

Regeneration of *Eucalyptus delegatensis* R.T.Baker subsp. *delegatensis* (Alpine Ash) in Kosciuszko National Park after the severe 2003 and 2020 fires

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Abstract: *Eucalyptus delegatensis* R.T. Baker subsp. *delegatensis* (Alpine Ash) is the dominant canopy species in large areas of montane forest in the Australian Alps. As the species is killed by high severity fire, minimal intervals between fire are required for the species to germinate and to reach reproductive maturity to ensure stand persistence. In 2003 and again in 2020, extensive high severity fires occurred in southeastern Australia. These burnt through large tracts of Kosciuszko National Park in New South Wales, where the 9309 ha of *Eucalyptus delegatensis* that burnt at high severity in both 2003 and 2020 is of particular management concern.

In 2021, using an existing array of *Eucalyptus delegatensis* dominated monitoring plots set up between 2008 and 2013, we undertook a survey of seedling regeneration in plots burnt either at low severity in 2003 and high severity in 2020 or burnt at high severity in both 2003 and in 2020. We found a highly significant tendency for greater recruitment in plots only burnt at high severity 2020 as compared with plots burnt at high severity in both 2003 and 2020. Despite this significant difference, there was still robust recruitment in the plots burnt twice at high severity and there were no plots where recruitment failure was observed. In mixed stands with other re-sprouting eucalypt species present, the overwhelming majority of seedlings post-fire were of *Eucalyptus delegatensis*. For plots burnt twice at high severity, greater recruitment of *Eucalyptus delegatensis* occurred in mid-elevation stands, as compared to stands at the lower and upper limits of the elevational range of the species within Kosciuszko National Park.

Despite the downward trend in *Eucalyptus delegatensis* seedling recruitment with short inter-fire intervals, the 17 year interval between 2003 and 2020 allowed early maturing saplings to establish a viable canopy seed bank. Monitoring the growth and survival of the post-2020 cohort of seedlings will be critical to inform appropriate fire management. Our dataset makes a significant contribution to understanding recruitment and survival in eucalypts post-fire in the Australian Alpine Bioregion and it will be important to continue to document the time to first flowering and fruiting of individuals in fire affected stands and to track the proportion of saplings reaching reproductive maturity over time, to gauge stand vulnerability to further high severity fires over coming decades.

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Introduction

Eucalyptus delegatensis R.T.Baker subsp. *delegatensis* (Alpine Ash) is a forest tree growing up to 40 metres in height. This subspecies occurs in montane forest communities in south-eastern Australia from the northern Brindabella Range in New South Wales southwards into eastern Victoria through to Mt Macedon. (Boland *et al.* 2006; Brooker and Kleinig 2006), with *Eucalyptus delegatensis* subsp. *tasmaniensis* Boland occurring in central, northern and eastern Tasmania (Boland and Dunn 1985). Individuals of subspecies *delegatensis* are killed after 100% canopy scorch, but adults can survive lower intensity surface or understorey fires where canopy scorch does not occur (Bowman and Kirkpatrick 1986a). In contrast, subspecies *tasmaniensis* is a strong epicormic resprouter (Rodriguez-Cubillo *et al.* 2020).

In New South Wales (NSW), *Eucalyptus delegatensis* is found primarily on steep to moderately sloping terrain across a wide range of aspects, occurring both in monospecific stands and in association with other eucalypts, particularly *Eucalyptus dalrympleana* subsp. *dalrympleana* (Mountain Gum) and *Eucalyptus pauciflora* (Snow Gum). Other less common associates are *Eucalyptus robertsonii* subsp. *robertsonii* (Robertson's Peppermint), *Eucalyptus dives* (Broad-leaved Peppermint), *Eucalyptus viminalis* (Manna Gum) and in northern areas *Eucalyptus fastigata* (Brown Barrel) (Costin 1954; Gellie 2005). The understorey found in *Eucalyptus delegatensis* stands varies from shrubby to grassy, with common high cover shrub species including *Daviesia mimosoides* subsp. *mimosoides*, *Daviesia latifolia*, *Daviesia ulicifolia*, *Acacia obliquinervia*, *Coprosma hirtella* and *Polyscias sambucifolia*. Herb and grass layers typically have a high cover of *Lomandra longifolia*, *Stellaria pungens*, *Asperula scoparia*, *Viola betonicifolia* and *Poa phillipsiana*.

Eucalyptus delegatensis dominated forests occupy approximately 105,000 ha of NSW, extending over 150 km from the Victorian border, through Kosciuszko National Park (KNP) and Bimberi Nature Reserve to Brindabella National Park, with the northern limit occurring immediately north of Mt. Coree. Within KNP, *Eucalyptus delegatensis* dominated forests occupy approximately 77,050 ha, representing 73% of the NSW extent of the species (Figure 1). Most stands of *Eucalyptus delegatensis* in KNP occur on slopes in the montane zone between 1000 m and 1400 m elevation, but the species can occur up to 1750 m elevation into the subalpine zone. Annual average rainfall across *Eucalyptus delegatensis* stands in KNP ranges from 850 mm-1700 mm per annum with an annual average temperature range of approximately 6.5°C -11.5°C. Most stands occur on plutonic rock types, but the species can also occur on volcanic and sedimentary geology.

Being fire-interval sensitive and subject to 'interval squeeze' (Enright *et al.* 2015), *Eucalyptus delegatensis* is likely to be adversely impacted by changes in climate and fire regimes (Bowman *et al.* 2014). In Victoria in 2003, several stands were fire-killed that had either been burned twice or logged in the preceding 20 years. These were predicted to mostly return as shrublands dominated by *Acacia* species, and a major effort was undertaken to reseed many of these areas, at a cost of

around \$1000 per hectare (Bassett 2013; Bassett *et al.* 2015; Fagg *et al.* 2013). However, it is unclear how much of the affected areas had no *Eucalyptus delegatensis* regeneration in the absence of aerial seeding. Boland (1985) raised a cautionary note regarding re-seeding and the potential for hybridisation between different provenances affecting the genetic integrity of natural populations, an issue first raised by Pederick (1976). At this stage, in the case of stands in KNP and adjacent reserves, no artificial re-seeding has been undertaken and the current management and monitoring regime which we outline below can be regarded as a 'natural experiment' (Diamond 1983; Green 2009).

