Comparative change in the spatial and temporal dynamics of alpine and subalpine treelines across the Victorian Alps, Australia

---

Aviya Naccarella

Thesis follows the publishing convention of the Australian Journal of Botany

A thesis submitted in partial fulfilment of the requirements

for the degree of BSc (Hons)

in the

Department of Ecology, Environment & Evolution

La Trobe University

Bundoora, Victoria

23 April 2018

Words:11,912

Declaration

I certify that the attached document is my original work. No other person's work has been used without due acknowledgement. Except where I have clearly stated that I have used some of this material elsewhere, it has not been presented by me for examination in any other course or subject at this or any other institution. I understand that the work submitted may be reproduced and/or communicated for the purpose of detecting plagiarism.

None of the research undertaken in connection with this thesis required approval by a University Ethics Committee.

Full name: Aviya Naccarella

Subject: Bachelor of Science Honours Thesis

Document: Comparative change in the spatial and temporal dynamics of alpine and subalpine treelines across the Victorian Alps, Australia

Student signature:

Student Number:19062995

Date: 23rd April 2018

Thesis follows the publishing convention of the Australian Journal of Botany with exception of the word limit which follows the thesis guidelines of 12,000 words excluding figures, tables, references and appendices.

Contents

Abstract

Treelines are one of the most conspicuous vegetation transition zones driven by the sensitivity of trees to low temperatures. Consequently, treelines are predicted to advance beyond their current position in response to rising global temperatures. Currently, however, treelines across the globe are not responding as predicted. Despite the prominence of treeline studies globally, Australian treeline studies remain underrepresented. A recent increase in bushfire occurrence (2003, 2007 and 2013) across the Victorian Alps provided the opportunity to study the combined effects of rising temperature and fire frequency on alpine and subalpine treelines formed by Snow Gum (*Eucalyptus pauciflora*). This study used repeat photography dating back ~100 years, re-visitation surveys over the last ~20 years and dispersal modelling to assess temporal and spatial change. Treeline dynamics and woodland structure have remained relatively stable at landscape and local scales. Seedling recruitment has continued above treeline. However, high turnover of individuals suggests there are limiting factors impacting survival and growth (e.g. competition, drought, frost and recruitment limitation). Bushfires had marginal effects on dynamics, with high overall survival. Two fires within ten years may have impacted recruitment processes in conjunction with site-specific influences. Dispersal modelling of treeline species showed no clear trends between advance and dispersal distance. *E. pauciflora* was at the lower end of the dispersal spectrum, suggesting Australian treelines may be slower to advance than treelines elsewhere in the world. This study suggests the stability of Victorian alpine and subalpine treelines is likely due to a combination of limiting factors which continue to inhibit establishment and persistence of *E. pauciflora* above treeline. These findings resonate with global studies suggesting site-specific limiting factors are driving the variable response of global treelines to rising temperatures. Ultimately longitudinal studies on these factors will reveal the response of treelines to environmental change in the future.

1. Introduction

Treelines can be indicators of climate change, with the position of the treeline commonly used as a proxy for changes in climatic conditions over recent history (Slatyer and Noble 1992; Compostella and Caccianiga 2017). This is due to treelines being a thermal boundary, sensitive to changes in climatic conditions (Körner 2003, 2012). Global average temperatures have risen by ~0.85 °C since 1880, with the most rapid and significant increases occurring in high altitude and latitude regions (IPCC 2013). Global average temperatures are predicted to continue to rise by up to 4.8 °C by 2100 (IPCC 2013). This increase in temperature is predicted to cause alpine treelines to advance upslope, and subalpine areas to be invaded by trees as conditions become increasingly favourable for tree growth (Wearne and Morgan 2001; Holtmeier and Broll 2005; Körner 2007; Harsch *et al.* 2009).

There are a range of factors that influence the position of the treeline including precipitation, competition, herbivory, availability of safe sites, frost, regeneration, nutrient limitation or disturbance (Körner 1998; Holtmeier and Broll 2005). On a global scale, thermally inhibited treelines are driven by the inability of trees to utilize the products of photosynthesis and thus maintain a positive carbon balance at low temperatures (Slatyer and Noble 1992; Körner 1998; Grace *et al.* 2002; Paulsen and Korner 2004). Globally, this corresponds to a mean growing season soil temperature between 5-8 °C (Paulsen and Korner 2004). Subalpine grasslands are more strongly driven by local factors, specifically the occurrence of radiation frosts (Moore and Willaims 1976).

Australia contains two distinct treeline forms- alpine and subalpine. Alpine treelines are defined as the boundary between the upper limit of subalpine woodland and treeless alpine vegetation, dominated by *Eucalyptus pauciflora* subsp. *niphophila* and subsp. *pauciflora* (Slatyer 1989; Paulsen *et al.* 2000). There are strong aspect effects determining treeline altitude, extending up to ~1900 m on the warmer and drier northern and western aspects, and up to ~1750 m on cooler and wetter southern and eastern aspects (Slatyer 1989). Subalpine treelines border frost hollows and are defined as the boundary between subalpine grassland and subalpine woodland, dominated by *E. pauciflora* subsp. *pauciflora*, and *Eucalyptus stellulata* and *Eucalyptus perriniana* at lower elevations (Slatyer and Morrow 1977; Wearne and Morgan 2001).

Treeline response to climate

Despite warming, treelines are not responding predictably. Treeline advance, stability and retreat has been observed (Walther 2003; Harsch *et al.* 2009; Harsch and Bader 2011). A pivotal global meta-analysis by Harsh *et al.* (2009) found 52% of global altitudinal and latitudinal treelines had advanced over the last century, despite the majority of sites experiencing warming. Additionally, 1% had receded over this period. Treelines with a diffuse form and those that had experienced significant winter warming were more likely to have advanced, and those that had receded had evidence of disturbance. Increases in growth rates and infilling have been more commonly observed than spatial advance (Walther 2003; Körner 2012). This suggests that other local limiting factors may be overriding the influence of temperature, causing treeline positions to lag behind climate warming (Harsch *et al.* 2009).

The Victorian Alps have warmed by an average of ~0.4 °C since 1992 and are predicted to continue to warm by 0.6-2.9 °C by 2050 (Hennessy *et al.* 2008; BOM 2018). As such, treeline advance would be predicted to have already occurred. Slatyer (1978) calculated an altitude-temperature relationship (i.e. the lapse rate) for the Snowy Mountains, NSW Australia of 5.9 °C/km. Therefore, if temperature controls were greater than other modulating factors, there should be an advance of up to ~68 m, based on recent warming trends.

Treeline response to bushfires

There have been multiple fires in the Victorian Alps over the last two decades. Bushfires have historically been a relatively rare occurrence in Australian alpine areas with a predicted pre-European interval of 50-100 years (Williams *et al.* 2006, 2014). The recent atypical fire occurrence has stimulated discussion on the effects of bushfires on treeline dynamics and resilience of treeline populations in the future, as fire frequency and severity is predicted to increase with climate change (Williams *et al.* 2008, 2014; Bradstock *et al.* 2014; Coates 2015).

E. pauciflora is a facultative seeder, capable of regenerating through seed reserves in the canopy, epicormic regrowth from meristematic tissue in stems and basal regeneration from meristematic tissue in lignotubers following disturbances including bushfires, herbivory and severe frost (Bond and Midgley 2001; Pickering and Barry 2005). *E. pauciflora* is characterized as a “niche persistor” due to its capacity to reoccupy sites after disturbance, a trait most likely derived from the severe climatic conditions which constrain seedling establishment at high elevations (Billings 1969; Loveys *et al.* 2010; Green and Venn 2012; Coates 2015). As such, *E. pauciflora* treelines are largely unaltered by fire. However, resprouting capacity is dependent on lignotuber survival, which has been shown to decline with multiple fires (Coates 2015). Therefore, fire frequency and severity may be an important determinate on whether treelines reach their potential elevational limit under higher global temperatures with climate change (Colombaroli *et al.* 2010).

Limited research has been conducted on the dynamics of alpine and subalpine treelines in Australia, particularly within a global context. *E. pauciflora* physiology and forest ecology have been extensively studied in the past, including investigations into woodland-grassland boundary dynamics, germination, population structure, fire and grazing effects and altitudinal variability (e.g. Moore and Willaims 1976; Slatyer and Morrow 1977; Beardsell and Mullett

1984; Barker 1988; Ferrar *et al.* 1988; Ball *et al.* 1991). Studies have also provided further insight into treeline dynamics, including the effects of a single bushfire on alpine treelines, the formation and expansion of ‘tree ribbons’ above alpine treelines, and tree invasion into subalpine grasslands (Wearne and Morgan 2001; Pickering and Barry 2005; Green 2009; Green and Venn 2012; Coates 2015). However, few studies have investigated temporal change in *E. pauciflora* woodlands focusing on the treeline ecotone and in response to multiple bushfires. A recent study by Fairman *et al.* (2017) indicated multiple short-interval bushfires threaten the persistence of lower elevation *E. pauciflora* woodlands. The recent atypical bushfire occurrence has put into question if treeline populations are equally vulnerable to multiple short-interval bushfires. The negative consequences of rising bushfire frequency may impede treeline advance predicted to occur under warmer climates (Colombaroli *et al.* 2010).

This study aims to identify the current status of treelines in the Victorian Alps. In particular, the aims were to:

1) Investigate change in treeline position at the landscape-scale over ~100 years through the comparison of historical and modern photographs.

2) Explore how local treeline dynamics and woodland structure have changed over a ~20 year period in light of rising average temperatures and a recent increase in bushfire occurrence, using a re-visitation approach.

3) Explore seed dispersal as a potential constraint to treeline advance to determine if dispersal limitation may be driving the inconsistent response of global treelines to warming temperatures.

2. Materials and Methods

2.1 Assessment of landscape-scale change in treelines across the Victorian Alps through repeat photography

To determine the change in treeline position at the landscape-scale over ~100 years, historical images were interpreted and compared to current images of the same locations. Four historical ground and two aerial photographs of the Victorian Alps region were sourced from publically accessible archives (State Library of Victoria and National Library of Australia Trove) and private collections. These images were taken during the period of 1928 to 1961. Ground-based photographs were relocated, aligned and re-photographed between 2016 and 2018. Aerial photographs were relocated and modern photographs sourced from publically accessible satellite imagery (Google Earth 2018).

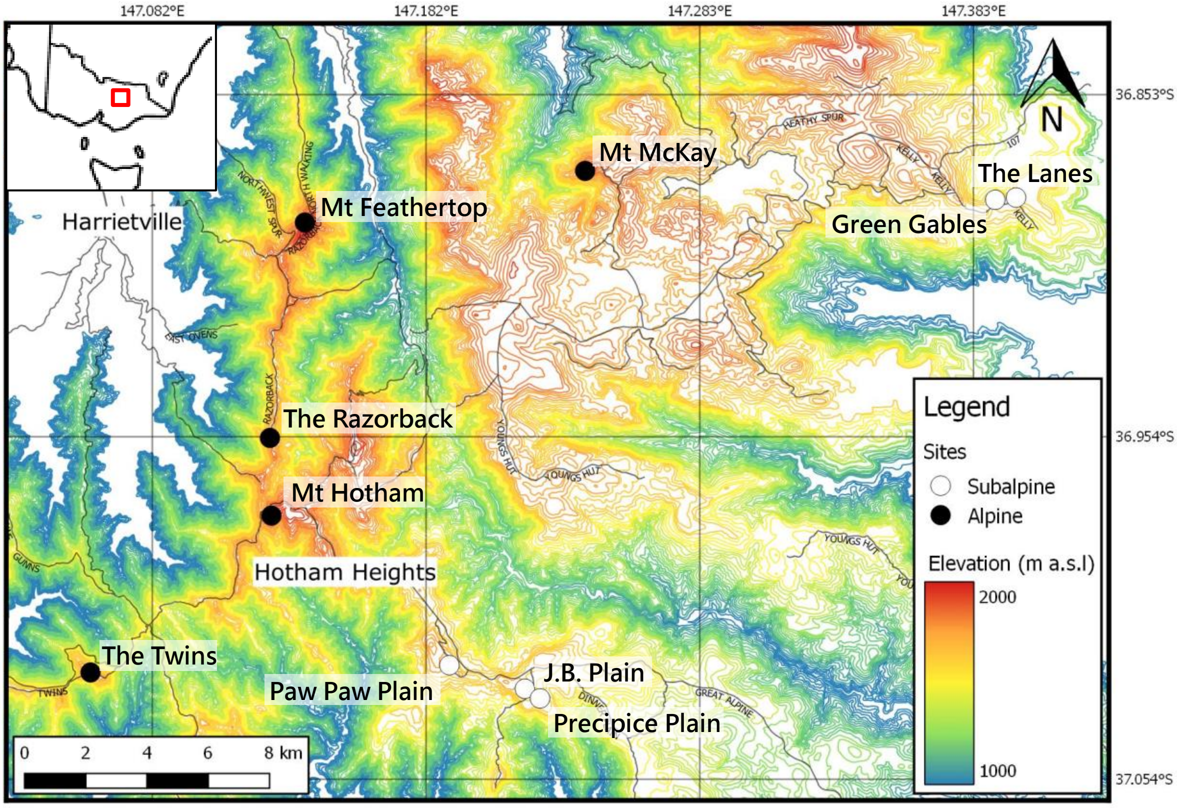
Quantitative comparisons of treeline elevation or tree density were unable to be estimated due to: image quality, inability to differentiate tree and shrub cover, and image resolution where resprouts from basal lignotubers were unclear. Thus, photographs were compared qualitatively to provide a longer time sequence and broader landscape scale perspective to complement the short-term revisitation study (described below). Qualitative analyses were conducted by focusing on select areas in the landscape within photographs and comparing the relative position of the treeline, the presence of outpost trees, and observed density of trees between time periods.

2.2 Assessment of the current state of alpine and subalpine treelines through re-visitation surveys

Study Area

To determine change in treeline position and subalpine woodland structure at the local-scale, a network of alpine and subalpine treeline sites (dating back ~ 20 years) were resurveyed. The re-visitation study was conducted in the Mount Hotham (36.98 °S, 147.13 °E) and Falls Creek regions (36.87 °S, 147.28 °E) of the Victorian Alps, Australia. These regions are characterised by low temperatures, with an annual mean maximum temperature between 8-9.4 °C and minimum temperature between 1.9-2.6 °C (Mount Hotham, BOM 2018). Annual mean precipitation is 1274-1454 mm, falling predominantly as winter snow (BOM 2018). Frost frequency varies inter-annually. Over the last five years, frost frequency has ranged from 8-23 % of days during the growing season (October to March) (BOM 2018). Alpine soils are influenced by a combination of the parent rock, topography and climate (Slattery 2015). There were no clear differences in recorded soil characteristics (moisture, pH, electrical conductivity or depth) across the treeline ecotone (Appendix A).

Four alpine peaks and five subalpine grasslands were selected for resurveying based on surveys by Wearne (1998), Cutler (2002) and J. Morgan (unpubl. data) (Figure 2.1, Table 2.1)(Appendix C Table 1). Grazing has occurred historically throughout this region from the early 1800’s (Lawrence 1999). Grazing history is variable across sites with cessation of grazing from 2005 across all sites (Table 2.1).



Data sourced from Department of Environment, Land, Water and Planning

Figure 2.1 Location of alpine and subalpine sites across the Mount Hotham and Falls Creek Region, Victoria, Australia.

Table 2.1 Characteristics of alpine and subalpine sites. Grazing history sourced from Lawrence (1999).

Treeline Form	**Site**	**Previously surveyed**	**Transect**	**Aspect**	**Altitude (m a.s.l)**	**Grazing Removed**
Alpine	Mount Feathertop	Cutler (2002)	1	N	1789	1958
			2	NW	1785	
			3	W	1881	
			4	W	1776	
	The Razorback		1 (added)	E	1648	1958
			2 (added)	NW	1746	
	Mount Hotham	Cutler (2002)	1	W	1796	1958
			2	W	1830	
			3	NW	1795	
			4	SW	1792	
			5	SW	1794	
	Mount McKay	Cutler (2002)	1	NW	1770	1981
			2	S	1710	
			3	S	1684	
			4	NW	1799	
	The Twins	Cutler (2002)	1	N	1657	2003
			2	N	1649	
			3	N	1659	
			4	W	1677	
			5	W	1681	
			6	W	1673	
Subalpine	Paw Paw Plain	Wearne (1998)	1	E-W	1655	2004
			2	E-W	1648	
			3	E-W	1639	
	Precipice Plain	Wearne (1998)	1	N-S	1605	2004
			2	N-S	1605	
			3	N-S	1603	
	JB Plain	Wearne (1998)	1	E-W	1645	2004
			2	E-W	1634	
			3	E-W	1626	
	The Lanes	J. Morgan, unpubl. data (2001, 2011)	1	NE-SW	1572	2005
			2	NE-SW	1572	
			3	NE-SW	1572	
	Green Gables	J. Morgan, unpubl. data (2001, 2011)	1	N-S	1590	2005
			2	N-S	1590	

Study sites were burnt in the 1926 bushfires, which burnt all subalpine sites and Mount Feathertop, and the widespread landscape scale 1939 fires which burnt all sites (Lawrence 1999). Since last surveyed, sites have been burnt unevenly in the 2003, 2007 and 2013 bushfires (Table 2.2, Figure 2.2).

Table 2.2 Recent fire history (2003, 2007 and 2013 bushfires) per site based on The Victorian State Department of Environment, Land, Water and Planning spatial data. X indicates sites burnt in each fire.

Treeline Form	Site	2003	2007	2013
Alpine	Mount Feathertop	X		
	The Razorback	X		X
	Mount Hotham			
	Mount McKay	X	X	
	The Twins	X	X	X
Subalpine	Paw Paw Plain	X		
	Precipice Plain	X		
	JB Plain	X		
	The Lanes	X		
	Green Gables	X		

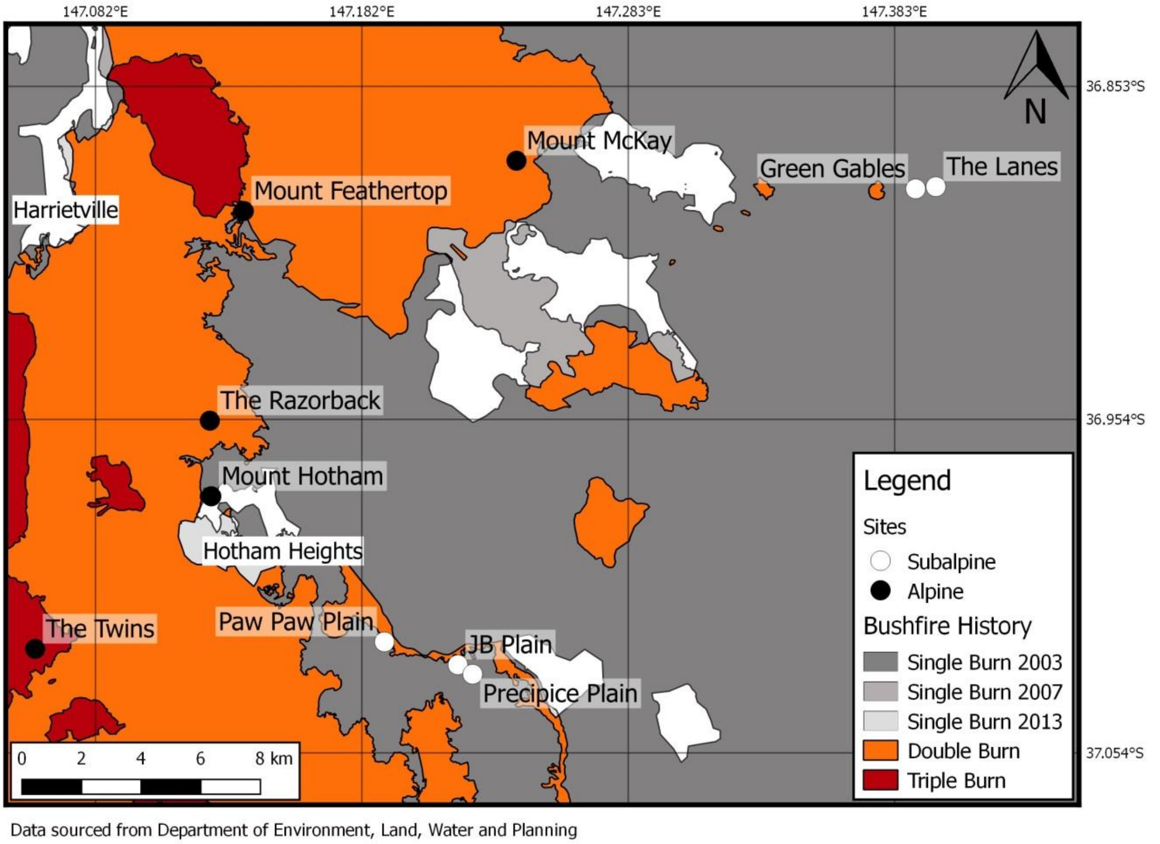


Figure 2.2 Location of alpine and subalpine sites in relation to recent fire history of the Victorian Alps region.

Field Methods

Environmental Variables

To quantify differences in environmental conditions below and above treeline soil and air temperature was recorded throughout the growing season (November 2017 to March 2018) at two representative alpine (Mount Hotham and Mount McKay) and subalpine sites (Green Gables and Paw Paw Plain). Measurements were made at ~40 m below treeline, at the treeline and ~40 m above treeline.

Soil temperature was measured approximately 10 cm below ground. Air temperature was measured at ground level (0 cm), 30 cm and 60 cm above ground (Figure 2.3). These heights were chosen to quantify changes in temperature with height as trees grow amongst (0 cm) and above (30 cm and 60 cm) the surrounding vegetation. This investigation was stimulated by research on the thermal inhibition of *E. pauciflora* by surrounding grass and suggestions of a thermal height threshold inhibiting seedling growth (Ball *et al.* 1991, 2002; Cutler 2002). Thermochron i-button loggers recorded temperature at two-hour intervals. Based on availability, DS1921G-F5 (minimum temperature recording -40 °C) were preferentially used above ground and for above treeline positions, and Thermochron i-Button DS1922T (minimum temperature recording -1.2 °C) were preferentially used for -10 cm positions, as soil temperatures are generally above zero, and below treeline positions. Hence, comparisons of Growing Degree Days (GDDs) and frost days between locations and heights are made, rather than evaluation of exact temperature minima or maxima. i-Buttons were covered in waterproof silicon tape and those within the soil and at ground level further placed in three plastic zip lock bags to prevent water damage. Two i-Buttons were left without silicon tape to determine the influence of tape on temperature. Air temperature loggers were positioned within 10 cm x 10 cm Stevenson screen boxes constructed of corrugated cardboard, with vented sides to shield the loggers from direct sunlight (Terando *et al.* 2017). Data from i-

Button loggers was subsequently calibrated to account for the warming effect of the silicon tape (+1.81 °C).

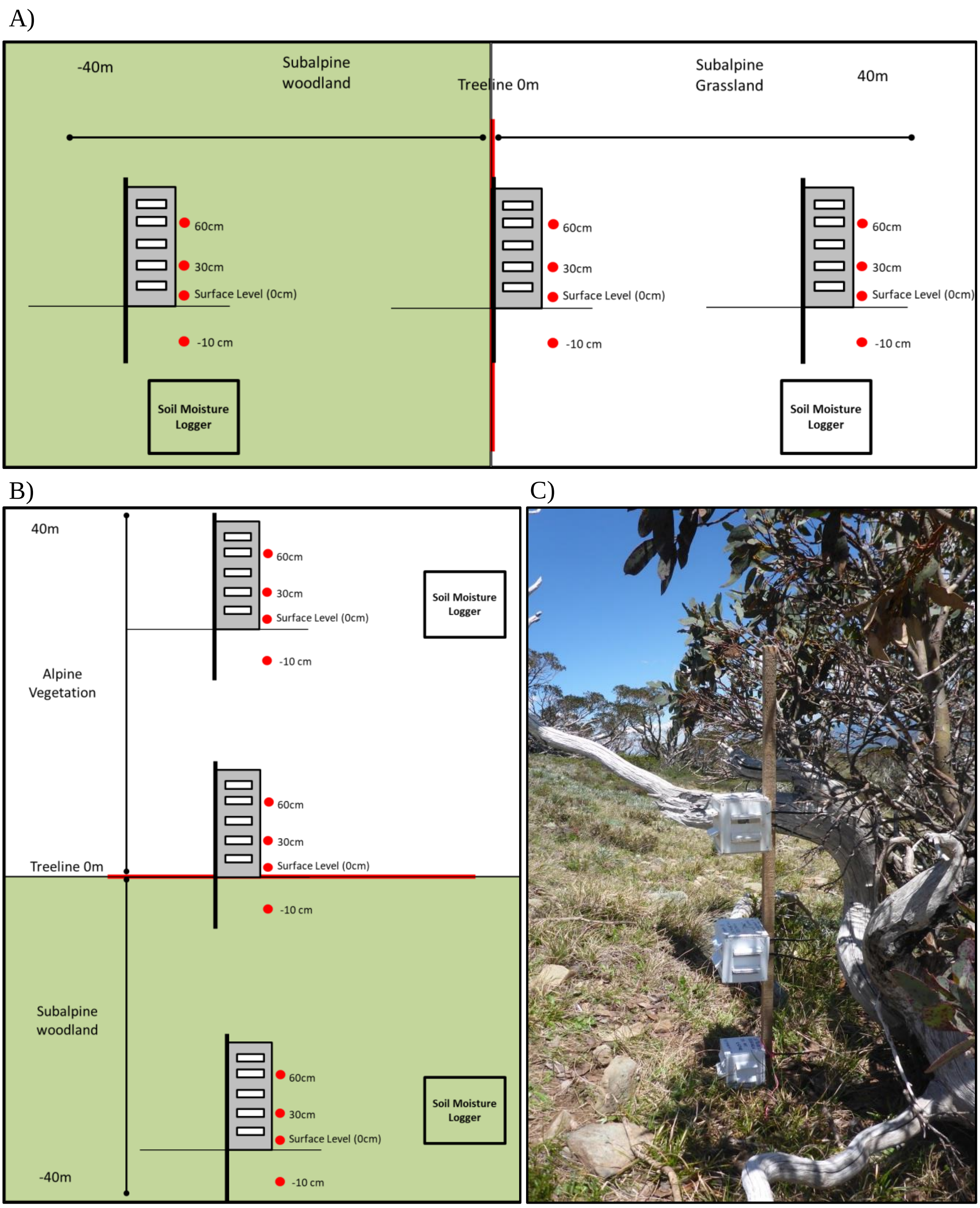


Figure 2.3 Position of temperature and soil moisture loggers at subalpine sites (A), alpine sites (B) and an example of Stevenson screens housing i-Button temperature loggers at varying heights above ground at Mount Hotham. Green areas represent woodland and white areas represent alpine or grassland vegetation. Soil moisture logger methods referred to in Appendix A.

