forest in the Lake Mackenzie area by the Mersey Complex Fires (Senate ECRC 2016). The fire reached this highland plateau area on 19th January, when the fire danger was very high (Forest Fire Danger Index was 28) and the fire behaviour was at its most extreme. Most of the fire damage to alpine and subalpine vegetation occurred prior to the arrival of interstate fire-suppression resources on 23rd January, although the fires continued to burn at low fire intensities and under mild fire weather until March (DPIPWE 2017). The fires also ignited peat soils, which continued to smoulder in sphagnum bogs and other vegetation long after the fire front passed, and were not fully extinguished until May 2016.

Study species

Athrotaxis cupressoides is a very long lived (>1000 years), slow growing, endemic Tasmanian conifer (Allen *et al.* 2011; Ogden 1978). This species, as well as *A. selaginoides*, are the only extant species from the *Athrotaxis* genus, which is 150 million years old (a hybrid of the two species, *A. laxifolia*, also exists) (Worth *et al.* 2016a). Today, *A. cupressoides* is found in the alpine regions of central and western Tasmania, concentrated on

the Central Plateau, which accounts for 76% of its total distribution (Harris and Kitchener 2005). These species are considered ‘palaeoendemic’ and are important living links to Gondwanan flora because of their antiquity and current restricted geographical range (Jordan *et al.* 2016).

Athrotaxis cupressoides exhibits diverse physical forms, ranging from tall (30 m) trees in sheltered habitats to dwarfed (< 5m) trees in exposed sites. It is extremely frost tolerant, though shade intolerant and regarded as sensitive to all but the lowest intensity fires (Cullen and Kirkpatrick 1988b; Holz *et al.* 2015). *Athrotaxis 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, vegetative reproduction is more common, whereby *A. cupressoides* regenerates vegetatively via root suckers (Worth *et al.* 2016b). On average, about 60% of stems (ramets) are clonal, and are often aggregated in clusters that arise from the same genet; some genets can produce multiple clusters up to 38 m apart, interspersed with stems from other genets (Worth *et al.* 2016b).

Field surveys

Field observations of fire damage to *A. cupressoides*, physical site attributes and juvenile presence were initially undertaken in February - April of 2017, 13-15 months after the January 2016 Mersey Complex Fire (Fig.1), as described in detail by Bowman *et al.* (2019) and Bliss (2017). At three sites near Lake Mackenzie, a total of 300 plots were chosen within the fire-boundary to sample most of the accessible *A. cupressoides* populations burnt in this fire event. An additional 20 plots were located in adjacent unburnt areas. Two of the three sites (‘Scree East’ and ‘Scree West’) were on scree slopes, and the third (‘South Bog’) was in a flat, boggy depression surrounded by rocky slopes covered in low *Eucalyptus coccifera* woodland and subalpine shrubs. At each site a systematic sweep of the *A. cupressoides* population was conducted, using adjacent 10 m radius circular plots. The plots were centred on large target trees to give an adequate representation of all size classes. A ‘tree’ was operationally defined as stems joined at the base above ground or within 30 cm of each other. Stems of a ‘tree’, as so defined, usually belong to a single genet, but a genet often comprises

more than one ‘tree’, as shown by the detailed genetic study of Worth *et al.* (2016b). Overall, each tree comprised an average 2.5 stems (maximum 19), and 56% were multi-stemmed. Within each plot, measurements were made on up to 10 trees and their stems. At the tree level, we estimated the percentage of the canopy scorched (browning of leaves, but no leaf mass consumed) and the percentage of the canopy consumed (Fig. 2). At the stem level, stems were assessed as ‘alive’ or ‘dead’ determined by the presence or absence of any green foliage (McHugh and Kolb 2003; Kobziar *et al.* 2006). The presence of fire scars was also noted (Fig. 2l). A 2 m radius circular subplot around the base of each tree, divided into four quadrants, was used to characterise environmental factors (including rock cover, unburnt soil cover and burnt shrub cover), presence of juveniles, which we operationally defined as either seedlings or root suckers less than 30 cm tall (noting it is difficult to distinguish between seedlings and root suckers in the field without damaging the plants). We also measured minimum diameter of burnt twigs, a proxy for fire severity, because more severe fires consume a greater proportion of biomass, and hence larger twigs, than less severe fires (Moreno and Oechel 1989; Whight and Bradstock 2000). The twig diameter of the five smallest twigs on burnt shrubs in each quarter was measured with calipers, and the average of these 20 measurements was used to calculate the minimum burnt twig diameter around each tree.

The trees were resurveyed in February and March 2020, to assess stem status and thereby quantify delayed mortality of stems, and to relate post-fire mortality to measurements of canopy damage and fire intensity made in 2017. Trees had not been tagged because of the sensitivity of this World Heritage area, but we were able to relocate 3151 (96%) of the original 3272 stems in 294 plots using GPS readings and DBH measurements (Table 1). Stems that were dead at the time of the 2016 fire were not considered in the 2020 study. We assessed whether stems were alive or dead, and visually estimated the percentage of canopy of each tree that was dead. These estimates of the percentage of canopy dead in 2020 were very similar to those of canopy scorched in 2017 ($r = 0.98$; Table 1), so were not used in further analyses. We also recorded whether stems were resprouting, and whether juveniles were present within a 2 m radius of the base of each tree (Fig. 2g-i).