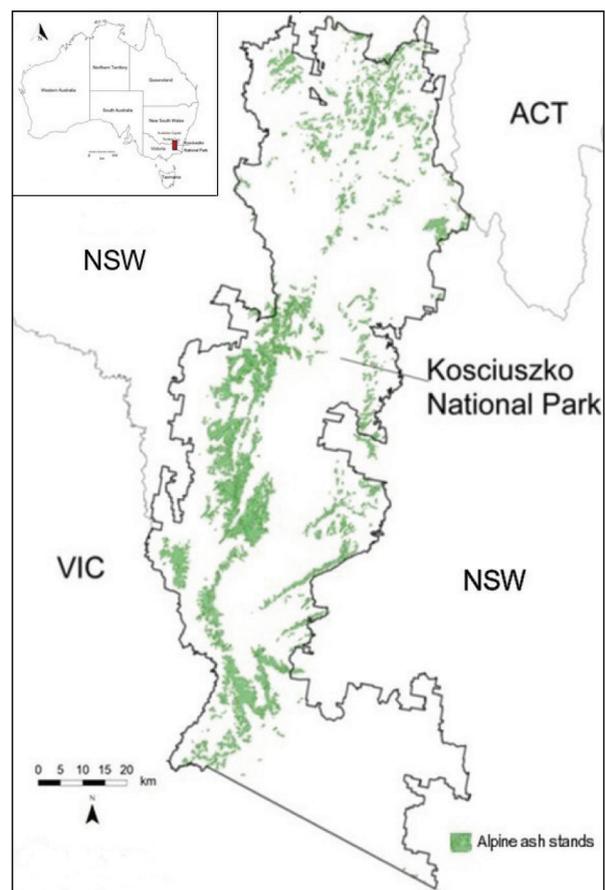


Figure 1. Distribution of Alpine Ash dominated stands in Kosciuszko National Park (Map: NSW Department of Planning & Environment).

KNP occurs in the Australian Alps bioregion (Thackway and Cresswell 1995) which is contained within the broader Southern Tablelands region of NSW. Climate change predictions for the Southern Tablelands are for a decline in rainfall, particularly in winter (NSW Office of Environment and Heritage 2014). Rainfall in winter is predicted to fall between 20-40%, with declines of up to 17% in spring and autumn, but an increase of between 18-29% in summer. The expected decline in winter rainfall is more significant than the increase in summer rainfall since most of the rain in the Australian Alps falls during the cooler months with the passage of cold fronts. It is the southward shift of these fronts that is expected to result in reduced rain and snowfall. Temperatures, both daily maxima and minima, are forecast to be 1.0 -2.5°C higher in all

seasons. Drier spells in the southern tablelands are likely to occur more often and there is likely to be an increased number of days of extreme fire danger. Severe and extensive wildfires usually occur after these conditions as for example occurred in 1926, 1939 and 2003 fires, which were each preceded by long periods of below average rainfall (Zylstra 2006). Such conditions are expected to become more frequent (Cai et al. 2014; Hennessy et al. 2005; Lucas et al. 2007).

Recent Fire history in Kosciuszko National Park

The most significant fire events in KNP since the 1939 fires (Zylstra 2006) are the large landscape fire events that occurred in 2003 and in 2020. While the majority of montane eucalypt species found within KNP resprout after even high severity fire, *Eucalyptus delegatensis* stands, being fire-killed, were significantly affected by these two fire events both singly and in combination.

In January 2003, approximately 49,500 ha (64.2%) of the 77,050 ha occupied by *Eucalyptus delegatensis* dominated stands in KNP was burnt. Fire severity mapping produced after these fires showed that of the 49,500 ha which burnt, 28,625 ha was burnt at high severity with 100% crown scorch, with the remaining 20,875 ha burnt at low severity without crown scorch (Barrett 2006). After the 2003 fire event, 37% of *Eucalyptus delegatensis* stands in KNP were in a fire-killed state with regeneration from canopy-stored seed required to re-establish stands. Seventeen years later in January 2020, the Dunns Road and northern Hume Complex fires burnt into the mid-northern and south-western parts of KNP (Figure 2) burning through approximately 25,100 ha (32.5%) of the area occupied by *Eucalyptus delegatensis* in the park. In the 2020 fire event, 19,077 ha burnt at high severity and 6,023 ha burnt at low severity. Of the total extent of *Eucalyptus delegatensis* in KNP, 25% burnt in both 2003 and in 2020.

However, because low severity fires do not kill adult *Eucalyptus delegatensis* trees, the area burnt on its own does not reflect the state of maturity and short-term fire sensitivity of *Eucalyptus delegatensis* stands.

The critical areas of concern are those stands that have burnt at high severity resulting in tree death either in 2003 or in 2020 and particularly stands that burnt at high severity in both fire events. The combined effects of the 2003 and 2020 fires in KNP have resulted in areas which fall into three categories:

- areas containing old mature trees that may be either long unburnt or which have only burnt at low severity in 2003 and/or in 2020,
- areas containing maturing sapling regrowth from the 2003 fires which did not burn in 2020,
- seedling regeneration in areas which burnt at high severity in both 2003 and in 2020, or at high severity only in 2020.