Resurveying Alpine and Subalpine Treelines

Treeline transects were re-surveyed across alpine and subalpine sites. In the absence of permanent markers, alpine transects were relocated as close as possible to the original transects in representative vegetation. At alpine sites a combination of GPS positions, assistance from the original researcher (S. Cutler *pers. comm.* January 2018), original field notebooks and historical tree distributions were used to relocate transects in areas of similar treeline structure (Cutler 2002). At two subalpine sites (The Lanes and Green Gables) permanent transect markers were available to accurately relocate transects and compare individual trees over time. The remaining subalpine sites transects were positioned in locations in the upper, middle and lower section of each grassland based on the methods described in Wearne (1998). As such, change over time (in most cases) represents local-scale changes in treeline dynamics and woodland structure as opposed to change in individual trees.

A total of 19 alpine and 14 subalpine transects were resurveyed in January 2018. Belt transects were positioned perpendicular to the treeline. Alpine transects followed methods by Cutler (2002). Transects were 5 m wide and ran 40 m downslope from the treeline. The area above the treeline was searched and transects extended to encompass all outpost individuals. At subalpine sites transects ran from one side of the woodland, across the grassland and into the woodland on the opposing side. At Paw Paw, Precipice and JB Plain subalpine sites 10 m wide transects were used and ran 40 m into the woodland on both sides as per methods by Wearne (1998). At Green Gable and The Lanes subalpine sites 5 m wide transects were used and transect length was transect specific as per methods by J. Morgan (unpubl. data) (Figures 2.4 and 2.5) (Appendix C Table 1).

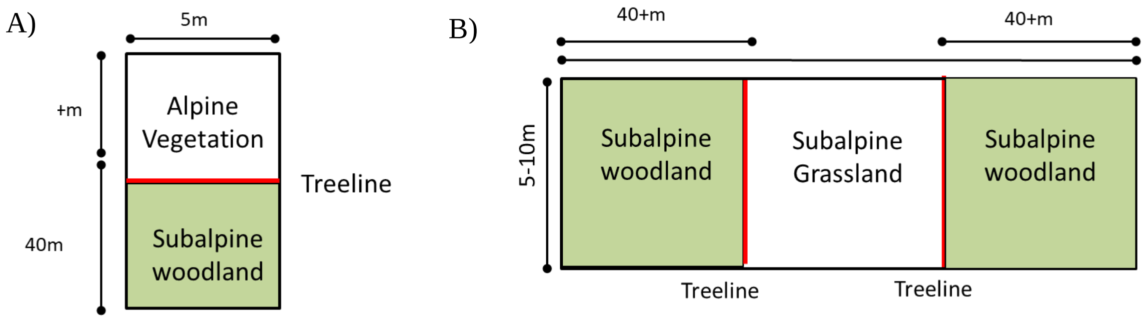


Figure 2.4 Design of alpine (A) and subalpine (B) transects based on methods conducted by Cutler (2002), Wearne (1998) and J. Morgan (unpubl. data).

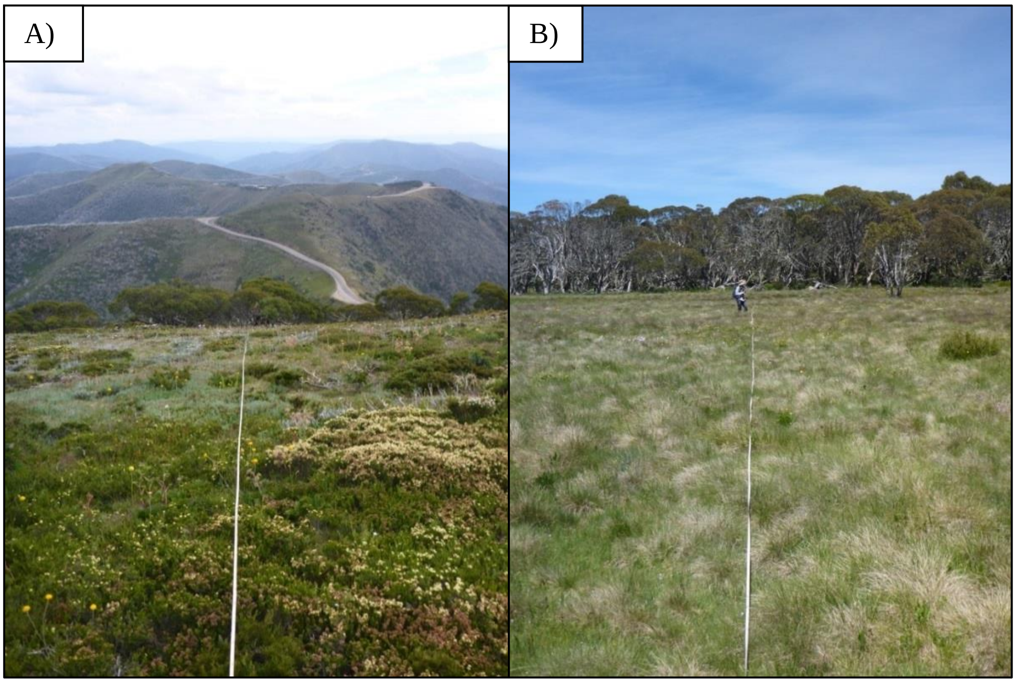


Figure 2.5 Example of alpine (A) (Mount Hotham) and subalpine (B) (JB Plain) transect arrangement oriented towards the treeline.

In each transect, individuals were assigned an X and Y coordinate. Height was measured for each individual and, when exceeding 3 m, visually estimated. Individuals were classed according to growth form (single or multi stemmed), condition (alive or dead), reproductive status (flowers, buds or capsules), resprouting (basal or stem), and canopy condition (intact or burnt). Fire history was determined by the presence of stems arising after each fire, defined as cohorts, determined by the relative size and conditions of stems (Figure 2.6).

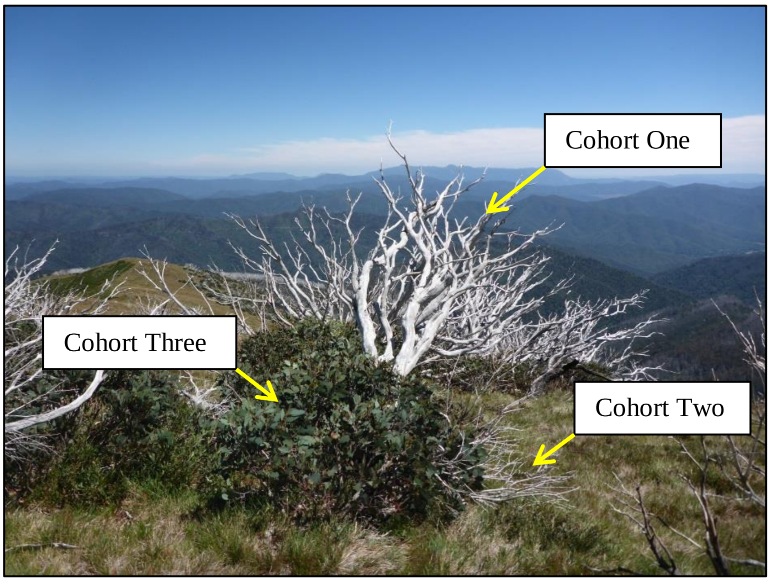


Figure 2.6 Example of a tree burnt twice in recent bushfires as evidenced by the three cohorts of stems; large burnt defoliated stems burnt in the first fire (cohort one), smaller burnt defoliated stems resprouting in response to the first fire and burnt in the second fire (cohort two) and the most recent alive resprouts resprouting from the most recent fire (cohort three). The Razorback trail, Mount Feathertop.

Diameter of five representative stems per cohort (stems arising from each fire) and basal girth was measured. Basal girth was used as the standard technique of girth at breast height is not possible due to the short stature and multi-stem form of *E. pauciflora* at the treeline (Barker 1988; Wearne and Morgan 2001). Percent ground cover in a 1 m radius circle around each tree located above treeline was estimated to determine if there was a relationship between vegetation cover and the occurrence of trees.

In addition to the four transects at Mount Feathertop previously surveyed by Cutler (2002), an additional two transects were surveyed along the Razorback trail towards Mount Feathertop. These transects were chosen to provide an additional twice burnt site, along with The Twins.

Data Analysis

Data analysis was conducted using R version 3.3.3 (2017-03-06) and R Studio version 1.0.153 (2009-2017). Significance was tested at the 0.05 level.

Regional Climate Trends

Climate records for Falls Creek (36.87 °, 147.28 °E, 1765 m a.s.l) and Mount Hotham (36.98° S, 147.13 ° E, 1849 m a.s.l) stations were sourced from the Bureau of Meteorology (BOM 2018). Mean yearly minimum and maximum temperature, and annual precipitation were calculated for the period 1990-2017. Percentage of frost days (days <0 °C) per growing season (October to March) were calculated from the available data.

Environmental Variables

Temperature data was used to calculate weekly GDDs based on the formula (McMaster and Wilhelm 1997):

GDD= (Tmax+Tmin/2) – Tbase (Tmax = daily maximum, Tmin=daily minimum, Tbase = base temperature for plant growth (1)

A 0 °C Tbase was chosen as a general baseline for growth, below which frost occurs. The number of frost days (days <0 °C) were calculated for each location and height above ground level. An analysis of variance was carried out on the effect of height (60, 30, 0,-10 cm) and location (at, above, below treeline) on weekly accumulated GDDs. Due to a significant result, a post-hoc Tukey honest significant difference (HSD) test was carried out on the effect of height on GDDs for alpine and subalpine sites and the interaction of height and location for subalpine sites.

Structural Change Over Time

To examine changes in woodland structure over time, size class distributions (SCDs) were analysed based on a model presented by Condit *et al.* (1998). Individuals were grouped into basal diameter classes (mm), based on the availability of historic data and structural demographics of *E. pauciflora* woodlands (Green 2009) (Table 2.3).

Table 2.3 Basal diameter classes (mm) used for size class distribution model based on Condit et al (1998) for alpine and subalpine sites.

	Alpine	**Subalpine**
Basal Diameter Class (mm)	0-5, 5.1-10,10.1-15,15.1-20,21-70,71-140,141-250,251-400,401-800,801-1400,1400-4000	0-5, 6-20, 21-50, 51-100, 101-400

The number of living individuals were counted per size class. To accommodate uneven size class width, the number of individuals (N_i) was divided by the width of the size class:

$$\mathrm{n}_i = \frac{100_{Ni}}{(dbh_{i+1} - dbh_i)} \qquad (2)$$

This gives the abundance per size class (n_i). The midpoint of each size class and abundance was natural log (ln) transformed and a regression calculated for each site in each survey period. The slope of the regression was then used as an indicator of population structure.

Changes in Treeline Dynamics Over Time

To determine differences in the number of seedlings (<25 cm basal girth) above treeline between survey periods, a chi-squared test was used. Assumptions of chi-squared tests were checked and upon failing assumptions, a Fisher exact test used.

To determine establishment trends above treeline between survey periods the year of establishment of individuals above treeline in all survey periods was calculated from basal girth, based on the function provided in Rumpff et al (2009):

$$\text{growth rings} = 3.62 \text{ x girth}^{0.63} \quad (3)$$

To determine establishment trends with aspect a linear regression was carried out on year of establishment against the number of individuals above treeline in 2018.

2.3 Dispersal limitation in *Eucalyptus pauciflora* and other global treeline forming species

To explore some of the possible limitations to recruitment beyond the treeline, the dispersal distances of 31 global treeline forming species were modelled. Species were selected from international literature and those referenced in Harsch *et al.* (2009). Maximum dispersal distance was calculated using the R package 'dispeRsal' developed by Tamme *et al.* (2014). The 'dispeRsal' package estimates maximum dispersal distance based on plant traits. Dispersal syndrome, growth form and mean seed mass traits were used. Seed mass data and dispersal syndrome was sourced from primary literature and the Kew Seed Information Database (Appendix D Table 1).

Results of maximum seed dispersal according to family was used for all species except *Nothofagus* species in which maximum seed dispersal according to order was used, due to the absence of model data at a species level. Maximum dispersal distance was then categorized by the occurrence and distance of treeline advance according to international literature (Appendix D Table 2). Advance was classified as a single observation of treeline advance at a site, thus this is not to say all treelines formed by this species have advanced over the last century.

3. Results

3.1 Assessment of landscape scale changes in treelines across the Victorian Alps through repeat photography

At the landscape scale, treelines within the Victorian Alps appear relatively stable over the last 50 to 100 years. Qualitative comparisons suggest there had not been substantial nor widespread advance, infilling or recession of treelines.

There were no dramatic differences in the distribution of trees between historical and modern photographs. Treeline stability is observed most prominently in Figures 3.1 and 3.2 (additional examples Appendix B Figure 1, 2). Figure 3.1 shows there has been no significant shift in treeline positions, such as on the ridge line or expansion, such as the cluster of trees in the center of the photograph. Similarly, Figure 3.2 shows a stable treeline with no observable advance of the treeline over the opposing slope. Burnt individuals, indicated by the defoliate dead stems, are prominent in both modern photographs. Determining whether these individuals have survived is questionable due to image resolution. However, personal observation along the Razorback trail towards Mount Feathertop suggests that at least at the landscape-scale majority of individuals have resprouted.

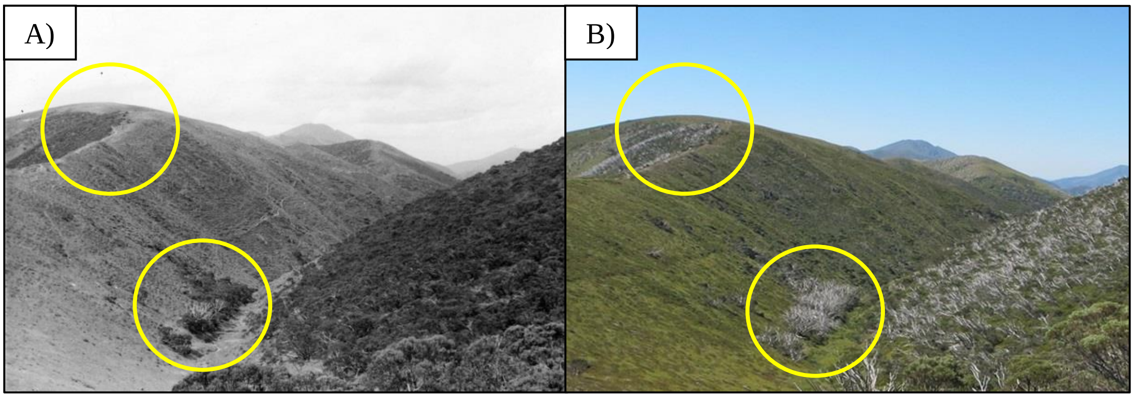


Figure 3.1 Historical (1967) (A) and modern (2016) (B) photographs of Diamantina valley looking north towards Mount Feathertop, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by Z. Walker (2016).

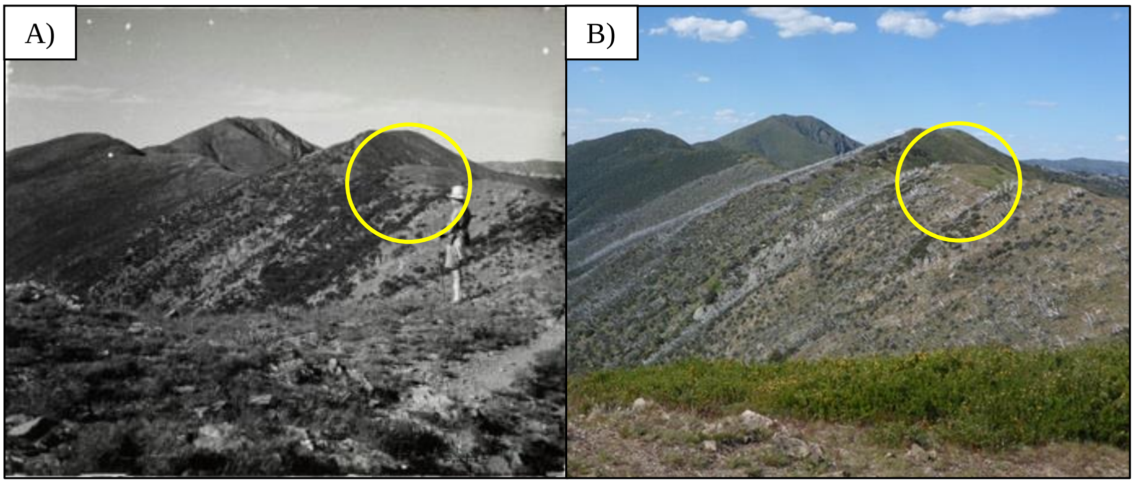


Figure 3.2 Historical (1928-35) (A) and modern (2017) (B) photographs looking north towards Mount Feathertop, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by A. Naccarella (2017).

Similarly basal resprouting is difficult to distinguish in aerial photographs of the Razorback trail towards Mount Feathertop (Figure 3.3) (additional example Appendix B Figure 3, 4). Despite this the overall distribution of trees within aerial photographs appears stable.

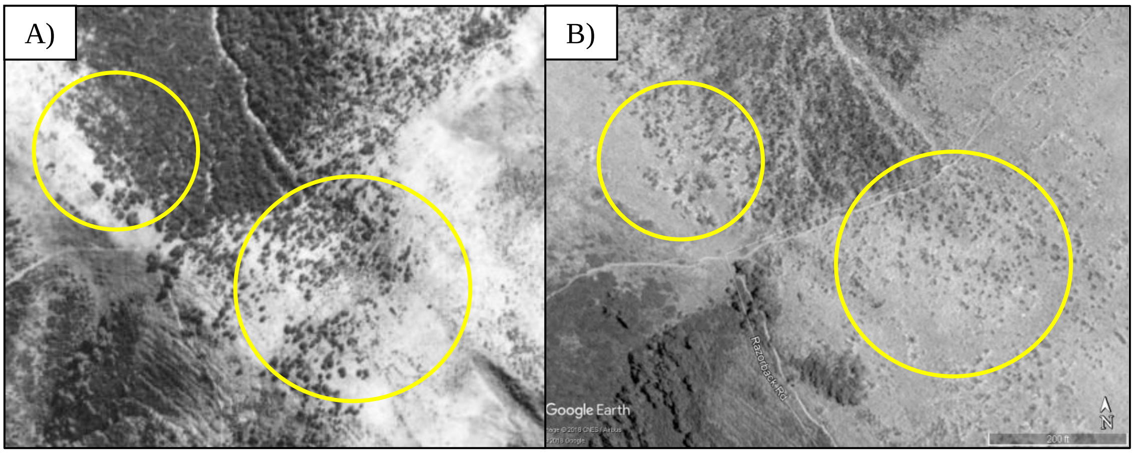


Figure 3.3 Historical (1961) (A) and modern (2017) (B) aerial photographs of junction between Bungalo Spur Walking Track (left), Razorback track (right foreground and center) and Northwest Spur track in the northwest, Victoria, Australia. Historical photographed sourced from Soil Conservation Authority courtesy of Keith McDougall private collection. Modern photograph sourced from Google Earth (2017).

Likewise, in aerials photographs of a subalpine grassland around Falls Creek, it is difficult to distinguish between trees and shrubs (Figure 3.4). The light grey areas in both modern and historical photographs appear to be trees, while the darker areas amongst these are shrubs and lighter areas in the centre is most likely dominated by grass. Based on these assumptions, there appears to have been expansion of trees into the outlying cluster of shrubs, however field validation is required to confirm this.

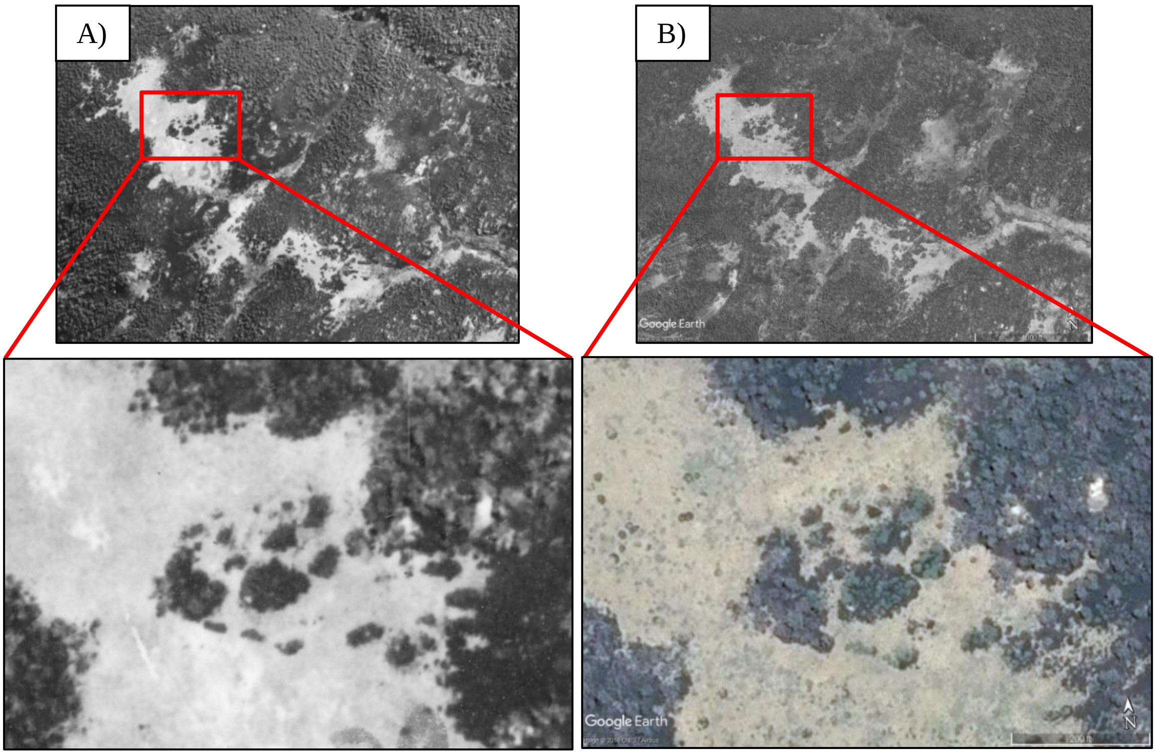


Figure 3.4 Historical (1961) (A) and modern (2017) (B) aerial photographs of Spion Kopje, Falls Creek, Victoria, Australia. Historical photographed sourced from Soil Conservation Authority courtesy of Keith McDougall private collection. Modern photograph sourced from Google Earth (2017).

Similarly, around Mount Hotham subalpine woodland areas appear to have increased in density over approximately the last 50 years (Figure 3.5) (additional example Appendix B Figure 5). Additionally, at Cross Cut Saw, establishment and growth of individuals appears to have occurred above treeline. These individuals may not have been present or were indistinguishable due to their small size in the historical photograph (Figure 3.6).

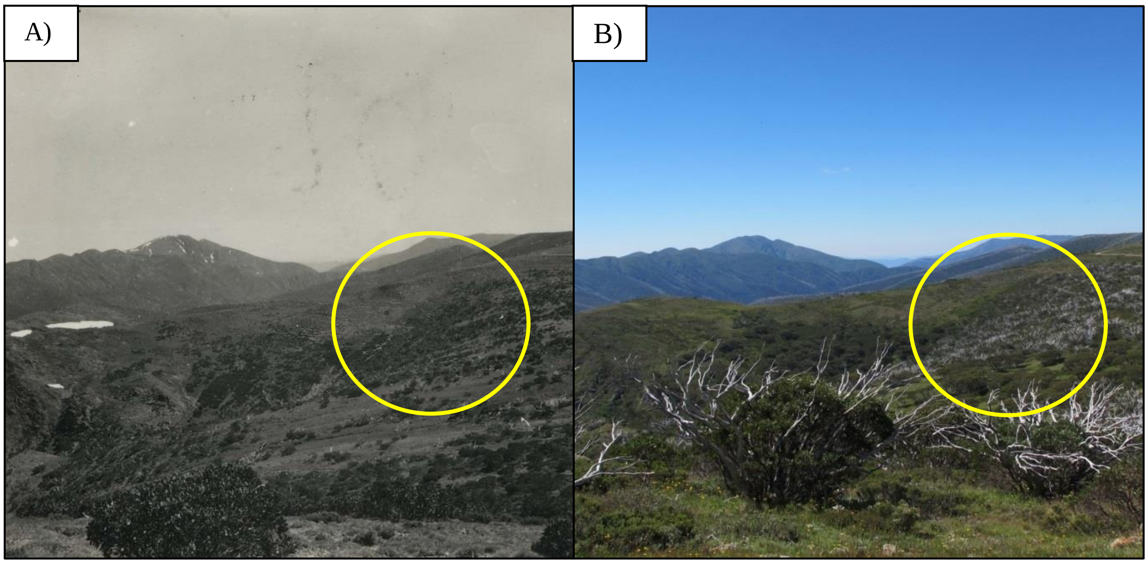


Figure 3.5 Historical (1950-1965) (A) and modern (2015) (B) photographs looking north- west towards Mount Feathertop, Hotham, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by Z. Walker (2015).

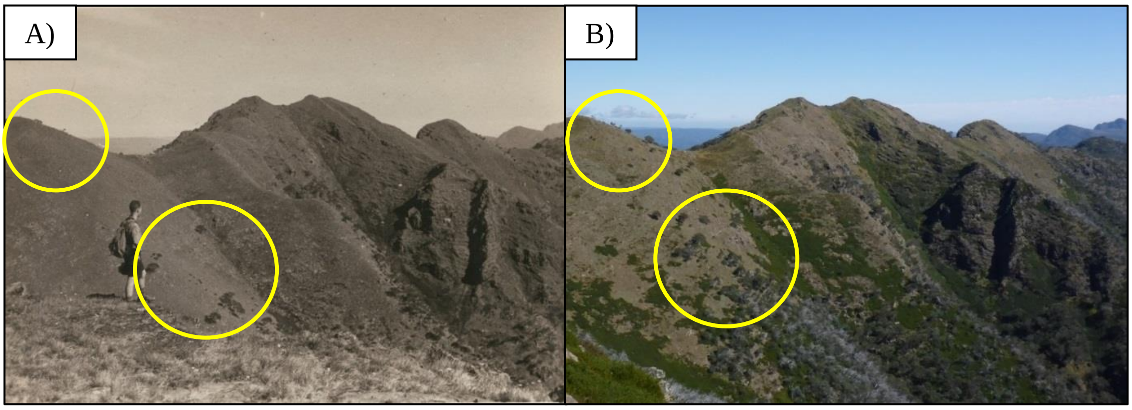


Figure 3.6 Historical (1935) (A) and modern (2015) (B) photographs of Cross Cut Saw looking north- west, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by A. Naccarella (2015).