Data analyses

Our analytical approach was to use generalised linear modelling (GLM) and model selection based on AICc, a modification of Akaike’s Information Criterion that is robust to small

sample size. The software R (R Core Team, 2020) was used for all analyses. Linear GLM was used for continuous variables, and binomial GLM with a logit link was used to analyse stem status (dead =0, alive =1) and juvenile presence. Our analyses focused on the burnt plots, with the small number of unburnt plots serving as controls to check for mortality unrelated to the 2016 fire. Complete subsets regression, in which candidate sets of models containing all combinations of predictor variables, without interactions, was used to assess effects of predictors.

We first examined variability in *A. cupressoides* population and environmental characteristics within and among sites, using generalised linear modelling and plot level observations. Response variables are listed in Table 1, and included stem status in 2017 and 2020, stem diameter, resprouting, canopy scorched, canopy consumed, minimum twig diameter, and juvenile presence. The AICc weights of the model with Site as a predictor variable were compared with the intercept-only model. Where stem-level response variables were analysed using a tree-level variable, the value of the tree-level variable was applied to all the stems that formed part of that tree.

Stem survival in 2020 was then analysed in relation to three measures of fire severity recorded in 2017 for each tree: percentage canopy scorched, percentage canopy consumed and the minimum twig diameter of burnt shrubs around the tree. We compared overall stem survival, and continued survival to 2020 of the 2017 survivors, using binomial GLMs that contained these three fire severity measures as explanatory variables. We also tested whether adding stem DBH and $(DBH)^2$ as explanatory variables significantly improved the models, given Bowman *et al.* (2019) found that medium to large stems were more likely to survive than small ones, albeit this was a humped relationship, with survival rates falling for very large stems. Note that survival in 2017 was not analysed in relation to canopy damage in that year because of considerable inherent circularity in the relationship, given that lack of green foliage was the criterion for stems to be considered dead. Although this circularity was to some extent carried through to survival in 2020, there was in principle some independence between the measurements, because it was possible that stems with completely burnt foliage could recover over three years. Therefore, we considered it legitimate to analyse the relationship between stem survival in 2020 and canopy scorched in 2017.

Relationships of canopy damage, resprouting and juvenile presence with minimum burnt twig diameter were also examined. Linear GLMs of both canopy scorched and canopy consumed in relation to minimum burnt twig diameter were compared with the intercept-only model using AICc. We used complete subsets regression and binomial GLMs to analyse

resprouting of stems in relation to canopy scorched, canopy consumed and minimum burnt twig diameter, with and without DBH as a predictor to examine the possible effect of stem size. We also explored presence of juveniles in both 2017 and 2020 in relation to the three severity variables and tree size. Because juveniles were measured at a tree level, we used the summed basal area of the constituent stems that were alive at the time of the 2016 fire as the tree size variable.

Results

Of the stems assessed in 2017, we were able to reassess a total of 154 stems in unburnt plots and 2997 stems in burnt plots in 2020 (Table 1). The canopy damage in burnt plots in 2017 in relation to minimum burnt twig diameter, and survival in 2020 in relation to these measurements, are described below. There were no statistically supported differences in stem survival among sites (Appendix 2). However, the minimum burnt twig diameter (our proxy for fire severity) was highest at the site ‘South Bog’, which also had the highest average stem DBH. This site also had the highest presence of juveniles in both 2017 and 2020. Site ‘Scree East’ had the lowest stem DBH and stand basal area, the highest proportion of resprouting, the highest canopy defoliation and the lowest juvenile presence.

Canopy damage and minimum burnt twig diameter

Our three measures of fire severity were strongly intercorrelated (r ranged from 0.49 for canopy scorched vs canopy consumed to 0.59 for canopy scorched vs twig diameter) (Appendix 3). Two-thirds of trees in the burnt plots were assessed as having 100% canopy scorched (Fig. 3d). Canopy consumption was much rarer, with 59% of trees in burnt plots assessed as having 0% canopy consumed (Fig. 3e). Both canopy scorched and canopy consumed were strongly related to minimum burnt twig diameter (Appendix 4 and Appendix 5). Trees surrounded by unburnt shrubs with a minimum burnt twig diameter of 0 mm had on average 6% of their canopy scorched and 0% consumed, compared with 99% and 64%, respectively, where the minimum burnt twig diameter was >7 mm. The models containing minimum burnt twig diameter received all the statistical support relative to the intercept-only model (Appendix 5).

Stem survival

All the unburnt stems were alive in both 2017 and 2020. By contrast, in the burnt plots, only 33.2% of stems were alive in 2017, declining slightly to 31.1% in 2020, as described below. Trees could survive a degree of canopy scorch: for example, there was 54% overall survival of stems of trees with 60-79% canopy scorch in 2017 (Fig. 3). However, stems of trees with 100% canopy scorch all died. By contrast, any canopy consumption was indicative of severe damage: only 5% of stems of trees with any canopy consumption were alive in 2017, and survival was only 0.6% for stems of trees with >20% canopy consumption. The probability of a stem being alive in 2020 was strongly, negatively correlated with the percentage of canopy scorched in 2017 (76% deviance explained). An additional 1.3% deviance was explained when DBH was added to the model (Appendix 6a). This model with canopy scorched and DBH received all the statistical support in the candidate model set ($w_i=1.000$). Percent canopy consumed (36% deviance explained) and minimum burnt twig diameter (34% deviance explained) were also correlated with stem survival, but had weaker explanatory power (Appendix 6a). DBH on its own only explained 3% of the deviance.