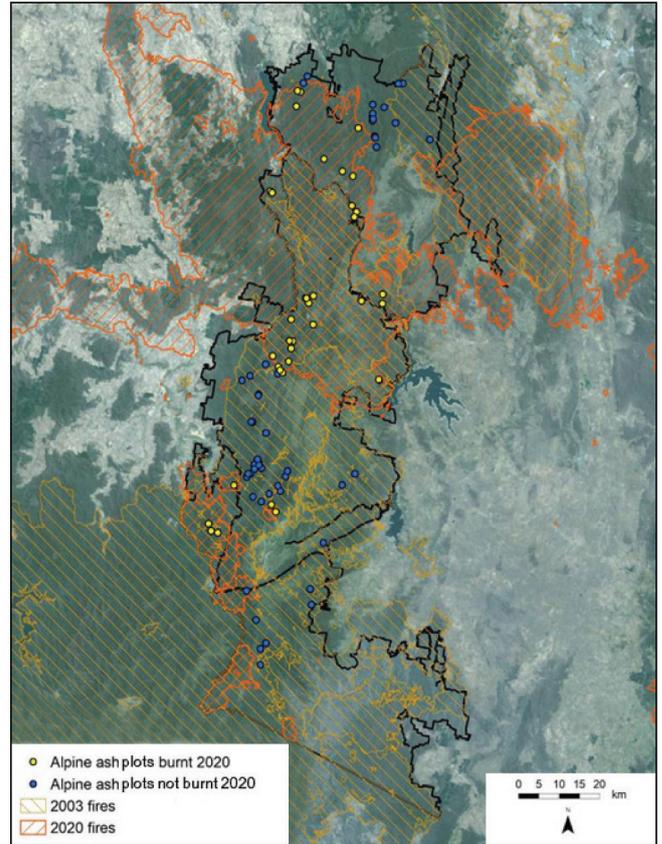


Figure 2. Alpine Ash monitoring plots in relation to the extent of the 2003 and 2020 fires in Kosciuszko National Park (Map: NSW Department of Planning & Environment).

A shift has occurred in these categories from 2003 to 2020, with only 38% of stands currently in a mature state (i.e. unburnt in 2003 and 2020, or else burnt in fires of low intensity which did not affect the canopy) and 62% of stands currently being either maturing saplings or recently germinated seedlings (Table 1).

Although the 2003 and 2020 fires had different footprints, of particular concern is the 9309 ha of *Eucalyptus delegatensis* that burnt at high severity in both 2003 and in 2020 (crosshatching in Figure 2). These twice-burnt areas had a 17 year recovery period which is a relatively short interval between stand-replacing fires for this species. *Eucalyptus delegatensis* saplings in these areas had not yet reached full maturity leaving these stands vulnerable to poor seedling recruitment or potential recruitment failure. The time to re-establish a canopy seed bank makes *Eucalyptus delegatensis* vulnerable to local extinction if a second fire occurs before adequate canopy seed is produced. Although the primary juvenile period of *Eucalyptus delegatensis* has generally been thought to be in the order of 20 years, recent evidence from stands in the Australian Capital Territory has shown that the species can produce viable seed in as little as 6 years post-fire (Doherty et al. 2017a). How widespread this phenomenon is across the full range of stands on mainland Australia is not yet documented.

Table 1. Regeneration status of stands of Alpine Ash in Kosciuszko National Park after the 2020 fires.

Regeneration Status	Pre-2003	12 months post-2003		12 months post-2020	
		Area (ha)	% of AA stands in KNP	Area (ha)	% of AA stands in KNP
Old Mature	77,050 ha	48,425	63	29,348	38
Sapling Maturing	Small area	0	0.0	38,393	50
Seedling Immature	Small area	28,625	37	9,309	12

Background to the Establishment of the Alpine Ash Monitoring Study in Kosciuszko National Park

In late October 2006, an unplanned fire started adjacent to Tooma Dam in KNP and burned 4000 ha of forest, all of which had also burned in 2003. Within the burn perimeter, *Eucalyptus delegatensis* stands occupied approximately 1000 ha. Because these stands had burnt in rapid succession in 2003 and 2006, there was an impetus to develop a monitoring programme to measure *Eucalyptus delegatensis* recovery specifically in the Tooma area and more broadly across KNP.

The life history of *Eucalyptus delegatensis* means that monitoring the species status and post-fire recovery in KNP must use fire history to ensure that plots are representative of the range of growth stages present in the park population. Monitoring of the *Eucalyptus delegatensis* plots has a short-term and a long-term aim: firstly to examine the impacts of and recovery from the 2003 and 2006 fire events and secondly, to monitor the impacts of climate change, focussing on any increases in fire frequency which have the potential to cause significant and lasting impacts on fire sensitive plant communities. The recent fires of 2019/2020 added further impetus to monitor *Eucalyptus delegatensis* stands for the impacts of recurrent fire. In this paper we report on the initial results of post-fire monitoring of *Eucalyptus delegatensis* germination and establishment in KNP after the 2003 and 2020 fires and outline areas for further research and monitoring.

Methods

Initial Stratification and Plot Selection

After the 2003 fires, a representative floristic and structural survey of *Eucalyptus delegatensis* dominated stands in KNP was developed using ArcGIS V9 (ESRI 2004) to stratify potential sample plot locations by fire history, elevation, and aspect. The primary stratification unit was fire severity mapping that was prepared after the 2003 fires (Barrett 2006). Work conducted after a fire near Tooma Dam in 2006 showed that the fire severity mapping categories of 'medium', 'high' and 'very high' were correlated with crown loss, with intact crowns corresponding to 'very low' and 'low' severities.

This allowed the entire area of the 2003 burn to be used in the stratification.

For all of KNP, the categories used were: 'not burnt', 'burnt but with an intact crown', or 'crown loss'. As the distribution of *Eucalyptus delegatensis* in KNP is strongly determined by elevation, a 25 m grid cell digital elevation model (DEM) was used to sub-divide the environment in which *Eucalyptus delegatensis* grows. Total annual radiation was also used in the stratification as radiation is a useful predictor of growth rate, with *Eucalyptus delegatensis* seed collected from plots of high insolation growing faster when planted in a range of different environments than seed from areas of low insolation (Garnier-Gere & Ades 2001). ArcGIS V9 was used to model radiation over the whole of KNP, in units of watt-hours/square metre. All layers were clipped to the boundaries of *Eucalyptus delegatensis* and associated canopy dominants using existing aerial photograph interpretation produced as part of the Southern Comprehensive Regional Assessment (Gellie 2005). The 'Combine' function was used to allocate grid cells to each combination of elevation, radiation and fire severity. Two classes of elevation and two classes of annual radiation were used in conjunction with the fire severity mapping to stratify the plot locations. An ArcGIS extension was used to randomly allocate eight replicate plots within each stratum. The potential plots were examined on the GIS, and repositioned where necessary to ensure that they were at least 50 metres from the boundary of the stratum.