3.2 Assessment of the current state of alpine and subalpine treelines through re-visitation surveys

Regional Climate Trends

There has been a marginal increase in mean annual minimum and maximum temperature of ~0.4 °C at Falls Creek and Mount Hotham over the last 25 years (Figure 3.7). Growing season (October to March) precipitation expresses high inter-annual variability, with no clear trends over time (Figure 3.8). The percentage of frost days (<0 °C) during the growing season (October to March) has substantial inter-annual variability, showing an overall decline since 1990 (Figure 3.9).

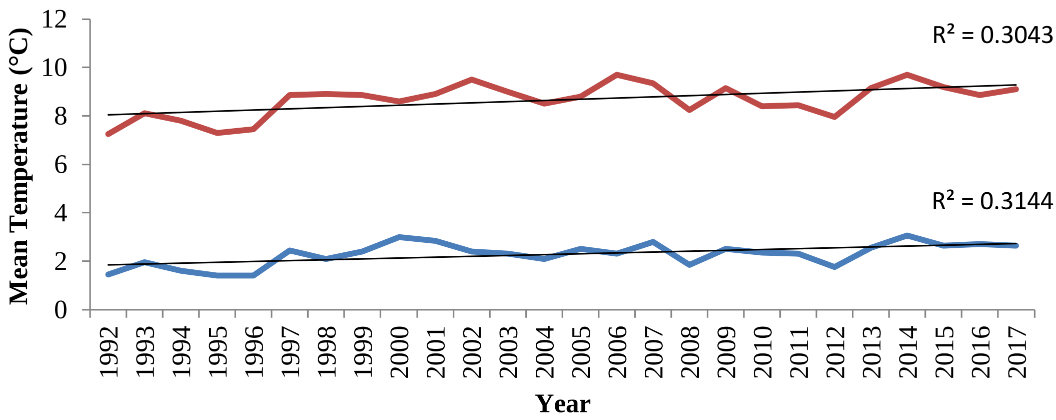


Figure 3.7 Mean yearly maximum (red) and minimum (blue) temperatures combined from Falls Creek and Mount Hotham from 1992 to 2017. Source: BOM, 2018.

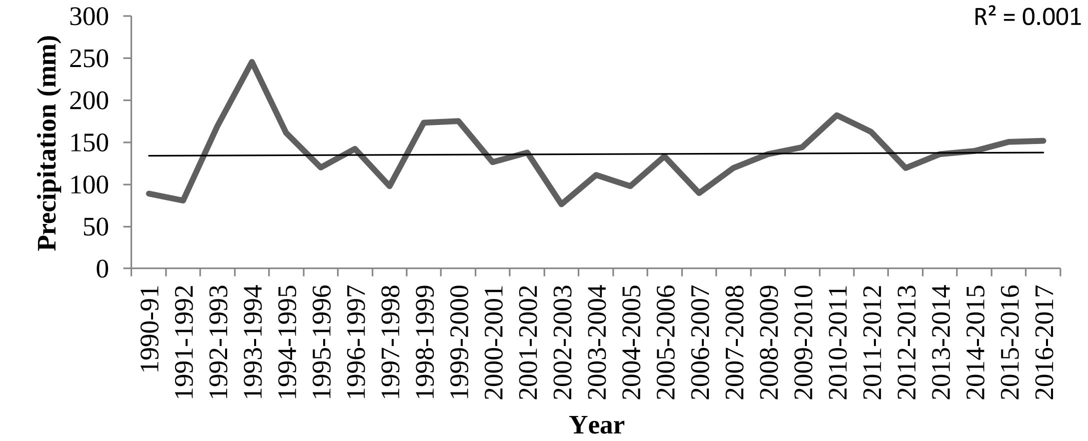


Figure 3.8 Mean growing season precipitation (mm) (October-March) for Falls Creek and Mount Hotham from 1990 to 2016. Source: BOM, 2018.

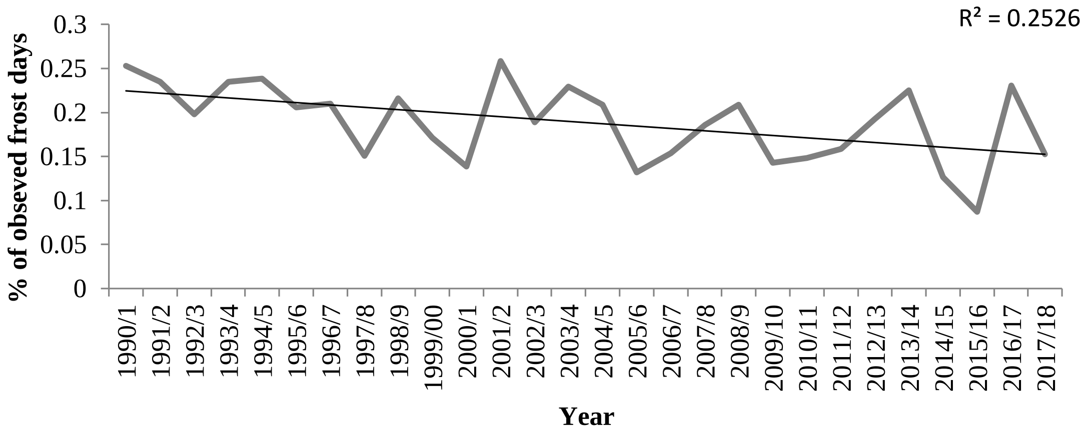


Figure 3.9 Percentage of days below <0 °C during the growing season (October to March) averaged across Falls Creek and Mount Hotham from 1990 to 2018. Source: BOM, 2018.

Environmental Variables

GDD trends between heights and locations were similar between alpine and subalpine sites (Figure 3.10, 3.11). GDDs varied between weeks; air temperatures were generally warmer at 30 cm followed closely by 60 cm, 0 cm and lowest at -10 cm. An analysis of variance revealed there to be a significant effect of height at alpine (P-value <0.001) and subalpine sites (P-value <0.001), and a significant interaction between height and location at subalpine sites (P-value= 0.024) (Appendix C Table 2). Tukey HSD tests revealed differences between a range of heights and locations, largely between soil and air temperatures, and 0 and 30 cm heights (Appendix C Tables 3, 4, 5).

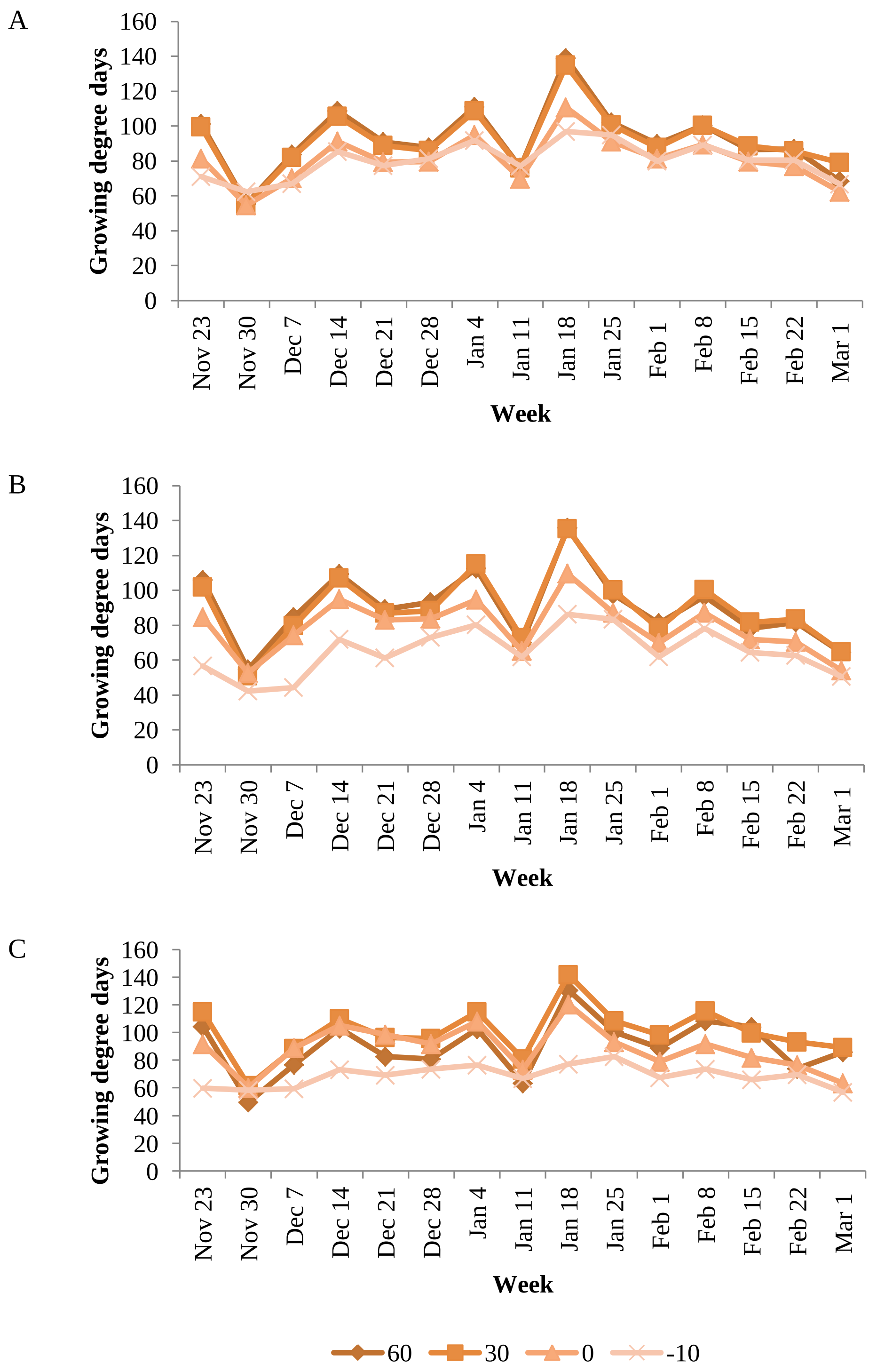


Figure 3.10 Weekly growing degree days (>0 C°) at 60cm, 30 cm and 0 cm above ground and 10 cm below ground recorded 40m above treeline (A), at treeline (B) and 40m below treeline (C) averaged across Mount Hotham and McKay alpine sites. Weeks run sequentially from 23rd November 2017 to 6th March 2018. Due to logger failure data for; Above treeline -10 cm only includes Hotham data, At treeline 0 cm includes only McKay data, Below 60 and 30 cm includes only McKay data and Below -10 cm includes only Hotham data.

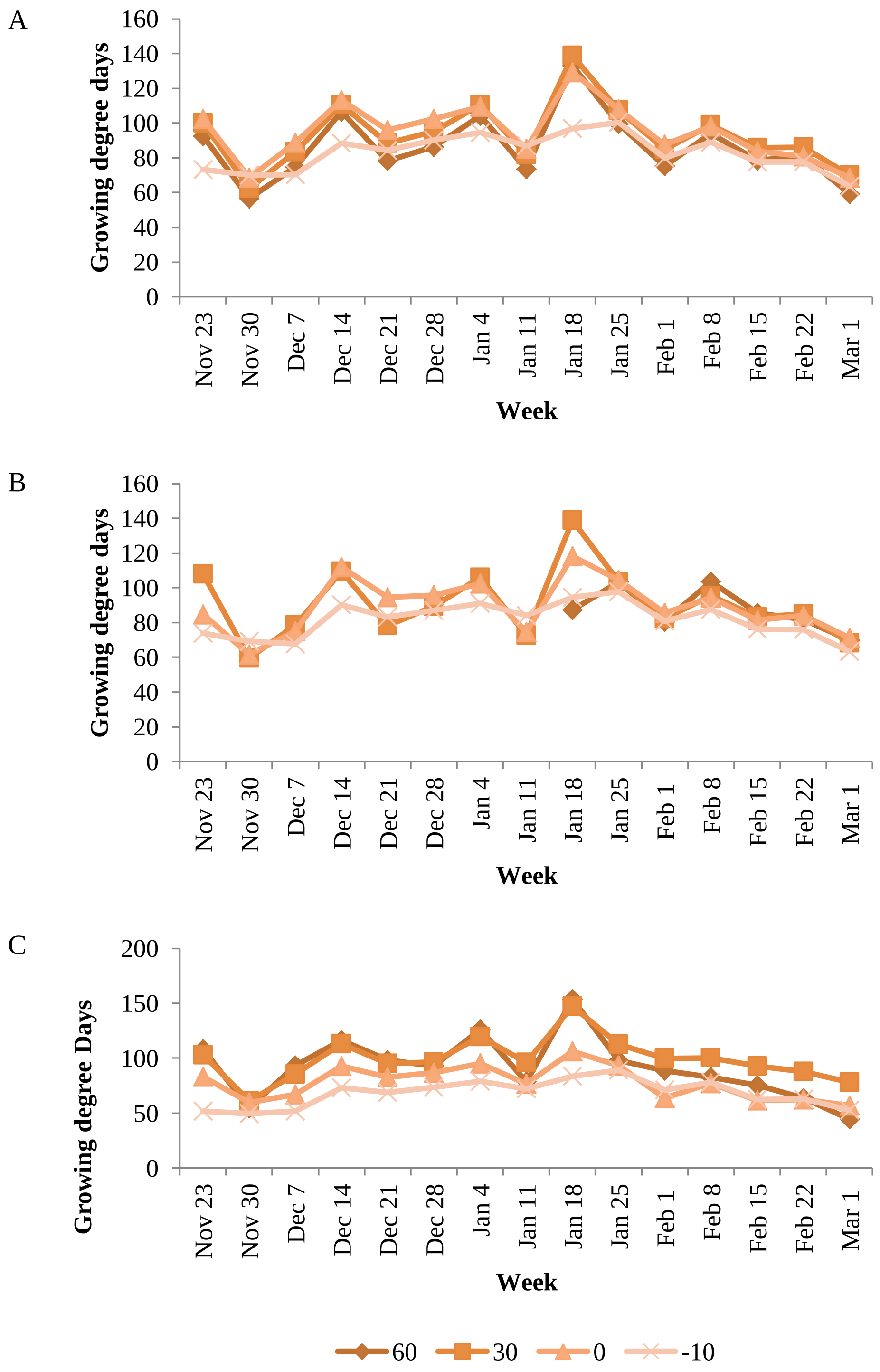


Figure 3.11 Weekly growing degree days (>0 C°) at 60 cm, 30 cm and 0 cm above ground at 40m above treeline (A), at treeline (B) and 40m below treeline (C) averaged across Paw Paw Plain and The Lanes subalpine sites. Weeks run sequentially from 23rd November 2017 to 6th March 2018. Missing data for is due to logger failure. Due to logger failure data for; Above treeline 0 cm includes only Paw Paw data, At treeline 60 cm records from 18th January 2018, At treelines 30 cm includes only Paw Paw until 22nd January 2018, At treeline 0 cm includes only The Lanes until 9th January 2018, Below treeline 60 cm includes only Paw Paw data and Below treeline 0 cm includes only The Lanes data.

The numbers of frost days were higher at 30 and 60 cm above ground, compared to 0 cm at both alpine and subalpine sites, with no clear trends between locations (Figure 3.12, 3.13).

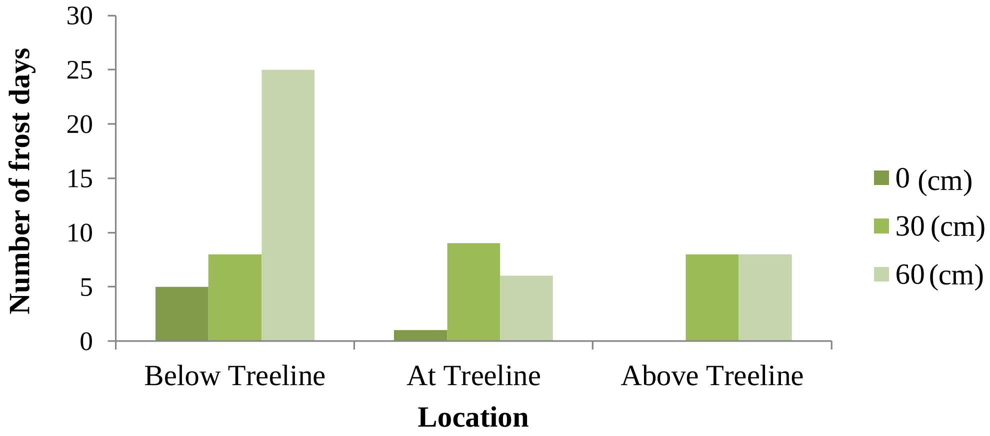


Figure 3.12 Total number of frost days per week across survey period (November 23rd 2017 to March 6th 2018) recorded at ground level (0cm), 30 cm above ground and 60cm above ground at monitoring stations 40 m below treeline, At treeline and 40m above treeline average across Mount Hotham and McKay alpine sites. Potential logger failure occurred Below Treeline at 60 cm which may have overrepresented frost days.

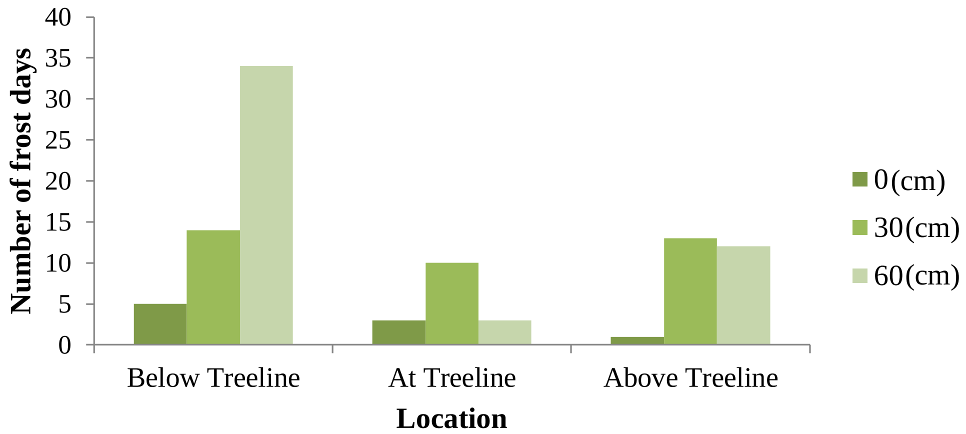


Figure 3.13. Total number of frost days across the survey period (November 23rd 2017 to March 6th 2018) recorded at ground level (0), 30 cm above ground and 60cm above ground at monitoring stations 40 m below treeline, at treeline and 40m above treeline averaged across Paw Paw Plain and The Lanes subalpine sites. Potential logger failure occurred Below Treeline at 60 cm which may have overrepresented frost days, and At Treeline which excludes 60 cm readings between November 23rd 2017 to January 17th 2018.

Structural Change Over Time

Fire History

Surveying revealed fire maps to be imperfect to determine fire history at the fine scale of transects. Observations revealed Mount Hotham transects to be unburnt, Mount Feathertop and McKay transects to have been burnt once in 2003, The Twins and The Razorback transects to have been burnt twice across the 2003, 2005 or 2013 fires, and all subalpine site transects to have been burnt once in 2003 (Figure 3.14, 3.15).

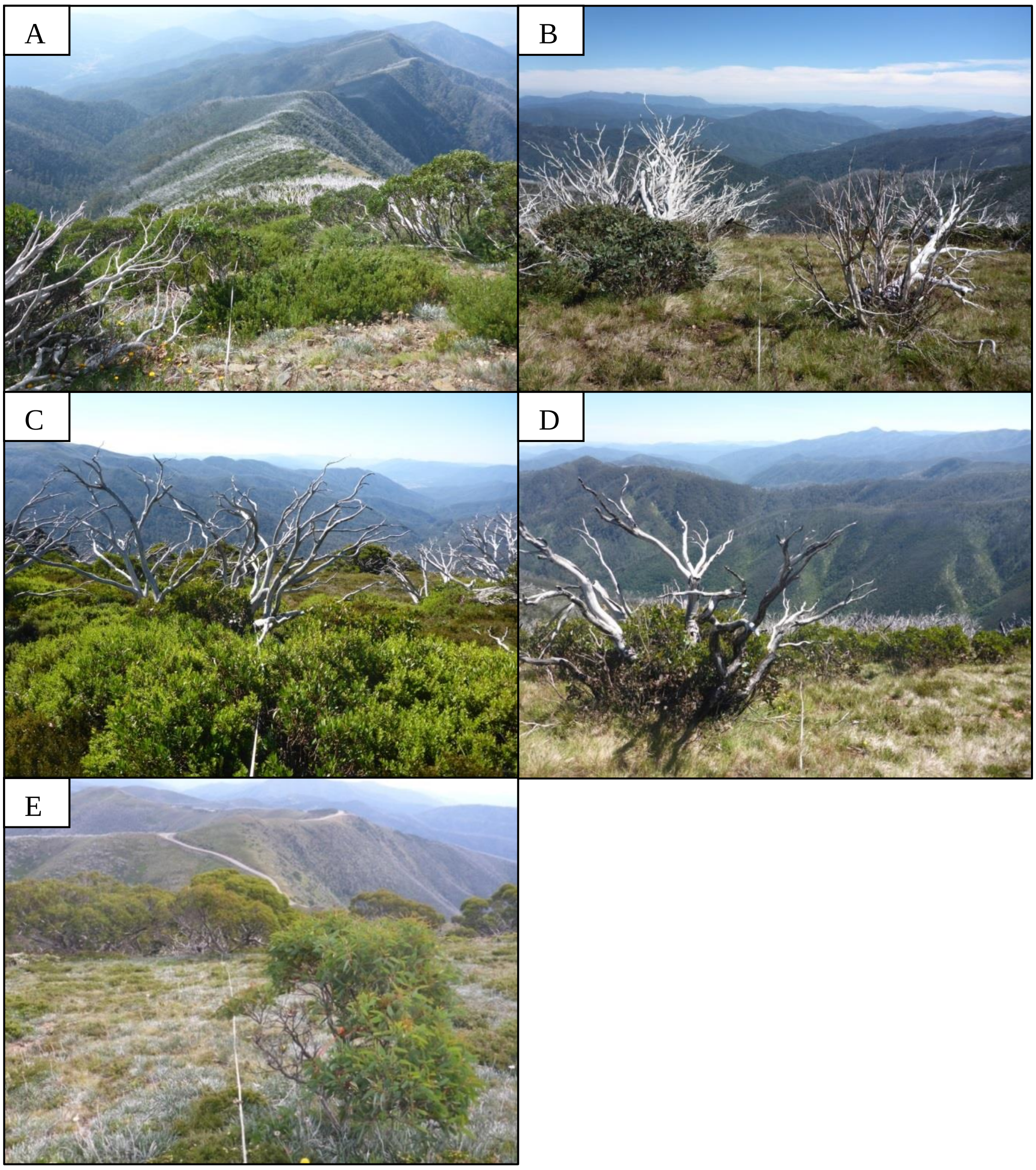


Figure 3.14 Characteristics of alpine transects, highlighting the variability in canopy cover, resprouting extent, density and ground vegetation type and cover. (A) Mount Feathertop (once burnt). (B) The Razorback (Twice burnt). (C) Mount McKay (once burnt). (D) The Twins (Twice burnt). (E) Mount Hotham (unburnt).

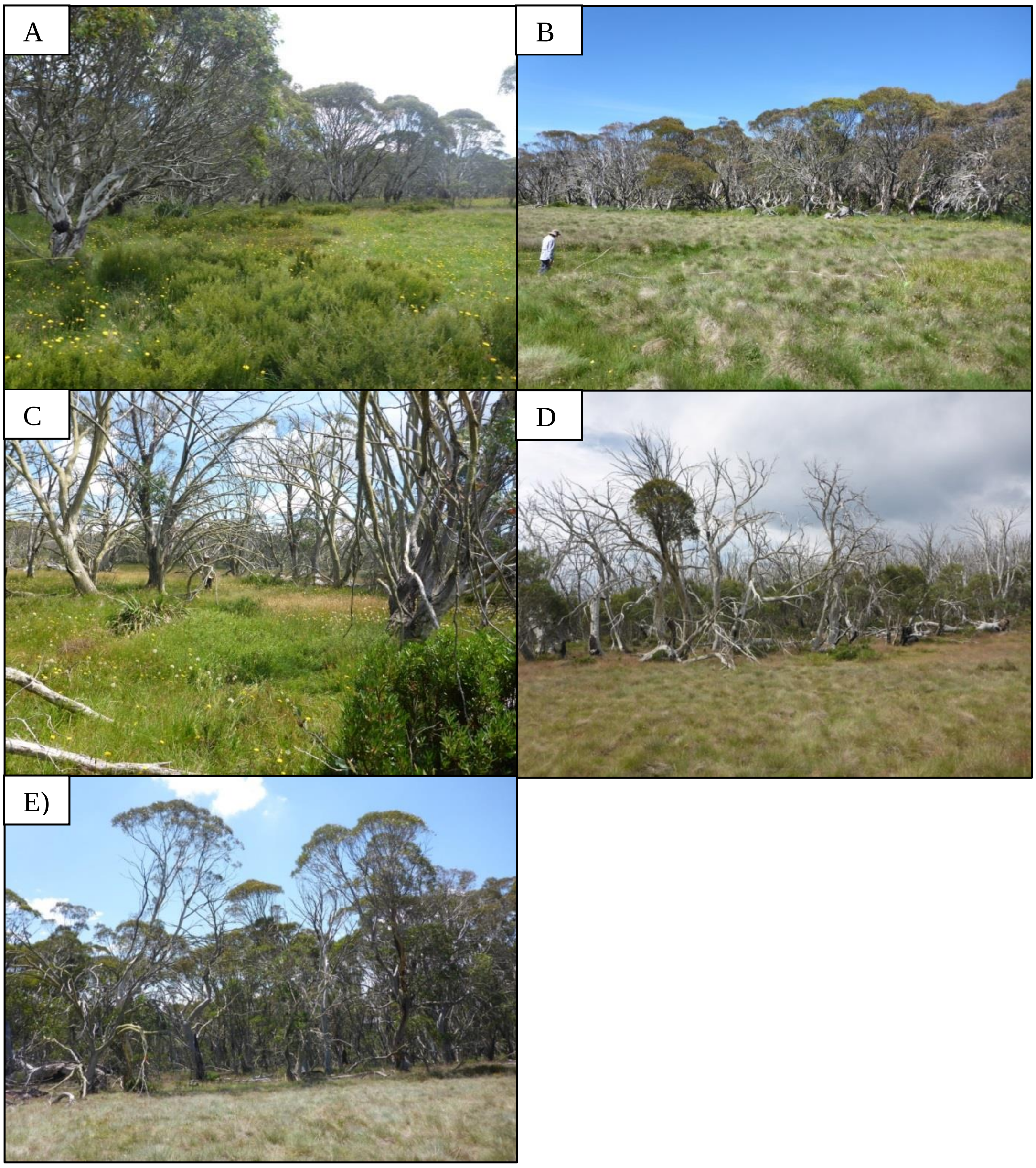


Figure 3.15 Characteristics of subalpine transects highlighting the variability in canopy cover, resprouting extent, density and ground vegetation type and cover. (A) Paw Paw Plain. (B) JB Plain. (C) Precipice Plain. (D) The Lanes. (E) Green Gables. All sites were burnt once.