Inspection of the data showed that survival tended to decrease in very large trees (Appendix 7). Adding a $(\text{DBH})^2$ term to the top model (canopy scorched + DBH) explained a further 2% of the deviance explained (Appendix 6c), and predicted that survival increased with DBH up to about 65 cm, then decreased.

Of the 468 multi-stemmed trees, 63% had stems that were all dead, 25% were all alive, and 11% were of mixed status (Table 2). Trees with all stems dead experienced the most severe fire (according to all three measures), and trees with all stems alive experienced the least severe fire, and trees with the mixed status stems experienced intermediate severity fire (Table 2).

Delayed mortality

In the burnt plots, a total of 2062 stems were recorded as dead in 2017, and 2122 were dead in 2020. Thus, 97% of the 4-year mortality occurred within one year of the fire. Of the stems recorded as dead in 2017, only 4 (0.2%) were found to be alive in 2020, and this number was so low no further analysis was done (Table 3). Conversely, of the 935 stems recorded as alive in 2017, 64 (6.8%) were found to be dead in 2020. The factors predisposing the burnt stems alive in 2017 to dying in the next three years were similar to those increasing the probability of stems being dead in 2017, although the effects were weaker. Mortality of the stems alive in

2017 was 36% for stems of trees with >20% canopy scorch, compared with only 6.5% for stems of trees with $\leq 20\%$ canopy scorch. Our modelling found the percentage of scorched canopy in 2017 explained 24% of the deviance in delayed mortality, and there were also weak positive correlations of delayed mortality with canopy consumed (2.4% of deviance) and minimum burnt twig diameter (2.1% of deviance) (Appendix 6b). Delayed mortality was more likely in small trees: the canopy scorched and twig diameter models were improved slightly by adding stem DBH, which on its own explained 0.2% of the deviance. Adding a $(\text{DBH})^2$ term to the top model (canopy scorched + DBH) was not supported, and slightly increased AICc (by 0.9) (Appendix 6d).

Resprouting

Overall, only 54 of the 2997 stems (1.8%) in burnt plots were resprouting in 2020. We observed apical resprouting at the tips of branches and some epicormic resprouting along branches. There was a peaked relationship between resprouting and percent canopy scorched (Fig. 4), with the quadratic model receiving most of the statistical support (Appendix 8). The proportion of stems resprouting was low (0.03) in stems with less than 20% canopy scorched, rising to a maximum of 0.09 for stems with 40-60% canopy scorched (Fig. 4a). There was no resprouting in all 1927 stems that had 100% of their canopy scorched. There was no resprouting in stems that were >20% consumed (Fig. 4b), and the linear canopy consumed model received most of the statistical support (Appendix 8). There was no statistical support for adding DBH to the canopy scorched or canopy consumed models (Appendix 8). There was also a negative relationship between resprouting and minimum burnt twig diameter; in this model set, the model with minimum burnt twig diameter and DBH received most of the statistical support, with resprouting slightly more likely in large stems (Appendix 8).

Juvenile presence

Of the 1164 trees in burnt plots, the number of trees with surrounding juveniles declined substantially from 115 in 2017 to 21 in 2020. However, while 105 trees lost all surrounding juveniles during this period, new juveniles established around 11 trees. Juvenile presence in both years was negatively correlated with all three fire severity measures (Fig. 5; Appendix 9). In 2020, four years after the fire, no juveniles were found beneath trees that suffered any canopy consumption (Fig. 5). Juvenile presence was also positively related to tree size

(summed basal area of stems alive at the time of the 2016 fire), although the statistical support for this was much weaker.

Discussion

This study has added to our knowledge of post-fire survival and regeneration of an iconic Tasmanian palaeoendemic conifer. From a management perspective, important findings are the dearth of juveniles and that measurements made one year after a fire provide a reliable indication of post-fire survival of *A. cupressoides* stems.

Recruitment failure

Overall, only 2% of burnt trees had juveniles present near their base in 2020. Other studies of *A. cupressoides* have found juveniles are uncommon in burnt areas, especially when adult stems were fire-killed. For example, a large-scale geographic survey found 47% of transects with evidence of past fire contained no juveniles, compared with 28% of unburnt transects; in transects without live adult trees, 86% of burnt transects contained no juveniles (Bowman *et al.* 2019). Similarly, Holz *et al.* (2015) found a much lower density of small seedlings in *A. cupressoides* stands burnt by wildfire several decades previously than in unburnt stands, and a total absence of larger saplings in burnt stands. Small *A. cupressoides* plants (< 50 cm tall) have been shown to have no capacity to recover from even very low severity fires (Prior *et al.* 2018). Even in the absence of fire, juvenile recruitment appears precarious: this has been attributed to herbivory by both native and non-native herbivores (Cullen and Kirkpatrick 1988a), although little recruitment was detected in *A. cupressoides* stands on herbivore-free islands, implicating additional factors (Bowman *et al.* 2019). The effects of herbivory could be particularly severe immediately following fire, when there is little other food in the landscape, and new shoots are clearly visible (Holz *et al.* 2015). The paucity of juveniles in populations damaged by severe fire is particularly problematic because *A. cupressoides* does not produce a long-lived seedbank, and population recovery requires live trees as a source of seed and/or root suckers. *A. cupressoides* seed is poorly dispersed, with one study reporting a maximum distance of a seedling from a parent tree of only 9 m (Cullen and Kirkpatrick 1988a). While it is possible that a very rare and different process could disperse seed much further than this (Higgins and Richardson 1999; Trakhtenbrot *et al.* 2005), natural recolonization of extirpated populations would be extremely slow, given the patchy

distribution, infrequent mast seeding and slow growth rates of this species (Fitzgerald *et al.* 2011).