Plot Sampling Regime

Initial sampling of 75 *Eucalyptus delegatensis* plots was undertaken from 2008-2010. After this initial sampling, an Australian Alps Liaison Committee (AALC) funded project was established in 2013 to re-monitor *Eucalyptus delegatensis* stands burnt at high severity in 2003 and those plots which re-burnt in 2006. New plots were also established to ensure that the full geographic range of *Eucalyptus delegatensis* within KNP was sampled. During this survey an additional 12 plots were established in *Eucalyptus delegatensis* stands. In total, between 2008 and 2013, 87 monitoring plots across the range of *Eucalyptus delegatensis* dominated vegetation were established and sampled by the NSW Department of Planning, Industry and Environment (DPIE) and Southern Branch of the NSW National Parks and Wildlife Service (NPWS). Plot size was consistent across all the plots sampled (see plot sampling methods below).

In April 2020 prior to the 2021 re-sampling and before any *Eucalyptus delegatensis* seedling recruitment had occurred, traverses were undertaken in selected areas that were burnt at high severity in both 2003 and in 2020 to ascertain the degree of capsule development on saplings that germinated after 2003. In total, 816 trees were examined in ten traverses in stands on Alpine Creek fire trail, Sawyers Hill, the Link Road, around Cabramurra, Snow Ridge Road, and Tooma Rd west of Round Mountain. All trees on the path of the traverse were assessed for capsule development. The time spent in each stand was proportional to stand size and varied from thirty minutes to two hours.

In 2021, 35 of the 37 *Eucalyptus delegatensis* plots identified as having been burnt in January 2020 were re-sampled. These plots were allocated into two categories based on the severity of the 2020 fires:

- a) Crown Loss 2020 (High Severity): 21 plots, of which 12 were burnt at high severity in 2003 and nine were burnt at low severity in 2003,
- b) Crown Intact 2020 (Low Severity): 14 plots, of which four were burnt at high severity in 2003 and 10 were burnt at low severity in 2003.

This paper discusses only those 21 plots where crown loss occurred after high severity fire in 2020.

Plot Sampling Methods

For the establishment of the initial plots up until 2013 a centre post was established at each plot and location was recorded to +/- 5m with a handheld GPS, so plots could be relocated. Portrait and landscape photographs were taken from the rear of each plot looking downslope. At each plot, a square plot of 20m x 20m around the centre post was used to record vegetation structure and vascular plant cover abundance, using a 0-6 modified Braun-Blanquet scale (Poore 1955).

For tree measurements, a 17.8 m radial plot (0.1 ha) from the centre of the plot was used in which seedlings, saplings (<2 m) and the diameter at breast height (DBH; 1.3 m above ground) of trees greater than two metres in height were recorded. Tree measurements were undertaken by each quarter of the radial plot for ease of counting.

For plot resampling in 2021, the same approach was used and ground truthing of the mapped fire severity class was also undertaken to confirm canopy loss. In addition, seedling counts were undertaken in each quarter of the radial plot, added together, and rounded to the nearest five seedlings for each plot. In this paper, we only report on the results of the seedling count analysis from 2021.

Analysis

Seedling counts were log transformed to bring the data closer to a normal distribution. To test for significant differences between the treatments, a two-sample t-test assuming unequal variances was undertaken on the transformed data in EXCEL. Model fitting was also undertaken on the transformed data, using a negative binomial GLM, with a log link function, in R (R Core Team 2020).

Stem data collected in 2013 also provided a basis to compare seedling germination post-2020 with pre-fire stand characteristics. For those plots burnt at high severity in both 2003 and in 2020, seedling counts were compared to sapling counts (DBH < 10cm). For those plots burnt at low severity in 2003 and high severity in 2020, seedling counts were compared to stem counts (DBH > 10cm) and mean DBH.

Results

Capsule Counts

Of the 816 standing dead *Eucalyptus delegatensis* trees which were assessed six months after the 2020 fires, 63.4% had no capsules (Table 2).

In these instances, it is unlikely that capsules had been consumed during the 2020 fire as overall, trees that had been burned with sufficiently high severity to consume all the branchlets still possessed capsules. Of the trees that did have capsules, 22.9% had >10 capsules per tree.

This was compared to data collected in 2014 on 24 plots which were burned at high severity in 2003. At 11 years post-fire, the percentage of regenerated saplings with fruit in 15 of these plots ranged from 3.4% to 38.7%. A further nine plots surveyed at the same time had much lower numbers of saplings. Five of these plots had no fruiting saplings 11 years post-fire, the other four plots had between one and nine fruiting individuals.

Table 2. Capsule counts on Alpine Ash saplings which germinated after the 2003 fires. Counts were undertaken in April and May 2020.

Number of Capsules per Tree	Number of Trees	%
>100	36	4
10-99	143	18
<10	120	15
None	517	63
TOTAL	816	100

The DBH was measured for 108 fruiting and 244 non-fruiting saplings during the survey work, but there was no significant difference in mean diameter between fruiting (mean DBH 6.1 cm) and non-fruiting (mean DBH 5.3 cm) saplings (t=1.52; df=172; P=0.12).

Alpine Ash Seedlings

For the 12 plots burnt at high severity in both 2003 and 2020, the seedling count ranged from 8 to 1835 seedlings per 0.1 ha, with a mean count of 646 per 0.1 ha (Figure 3). Plot 26 above Tumut Pondage and Plot 69 at Sawyers Hill had very low seedling counts of eight and 26 seedlings per 0.1 ha respectively. For the nine plots burnt at low severity in 2003 and high severity in 2020, the seedling count ranged from 385 to 6930 seedlings per 0.1 ha, with a mean count of 2305 per 0.1 ha (Figure 3).