Alpine

Alpine treelines were exclusively composed of *E. pauciflora*. Transects comprised large old individuals exceeding 500 cm basal girth with evidence of long-term stability with treeline trees between 90 to >500 cm basal girth. Mature trees were up to 3.5 m tall and seedlings (<25 cm basal girth) were generally under 1.5 m tall. Buds and capsules were commonly found across transects. Flowering was solely observed at Mount Hotham. Stem and basal resprouting was common at single burn sites (Mount McKay and Feathertop). Basal resprouting was more common at double burn sites (The Twins and The Razorback) and present but not prolific at the unburnt site (Mount Hotham). A high proportion of semi-intact canopies (<50 % full) were observed at single burn sites, absent canopies with intact resprouting canopies at double burn sites and relatively intact canopies at the unburnt site. The presence of seedlings, mortality and woodland structure were site and transect dependent showing trends with burn history.

Overall, treeline dynamics and structure remained relatively consistent between survey periods and across sites. Evidence of stability between survey periods was observed, with similar abundance or absence of individuals above treeline (Figure 3.16). Increases in seedlings above treeline were seen at a number of unburnt and single burn site transects, where seedlings above treeline were both previously common in 2002 (Mount Hotham transect 1) and near absent in 2002 (Mount McKay transect 1) (Figure 3.17). Reductions in seedlings above and below treeline were observed at The Twins double burn site (Figure 3.18). This was not the case for The Razorback double burn site in which seedlings were present above and below treeline (Figure 3.18). There were low proportions of dead individuals across most sites, with the exception of McKay transect 2 and The Twins transect 2 (Figure 3.18, 3.19)(Appendix C Figures 1-6 for complete transects).

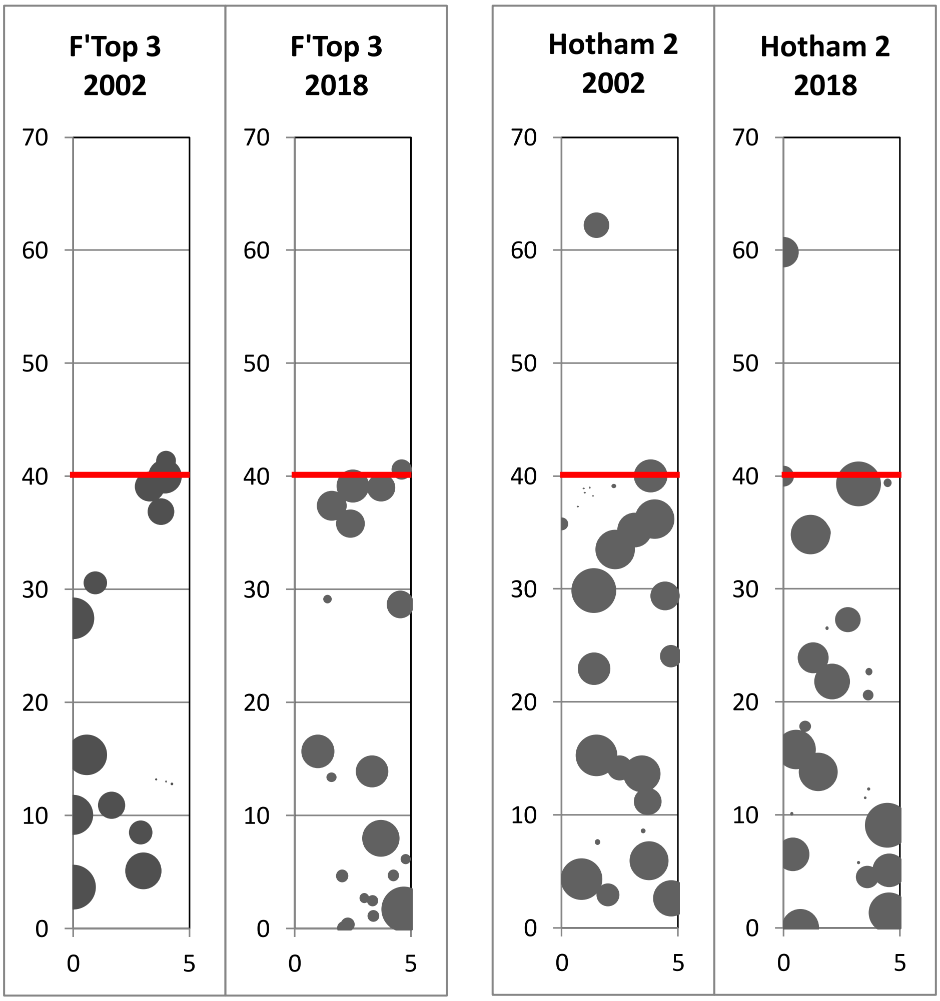


Figure 3.16 A visual representation of *E. pauciflora* individuals across Mount Feathertop transect 3 and Mount Hotham transect 2 in 2002 and 2018 expressing stability between survey periods. Mount Feathertop transect 3 aspect = W. Mount Hotham transect 2 aspect = W. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

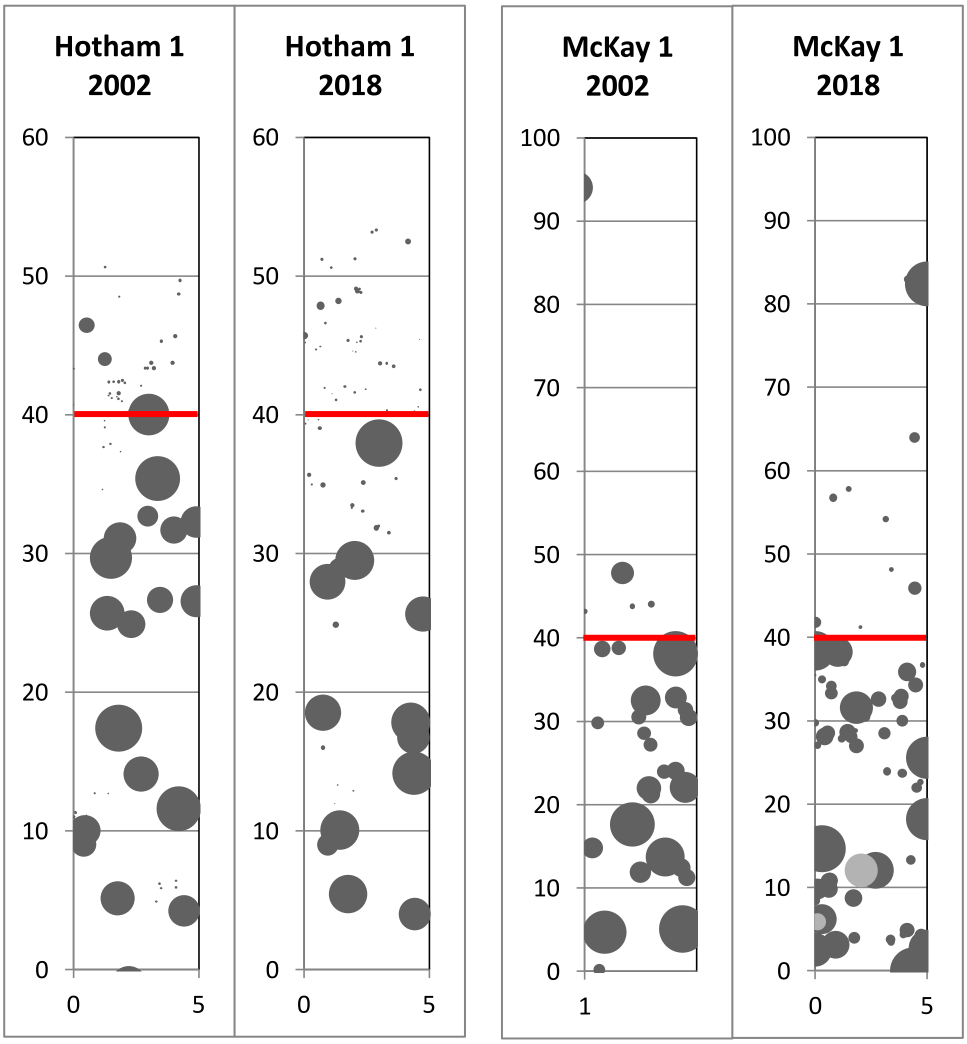


Figure 3.17 A visual representation of *E. pauciflora* individuals across Mount Hotham transect 1 and Mount McKay transect 1 in 2002 and 2018 expressing an increase in the number of seedlings in 2018. Mount Hotham transect 1 Aspect = W. Mount McKay transect 1 aspect = NW. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

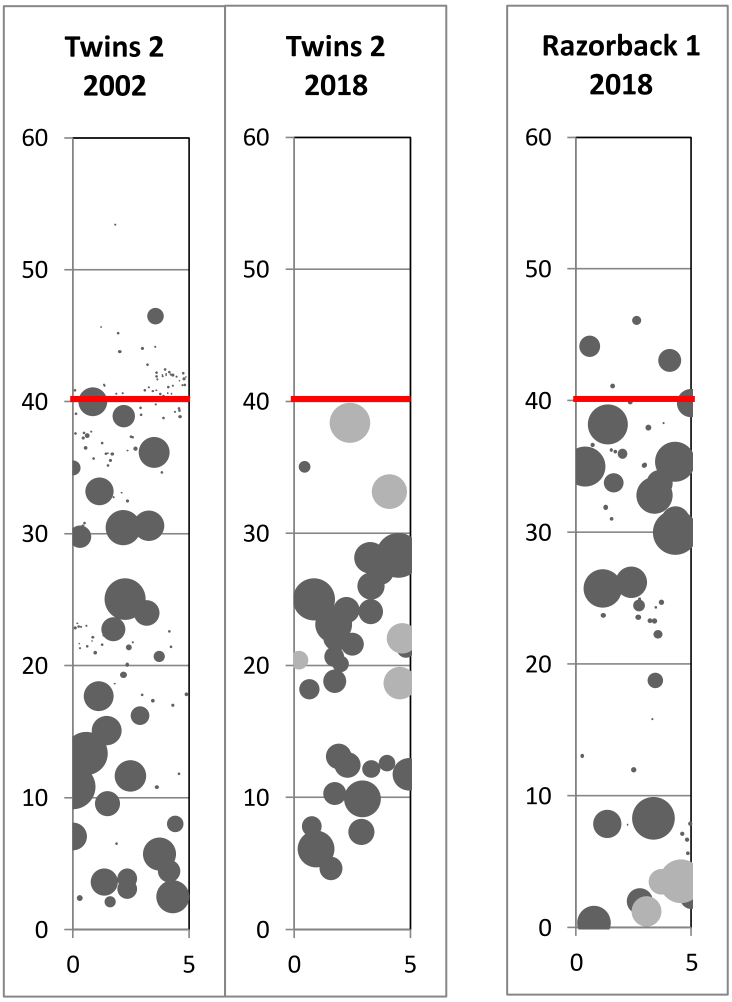


Figure 3.18 A visual representation of *E. pauciflora* individuals across transect 2 at The Twins in 2002 and 2018 and The Razorback transect 1 expressing differences in seedling abundance between double burn sites. The Twins transect 2 aspect = N. The Razorback transect 1 aspect = E. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40 m, y<40 m within the woodland, y>40 m above treeline.

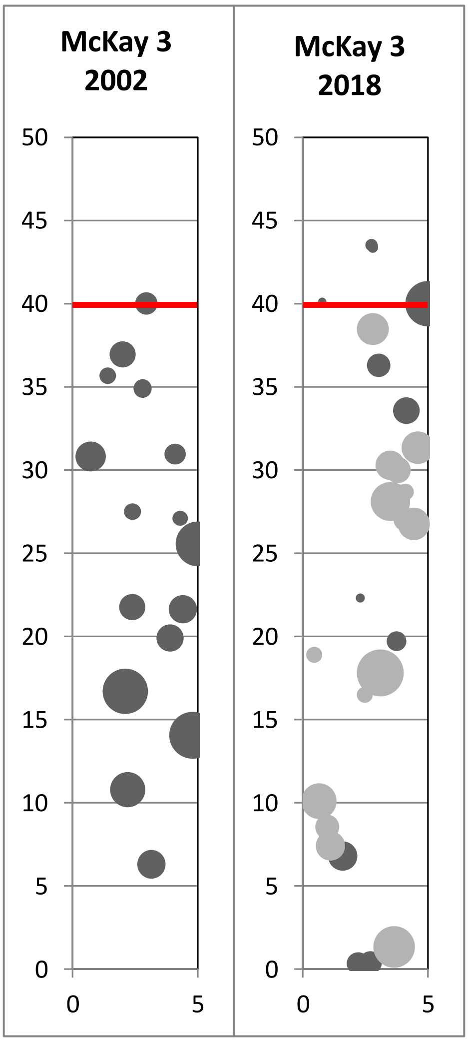


Figure 3.19 A visual representation of *E. pauciflora* individuals across transects at Mount McKay in 2002 and 2018 expressing high mortality found in few transects. Transect 3 aspect = S. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

SCDs indicated forest structure was similar between survey periods across unburnt and single burn sites and varied at the double burn site. Size distribution slopes were negative, indicating higher proportions of seedlings and sapling to mature trees. Mount Hotham had a steep size distribution slope which was consistent between survey periods (Figure 3.20). A slight shift in structure occurred at Mount Feathertop with a steepening of the slope due to the absence of smallest size classed individuals and reduction in saplings in 2018 (Figure 3.21). At Mount McKay forest structure shifted slightly with an increase in seedlings which were previously absent in 2002 and an increase in saplings causing a steepening of the slope in 2018 (Figure

3.21). Forest structure at The Twins had shifted more substantially with a flat size distribution slope in 2018 compared to a steep size distribution slope in 2002, due to reductions in seedlings and saplings leading to a more even aged stand in 2018 (Figure 3.22). The Razorback had a steep size distribution in 2018 (Figure 3.22).

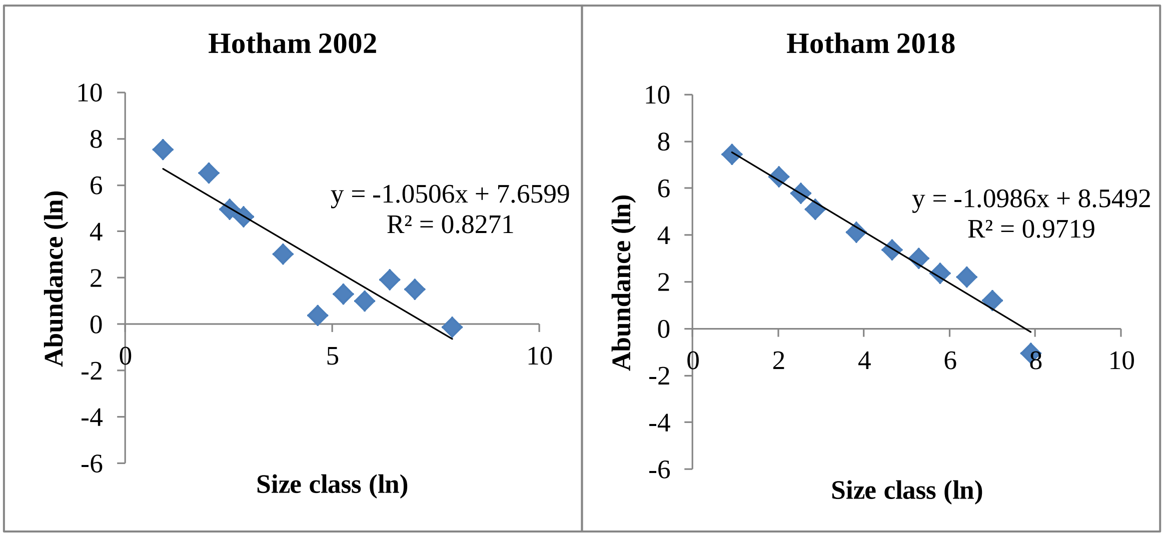


Figure 3.20 Size class distribution of size class natural log transformed against abundance (individuals per size class corrected) natural log transformed based on Condit *et al.* (1998) model for Mount Hotham, unburnt site, in 2002 and 2018.

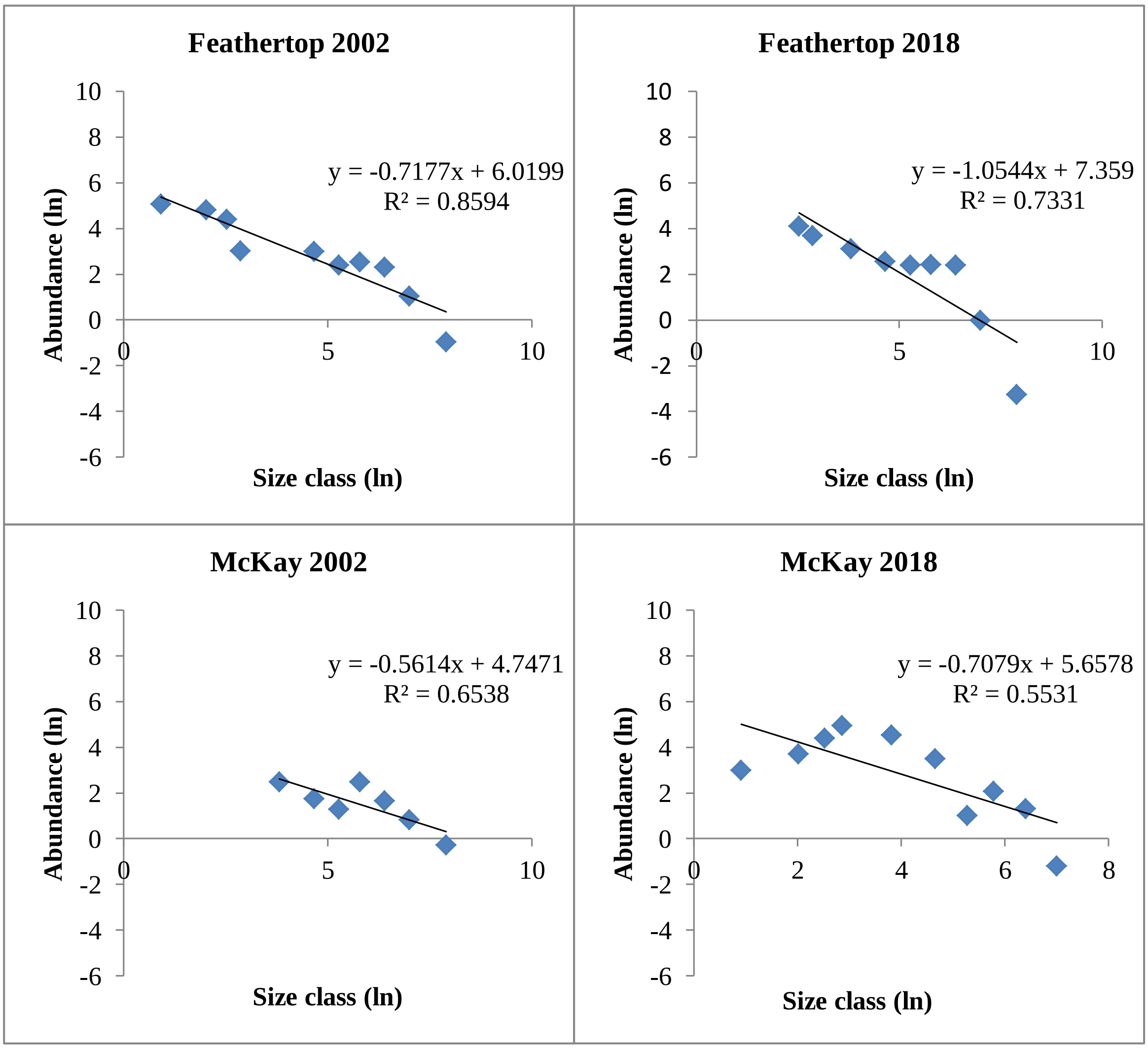


Figure 3.21 Size class distribution of size class natural log transformed against abundance (individuals per size class corrected) natural log transformed based on Condit *et al.* (1998) model for Mount Feathertop and Mount McKay, single burn sites, in 2002 and 2018.

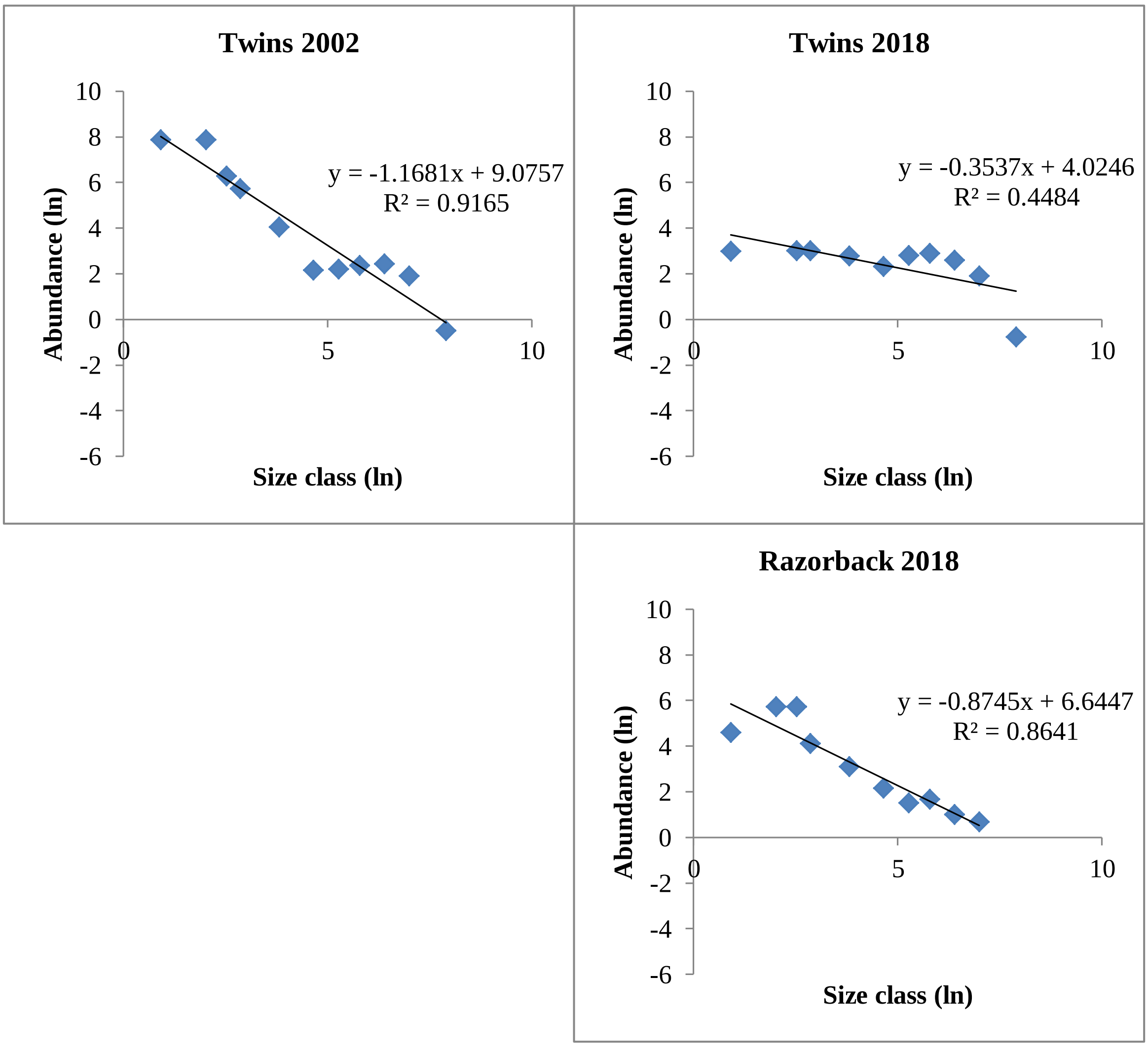


Figure 3.22 Size class distribution of size class natural log transformed against abundance (individuals per size class corrected) natural log transformed based on Condit *et al.* (1998) model for The Twins in 2002 and 2018 and The Razorback in 2018, double burn sites.

Subalpine

Subalpine treelines were exclusively composed of *E. pauciflora*, with observations of *E. stellulata* at Precipice Plain outside of transects. Transects comprised large old individuals exceeding 800 cm basal girth with evidence of long term stability with treeline trees between 60 to >800 cm basal girth. Mature trees reached heights of 16 m tall and seedlings (<25 cm basal girth) were generally under 2 m. Buds and capsules were common at Paw Paw Plain and uncommon across all other sites. Flowers were present at JB and Paw Paw Plain however infrequent. Stem and basal resprouting was present at all sites, however less common at Paw

Paw and JB Plain. Semi-intact canopies were common across sites, excluding JB Plain where majority were intact and Paw Paw Plain in which equal numbers of individuals were semi intact and intact.

Treeline structure and dynamics varied across transects and sites, however remained relatively stable between study periods. JB, Precipice and Paw Paw Plain had high seedling abundance below treeline. JB and Paw Paw Plains had high overall seedling abundance and an increase over time, with particularity high seedling abundance above and below treeline at Paw Paw Plain (Figure 3.23). There were low proportions of dead individuals across JB, Precipice and Paw Paw Plain transects (Appendix C Figures 7-18 for complete transects). Green Gables and The Lanes had fewer seedlings below and above treeline over time (Figures 3.24, 3.25). Evidence of seedling survival and subsequent growth, and death of treeline individuals was observed at The Lanes transect 1 (Figure 3.25). There were low proportions of dead individuals on average across Green Gables and The Lanes (Appendix C Figures 19-23 for complete transects).