There were few *A. cupressoides* juveniles at Lake Mackenzie in 2017, highlighting the poor seedling regeneration and minimal production of root suckers following the 2016 fire. Moreover, fewer juveniles were present around the most severely burnt trees than around those where fire was mild. There were even fewer juveniles in 2020 than in 2017: juveniles had disappeared from 90% of trees where they had previously been present. It was unclear from our field survey whether juveniles detected around the same trees in 2017 and 2020 had persisted since 2017, or were newly established. The detection of 11 juveniles in new areas in 2020 shows juveniles have established since 2017. Although we did not measure juvenile height, we observed most juveniles were between 1-3 cm tall, with no obvious difference in size of juveniles between 2017 and 2020. Thus, it is likely that the juveniles detected in 2017 died and new ones re-established before 2020, but it is also possible some seedlings survived between surveys, but grew very little. This putative low survivorship and slow growth of seedlings could be due to herbivory, drought stress or both. Reduced growth and survivorship could also have been associated with drought because while total rainfall was close to average between the time of the fire in 2016 and our remeasurements in 2020, the second half of 2019 was very dry, with persistent rainfall deficits (Appendix 1).

Stem mortality

Most stem mortality (97%) occurred within one year of the fire. The factors predisposing live stems to die between 2017 and 2020 were similar to those predicting the probability of being dead in 2017, although they were statistically less important because of lower replication. Continuing survival of burnt stems declined with increasing fire severity. Overall, as was found in the first year, large stems that survived the first year were less likely than small ones to subsequently die, but there were too few deaths between 2017 and 2020 to statistically detect higher mortality in very large stems.

Our three measures of fire severity, canopy scorch, canopy defoliation and minimum twig diameter, were all intercorrelated and useful in predicting the ultimate fate of a stem, especially in combination with its DBH. The degree the canopy was scorched was the strongest predictor of survival, resprouting and juvenile establishment. We also found any amount of canopy defoliation caused severe demographic impacts, with only 0.6% of these stems surviving, none resprouting, and no juveniles present at the base of these trees in 2020

(four years after the fire). Minimum burnt twig diameter proved to be a useful measure of fire severity, as has been found in other studies (Moreno and Oechel 1989; Whight and Bradstock 1999; French *et al.* 2016). There were strong relationships between it and stem survival, resprouting and juvenile presence.

Clonality has been shown to be important in *A. cupressoides* populations, with up to 63% of genets within a population having more than one ramet (i.e. being multi-stemmed), and up to 62 ramets observed from one genet (Worth *et al.* 2016b). We found the stems of most multi-stemmed trees shared the same status (either all alive or all dead), probably in part because stems on the same ‘tree’ were exposed to a similar fire intensity. However, 11% of multi-stemmed trees had both live and dead stems, suggesting that the death of some stems does not necessarily impact survival of the greater clonal organism.

Large *A. cupressoides* stems have thick fibrous bark, which appears to confer some fire protection against low severity surface fires. Previous work has shown that *A. cupressoides* stands have multiple size classes, with most large stems bearing fire scars (Bowman *et al.* 2019) demonstrating they have survived past mild fires (Holz *et al.* 2015; Stahle *et al.* 2016; Worth *et al.* 2016b). In addition, at Lake Mackenzie some partially scorched stems resprouted, showing that, contrary to common belief, *A. cupressoides* can potentially resist and recover from mild fire. However, the lack of resprouting and absence of juveniles observed around the more severely burnt trees (as indicated by higher minimum burnt twig diameters) indicates that the intensity of the 2016 fire exceeded the fire-tolerance of this species, as Holz *et al.* (2015) concluded was the case for the fires that occurred in 1960-61.

To test the proposition that *A. cupressoides* is a particularly fire sensitive species, we compared the survival of its stems with rates reported in a large study for 11 common tree species in the western USA following planned burns (Kane *et al.* 2017) (Fig. 6; Appendix 10). Survival of *A. cupressoides* was within the range reported for the American species, despite the fact that the wildfire in our study caused more canopy scorch (and was likely more intense) than the planned fires in the American studies. It is also worth noting that the average DBH in the study by Kane *et al.* (2017) was larger than in our study, which could also have increased their reported survival rates because the trees are taller and have thicker bark. Nonetheless, the relationship between canopy damage and survival was similar in the two studies. We could find no detailed data for survival vs crown damage in Australian conifers, but it has been reported that the only way individuals of several *Callitris* species from fire-prone areas of Australia survive fire is by avoiding crown scorch (Denham *et al.*

2016), and there is 100% mortality of trees <25 cm diameter when char height exceeds 1 m (Cohn et al. 2011). Similarly, in the Northern Territory conifer *Callitris intratropica*, canopy damage was strongly linked to mortality (Bowman et al. 2014).

These findings all suggest that by world standards, adult *A. cupressoides* stems are not unusually prone to be killed by fire. Rather, it appears the susceptibility of *A. cupressoides* arises because it has no reliable mechanisms by which to recover from severe fire, either vegetatively or from a fire-resistant seed source.