There was a large apparent difference in means between the treatments, but a high variance associated with the data. The seedlings numbers in the Low/High treatment in particular show a wide range of variation across the plots and there is a large degree of overlap in the number of seedlings with the High/High treatment. After log transformation, results from the t-test indicated that there was a weak but significant tendency (t=2.49; df=19; P<0.05) for higher germination rates in the Low/High severity combination.

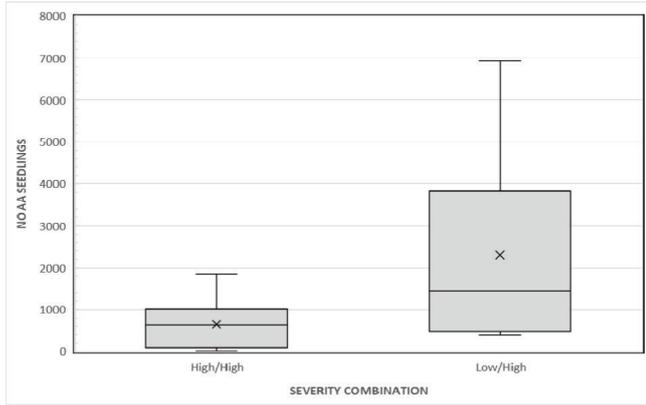


Figure 3. Box and Whiskers plot showing Alpine Ash seedling count raw data mean (cross within box), median (horizontal line within box), 25th and 75th-percentile (box boundaries) and highest and lowest values (whiskers) between areas burnt at high severity in 2003 and in 2020 (LHS) and areas burnt at low severity in 2003 and high severity in 2020 (RHS).

The application of a negative binomial GLM to the data showed a highly significant tendency ($P < 0.01$) for higher germination rates in the Low/High severity combination:

The limited data from capsule counts shows a moderate linear correlation with seedling counts ($R^2 = 0.73$; $P < 0.05$), but with a high degree of variability from plot to plot (Figure 4). The data suggest that by the time 25% of individuals in a stand are fruiting, the post-fire seedling response after high severity fire is likely to be adequate for stand re-stocking.

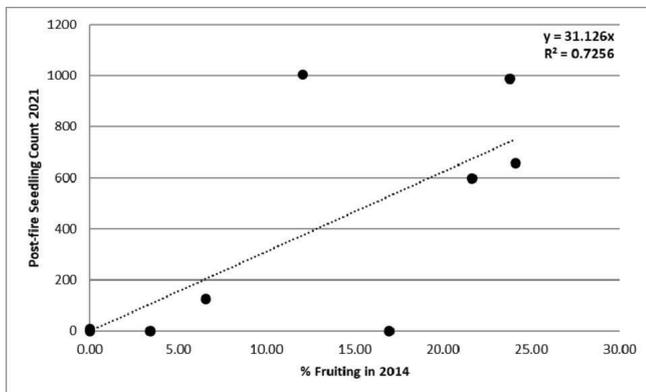


Figure 4. Relationship between fruiting on Alpine Ash saplings that germinated post-2003 and counted in 2014, to Alpine Ash seedling counts post-2020, for 9 of 12 plots burnt at high severity in 2003 and 2020.

The relationship between seedling emergence and elevation varied between those plots burnt twice at high severity and those only burnt at high severity in 2020. In the former, there was a moderately strong polynomial relationship ($R^2 = 0.61$; $P < 0.05$) with a peak of seedlings at middle elevations (1200-1300 m) and drop in numbers at both lower and higher elevations (Figure 5). In the latter case, there is a similar but weak polynomial relationship ($R^2 = 0.28$; $P = 0.46$) with a general increase in seedling numbers with increasing elevation (Figure 6).

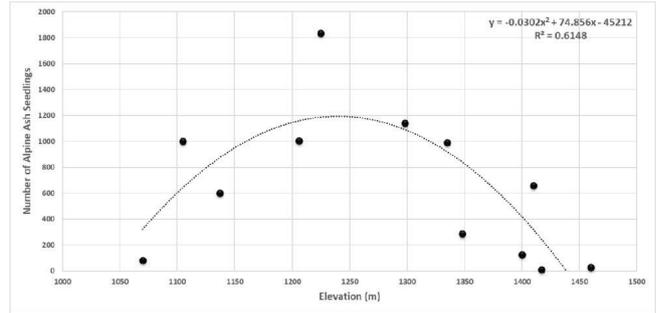


Figure 5. Relationship between elevation and numbers of Alpine Ash seedlings for 12 plots burnt at high severity in 2003 and high severity in 2020.

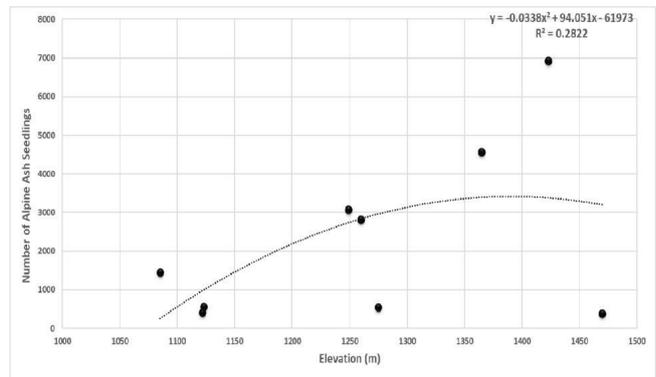


Figure 6. Relationship between elevation and numbers of Alpine Ash seedlings for 9 plots burnt at low severity in 2003 and high severity in 2020.

Using 2013 data, the relationship between elevation and stem counts 10 years after the 2003 fires was used for comparison. For plots burnt at high severity in 2003, the resulting pattern of numbers of saplings showed a weak polynomial relationship ($R^2 = 0.12$; $P = 0.72$) with a peak in the number of saplings found in stands of *Eucalyptus delegatensis* at intermediate elevations (Figure 7).