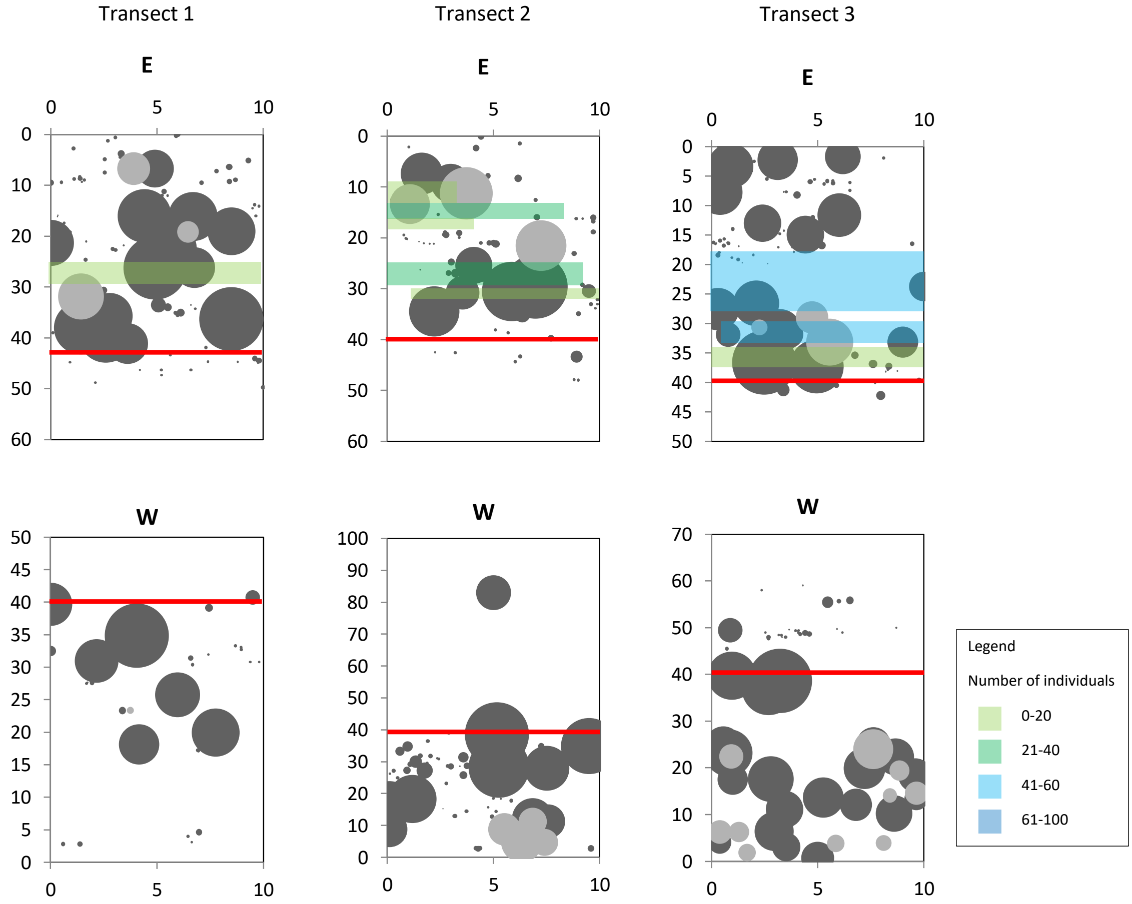


Figure 3.23 A visual representation of *E. pauciflora* individuals across transects 1, 2 and 3 at Paw Paw Plain in 2018 expressing high seedling abundance both above and below treeline. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the x and y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Excludes 1998 transect data due to the absence of spatial data (Appendix C Figures 15, 16, 17).

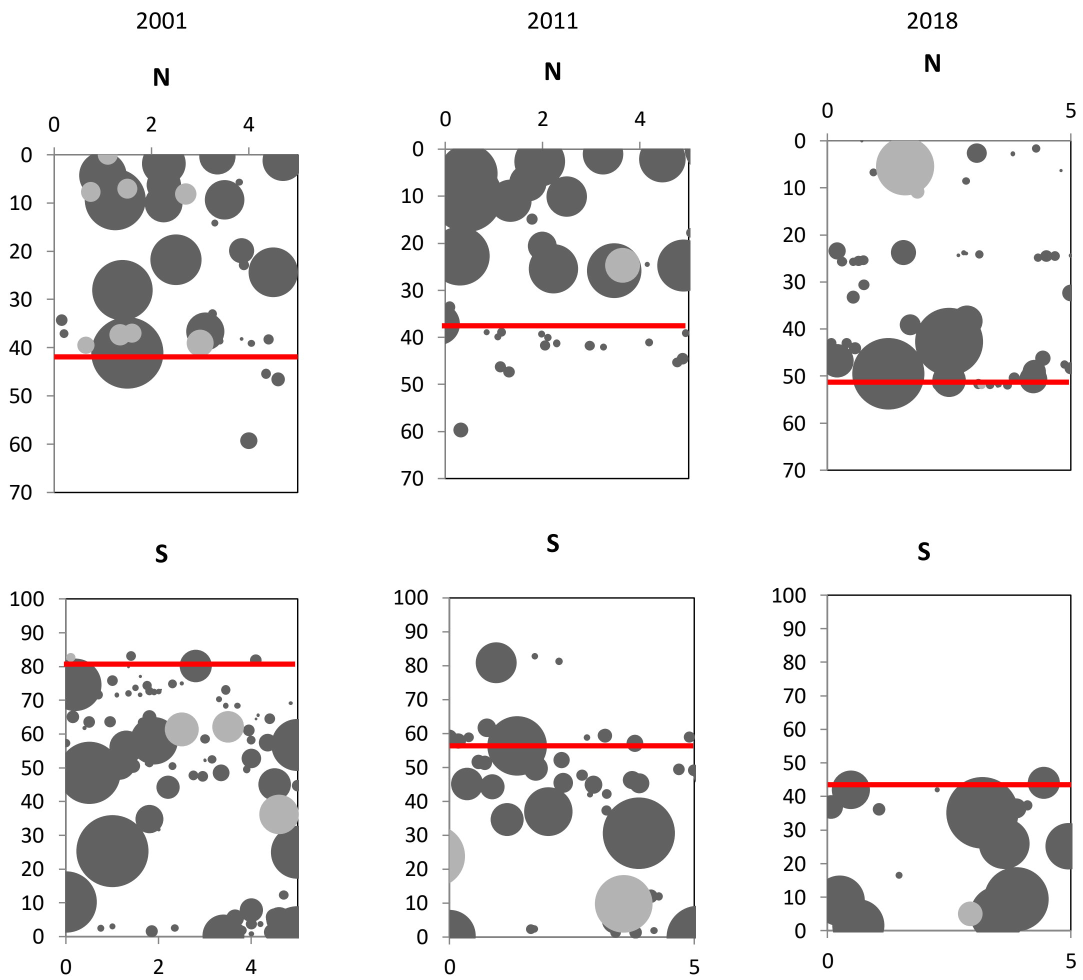


Figure 3.24 A visual representation of *E. pauciflora* individuals across transect 1 at Green Gables Plain in 2001, 2011 and 2018 expressing reductions in seedlings over time. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the x and y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline position for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

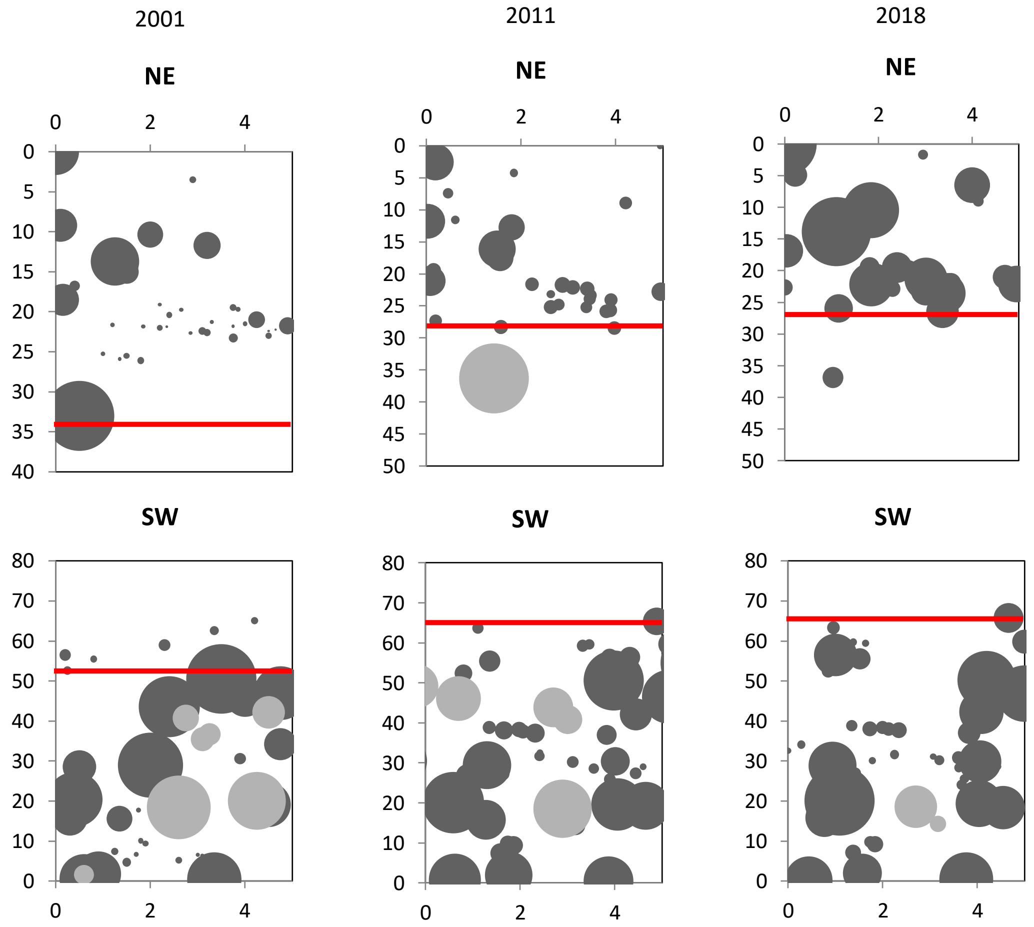


Figure 3.25 A visual representation of *E. pauciflora* individuals across transect 1 at The Lanes Plain in 2001, 2011 and 2018 expressing seedling survival and growth over time, and death of treeline individuals. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the x and y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline position for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

SCDs indicated forest structure was similar between survey periods across subalpine sites, with strong negative size distribution slopes indicating higher proportions of seedlings and sapling to mature trees. Paw Paw, Precipice and JB Plain had a steeper size distribution slope in 2018 due to an increase in seedlings and saplings compared to 1998 (Figure 3.26). Green Gables and The Lanes had a marginally steeper size distribution slope in 2018 due to slight reduction in smaller size class individuals and an increase in larger size class individuals in 2018 compared to 2001 and 2011 (Figure 3.27).

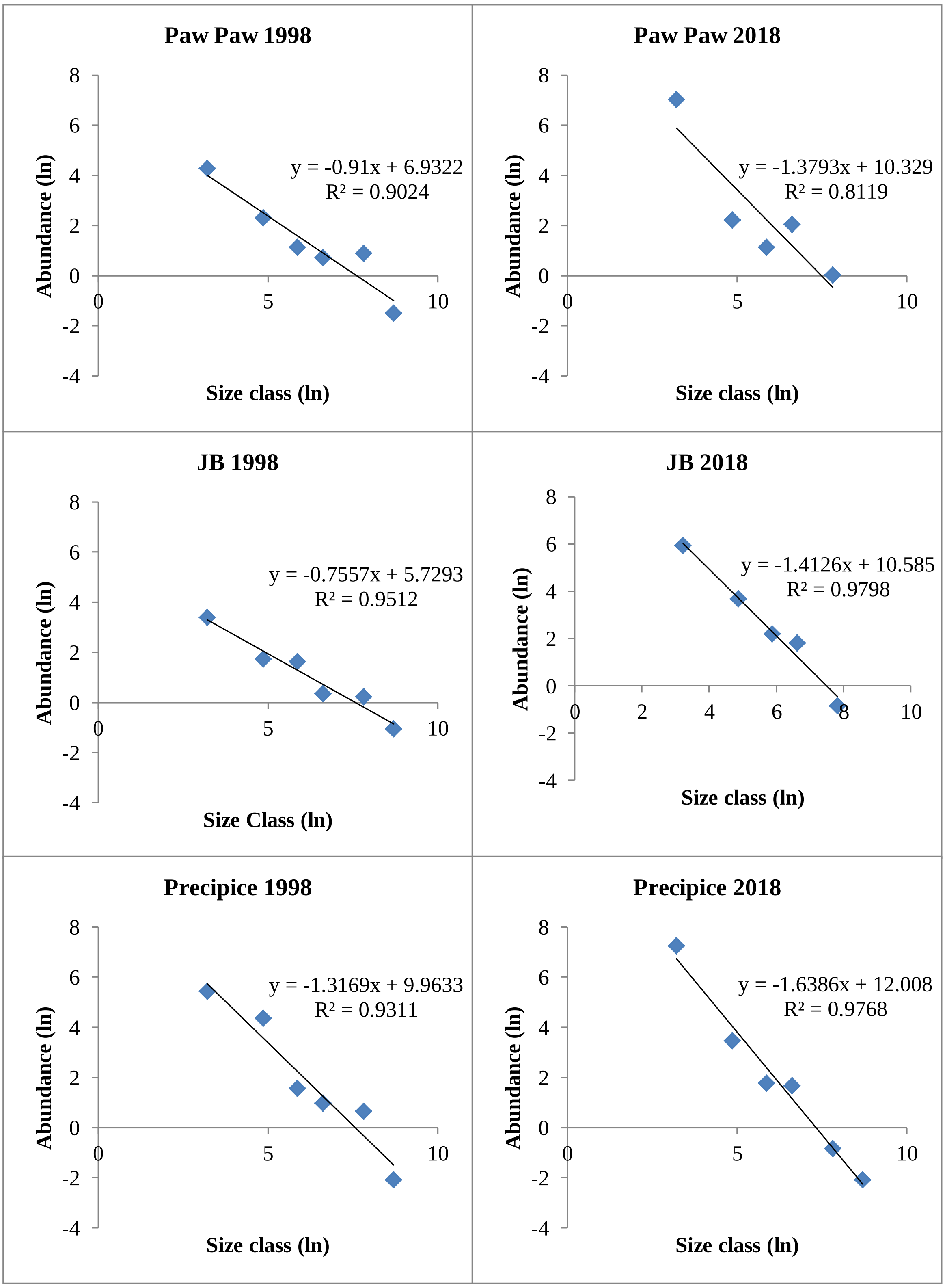


Figure 3.26 Size class distribution of size class natural log transformed against abundance (individuals per size class corrected) natural log transformed based on Condit *et al.* (1998) model, for Paw Paw Plain transects combined in 1998 and 2018, JB Plain transects combined in 1998 and 2018 Precipice Plain transects combined in 1998 and 2018.

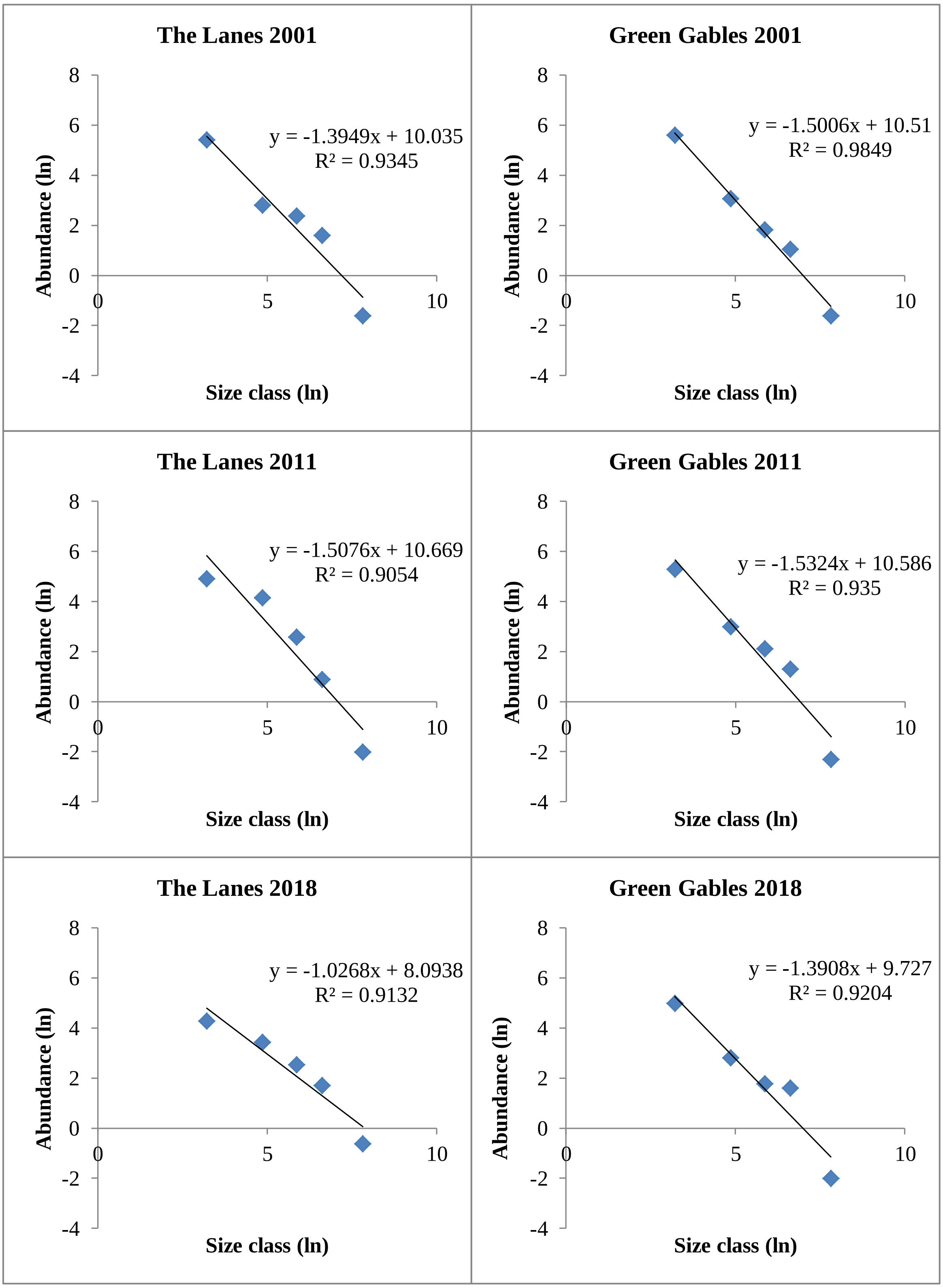


Figure 3.27 Size class distribution of size class natural log transformed against abundance (individuals per size class corrected) natural log transformed based on Condit *et al*. (1998) model for The Lanes 2001, 2011, 2018 and Green Gables 2001, 2011, 2018.

Changes in Treeline Dynamics Over Time

Alpine

Changes in treeline dynamics varied between sites and transects. A total of 87 seedlings (<25 cm basal girth) were located above treeline in 2018. Majority of seedlings found above treeline were located within 5 to 10 m of the treeline and were less than 57 cm in height (Figure 3.28). The number of seedlings above treeline varied between survey periods on a transect level, and more broadly between sites and fire occurrence. There was an increase in seedlings above treeline at Mount Hotham, Feathertop and McKay and a substantial decline at The Twins (Figure 3.29).

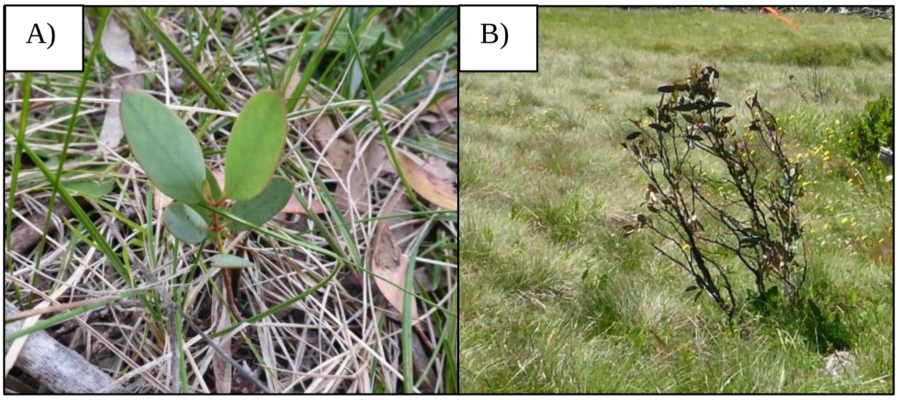


Figure 3.28 Examples of the variable age and height of seedlings located above treeline at Paw Paw Plain (A) and JB Plain (B).

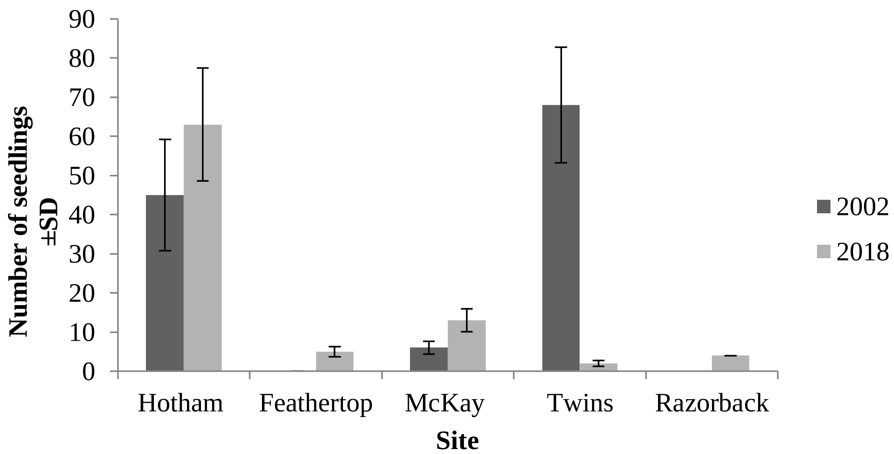


Figure 3.29 Total number of seedlings (<25 cm basal girth) above treeline (±standard deviation) between survey periods for alpine sites. Hotham was unburnt, Mount Feathertop and McKay burnt once, The Twins and The Razorback were burnt twice in recent bushfires. The Razorback does not include 2002 data as transects were first surveyed in 2018.

There was a significant difference in seedling numbers above treeline between 2002 and 2018 compared to expected values at Mount Hotham (P-value <0.001) and The Twins (P-value= 0.008)(Appendix C Table 6). Age modelling of individuals above treeline indicated the majority of individuals had established since 1995 in 2002 surveys and since 2012 in 2018 surveys (Figure 3.30). Few individuals present in 2018 surveys had established before the 2002 survey, indicating high turnover and mortality.

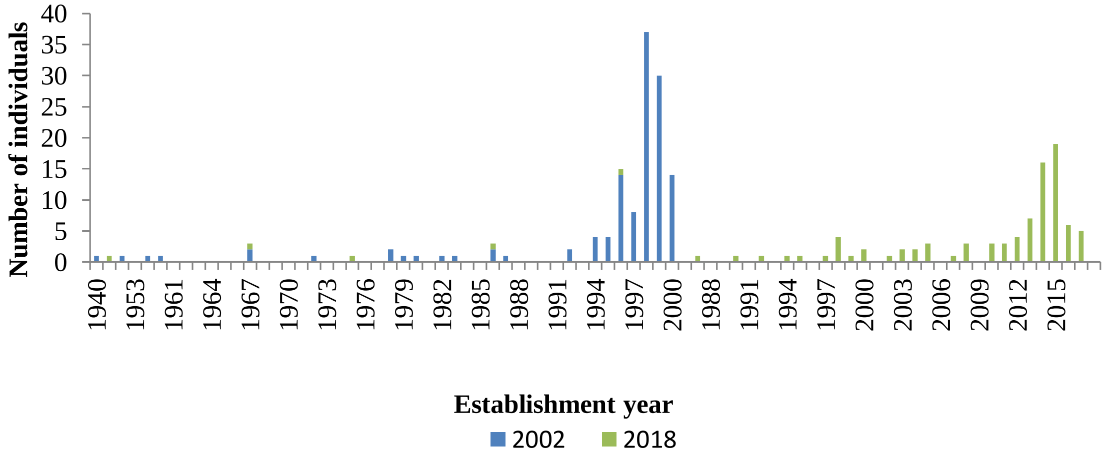


Figure 3.30 Estimated year of establishment of individuals located above treeline across alpine sites in 2002 and 2018. Year of establishment calculated based on Rumpff *et al*. (2009) model, as such trees with girth >115 cm (establishment data pre-1938) were excluded. Excluding The Razorback site which was first surveyed in 2018.

Linear regression revealed a potential aspect effect on seedling recruitment above alpine treelines over time (Figure 3.31). A significant increase in seedling establishment through time occurred on western aspect transects (P-value <0.001) (Appendix C Table 7). All other aspects showed a positive relationship but this was not statistically significant.