Overall, our findings confirm that *A. cupressoides* is a fire-intolerant facultative resprouter/seeder because: it is a mast seeder that lacks a long-lived soil or aerial seedbank; commonly uses vegetative root-suckering for regeneration; is vulnerable to being killed by canopy fire; has poor post-fire seedling and vegetative regeneration; and has effectively no recolonization ability (Prior and Bowman 2020). *Athrotaxis cupressoides*, and other fire-intolerant palaeoendemic species, are restricted to areas with cool, moist climates that are largely fire-free (Grandcolas et al. 2014; Jordan et al. 2016). Climate change is projected to lead to increased temperatures and less reliable rainfall (Fox-Hughes et al. 2014; Jordan et al. 2016), threatening the integrity of these refugia due to drought and associated intense fires. Furthermore, poor dispersal limits the ability of *A. cupressoides* populations to migrate to any new refugia, such as areas above the current tree line. Ultimately, if chronic environmental stresses such as drought and extreme fire events continue unabated, *A. cupressoides* ecosystems could collapse (Bergstrom et al. 2021).

Management implications

We can draw some management recommendations from our study. Importantly, assessments of fire impacts on *A. cupressoides* populations can be made one year post-fire, given that 97% of the 4-year mortality had already occurred by then. It is possible that useful assessments could be made as early as at the end of the same summer as the fire, although this would need to be verified. We recommend visiting populations affected by the fire and visually estimating the percent crown volume scorched, which was the best predictor of a stem's fate. Ideally all trees should be assessed, but if a large area is burned then a representative sample of trees in a fire affected population should be sampled. Assessments of canopy consumed are also very useful, as any amount of canopy consumption indicates severe damage, with no prospects of resprouting or seedling recovery. Such an assessment

would provide a reliable indication of the impact of the fire on a population, and whether remedial measures would be required to sustain it.

Our findings that *A. cupressoides* can tolerate low intensity fire show that in theory controlled burns could be used to reduce fuel loads and slow the establishment of woody shrubs surrounding trees. However, this presents numerous practical and social challenges. Using low-intensity fire to reduce fuel would be difficult because montane vegetation only carries fire when conditions are unusually dry, so safe burning conditions when fires are controllable are very rare and likely hard to reliably predict. The natural and cultural values of the environment lead to an extremely low management tolerance to risk of the fire escaping control or causing environmental harm. Indeed, a back-burn set by fire fighters to protect a mountain hut during the bushfire killed several *A. cupressoides* trees (Senate ECRC 2016). A safer alternative could be to protect stands from the worst effects of fire through mechanical removal of shrubs surrounding the base of trees, given the relationship between shrubs, fire severity and canopy damage (Bowman *et al.* 2019), although such interventions are likely to be also socially controversial as they directly modify the environment.

As climate change leads to increasingly frequent and severe fire in the montane areas of Tasmania, restoration programs for palaeoendemics plants become increasingly important. For instance, to avoid substantial range contraction of *A. cupressoides*, sowing seed or transplanting seedlings or cuttings to re-establish burnt populations, together with protection from herbivores, will be required. These measures are currently being tested in the fire-affected areas around Lake Mackenzie, and if successful, could mitigate the deleterious demographic effects of fire on remaining *A. cupressoides* populations.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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Table 1. Summary of variables according to level of measurement (plot, tree and stem)

Counts of plots, trees and stems in burnt and unburnt plots are shown in italics, with the variable type, overall means and s.e.m.s also shown for continuous variables. All variables, except those labelled 2020, were measured in 2017. Stand BA (basal area) and stem density apply to all *Athrotaxis* stems that were alive at the time of the 2016 fires. ‘n.a.’ is not appropriate, because the data are binary

Variable	Type	Unit	Burnt		Unburnt	
			average	s.e.m.	average	s.e.m.
Plot level		<i>Count</i>	<i>294</i>		<i>20</i>	
Stand BA	continuous	m ² ha ⁻¹	11.6	0.9	16.7	4.5
Stem density	continuous	ha ⁻¹	328	20	249	43
Tree level		<i>Count</i>	<i>1164</i>		<i>75</i>	
Canopy scorched	continuous	%	75.4	1.1	0	0
Canopy consumed	continuous	%	31.4	1.2	0	0
Canopy dead- 2020	continuous	%	74.3	1.2	0	0
Burnt twig diameter	continuous	mm	2.76	0.06	0	0
Juveniles- 2017	binary	% ¹	9.9	n.a.	8.0	3.2
Juveniles- 2020	binary	% ¹	1.8	n.a.	0	n.a.
Stem level		<i>Count</i>	<i>2997</i>		<i>154</i>	
Live stems - 2017	binary	% ²	31.2	n.a.	1.00	n.a.
Live stems - 2020	binary	% ²	29.2	n.a.	1.00	n.a.
Resprouting	binary	% ²	1.8	n.a.	0	n.a.
DBH	continuous	cm	15.8	0.3	23.1	1.5

¹ percentage of all trees with juveniles within a 2 m radius of the base

² as a percentage of all stems that were alive at the time of the fire

Table 2. Status of stems of the 468 burnt, multi-stemmed trees.

The count and percentage of trees with stems all alive, all dead, or with mixed status is listed, as well as mean canopy scorched, canopy consumed and minimum burnt twig diameter for each category.