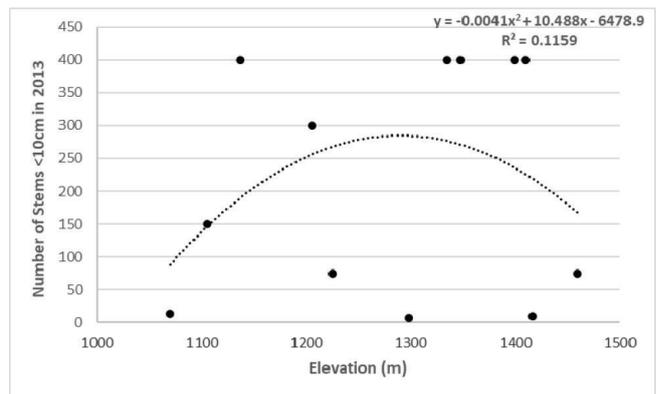


Figure 7. Relationship between elevation and number of Alpine Ash stems found in 12 plots burnt at high severity in 2003, as measured in 2013.

For plots burnt at low severity in 2003, the resulting pattern of numbers of large stems in 2013 showed a weak polynomial relationship ($R^2 = 0.30$; $P = 0.44$) with a peak in the number of stems of trees at intermediate elevations (Figure 8).

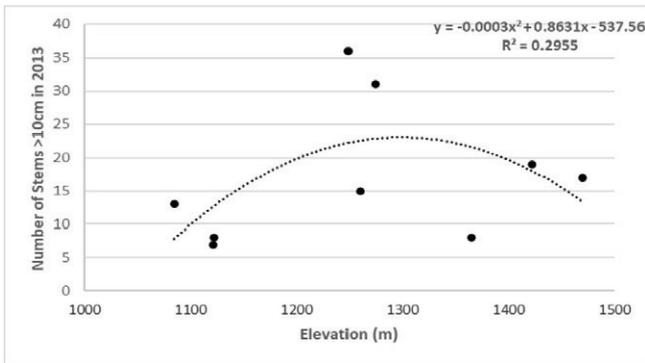


Figure 8. Relationship between elevation and number of Alpine Ash stems found in 9 plots burnt at low severity in 2003, as measured in 2013.

These data from the 2013 and the 2021 samples suggest that there is an optimum elevation for recruitment of *Eucalyptus delegatensis* between approximately 1200 m and 1300 m, in the middle of the altitudinal range of the species in KNP.

There was only a weak relationship ($R^2=0.16$; $P=0.61$) between number of sapling stems <10cm DBH and seedling recruitment in plots burnt at high severity in both 2003 and 2020 (Figure 9). The relationship suggests a peak of seedlings at intermediate numbers of saplings (approximately 200).

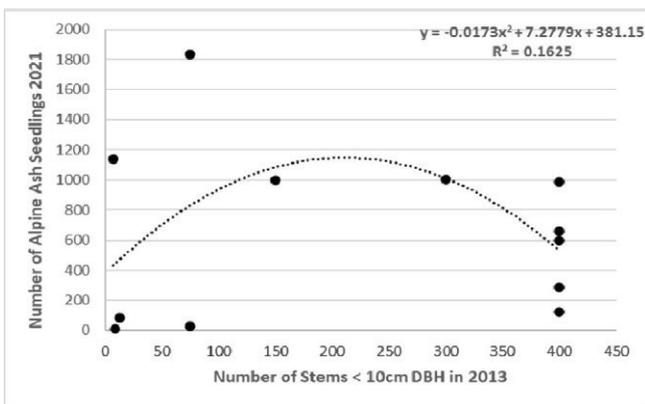


Figure 9. Number of stems of Alpine Ash <10cm DBH in 2013 vs Alpine Ash seedling count in 2021 for 12 plots burnt at high severity in 2003 and high severity in 2020.

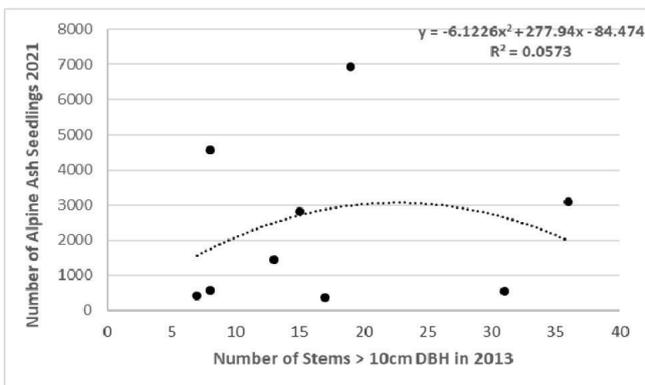


Figure 10. Number of Alpine Ash stems >10cm DBH in 2013 vs Alpine Ash seedling count in 2021 for 9 plots burnt at low severity in 2003 and high severity in 2020.

Similarly for those plots burnt at low severity in 2003 and high severity in 2020, there was a very weak polynomial relationship ($R^2=0.06$; $P=0.88$) between number of stems >10cm DBH (Figure 10) and post-fire seedlings with a similar mid-range peak of number of stems to number of seedlings post-fire.

All Eucalypt Seedlings

As well as a detailed count of *Eucalyptus delegatensis* seedlings on the plots sampled, seedlings of other co-occurring eucalypts were counted. The other common co-occurring eucalypts that grow with *Eucalyptus delegatensis* are *Eucalyptus dalrympleana* subsp. *dalrympleana*, *Eucalyptus pauciflora*, *Eucalyptus robertsonii* subsp. *robertsonii* and *Eucalyptus viminalis*. All these species will resprout after high severity fire and given the re-sprouting ability of these species, they are not dependent on seedling recruitment after fire in the short term (Bryant 1971; Noble 1984).

The overwhelming majority of seedlings observed on plots burnt at high severity in 2020 were *Eucalyptus delegatensis* (Figure 11). There is a slightly higher percentage of *Eucalyptus dalrympleana* subsp. *dalrympleana* seedlings in the plots burnt twice at high severity, but this difference is still only a very small percentage of the total number of seedlings counted.