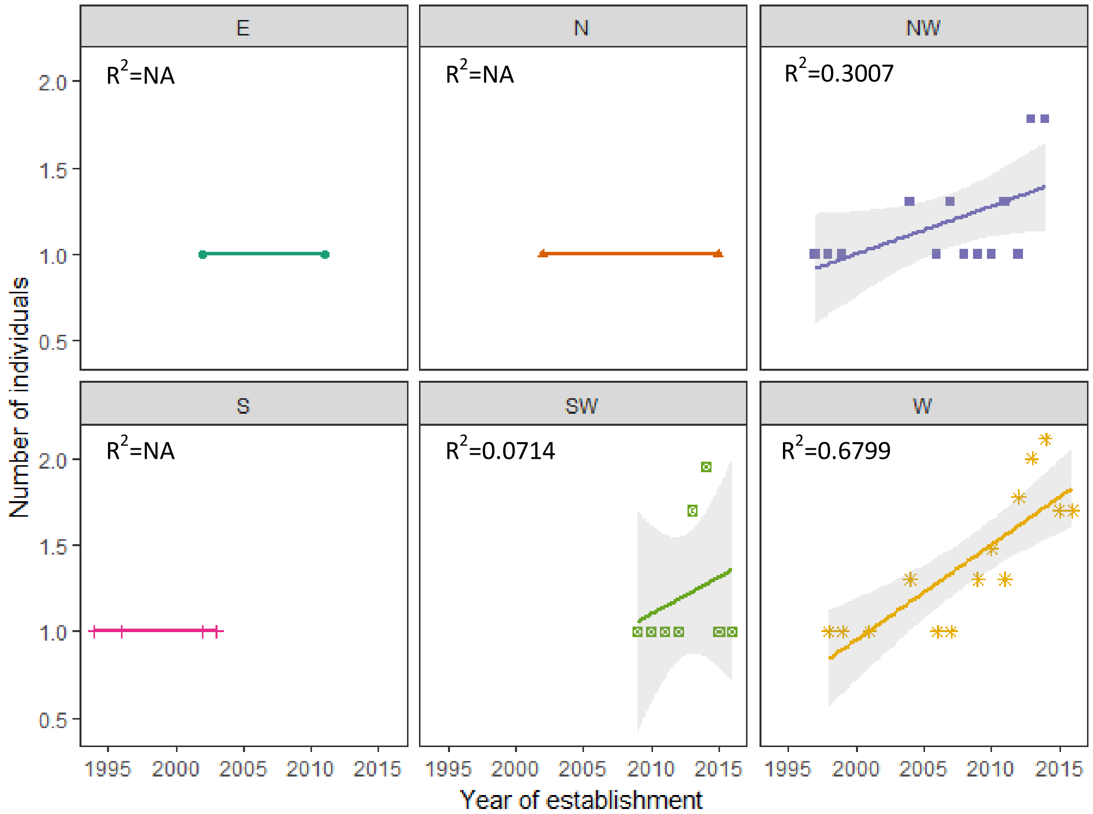


Figure 3.31 Linear regression of the number of seedlings (<25 cm girth) located above treeline in 2018 and year of establishment across alpine sites categorised by aspect. Number of transects per aspect are as follows; E =1, N=4, NW=5, S=2, SW=2, W=7. Year of establishment calculated based on Rumpff *et al.* (2009) model.

There were no clear trends of surrounding ground cover around individuals located above treeline, with graminoid and shrub the most prominent ground covers (Figure 3.32).

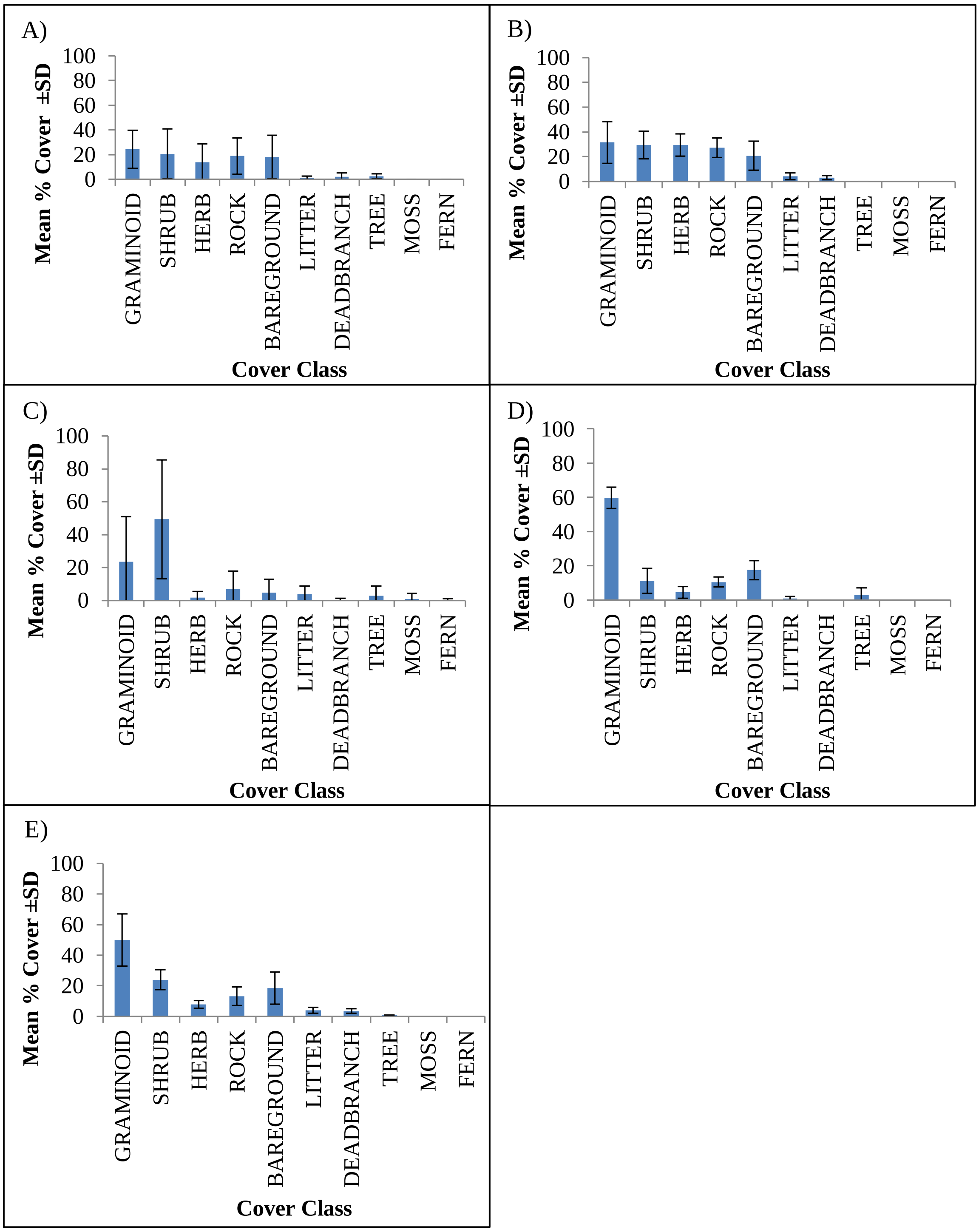


Figure 3.32 Mean % ground cover of vegetation forms or features in a 1 m radius circle around individuals above treeline per site. (A) Mount Hotham. (B) Mount Feathertop. (C) Mount McKay. (D) The Twins. (E) The Razorback.

Subalpine

Changes in treeline dynamics over time varied between sites and transects. A total of 100 seedlings (<25 cm basal girth) were located above treeline in 2018. The majority of seedlings located above the treeline were found within 5 to 10 m of the treeline and were less than 56 cm in height. Changes in the number of seedlings above treeline between survey periods varied between transects and sites. There was an increase in seedlings above treeline at JB and Paw Paw Plain and declines at Precipice Plain, The Lanes and Green Gables (Figure 3.33). Statistical analyses revealed a significant difference in seedling number above treeline between survey periods at all subalpine sites (Appendix C Table 8).

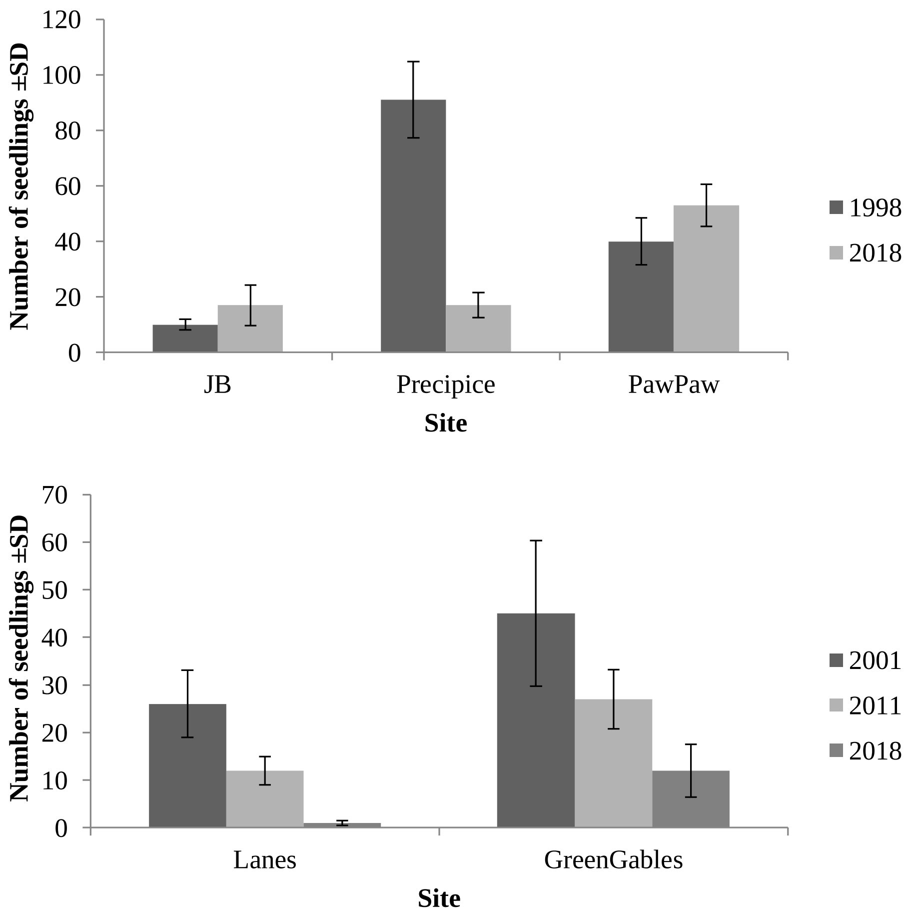


Figure 3.33 Total number of seedlings (<25 cm basal girth) above treeline (± standard deviation) between survey periods for subalpine sites. All sites were burnt once in recent fires.

Establishment year of individuals above treeline combined for JB, Paw Paw and Precipice Plain subalpine show that the majority of individuals had established since 1985 in 1998 surveys and since 2007 in 2018 surveys, with few individuals present in 2018 having established before 1998 surveys, indicating high turnover and mortality (Figure 3.34). At Green Gables and The Lanes, the majority of individuals had established since 1989 in 2001 surveys, 1997 in 2011 surveys and 2009 in 2018 surveys. Few individuals present in 2018 surveys had established before 2001 surveys (Figure 3.35).

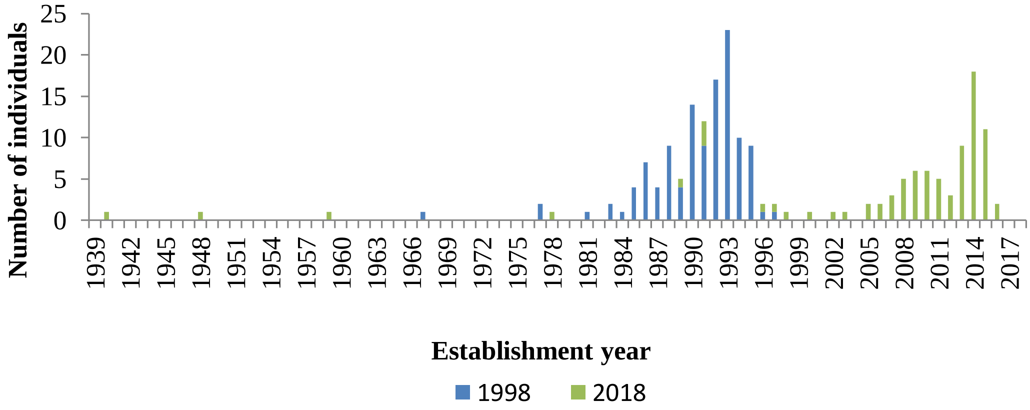


Figure 3.34 Estimated year of establishment of individuals located above treeline across alpine sites in JB, Paw Paw and Precipice Plains in 1998 and 2018. 1998 only presents seedlings based on availability of historic data. Year of establishment calculated based on Rumpff *et al*. (2009) model, as such trees with girth >115 cm (establishment data pre-1938) are excluded.

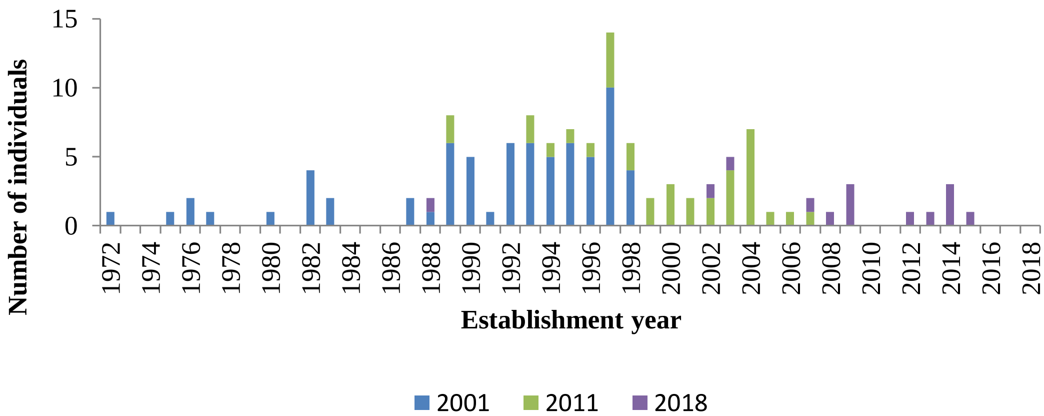


Figure 3.35 Estimated year of establishment of individuals located above treeline across subalpine sites in Green Gables and The Lanes in 2001, 2011 and 2018. 1998 only presents seedlings based on availability of historic data. Year of establishment calculated based on Rumpff *et al.* (2009) model, as such trees with girth >115 cm (establishment data pre-1938) are excluded.

Linear regression revealed a potential aspect effect on seedling recruitment trends above treeline over time, with a significant increase in seedling establishment through time on western and eastern aspects (P-value= 0.009 and 0.019 respectively) (Appendix C Table 9) (Figure 3.36). Northern aspect showed a positive relationship and southern aspect showed a negative relationship, but these were not statistically significant.

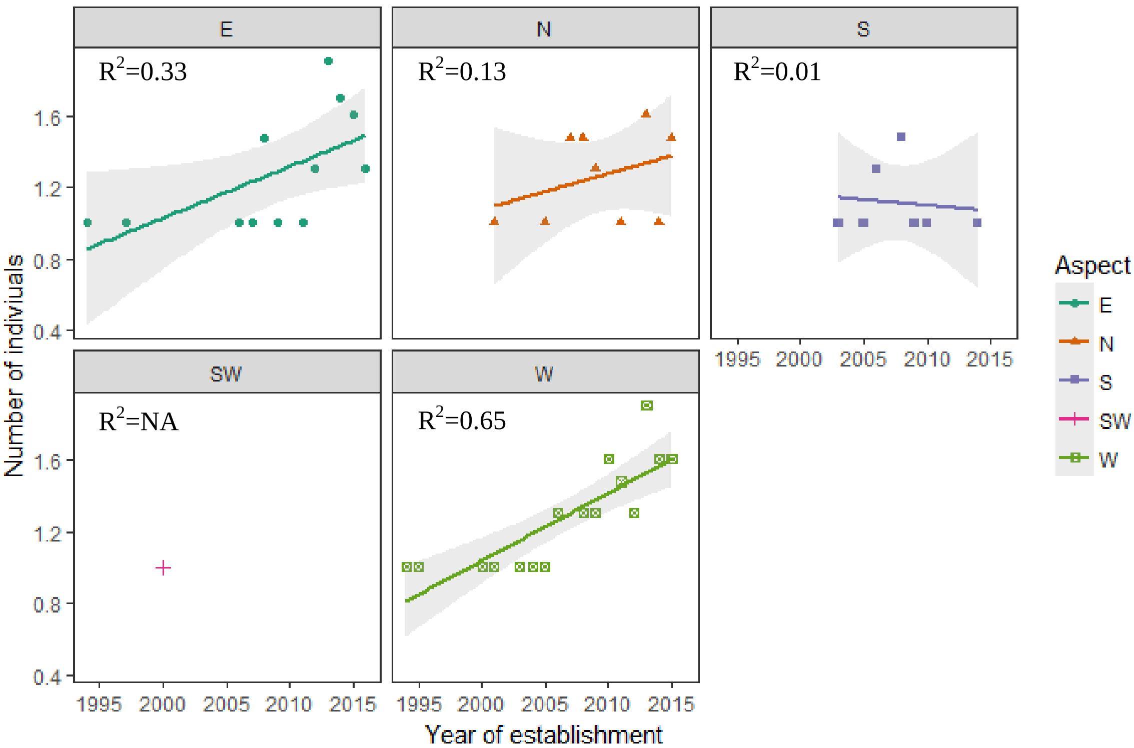


Figure 3.36 Linear regression of the number of seedlings (<25 cm girth) located above treeline in 2018 and year of establishment across subalpine sites categorised by aspect. Number of transects per aspect are as follows; E=6, N=5, S=5, SW=3, W=6. Year of establishment calculated based on Rumpff *et al.* (2009) model.

There were no obvious trends of surrounding vegetation cover around individuals located above treeline, with graminoid the most prominent ground cover (Figure 3.37).

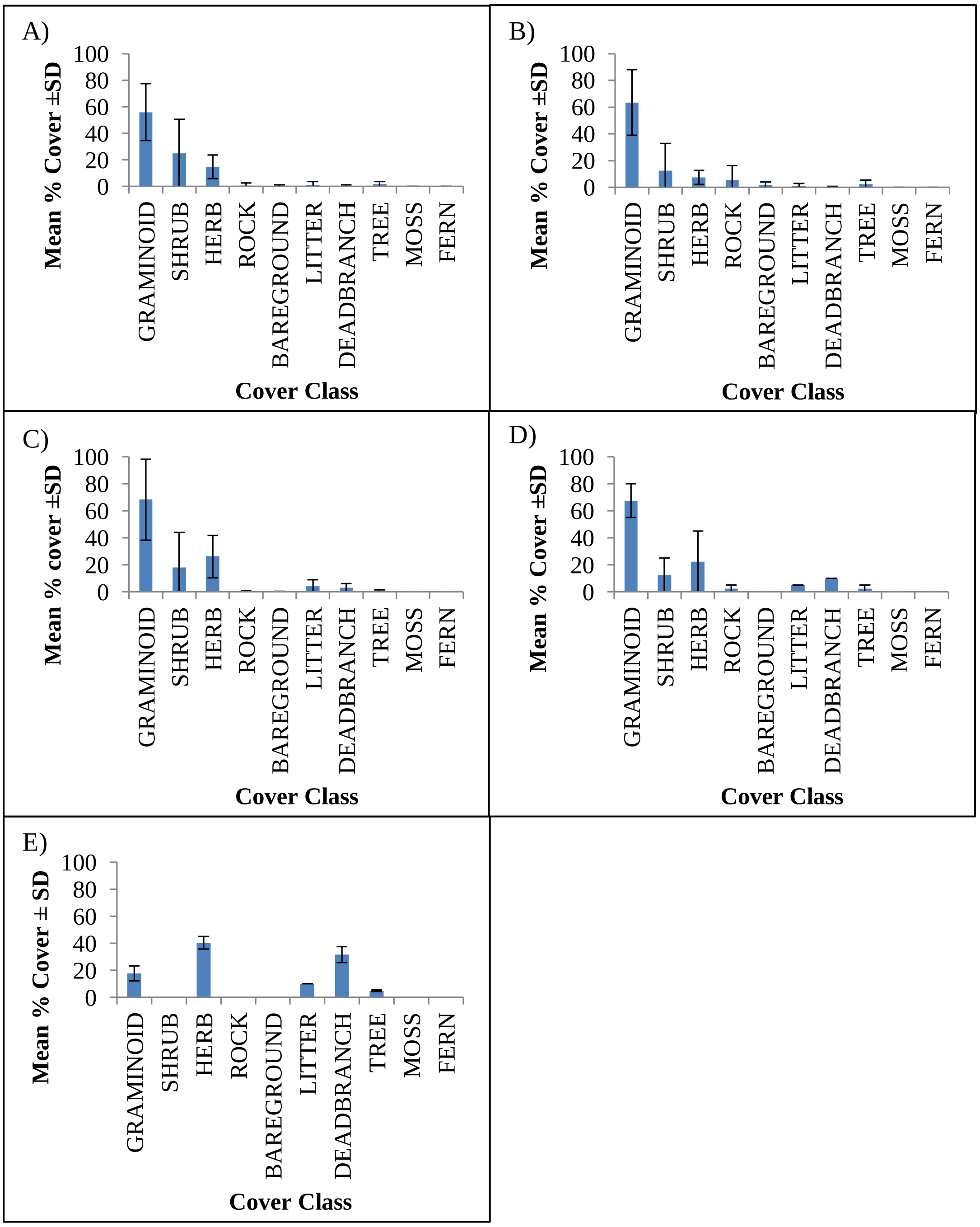


Figure 3.37 Mean % ground cover of vegetation forms or features in a 1 m radius circle around individuals above treeline per site. (A) JB Plain. (B) Paw Paw Plain. (C) Precipice Plain. (D) The Lanes. (E) Green Gables.

Effects of fire

Alpine

The proportions of alive to dead individuals were high across all alpine sites: 100 % at unburnt sites, 92 % at single burn sites and 95 % at double burn sites. Individuals recorded as dead had greater basal girth on average, however wide variation in basal girth occurred across both single (135.54±91.15 cm basal girth) and double (194.55±87.45 cm basal girth) burn sites. Basal or stem resprouting occurred in a moderate number of individuals in unburnt transects (27 %), just over half of individuals in single burn transects (53 %) and a high proportion of individuals in double burn transects (80 %). There were no observable differences in the number of stems or stem diameter across basal girth classes (Figures 3.38, 3.39). The Twins had evidence of big and small third cohort stems indicating two resprouting events following the second fire.

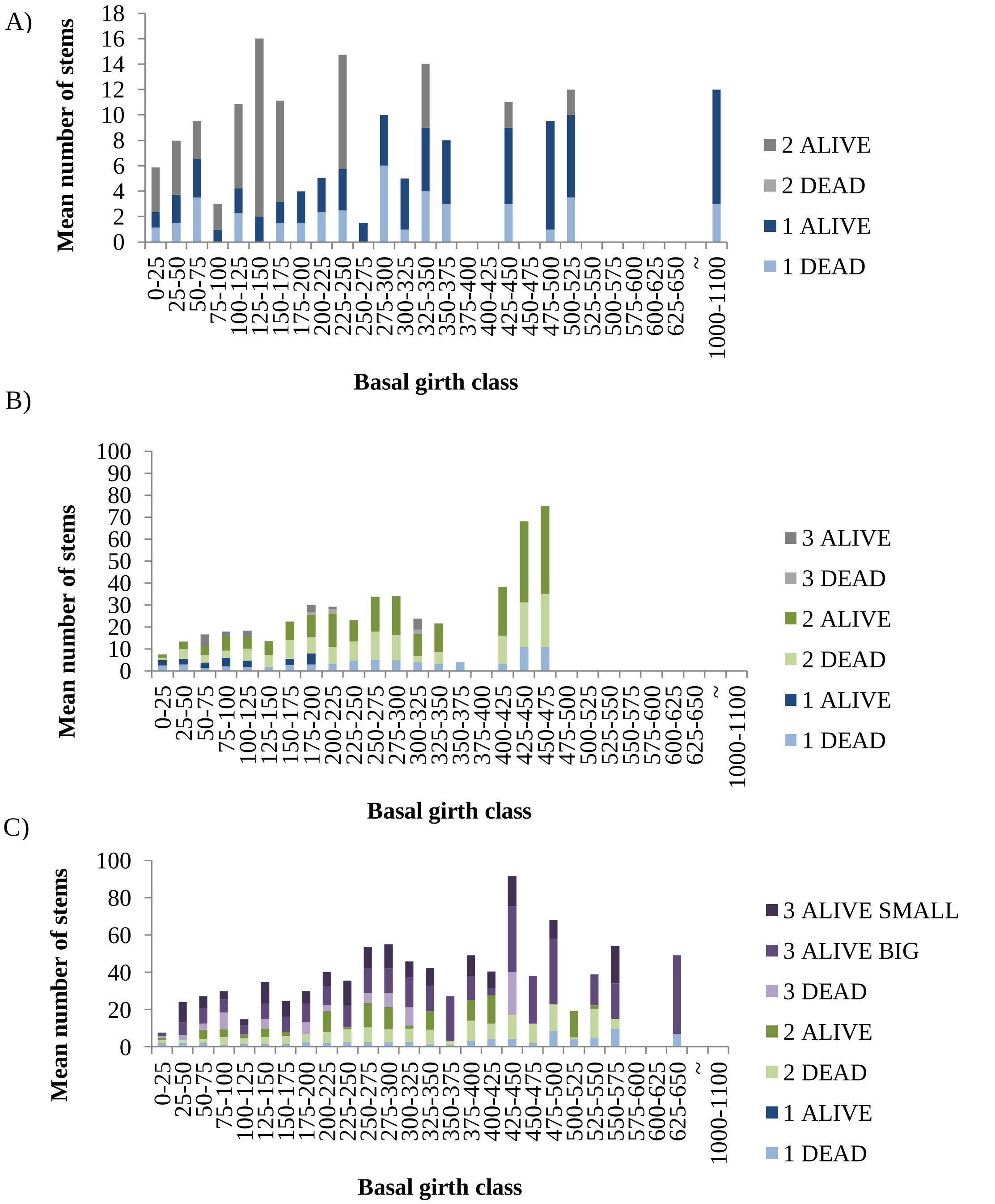


Figure 3.38 Mean number of stems per cohort for individuals in each basal girth class (cm) for alpine transects combined for transects not burnt since last surveyed (A), burnt once since last surveyed (B) and burnt twice since last surveyed (C). Grey indicates cohorts not resulting from fire.