Multi-stemmed trees	Count	%	Mean canopy scorched (%)	Mean canopy consumed (%)	Mean burnt twig diameter (mm)
Stems all alive	165	25.5	13.2	0.0	0.87
Stems all dead	411	63.4	99.3	47.6	3.61
Stems mixed	72	11.1	52.1	2.3	1.56

Table 3. Count of stems alive and dead, in burnt plots, in 2020 relative to status in 2017.
 (We were unable to relocate 121 stems in 2020, and these have been excluded from the current study)

Stem Status 2020	Stem Status 2017		Total
	Alive	Dead	
Alive	871	4	875
Dead	64	2058	2122
Total	935	2062	2997
(Missing)	(35)	(86)	

Fig. 1. (A) The Tasmanian Wilderness World Heritage Area (yellow) and location of the 2016 fires (red) within this Area. (B) Location of the *A. cupressoides* survey plots (green circles) at three sites ('Scree East', 'Scree West' and 'South Bog', to the north-east, north and south-west of Lake Mackenzie, respectively) within the 2016 Mersey Complex fire footprint (in red), in the north of the Tasmanian Wilderness World Heritage Area.

Fig. 2. Observations from within the 2016 fire perimeter in the Lake Mackenzie region. Variations in severity of canopy damage in *A. cupressoides* (a) no canopy damage (b) entire canopy scorched (c) complete canopy defoliation. Burnt *A. cupressoides* (d) soon after the fires in 2016; (e) one-year post fire, in 2017; and (f) four years post fire, in February 2020. Note the further loss of foliage near the top of the canopy. (g) & (h) 2020 field observations found resprouting in some stems that were partially burnt in 2016. (i) Juveniles were found within the burnt perimeter in both 2017 and 2020. (j) 2020 was a mast seeding year, with prolific cones on many trees. (k) *A. cupressoides* ‘survivors’, trees within the fire perimeter that were unburnt. Note the landscape features associated with the unburnt trees, specifically the absence of shrubs (l) Fire scar on *A. cupressoides* stem.
Photos: (d) Rob Blakers, all others Aimee Bliss

Fig. 3. The percentage of stems alive in 2017 and 2020 in burnt plots in relation to (a) canopy scorched, (b) canopy consumed, and (c) minimum burnt twig diameter of shrubs around each tree. For presentation, observations were binned into arbitrary classes, but actual values were used in the analysis. Frequency distributions of *A. cupressoides* stems in each class of (d) canopy scorched, (e) canopy consumed, and (f) minimum burnt twig diameter are also shown. All three fire severity measures received strong support as predictors of survival in both years (Appendix 7).

Fig. 4. The percentage of stems in burnt plots resprouting epicormically in 2020 in relation to 2017 measurements of (a) percent canopy scorched, (b) percent canopy consumed, and (c) minimum burnt twig diameter. For presentation, observations were binned into arbitrary classes, but actual values were used in the analyses. All three severity measures were important predictors of resprouting, with a peaked relationship in the case of canopy scorch (Appendix 8).

Fig. 5. The percentage of trees with juveniles present in 2017 and 2020, in burnt plots only, in relation to 2017 measurements of (a) percent canopy scorched, (b) percent canopy consumed, and (c) minimum burnt twig diameter. For presentation, observations were binned into arbitrary classes, but actual values were used in the analyses. All three fire severity measures received strong support as predictors of juvenile presence in both years (Appendix 9).

Fig. 6. Stem survival after fire in relation to the weighted average crown volume scorched for *Athrotaxis cupressoides* (star) and some common tree species from the Western USA, reported by Kane et al. (2017) (squares). Closed symbols represent conifers and open symbols, broadleaf species. The data of Kane et al. (2017) were from prescribed burns, which were less severe (less leaf scorch) than the wildfire in our study. Details are shown in Appendix 10.

Supplementary Information for Lack of reliable post-fire recovery mechanisms makes the iconic Tasmanian conifer *Athrotaxis cupressoides* susceptible to population decline

Authors: Aimee Bliss, Lynda D. Prior and David M. J. S. Bowman

Appendix 1. Monthly rainfall totals in relation to long-term averages between January 2013 and June 2020 at (a) Western Creek and (b) Liawenee rainfall stations. (c) 3-month running average monthly rainfall at Western Creek and Liawenee as a percentage of their respective long term running 3-month averages. Note the rainfall deficiencies immediately before the fire (red arrow) and again in late 2019. The correlations between monthly rainfall at Lake Mackenzie and (d) Liawenee, and (e) Western Creek, between January 1974 and December 1992, when the rainfall station at Lake Mackenzie was open, are also shown. Western Creek is the rainfall station closest to Lake Mackenzie (12 km away), but is only at 417 m a.s.l., while Liawenee is the closest, high-altitude station (1057 m a.s.l., 31 km away). Based on data from Bureau of Meteorology (2020).

Appendix 2. Summary of sample counts and results, for the three sites and overall, in (a) the burnt and (b) the unburnt plots.

Only survival is shown for the unburnt plots, but for the burnt plots, *Athrotaxis* population and fire severity characteristics are also shown. Measurements were made at the plot, tree and stem levels, but the means, s.e.m.s and analyses shown here are based on plot means (enabling analysis of variability among sites; note that overall means based on these values will differ slightly from means based on pooled data). Values shown in italics are counts. All measurements, except those labelled 2020, were made in 2017. Stand BA (basal area) and stem density apply to all *Athrotaxis* stems that were alive at the time of the 2016 fires. The statistical support for differences among sites is shown by Akaike weights (w_i) of the site model relative to the intercept only model, and the percent deviance explained by the site model. Values of $w_i > 0.73$, which correspond to AIC_c being at least 2 less than that of the null model, are indicative of support for the model and are shown in bold.