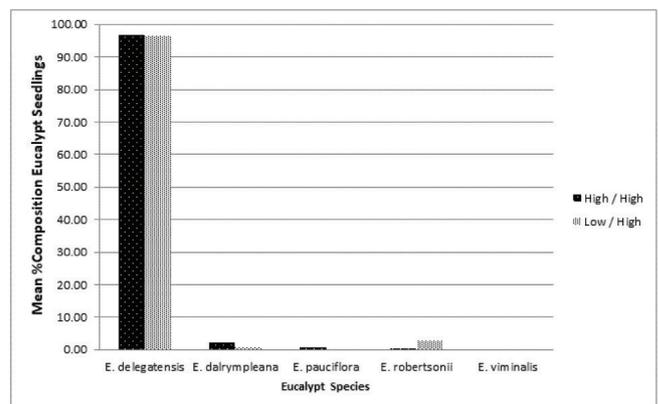


Figure 11. Percentage composition of eucalypt seedlings in plots burnt at high severity in 2020. High/High plots burnt at high severity in 2003 and in 2020; Low/High plots burnt at low severity in 2003 and at high severity in 2020.

Discussion

Capsules

Despite the relatively short 17-year interval between high severity fires in 2003 and 2020 in KNP, successful seedling recruitment of *Eucalyptus delegatensis* has occurred on all plots burnt at high severity in 2020. The relatively low numbers of fruiting capsules in many stands burnt at high severity in 2003 is not surprising, but the high variability between plots with the same fire history means that some plots have much higher capsule counts. The resulting trend that hundreds of seedlings are likely to establish when more than 25% of trees in a stand have fruited was partially a time-since-fire

effect, but also a function of differential growth rates post-fire between plots.

In *Eucalyptus delegatensis*, flowering and fruiting can begin from at least six years of age, so a small but growing canopy seed bank was accumulating for 11 years between the two high severity fire events. Wright and Robertson (2014) found evidence of *Eucalyptus delegatensis* stands in KNP producing fruit within 10 years of the 2003 fires and it has been established that *Eucalyptus delegatensis* seedlings can produce fruit and importantly, viable seed, from at least six years after stand replacing fires in the northern parts of the Australian Alps (Doherty et al. 2017a). Given that the time from bud initiation to fruit development can take over three years (Cremer et al. 1984), some individuals may be beginning to develop buds as early as three to four years after germination. Field observations to date suggest that suppressed individuals in *Eucalyptus delegatensis* stands are more likely to flower and fruit earlier than fast growing individuals. This contrasts with *Eucalyptus regnans* (Mountain Ash) in Victoria, where rapidly growing individuals are more likely to produce seed (von Takach Dukai et al. 2018). Early flowering and fruiting has also been recorded in other fire-killed ash group eucalypts in NSW including *Eucalyptus oreades* (Blue Mountains Ash) (Glasby et al. 1988) and *Eucalyptus fraxinoides* (White Ash) (Newbery et al. 2022).

Seedlings

Although *Eucalyptus delegatensis* seedling numbers at plots which burnt *only* at high severity in 2020 are significantly higher than those at plots burnt at high severity in *both* 2003 and 2020, this initial difference may not necessarily affect stand structure in the medium to long term. Larger numbers of *Eucalyptus delegatensis* seedlings emerging post-fire increases the probability of at least some individuals persisting and ultimately attaining reproductive maturity. However, there is naturally a very high attrition rate of seedlings and saplings until a mature forest structure is attained (Forestry Tasmania 2010). Most of the germinating seedlings will ultimately die during the time it takes to establish a mature tall open forest structure. Conceptually, a stand could reach a mature structural state after self-thinning from a very large initial number of seedlings developing into saplings over many decades, or else a stand could reach a similar structure through a less intensely competitive process starting with significantly fewer seedlings. At present, there is insufficient information to evaluate the relative time frames of either scenario, particularly under short-interval fire. However, at this time post-fire in the areas surveyed, there is adequate seedling recruitment to naturally re-stock stands burnt at high severity in 2020, notwithstanding any future high severity fire events that may occur.

For stands burnt twice at high severity the mid-elevation peaks in seedlings post-fire - with low numbers at the low and high ends of the altitudinal range of the species - suggests that macro-climatic and micro-climatic factors e.g. length of snow cover, severity of frost and solar radiation may play a part in keeping seedling numbers lower post-fire at the

extremes of the species range (Battaglia and Reid 1993; Bowman and Kirkpatrick 1986b; Florentine et al. 2008). These post-fire environmental factors and the interaction with fire frequency and fire severity likely bound the realised niche of *Eucalyptus delegatensis* in the Australian Alps (Gale and Cary 2021; Singh et al. 2021). But whether there are thousands or hundreds of seedlings in a stand, they are equally susceptible to short-interval fires.

High severity fire not only provides the necessary conditions for successful *Eucalyptus delegatensis* seedling regeneration, but also for the regeneration of other co-occurring eucalypts. Over evolutionary time, the interaction of fire regimes with climate, micro-climate and substrate has produced both pure and mixed stands of *Eucalyptus delegatensis* in KNP. In mixed stands, there are at least some individuals of *Eucalyptus dalrympleana* subsp. *dalrympleana*, *Eucalyptus robertsonii* subsp. *robertsonii* or *Eucalyptus pauciflora* present. The mixing of other eucalypt species within *Eucalyptus delegatensis* dominated stands, as well as the proximity of *Eucalyptus delegatensis* stands to other montane forest types dominated by other eucalypt species, would suggest that the composition of stand dominants could change after high severity fire with seedling recruitment from a range of eucalypt species. However, evidence to date in the northern extent of the range of *Eucalyptus delegatensis* suggest that this is not happening in the short term, with stand boundaries stable after high severity fire (Vivian et al. 2008).