589

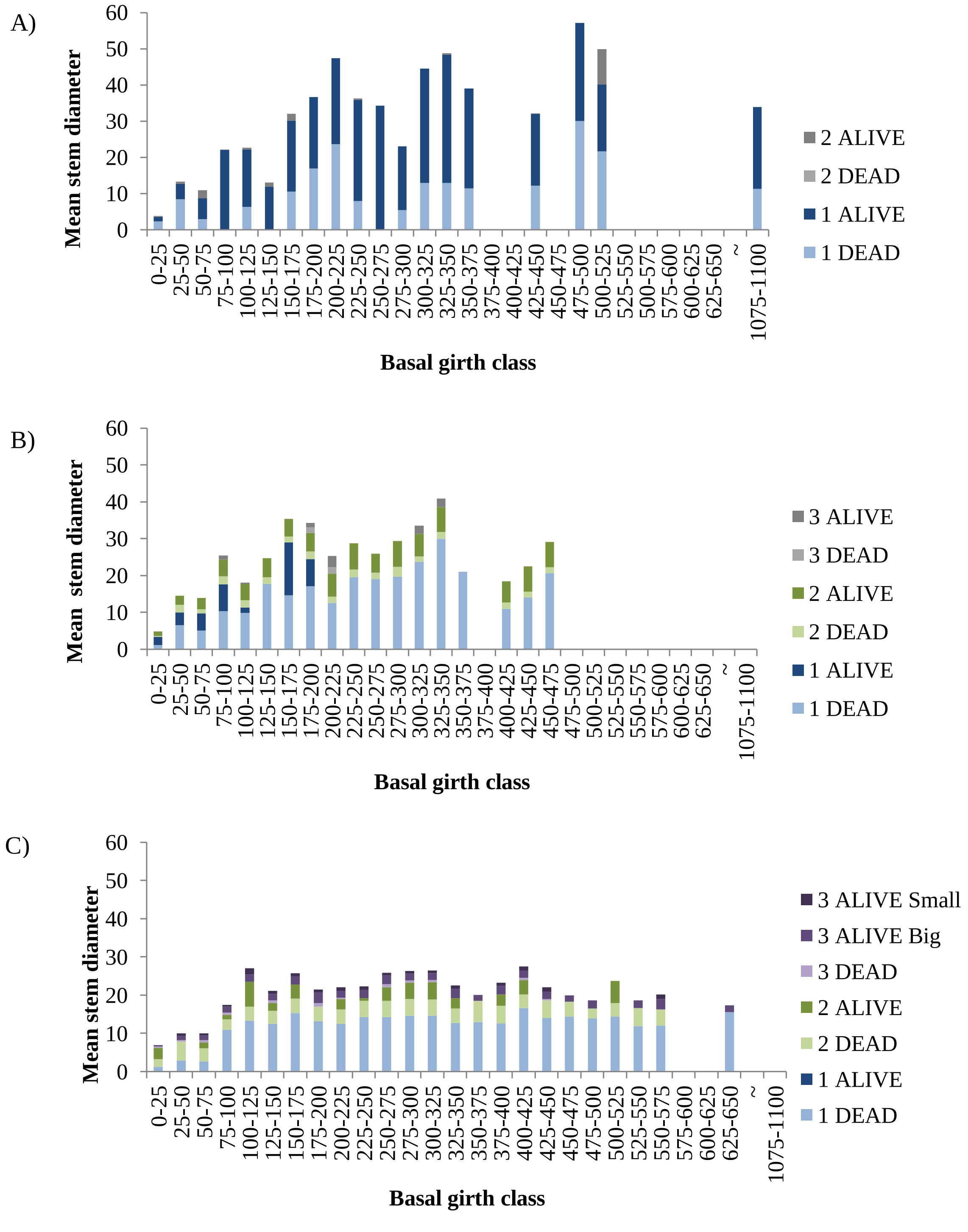


Figure 3.39 Mean stem diameter per cohort for individuals in each basal girth class (cm) for alpine transects combined for transects not burnt since last surveyed (A), burnt once since last surveyed (B) and burnt twice since last surveyed (C). Grey indicates cohorts not evolving from fire.

Subalpine

The proportions of alive to dead individuals were high (90 %) across subalpine sites. Individuals recorded as dead had greater basal girth on average, however wide variation in basal girth occurred across sites (133.45±137.54 cm basal girth). The proportions of individuals with basal and/or stem resprouting was variable across sites. Low numbers of resprouting individuals were seen at Paw Paw (13 %) and JB Plain (11 %), slightly higher at Precipice Plain (29 %) and over half of individuals at The Lanes (65 %) and Green Gables (59 %). There were no observable differences in stem number or diameter with basal girth size, with the exception of some larger individuals which survived the fires and were not observed resprouting. (Figures 3.40, 3.41).

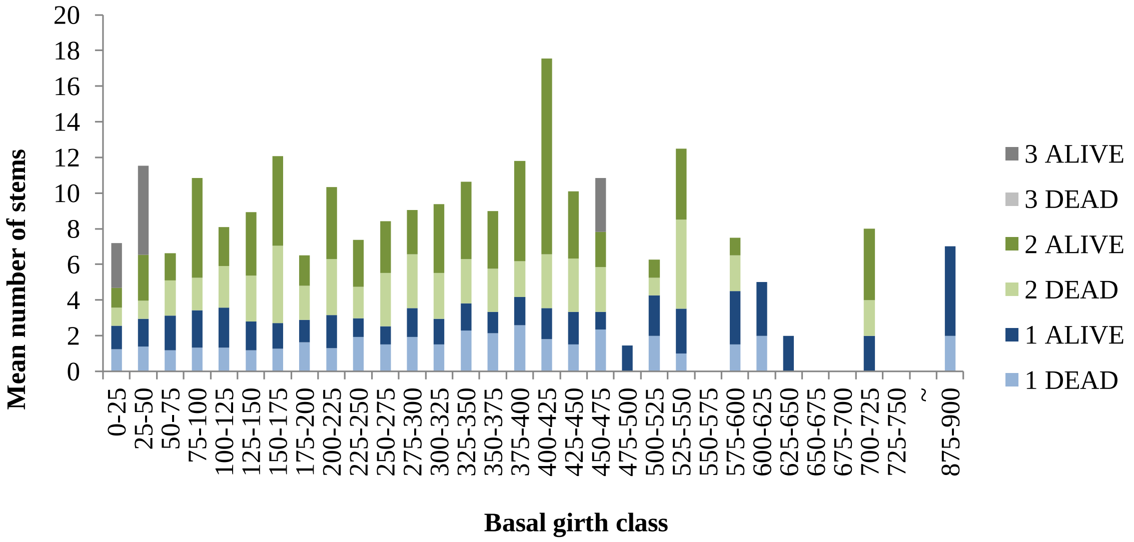


Figure 3.40 Mean number of stems per cohort for individuals in each basal girth class (cm) for subalpine transects combined. All transects have been burnt once since last surveyed. Grey indicates cohorts not evolving from fire.

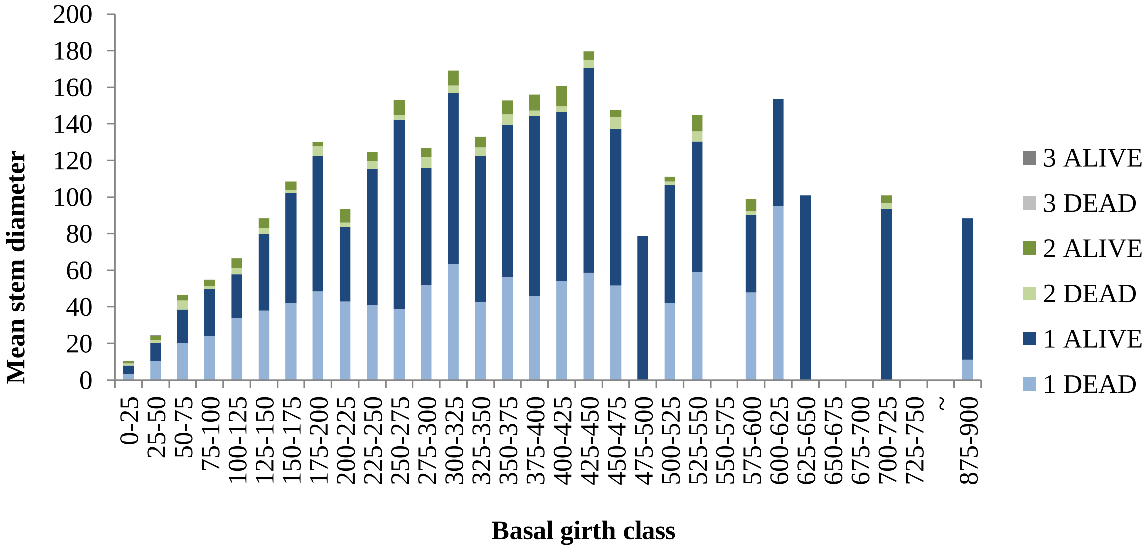


Figure 3.41 Mean stem diameter per cohort for individuals in each basal girth class for subalpine transects combined. All transects have been burnt once since last surveyed. Grey indicates cohorts not evolving from fire.

3.3 Dispersal limitation in *Eucalyptus pauciflora* and other global treeline forming species

There was a wide variation in modelled maximum dispersal distance across treeline forming species**.** Seeds dispersed by wind, but which do not possess dispersal appendages (gravity dispersal), including the study species *E. pauciflora*, had the shortest modelled dispersal distance (Figure 3.42). The relationship between observed treeline advance over the last century and maximum modelled dispersal distance is unclear (Figure 3.43). Species which have evidence of advance were distributed across a range of dispersal distances. There was no strong trend between maximum modelled dispersal distance and the distance of treeline advance (Figure 3.44).

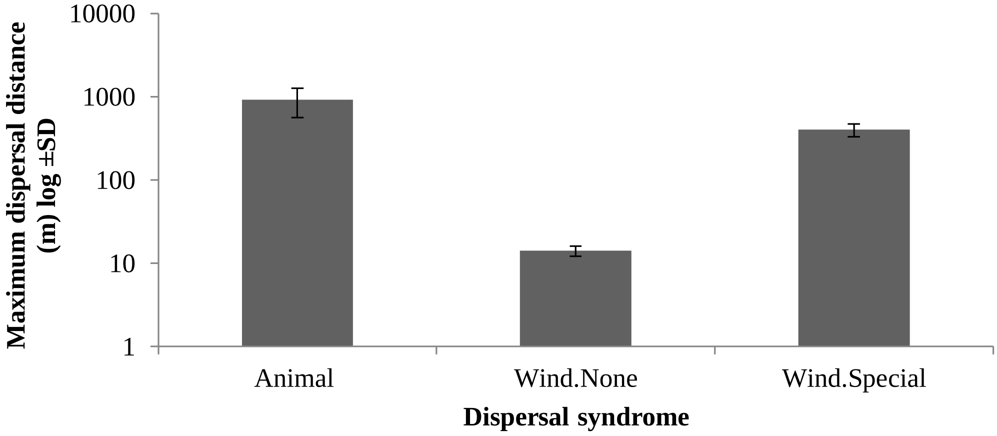


Figure 3.42 Mean modelled maximum dispersal distance of selected global treeline forming species categorised by dispersal syndrome. Animal= animal aided dispersal. Wind.None = gravity dispersal. Wind.Special= wind dispersal aided by dispersal appendages (e.g. wings).

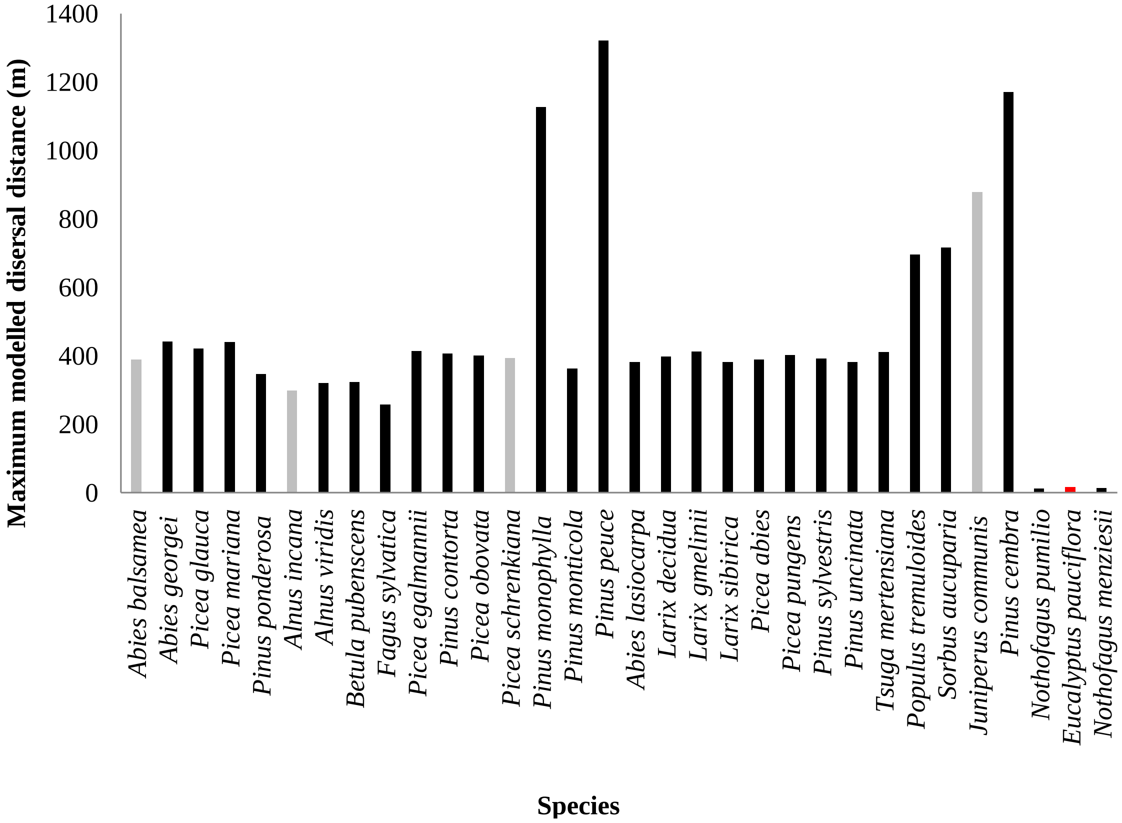


Figure 3.43 Maximum modelled dispersal distance of 32 global treeline forming species categorised by evidence of treeline advance over the last century and hemisphere origin. Advance is classified as a single observed treeline advance at a site thus this is not to say all treelines formed by this species have advanced over the last century. Black= observed advance. Grey= no observed advance. Red = study species.

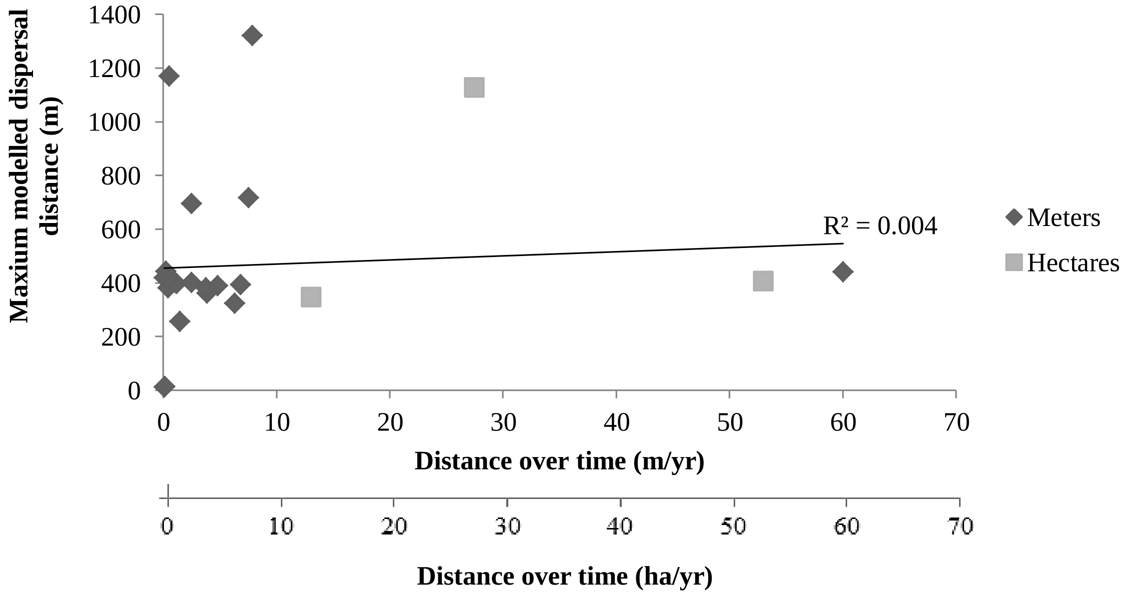


Figure 3.44 Maximum modelled dispersal distance against overserved distance (meters or hectares) of treeline advance.

4. Discussion

Alpine and subalpine treelines across the Victorian Alps appear stable. Historical photographs revealed that neither substantial treeline advance nor infilling has occurred at landscape-scales over the last ~100 years. Re-visitation surveys indicated there has been no significant shift in treeline positions or dynamics over the last 20 years. Marginal recruitment has continued to occur above the treeline at a number of sites. However, a high turnover rate of individuals suggests persistence above the treeline is still constrained by limiting factors. The occurrence of two bushfires over the last decade has negatively affected recruitment, but the presence of fruits on regenerating trees suggests recruitment may rise in the near future. Contrary to predictions, bushfire occurrence does not appear to have suppressed or facilitated treeline advance. Additionally, the substantially lower maximum dispersal distance of *E. pauciflora* relative to treeline species elsewhere suggests Australian treelines may lag behind climate to a greater degree than species with high dispersal capacity. Overall this study's findings do not support the predictions of treeline advance with rising global temperatures.

4.1 Assessment of landscape-scale changes in treelines across the Victorian Alps through repeat photography

Historical photographs provide a rare opportunity to study landscape-scale changes over longer timescales than what is usually possible with re-visitation studies. Through qualitative comparisons of historical and modern photographs, this study revealed distributions of *E. pauciflora* individuals at several alpine and subalpine treelines across the Victorian Alps have remained relatively stable over the last ~100 years. This contrasts to predictions of treeline advance with rising temperatures (Körner 1998). Elsewhere, a combination of treeline advance, stability and recession has been observed globally over similar timescales (e.g. Klasner and Fagre 2002; Hemp 2005; Stueve *et al.* 2009).

Despite overall stability of alpine and subalpine treelines, there has been some infilling and establishment of trees beyond historic alpine treelines around Mount Hotham and Cross Cut Saw, and expansion of trees into subalpine grasslands near Falls Creek. Infilling of trees into treeless vegetation on the Bogong High Plains, Victoria has previously been recorded between 1936 and 1980 (McDougall 2003). However, McDougall (2003) suggests this increase may be the result of canopy expansion over a long fire-free period. Infilling has similarly been observed in the Swiss Alps (Gehrig-Fasel *et al.* 2007) and Spanish Pyrenees (Camarero and Gutiérrez 2004). The prominence of infilling rather than spatial advance may be the result of a high degree of inertia in vegetation above and below treeline. This may result from the density-dependent positive feedback between canopy cover facilitation and seedling recruitment (Maher and Germino 2006). Conversely, the closed vegetation cover and prominence of vegetative reproduction above treeline may maintain treeline boundaries (Slatyer 1989; Halpern *et al*. 2010). Slatyer (1989) concluded that due to the positive feedback between subalpine woodland and alpine or grassland communities, there must be a significant shift in either climate or vegetation structure to enable shifts in tree distribution. This is similarly the case for many grassland communities, such as savannas which require disturbance to create gaps in the vegetation (Noble 1980; Loveys *et al.* 2010). The overall stability of treelines across these longer time scales, despite rising temperature and recent bushfire occurrence, indicates this inertia has not been overcome. This suggests temperature rise has not yet have overcome this thermal threshold to permit treeline advance and overcome constraints of other limiting factors.

4.2 Assessment of the current state of alpine and subalpine treelines through re-visitation surveys

Treeline dynamics and forest structure have remained broadly similar between survey periods, with no evidence of widespread recruitment above treeline due to rising temperatures or mass mortality due to bushfire occurrence. The Twins, double burn site has been more substantially affected by bushfires, with significant reductions in seedlings above and below treeline. However, this may only be a short-term effect. A high turnover rate of individuals above treeline between survey periods, however suggests persistence above the treeline is still constrained by a range of limiting factors, other than bushfire occurrence.

Regeneration Trends

The capacity of *E. pauciflora* to resprout from stem and basal lignotubers in response to bushfires means the position of Australian treelines remains largely unaltered. Adaptations to fire also occur across a number of boreal tree species including resprouting from roots and stumps (e.g. *Betula* spp., *Populus* spp.) and serotinous cones which require heat to release seed (e.g. *Pinus* spp.) (Li and Barclay 2000; Brown 2010). In contrast to Australian treelines, the reliance on regeneration from seed can cause immediate reductions in treeline position and long-term treeline recession if post-fire establishment is constrained (Shankman and Daly 1988; Stueve *et al.* 2009). Hence, fires (and particularity frequent fires) have been found to cause treeline recession across a range of global treelines (Butler and DeChano 2001; Hemp 2005; Coop and Givnish 2007; Cansler *et al.* 2016).

Theoretically, mature *E. pauciflora* have an unrestricted capacity for resprouting as buds stored in lignotubers are retained throughout the life of the tree (Carr *et al.* 1984). However, resprouting capacity may decline with age and size of the lignotuber, as resources are preferentially allocated to growth and reproduction rather than starch storage in lignotubers as the tree matures (Bond and Midgley 2001). Additionally, an increasing lignotuber size may act as a barrier to bud emergence (Burrows 2002; Pickering and Barry 2005). However, no differences in resprouting capacity (no reduction in the presence or relative number of resprouting stems) were observed between individuals of differing size in the present study. Furthermore, there were no clear trends between mortality and basal girth, with a wide variation in the basal girth of dead individuals across sites. Elsewhere, multiple fires have caused lignotuber death and thus death of mature trees (Barker 1988; Noble 2001). Although high mortality was observed in some transects, such as at The Twins (transect 2) and The Lanes (transect 1) where treeline individuals were killed, this was not widespread across study sites. Relatively few individuals were recorded as dead across all sites (<10 %). As such, while there may be some treeline recession on the scale of a few individual trees, there was no observed treeline recession at a slope or site scale.

The proportion of trees exhibiting resprouting was lower than previously found following a single fire in Kosciusko, NSW. Pickering and Barry (2005) observed 96 % regeneration after one year. In the current study, basal resprouting, and to a lesser extent, stem resprouting occurred in over half (53 %) of individuals in single burn transects and the majority (80 %) in double burn alpine sites. Resprouting at subalpine sites (burnt once) was variable (11-65 %). Lower resprouting may reflect lower fire intensity, as resprouting following low-intensity prescribed burns has been recorded as low as 7 % (Good 1982). Frost or drought stress post-fire has also been found to induce lower resprouting levels across *Eucalyptus* species (Bell and Williams 1997).

The results of the present study contrast to studies focusing on lower elevation *E. pauciflora* woodlands which found rising bushfire frequency led to shifts in forest structure through increasing tree and stem density (Coates 2015). Furthermore, Fairman *et al.* (2017) recently found a weakening of the persistence niche of *E. pauciflora*, due to reduced resprouting and seedling regeneration after multiple fires. In the present study forest structure was broadly similar between survey periods across single burn study sites. Although a slight shift in woodland structure occurred at The Twins double burn site due to reductions in small basal class individuals, the presence of buds and fruits all suggests recruitment may rise in the near future. Thus, woodland structure may only have shifted within the short-term. Mortality at The Twins was notably lower (5 %) than that recorded in double burn lower elevation subalpine woodlands (19±8 %) (Fairman *et al.* 2017). Additionally, there were no substantial declines in the number of resprouting stems between single and double burn sites as found by Fairman *et al.* (2017). There was also no substantial increase in stem density as found by Coates (2015). Similarly to Fairman *et al.* (2017), mortality was highest in small size classed individuals. This suggests seedlings are more vulnerable to short-interval bushfires. Therefore, the resilience of treeline populations may be compromised in the event of three or more consecutive fires, if mortality occurs within mature individuals, resprouting capacity is effected and recruitment post-fire is constrained, as seen at lower elevations. Importantly, the present study highlights that the response and resilience of *E. pauciflora* to bushfire may not be uniform across the species elevational range.

Recruitment Trends

General trends

Alpine and subalpine treelines exhibit evidence of long-term stability by the presence of trees exceeding 500 cm basal girth within the treeline ecotone. This is consistent with observations by Wearne (1998), Cutler (2002) and J. Morgan (unpubl. data). Treelines across the study area were found to be abrupt with outpost mature trees occurring infrequently up to 54 m above alpine treelines and 43 m from subalpine treelines. Similar to Wearne (1998), Cutler (2002) and J. Morgan (unpubl. data) surveys, seedlings were typically within 10 m of the treeline. This is consistent with global trends as this ecotonal environment has high seed rain and greater habitat modification via canopy cover which favour establishment (Holtmeier and Broll 2007; Körner 2012). Strong aspect effects were observed, with higher numbers of seedlings on warmer aspects, as predicted due to higher solar radiation and temperature (Slatyer 1989; Körner 2012).

Wearne (1998) and Cutler (2002) observed establishment above alpine and subalpine treelines. Recruitment peaked above alpine treelines from 1981 and subalpine treelines between 1991 and 1995 (Wearne 1998; Cutler 2002). There was no correlation between seedling recruitment and grazing history, suggesting seedling establishment in the past may have been attributed to higher minimum temperatures post-1980. The majority of individuals above treeline in the present study established post-2012, with little overlap with past surveys. This contrasts to predictions of treeline advance, suggesting there are sustained constraints on survival above treeline (Körner 2003; Harsch *et al.* 2009).

Single Burn Site Trends

SCD models indicated forest structure at single burn sites has remained relatively stable between survey periods, with a higher proportion of seedlings and saplings to mature individuals, indicating a healthy, potentially growing population (Condit *et al.* 1998). However, changes in treeline dynamics and marginal changes in structure were observed, suggesting site to site variation. Increases in the number of seedlings above treeline occurred at alpine sites Mount McKay and Feathertop, and at the subalpine sites JB and Paw Paw Plain. This suggests post-fire conditions may be beneficial for recruitment such as through the release of nutrients, reduction in competition and creation of bare ground, a key component of *E. pauciflora* regeneration niche (Noble 1980; Slatyer 1989; Slatyer and Noble 1992). Although increases were observed, on average the magnitude of these changes were relatively small.

Fire theoretically improves conditions for establishment. However, the lack of a pulse in recruitment and establishment above treelines post-fire suggests recruitment constraints persist, such as unfavorable conditions or limited seed availability. These constraints may differ between alpine and subalpine treelines. SCD models indicated regeneration is occurring, with high numbers of seedlings and saplings across JB and Paw Paw Plain, suggesting seed availability is not limited. Wimbush and Forrester (1988) have previously observed high mortality of seedlings which had established above subalpine treelines post-fire. High mortality was attributed to frost, drought and competition, suggesting post-fire conditions may be unfavourable within subalpine grasslands. Conversely, seedlings were less common at Mount McKay and Feathertop suggesting seed availability may be affecting recruitment both above and below treeline. Poor recruitment may also be a function of the life history tradeoff between resprouting and seedling recruitment (Bond and Midgley 2001). Additionally, the lack of an establishment pulse specifically above treeline may be due to the inability of seed to disperse upslope (Slatyer 1989; Green 2009).