Site		‘Scree East’		‘Scree West’		‘South Bog’		Site differences	
	Unit	average	s.e.m.	average	s.e.m.	average	s.e.m.	w_i	Deviance explained (%)
(a) Burnt plots									
Plot level	<i>Count</i>	<i>110</i>		<i>111</i>		<i>73</i>			
	m ² ha ⁻¹								
Stand BA		5.5	0.8	16.8	1.9	12.8	1.4	1.00	10.5
Stem density	ha ⁻¹	307	36	415	33	229	27	0.99	4.6
Tree level	<i>Count</i>	<i>369</i>		<i>563</i>		<i>232</i>			
Canopy scorched	%	75.8	3.5	75.0	2.9	69.1	4.4	0.24	0.62
Canopy consumed	%	33.3	3.4	22.2	3.1	24.0	3.9	0.77	2.19
Canopy Dead-2020	%	74.6	3.7	73.9	3.0	67.5	4.6	0.26	0.65
Burnt twig diameter	mm	2.69	0.16	2.60	0.15	3.31	0.27	0.82	2.4
Juveniles-2017	% ¹	2.7	1.3	11.3	2.6	13.7	3.6	0.97	3.7
Juveniles-2020	% ¹	0	0	1.0	0.6	6.6	2.7	0.99	4.7
Stem level	<i>Count</i>	<i>1050</i>		<i>1427</i>		<i>520</i>			
Live stems - 2017	% ²	29.0	4.0	32.9	3.5	40.1	5.1	0.41	1.13
Live stems - 2020	% ²	28.3	3.9	29.5	3.3	38.0	5.1	0.36	1.01
DBH	cm	14.7	0.9	19.9	1.2	26.5	1.4	1.00	13.6
Resprouting	% ²	6.8	2.2	1.6	1.0	1.3	0.8	0.86	2.6

(b) Unburnt plots									
<i>Plot level</i>	<i>Count</i>	<i>6</i>		<i>8</i>		<i>6</i>			
<i>Tree level</i>	<i>Count</i>	<i>23</i>		<i>28</i>		<i>24</i>			
<i>Stem level</i>	<i>Count</i>	<i>49</i>		<i>55</i>		<i>50</i>			
Live stems - 2017	% ²	100	0	100	0	100	0	n.a.	n.a.
Live stems - 2020	% ²	100	0	100	0	100	0	n.a.	n.a.

¹ percentage of trees with juveniles within a 2 m radius of the base

² as a percentage of all stems that were alive at the time of the fire

Appendix 3. Correlations matrices for survival of *A. cupressoides* stems and fire severity attributes (tree level data) in burnt plots only. The variables (from top left) are the proportion of stems alive in 2017 and 2020 in each tree, percent canopy scorched and percent canopy consumed in 2017, percent canopy dead in 2020, and minimum burnt twig diameter of shrubs around the tree in 2017. The top of each matrix shows the Pearson correlation coefficient and the significance of the correlation (‘.’ indicates $P < 0.10$, ‘*’ $P < 0.05$, ‘**’ $P < 0.01$, ‘***’ $P < 0.001$). The bottom of the matrix shows bivariate scatterplots, with a fitted line. The R package PerformanceAnalytics (Peterson and Carl 2014) was used to generate the matrices.

Peterson, B.G. & Carl, P. (2014). PerformanceAnalytics: Econometric tools for performance and risk analysis. R package version 1.4.354.

<http://CRAN.R-project.org/package=PerformanceAnalytics>

Appendix 4. (a) Canopy scorched, and (b) canopy consumed, in relation to minimum burnt twig diameter of shrubs around each tree, in burnt plots only. All variables were measured in 2017, at tree level. Twigs were binned into 1-mm classes for presentation, but actual values were used in analyses.

Appendix 5. Comparison of models describing canopy scorched and canopy consumed in relation to minimum burnt twig diameter and DBH .

Fire severity variables were recorded in 2017, at tree level, in burnt plots only. DBH was recorded at stem level in 2017, and in this analysis, was averaged for each tree.

Model	Canopy scorched		Canopy consumed	
	w_i	Explained deviance (%)	w_i	Explained deviance (%)
Twig diameter	1.000	34.8	1.000	21.1
Intercept only	<0.001	n.a.	<0.001	n.a.

Appendix 6. Comparison of models to evaluate (a) stem survival in 2020 and (b) the probability of survivors in 2017 surviving to 2020, in relation to three 2017 fire severity measures (percentage canopy scorched, percentage canopy consumed and minimum burnt twig diameter).

Summaries of the stem-level analyses demonstrating support for a peaked relationship with stem diameter (DBH) for (c) stem survival in 2020, but (d) not for stem survival between 2017 and 2020, are also shown. Burnt plots only were used in these analyses. Models are listed in order of decreasing statistical support.

	log(l)	K	AICc	Delta.AICc	wi	expdev
(a) Survival in 2020						
Canopy scorched + DBH	-378	3	764	0	1.000	77.5
Canopy scorched	-399	2	805	41	0.000	76.2
Canopy consumed + DBH	-1038	3	2084	1319	0.000	38.2
Twig_Diam + DBH	-1038	3	2084	1320	0.000	38.1
Canopy consumed	-1066	2	2137	1373	0.000	36.5
Twig_Diam	-1112	2	2231	1466	0.000	33.7
DBH	-1626	2	3259	2495	0.000	3.1
intercept only	-1678	1	3360	2596	0.000	NA
(b) Survival between 2017 and 2020						
Canopy scorched + DBH	-149	3	306	0	0.881	25.7
Canopy scorched	-152	2	310	4	0.119	24.2
Canopy consumed	-195	2	397	91	0.000	2.4
Twig_Diam + DBH	-195	3	397	92	0.000	2.8
Canopy consumed + DBH	-195	3	398	92	0.000	2.7