Because all eucalypt species carry a canopy seed bank there are opportunities for all species present to regenerate from seed post-fire (Hillis and Brown 1984; House 1997; Pryor 1976). The advantage that other co-occurring eucalypt species have over *Eucalyptus delegatensis* is that they are able to resprout from epicormic shoots or basally, enabling a greater ability to persist under recurrent fire irrespective of seedling recruitment (Gill 1975; 1981). It is therefore expected that changing fire frequencies and severities under climate change will put selective pressure on stand composition and structure. The resprouting ability of eucalypt species other than *Eucalyptus delegatensis* may lead to a transition in composition and structure from fire-killed *Eucalyptus delegatensis* stands to more fire tolerant mixed eucalypt stands, but whether this happens naturally or needs to be facilitated is an open question (Colloff et al. 2016; Doherty et al. 2017b). Although fire-killed *Eucalyptus delegatensis* stands with little or no natural regeneration have been successfully re-seeded in some parts of the Victorian alps (Bassett et al. 2015), such stands remain vulnerable to repeated fire despite a large financial re-investment in re-seeding. Additionally, given the potential for differential performance of the species across its elevational range based on existing genotypic variation, we suggest a cautionary approach is warranted to broad area re-seeding until more is known about the mixing of *Eucalyptus delegatensis* genotypes.

Observations of current sapling and seedling regeneration show that most of the current extent of *Eucalyptus delegatensis* tall open forest in KNP is either mature or else is still capable of growing into mature tall open forest contingent on the next high severity fire event. However, with very frequent high severity fire, *Eucalyptus delegatensis* stands could become open with few stems, potentially moving in a trajectory toward shrubland or grassland. Such transitions have to date occurred in small areas, as for example in some stands of *Eucalyptus regnans* in Victoria after the 1939 fires (Ashton 2000; Costermans 2010) but there is concern that much larger areas of montane forest will be susceptible to rapid transitions to non-forest vegetation under a future of short-interval high severity fires (Bowd et al. 2023). Alternatively, in mixed stands where there are also some resprouting eucalypt species present, a trajectory toward increasing dominance by resprouting species could occur, involving a transition to a different forest type rather than a transition from forest to shrubland or grassland (Doherty et al. 2017b). Both possibilities could occur in KNP.

There are signs in some plots of what a transition may look like if fire frequency increases. An example is Plot 69 (Figure 12), which was burnt in 1939 and had successful recruitment and regeneration after the 2003 fire event, but which has had poor recruitment after the 2020 fires, with only 26 seedlings counted in 2021. This plot had a mature but open structure prior to being burnt at high severity in 2003. In more typical mature stands which only burnt at high severity in 2020, the structure showed a greater density of dead stems reflecting the higher stem densities in forest which have as yet not undergone a regime of too frequent high severity fire events (Figure 13).



Figure 12. Alpine Ash stand at Sawyers Hill burnt at high severity in 2003 and at high severity in 2020. Large dead standing trees are those killed in 2003. Layer of dead saplings are those trees which germinated after 2003 and were killed in 2020. Plot 69, elevation 1460 m. (Photo: M. Doherty).



Figure 13. Alpine Ash stand near Cabramurra burnt at low severity in 2003 and at high severity in 2020. Large dead standing trees are those killed in 2020. Plot 25, elevation 1417 m. (Photo: M. Doherty).

In all cases where plots were burnt at high severity, there was a marked flush of shrub, herb and grass re-growth, particularly large tussocks of multiple species of *Poa*. However, there is no evidence that this affected the ability of *Eucalyptus delegatensis* seeds to germinate and establish. The rapid growth rates of *Eucalyptus delegatensis* seedlings in the first twelve months post-fire ensures that they establish well before the re-establishment of shrub, herb, and grass layers (Figures 14 and 15). These understorey layers typically begin to accrue a high biomass and cover approximately two years post-fire and beyond (Doherty and Wright 2004; 2005).

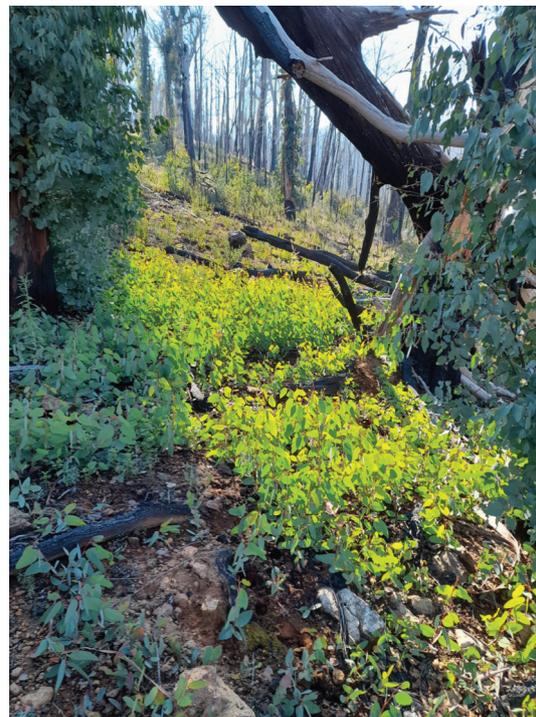


Figure 14. Alpine Ash seedlings north of Yarrangobilly 15 months post-fire. Taller re-sprouting trees on left and right and at rear are Mountain Gum. Near Plot 61, elevation 1225 m, burnt at high severity in 2003 and 2020. (Photo: M. Doherty).



Figure 15. Advanced Alpine Ash seedling 55 cm high northeast of Alpine Hill, 15 months post-fire. Plot 68, elevation 1348 m, burnt at high severity in 2003 and 2020. (Photo: M. Doherty).

In these first two years post-fire, seedling recruitment and regeneration from re-sprouting ensure a rapid establishment of overall plant cover. After this initial flush, plant growth rates slow as competition for light, water and nutrients becomes more intense.

Fire extent and frequency are expected to increase in the medium to long term in southeastern Australia, putting further pressure on fire-killed ash stands (Bowman *et al.* 2016; McColl-Gausden *et al.* 2021). Our dataset makes a significant contribution to understanding recruitment and survival in eucalypts post-fire in the Australian Alpine Bioregion. Monitoring the growth and survival of the post-2020 cohort of *Eucalyptus delegatensis* seedlings will be critical to inform appropriate fire management and it will be important to document the time to first flowering and fruiting of individuals in fire-affected stands and to track the proportion of saplings reaching reproductive maturity over time, to gauge stand vulnerability to further high severity fires over coming decades.

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