Twig_Diam	-196	2	398	92	0.000	2.1
intercept only	-200	1	405	99	0.000	NA
DBH	-200	2	406	100	0.000	0.2

Adding a $(DBH)^2$ term to the top models

	log(l)	K	AICc	Delta.AICc	wi	expdev
(c) Survival in 2020						
Canopy scorched + DBH + $(DBH)^2$	-371	4	751	0	0.999	79.5
Canopy scorched + DBH	-378	3	764	13	0.001	77.5
(d) Survival between 2017 and 2020						
Canopy scorched + DBH	-148.8	3	305.6	0	0.706	25.7
Canopy scorched + DBH + $(DBH)^2$	-148.7	4	307.4	1.8	0.294	25.8

Appendix 7. (a) The percentage of stems alive in 2017 and 2020, in burnt plots only, in relation to diameter at breast height, and (b) the frequency distribution of stems according to diameter. For presentation, observations were binned into arbitrary classes, but actual values were used in the analysis. The support for a peaked relationship in 2020 is shown in Appendix 6(c).

Appendix 8. Comparison of models describing resprouting in relation to the fire severity measures canopy scorched, canopy consumed and minimum burnt twig diameter, in combination with DBH, in burnt plots only.

We anticipated there could be a peaked relationship, with little resprouting in undamaged and severely damaged stems, so included a severity² term to test for this. (Indeed, this was the case for canopy scorched). The w_i for the best supported model in each set is indicated in bold.

Model	Severity measure		Canopy scorched		Canopy consumed		Twig diameter	
			w_i	Exp dev (%)	w_i	Exp dev (%)	w_i	Exp dev (%)
severity ² + severity + DBH			0.342	22.2	0.092	12.2	0.186	12.3
severity ² + severity			0.658	22.1	0.178	12.1	0.160	11.9
severity + DBH			<0.001	8.3	0.250	12.2	0.347	12.2
severity			<0.001	8.2	0.480	12.1	0.307	11.7
DBH			<0.001	0.5	<0.001	0.5	<0.001	0.5
intercept only			<0.001	NA	<0.001	NA	<0.001	NA

Appendix 9. Comparison of binomial GLMs describing juvenile presence in relation to three fire severity measures (canopy scorched, canopy consumed and minimum burnt twig diameter), in combination with tree basal area (summed for all stems of the ‘tree’ that were alive at the time of the fire in 2016).

Burnt plots only were used in this analysis. The w_i for the best supported model in each set is indicated in bold.

Model	Severity measure	Canopy scorched		Canopy consumed		Twig diameter	
		w_i	Exp dev (%)	w_i	Exp dev (%)	w_i	Exp dev (%)
<i>In 2017</i>							
Severity + Tree.BA		0.806	19.49	0.846	14.72	0.992	20.4
Severity		0.194	18.84	0.154	14	0.008	18.64
Tree.BA		0.000	1.34	0.000	1.34	0.000	1.44
intercept only		0.000	NA	0.000	NA	0.000	NA
<i>In 2020</i>							
Severity + Tree.BA		0.473	18.58	0.491	13.49	0.428	3.457
Severity		0.527	17.72	0.509	12.57	0.356	2.267
Tree.BA		0.000	1.38	0.000	1.382	0.116	1.15
intercept only		0.000	NA	0.000	NA	0.100	NA

Appendix 10. Data used as the basis for Fig. 6 in main text (shaded green).

The Kane et al. (2017) study was based on a large dataset documenting effects of planned fires on canopy damage and tree survival in mixed conifer forests in the western USA. Conifers and broadleaf trees are grouped together. Weighted average crown volume scorched damage was calculated for live and dead trees combined, as an indication of fire severity. These planned fires were less severe overall than the wildfire in our study.

Species	Count			Crown volume scorched (%)			Mean DBH (%)	
	live	dead	%survival	live	dead	weighted average	live	dead
<i>Athrotaxis cupressoides</i>	875	2122	29	20	97	75	20	14
Kane et al. (2017) Table 3								
<i>Abies concolor</i>	371	2075	15	33	66	61	25	19
<i>Abies magnifica</i>	21	99	18	21	77	67	61	31
<i>Calocedrus decurrens</i>	112	581	16	21	77	68	33	20
<i>Juniperus osteosperma</i>	48	87	36	25	75	57	25	27
<i>Pinus contorta</i>	60	227	21	13	48	41	19	24
<i>Pinus lambertiana</i>	19	252	7	13	60	57	56	23
<i>Pinus ponderosa</i>	1890	1325	59	20	65	39	32	28
<i>Pseudotsuga menziesii</i>	494	290	63	38	71	50	19	28
Mean-conifers			29			55	34	25
<i>Populus tremuloides</i>	67	50	57	3	21	11	20	19
<i>Quercus gambelii</i>	31	91	25	20	54	45	16	13
<i>Quercus kelloggii</i>	33	150	18	37	40	39	25	23

Mean- broadleafs	34	32	20	18