The unfavorable conditions post-fire at subalpine treelines aligns with observations of declines in seedlings above treeline at Precipice Plain, The Lanes and Green Gables between survey periods. Although these reductions may be due to seedling death during the bushfires, *E. pauciflora* form a lignotuber at around 6 months of age, suggesting that seedlings should have the capacity to resprout post-fire after canopy loss (Carr *et al.* 1984). Additionally, continued declines have occurred at The Lanes and Green Gables over consecutive surveys 8 and 15 years post fire. This suggests mortality has remained high and limited recruitment has occurred, meaning dead individuals are not being replaced. Although bushfires theoretically improve conditions for *E. pauciflora* establishment, the consequences of canopy loss and rising competition as surrounding vegetation regenerates can negatively affect establishment (Noble 1980; Ball *et al.* 1991; Green 2009).

Tree canopies can facilitate seedling establishment by ameliorating microclimate leading to a positive association between canopy cover and seedling establishment (Germino *et al.* 2002; Smith *et al.* 2003; Holtmeier and Broll 2007). In this study, the majority of seedlings above treeline were confined to within 5-10 m of the treeline. This suggests influences of restricted seed dispersal and canopy facilitation. Canopy cover increases humidity buffering against drought (Gómez-Aparicio *et al.* 2005; Kane *et al.* 2011; Barros *et al.* 2017). Moisture stress has been shown to be a key determinant of the lack of recruitment above treelines in the Himalayas and post-fire drought has been found to reduce recruitment and survival in North American treelines post-fire (van Mantgem *et al.* 2013; Harvey *et al.* 2016; Chhetri and Cairns 2018). As such, moisture stress associated with low rainfall years such as the 2004-5 and 2006-7 growing seasons may have been intensified by canopy loss, leading to lower recruitment and high seedling mortality.

Canopies also reduce frost severity and occurrence through generating a warmer microclimate and providing shade from high intensity light (Ball *et al.* 1991; Körner 2012). Cold-induced photo-inhibition has been shown to limit establishment above Australian subalpine treelines and drive regeneration patterns across a variety of environments from Siberian pine glades to tropical alpine treelines in Ecuador (Ball *et al.* 1991; Slot *et al.* 2005; Bader *et al.* 2007). The current distribution of seedlings above subalpine treelines aligns with the risk of cold-induced photo-inhibition with higher seedling abundance on western and eastern aspects of the subalpine plains where seedlings would benefit from shade from the overhanging canopy (Ball *et al.* 1991). Therefore, loss of canopy cover may have increased frost damage, thereby reducing survival. Conversely, canopies can shade out seedlings causing reduced root zone temperature and limiting light access (Körner 2012). As such, the open canopy, created by the fires, in some cases may have relieved individuals from a suppressed state under the canopy (Ashton and Williams 1989; Loehle 2000; Coates 2015). This may have occurred at The Lanes (transect 1) where seedlings at the treeline survived the fire and have subsequently grown over survey periods. Competition is the second major limiting factor for seedling establishment in subalpine grasslands-woodland systems after frost (Slatyer and Noble 1992). Hence, tree establishment in grasslands often requires creation of gaps in the grass cover induced by disturbances such as fire (Connell and Slatyer 1977; Noble 1980; Loveys *et al.* 2010). However, the benefits of reduced ground cover may be short-lived and have associated negative consequences. Firstly, post-fire regeneration of forbs and graminoids in subalpine grasslands is rapid, recovering to ~64 % of pre-fire cover in one year (Bear and Pickering 2006). Although this rapid recovery assists in stabilizing soil, it does not provide *E. pauciflora* time to establish in a competition-free environment. This may be intensified if fires occur at the end of the summer season, such as in 2003 where bushfires burnt from January to February. As such, growth of *E. pauciflora* may have been negligible prior to winter, leaving them susceptible to being outcompeted by rapidly recovering vegetation the following spring (Slatyer and Noble 1992). This effect may be reduced at alpine sites as cover of alpine vegetation is more slowly regained post-fire and regeneration of alpine vegetation is more beneficial in slope stabilization (Walsh and McDougall 2004; Bear and Pickering 2006). Secondly, surrounding vegetation can have facilitative effects on *E. pauciflora* seedlings as a warm boundary layer is formed due to maximum heat accumulation and retention near the soil surface, increasing temperatures by up to 10 °C (Körner 2003). Previous studies have found higher mortality and lower growth rates in *E. pauciflora* seedlings located closer to grass tussocks (Harwood 1976; Noble 1980). This highlights the competitive influence of grass for shared resources including water and nutrients. However, seedlings located further away from grass tussocks were found to have increased frost damage as they did not benefit from the warm microclimate (Noble 1980; Ball *et al.* 1991; Slatyer and Noble 1992). While the loss of surrounding vegetation may be beneficial for saplings due to reduced competition, this loss may be detrimental to establishment, as seedlings are physiologically sensitive and thus benefit from the warm microclimate (Loranger *et al.* 2017). The combined influence of canopy and surrounding vegetation loss may have intensified frosts, potentially driving the reduction in seedlings above treeline at Precipice Plain, The Lanes and Green Gables. Overall, bushfires can be both beneficial and deleterious for *E. pauciflora* recruitment. The variable effects of fire are driven by its influence on the direction, magnitude and interactions of limiting factors which constrain tree establishment above the treeline.

Double Burn Site Trends

In contrast to single burn alpine sites, SCD models for The Twins, which was burnt twice in recent fires, indicated a scarcity of seedlings and saplings in 2018 leading to a more even aged and potentially declining population (Condit *et al.* 1998). This contrasts to surveys conducted by Cutler (2002) where seedling and saplings were prominent suggesting a shift in treeline dynamics over time and potentially with bushfire occurrence.

Low seedling numbers above and below treeline may be a direct result of multiple short-interval fires. Although seedlings should be capable of resprouting from lignotubers, which are formed at 6 months of age, seedlings are more vulnerable to high-intensity fires, as their lignotubers are less well protected by soil than older individuals (Jacobs 1955; Carr *et al.* 1984). Additionally, the period between the two fires may have been an insufficient interval for individuals to recover, leaving them more susceptible to lignotuber death during the second bushfire (Fairman *et al.* 2017).

The lack of seedlings below treeline compared to single burn sites suggests there may also have been no viable seed to germinate after the second fire. Interval squeeze, linked to immaturity risk, may occur when bushfires occur on shorter fire intervals than is required for individuals to grow and mature (Enright *et al.* 2015). This has been observed in mixed-conifer and subalpine forests where repeat fires and the occurrence of other disturbances pre-fire caused reduced seed availability (Harvey *et al.* 2014; Stevens-Rumann and Morgan 2016). *E.*

pauciflora seed is not able to survive for long periods within the soil, and without stimulation of a second dormancy period cold stratified seed generally persists for only a single growing season (Howard and Ashton 1967; Ferrar *et al.* 1988). As such, the occurrence of a second fire within 10 years may have been an insufficient period to allow regrowth from the previous fire to reach reproductive maturity (Keeley *et al.* 1999; Westerling *et al.* 2011; Enright *et al.* 2015).

E. pauciflora (subsp. *niphophila*) has been observed regenerating 15 years after fire in Kosciusko, NSW (K. Green unpubl. data). Observations of buds and fruits at The Twins suggest reproductive maturity may be reached within 5 to 11 years post-fire (depending on fire history of The Twins). Although the viability of seed was not assessed in the present study, Cutler (2002) had previously found viable seed in fruit collected from The Twins treeline. This ensures maturation of fruit can occur at the treeline, but suggests that fruit is potentially not yet mature and thus, recruitment may rise in the future. A bushfire interval threshold appears to exist, defining the minimum time between bushfires that allow trees to reach maturity and set seed (K. Green, unpubl. data).

Conversely, at The Razorback transects, which were similarly burnt twice, seedlings are present below and above treeline. This suggests that additional site factors may be affecting conditions at The Twins, rather than the occurrence of two fires alone. As with single burn sites unfavourable conditions may be constraining recruitment and growth post-fire. In particular, the effect of canopy loss may be greater than at subalpine sites due to the complete loss of canopy post-fire and slower growth rates at higher elevations (K. Green, unpubl. data). Furthermore, the prominence of basal resprouting at alpine sites, compared to stem resprouting at subalpine sites, leads to a denser woodland structure. This can lead to intraspecific competition reducing growth, potentially leading to longer time periods to a reproductive state and recovery to pre-fire canopy height and structure (Bellingham and

Sparrow 2000; Noble 2001; Coates 2015). This effect may reduce canopy facilitation, dispersal capacity and light availability within the woodland for up to 150-200 years before stems thin to pre-fire conditions and return to a more open woodland structure (Barker 1988; Noble 2001). Continued surveys are required to determine if recruitment increases in the future, as more individuals reach reproductive maturity. However, the substantial reduction in seedlings above and below treeline suggests multiple bushfires can negatively affect recruitment processes and thus may delay the potential for treeline advance in the future.

Unburnt Site Trends

SCD models indicated Mount Hotham, unburnt in recent bushfires, expresses a healthy, stable and potentially growing population (Condit *et al.* 1998). Increases in seedlings above treeline occurred between survey periods across a number of transects. However, modelling of age indicated that the majority of individuals above treeline had established since 2009. As such, few individuals have survived from surveys by Cutler (2002), suggesting high mortality and turnover. This implies there are still limitations to seedlings survival above treeline aside from temperature and bushfire effects.

The modelled age of seedlings above treeline at Mount Hotham does not correlate to a significant rise in temperature or shift in growing season precipitation since 2009. Conversely, the majority of seedlings present above alpine and subalpine treelines across all study sites both currently and in past surveys are approximately under 10 years of age. There is also a similarity in height of individuals, with the majority less than ~50 cm in Wearne (1998 and Cutler (2002) surveys and less than ~56 cm in current surveys. This similarity in age and height suggests that growth may become limited beyond this point, potentially corresponding to a height threshold, as previously suggested by Cutler (2002). This height threshold is common across treelines with this stunted shrub-like structure, ‘krummholz’, present across a range of European treelines (Körner 2012). The establishment of seedlings and their ability to persist and mature are strongly influenced by the physical and biological microenvironment at that site (Slatyer and Noble 1992). Körner (2012) identifies the most critical transition for a seedling is to the upright sapling and tree stage. This corresponds to a shift in climatic environment from within the warm microclimate amongst the short-statured surrounding vegetation, to above this vegetation layer where they become more closely coupled to atmospheric conditions. The most critical stress at treeline is freezing stress which is known to cause dieback at alpine treelines and is the major cause of subalpine treeline formation (Slatyer 1989; Körner 2012). Although mature *E. pauciflora* are relatively resistant to frost, seedlings less than 30 cm can be easily killed by substantial shoot dieback, such as from frost (Slatyer 1989). Seedlings require a prolonged period of frost-free damage to attain heights of over 1 m where frost occurrence and damage becomes less severe. Once seedlings exceed 50-100 cm, they are generally able to survive adverse events involving shoot dieback or breakage (Paton *et al.* 1979; Sakai *et al.* 1981; Slatyer 1989; Wearne 1998).

Freezing stress is highest immediately above the surrounding vegetation layer due to exacerbated radiative cooling (Ball *et al.* 1997). Ball *et al.* (1991) found that leaves of *E. pauciflora* seedlings above grass were 1-3 °C lower than air temperature as grass impedes heat flow from the soil. In the present study, grass was found to be the most common ground cover within a 1 m radius around seedlings above treeline across all sites, suggesting radiative cooling effects may be strong. In addition, frost days were found to occur more frequently at 30 and 60 cm above ground compared to ground level at both alpine and subalpine sites. This aligns with Ball *et al.'s* (1997) finding that the cooling effects are greatest within 20 cm of surrounding vegetation. Counterintuitively, temperatures were generally higher, with a greater number of GDDs at 30 and 60 cm. This suggests that it may not be overall growing season temperature which limits seedling growth beyond this height, but the occurrence of extreme temperature events (Holtmeier and Broll 2005). Therefore, freezing stress may be stunting upright growth beyond the surrounding vegetation layer. Predictions of reduced snowpack depth and duration as a consequence of warming and drought have the potential to increased frost occurrence (Ball *et al.* 1991; Slatyer and Noble 1992). Combined with reduced frost tolerance under elevated CO_2, this suggests *E. pauciflora* persistence above treeline may remain limited in the future despite increases in average temperatures (Woldendorp *et al.* 2008). If a number of individuals are able to overcome this height threshold, this could facilitate rapid upslope migration through infilling as suggested by Green and Venn (2012), whereby positive density depended feedbacks occur due to environmental amelioration and high seed rain (Holtmeier and Broll 2007; Dovčiak *et al.* 2015). Additionally, this height threshold may have made individuals more susceptible to bushfires due to their close proximity to the ground layer and surface fuels (Cansler *et al.* 2016).

In summary, local treeline dynamics and woodland structure appeared relatively stable over this ~20 year period. Bushfires have not facilitated nor suppressed treeline advance. Overall, immaturity risk and the idea of a threshold fire interval suggests that increasing fire frequency, predicted with climate change, has the potential to negatively affect *E. pauciflora* woodland persistence. Two fires within a decade have had negative effects on recruitment processes below and above treeline. Observations of bud and capsules, however, suggest recruitment may increase in the future as resprouting individuals reach reproductive maturity. The high turnover of seedling above treeline between survey periods across all sites indicates there are outstanding constraints on establishment, survival and growth of *E. pauciflora* above the treeline. Hence, treeline advance may remain limited until temperatures rise beyond the point at which to overcome other limiting factors.

4.3 Dispersal limitation in *Eucalyptus pauciflora* and other global treeline forming species

Constraints on seed production and dispersal can dictate potential treeline advance, leading to dispersal lags (Alexander *et al.* 2017; Kambo and Danby 2017). Rising temperatures have the potential to improve seed production and viability (Allen *et al.* 2014; Hacket-pain *et al.* 2015; Kambo and Danby 2017). However, without successful dispersal advance would be marginal (Körner 2012; Alexander *et al.* 2017; Neuschulz *et al.* 2017).

Despite the large variation in modelled maximum dispersal distance across species, there were no clear trends with observed treeline advance. For example, *Nothofagus pumilio* and *Nothofagus menziesii* have shown evidence of treeline advance despite having the shortest dispersal distances of all species (Wardle and Coleman 1992; Cuevas 2000). The occurrence of treeline advance, however, is not uniform across treelines composed of the same species (Harsch *et al.* 2009). *N. pumilio* and *menziesii* have also shown evidence of treeline stability over the last century (Cuevas 2000, 2002; Cullen *et al.* 2001; Daniels and Veblen 2003, 2004). Site-specific variability is high, making determination of global trends complicated. As such, the distance of advance was used to compare the relationship between dispersal and treeline advance. However, no clear trends were observed. In some cases, as would be expected, a greater distance of advance was found in species modelled to have a higher dispersal distance, e.g. *Pinus peuce* in Bulgaria (Meshinev *et al.* 2000; Walther 2003). Similarly, a shorter advance distance occurred in *Picea glauca* in Canada, as would be expected due to its shorter maximum dispersal distance (Szeicz and MacDonald 1995). Conversely, *N. pumilio* modelled to have the shortest maximum dispersal distance has shown evidence of advance in Chile (Cuevas 2000, 2002). This inconsistency highlights the likely prevalence of local factors in determining the response of treeline species to rising temperatures.

Dispersal modelling revealed *E. pauciflora* to have a maximum dispersal distance of ~16 m. This supports Slatyer (1989) prediction that *E. pauciflora* dispersal is largely limited to within a few widths of the canopy. This also aligns with the current study in which majority of seedlings were observed within 10 m of the treeline. The maximum dispersal distance of *E. pauciflora* was at the lower end of the dispersal spectrum among global treeline forming species, suggesting dispersal may be a greater constraint in Australian treelines. In addition, long life spans and a prolonged period to reach reproductive maturity are associated with dispersal lags (Alexander *et al.* 2017). Based on the traits of *E. pauciflora* and modelled dispersal distance, dispersal lags may be occurring, reducing the rate of treeline response to warming temperatures (Johnson *et al.* 2017). However, ~16 m should still enable transport of seeds above the current treeline. Therefore, the transport of seed uphill, as suggested by Green (2009), may be more influential in limiting advance than dispersal distance alone. Given *E. pauciflora* is largely dispersed by gravity, this may be more difficult than species which are wind-dispersed and thus, are easily carried up slope in the wind stream (Holtmeier and Broll 2005). Overall, the variability in dispersal distance of global treeline forming species and observed advance suggests treelines are still strongly influenced by local limiting factors. Hence, limited recruitment above alpine and subalpine treelines in Victoria is most likely the result of a combination of limiting factors such as availability of safe sites, frost occurrence, competition and moisture limitations rather than dispersal alone.

4.4 Future implications for Australian treelines in a global context

Rising global temperatures are predicted to cause treeline advance as regions above the treeline become climatically suitable for tree growth (Körner 1998; Holtmeier and Broll 2007). However, currently upslope advance is not a uniform global trend. Harsch *et al.* (2009) found evidence of treeline advance, stability and recession across 126 global treeline sites, with advance occurring in only 52% of sites. Despite the lower than expected number of advancing treelines, Harsch *et al.* (2009) highlight that both advance and stability would be expected to occur if treelines were responding to rising global temperatures in a directional manner, yet remain controlled by other limiting factors.

Harsch *et al.* (2009) found evidence of disturbance across treelines which had receded over the last century. Bushfires have been shown to cause treeline depression across a range of global treelines (e.g. Butler and DeChano 2001; Hemp *et al.* 2005; Coop and Givnish 2007; Cansler *et al.* 2016). An increase in the frequency and severity of bushfires in the Australian Alps is predicted with climate change (Bradstock *et al.* 2014; Williams *et al.* 2014). Contrastingly to global studies and low elevation subalpine *E. pauciflora* woodlands, the present study suggests treeline populations are resilient to up to two bushfires within a decade, with no evidence of treeline suppression or facilitation of treeline advance. This resilience, however, may be compromised under shorter fire intervals due to effects on recruitment processes and increased immaturity risk, particularity if bushfires occur regularly within 15 years (Enright *et al.* 2015; K. Green, unpubl. data). Additionally, predictions of declines in precipitation may further reduce the resprouting capacity of *E. pauciflora* and post-fire recruitment (Bell and Williams 1997; IPCC 2013; Harvey *et al.* 2016). The altered forest structure (increase in shrubs and tree stem density) arising from fire also has the potential to increase woodland flammability, stimulating and intensifying bushfires in the future, creating a positive feedback (Zylstra 2012; Camac 2017). Furthermore, warming has been shown to increase the productivity of alpine plant communities; therefore, competition for microsites and recourses will likely increase (Winkler *et al.* 2016). Hence, the fate of Australian treelines may depend on the strength of these negative consequences associated with rising temperatures, which may counteract the positive effects of increased growth and establishment under warmer climates.

The lack of treeline advance across Victorian alpine and subalpine treelines is not unprecedented, with evidence of stability, infilling and increased growth rates more common than an increase in spatial extent across global treelines (Harsch *et al.* 2009; Körner 2012). Additionally, substantial lags between treeline elevation and temperature isotherms have been observed across global treelines (Paulsen *et al.* 2000; Klasner and Fagre 2002; Camarero and Gutiérrez 2004; Gehrig-Fasel *et al.* 2007; Kullman and Öberg 2009). These lags may be due to high inter-annual variability and dispersal limitation, as may be the case for *E. pauciflora* (Holtmeier and Broll 2007; Alexander *et al.* 2017). The continued presence of individuals above alpine and subalpine treelines suggests *E. pauciflora* is responding to warming to some extent. However, growth and persistence above treeline remains constrained by other limiting factors (e.g. disturbance, competition, dispersal limitation, herbivory, frost or regeneration limitations). In the present study, the majority of seedlings located above treeline were observed on western and north-western aspects. This asymmetrical establishment is common across treelines globally due to aspect effects, with higher solar radiation and temperatures on these aspects enabling advance to occur under lower temperature rises (Slatyer 1989; Körner 2012). Furthermore, the similarity in predicted age and height of individuals above treeline suggests frost may be one major constraint of growth and persistence above treeline. As such, a reduction in frost events may also be required to allow for sustained growth past this critical height threshold and substantial treeline advance to occur (Moore and Willaims 1976). Hence, Victorian treeline advance may only occur after a threshold of warming has occurred over which the influence of other limiting factors becomes negligible (Rupp *et al.* 2001; Harsch *et al.* 2009).

Although the spatial and temporal scales of this study may limit the ability to extract broad scale patterns and trends, this study demonstrates short-term changes at alpine and subalpine treelines in the Victorian Alps, providing a base upon which to build future research. Consistent observations of treeline stability across sites and time scales (20 to 100 year periods), suggests these trends may be common across Australian treelines (uniquely composed of *E. pauciflora*). Similarly, access to historical surveys combined with recent bushfire events has enabled the study to provide insights into changes in treeline dynamics in response to fire frequency. This study contributes to the lack of Australian treeline studies within global meta-analyses, highlighting the stability in Victorian treelines is not uncommon within global trends, suggesting Australian treelines are responding to temperature rise yet remain controlled by limiting factors (Harsch *et al.* 2009).

5. Conclusion

This study aimed to contribute to the gap in the scientific literature on the current state of Australian alpine and subalpine treelines. The findings suggest alpine and subalpine treelines remain stable at landscape- and local-scales due to limiting factors other than temperature, which continued to prevent establishment and persistence of *E. pauciflora* above treeline. These factors may include disturbance, competition, dispersal limitation, herbivory, frost or regeneration limitations. Bushfires do not appear to have suppressed nor facilitated treeline advance. However, increasing bushfire frequency has the potential to compromise *E. pauciflora* resilience in the future through limiting recruitment and resprouting capacity. Whether limiting factors will continue to constrain treeline advance in Australia or temperature eventually reaches a threshold at which these factors become negligible is still unknown. These site-specific limiting factors have similarly led to the variable response of global treelines to warming over the last century. Building on short-term studies, such as the re-visitation study conducted here, will assist in determining long-term patterns and trends. Furthermore, longitudinal studies are required to investigate the influence of facilitating or limiting factors such as seed dispersal in the field, associations between mature trees and seedling establishment, drought or frost stress and competition. Studying the combined influences of rising temperature, drought and bushfire occurrence will be crucial to understand and predict how the balance of facilitating and limiting factors may shift. Ultimately these factors will determine how alpine and subalpine treeline dynamics will respond to environmental change in the future.

Acknowledgements

I would like to thank my supervisors Susanna Venn and John Morgan for their guidance and their help in the field. Thanks to Sera Cutler for her assistance in the field in relocating transects. Thanks to Simon Heyes for assistance with statistical analyses. Thanks to Zac Walker and Keith McDougall for modern and historical photograph collections. Lastly a special thanks goes to my field volunteers Lisa, Lucio and Martin for all their help and support throughout my honours.

6. References

Alexander JM, Burgess I, Essl F, Haider S, Kueffer C, Mcdougall K, Milbau A, Rabitsch W, Rew LJ, Sanders NJ (2017) Lags in the response of mountain plant communities to climate change. *Global Change Biology* 1–17. doi:10.1111/gcb.13976.

Allen RB, Hurst JM, Portier J, Richardson SJ (2014) Elevation-dependent responses of tree mast seeding to climate change over 45 years. *Ecology and Evolution* **4**, 3525–3537. doi:10.1002/ece3.1210.

Ashton DM, Williams RJ (1989) Dynamics of the sub-alpine vegetation in the Victorian region. 'Sci. significance Aust. Alps'. pp. 143–168. (Australian Alps Liaison Committee,: Canberra)

Bader MY, van Geloof I, Rietkerk M (2007) High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecology* **191**, 33–45. doi:10.1007/s11258-006-9212-6.

Ball M, Egerton J, L Lutze J, Gutschick V, Cunningham R (2002) Mechanisms of competition: Thermal inhibition of tree seedling growth by grass. *Oecologia* **133**, 120–130.

Ball MC, Egerton JJG, Leuning R, Cunningham RB, Dunne P (1997) Microclimate above grass adverseiy affects spring growth of seediing snow gum (Eucalyptus pauciflora). *Plant, Cell adn Environment* **20**, 155–166.

Ball AMC, Hodges VS, Laughlin GP (1991) Cold-Induced Photoinhibition Limits Regeneration of Snow Gum at Tree-Line. *Functional Ecology* **5**, 663–668.

Barker S (1988) Population Structure of Snow Gum (Eucalyptus pauciflora Sieb . ex Spreng.)

Subalpine. *Australian Journal of Botany* **36**, 483–501.

Barros C, Guéguen M, Douzet R, Carboni M, Boulangeat I, Zimmermann NE, Münkemüller T, Thuiller W (2017) Extreme climate events counteract the effects of climate and land-use changes in Alpine treelines. *The Journal of applied ecology* **54**, 39–50. doi:10.1111/1365-2664.12742.

Bear R, Pickering CM (2006) Recovery of subalpine grasslands from bushfire. *Australian Journal of Botany* **54**, 451–458.

Beardsell D, Mullett J (1984) Seed Germination of *Eucalyptus pauciflora* Sieb . ex Spreng . from Low and High Altitude Populations in Victoria. *Australian Journal of Botany* **32**, 475–480.

Bell D, Williams J (1997) Eucalypt ecophysiology. 'Eucalypt Ecol. to Ecosyst.' (Eds J. Williams, JC. Woinarski) pp. 168–196. (Cambridge University Press: Cambridge)

Bellingham P, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* **89**, 409–416.

Billings WD (1969) Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio* **19**, 192–207. doi:10.1007/BF00259010.

BOM (2018) Cliamte Data Online. *Aust. Gov. Bur. Meterology*. http://www.bom.gov.au/climate/data/.

Bond WJ, Midgley J. (2001) Ecology of sprouting in woody plants : the persistence niche. *Trends in Ecology and Evolution* **16**, 45–51.

Bradstock R, Penman T, Boer M, Price O, Clarke H (2014) Divergent responses of fire to recent warming and drying across south-eastern Australia. *Global Change Biology* **20**, 1412–1428. doi:10.1111/gcb.12449.

Brown CD (2010) Tree-line Dynamics: Adding Fire to Climate Change Prediction. *Arctic* **63**, 488–492.

Burrows GE (2002) Epicormic strand structure in *Angophora, Eucalyptus and Lophostemon (Myrtaceae)* – implications for fire resistance and recovery. *New Phytologist* **153**, 111–131. doi:10.1046/j.0028-646X.2001.00299.x.

Butler D., DeChano L. (2001) Environmental change in Glacier National Park, Montana: An assessment through repead photography from fire lookouts. *Physical Geography* **22**, 291–304.

Camac JS (2017) Climatic warming strengthens a positive feedback between alpine shrubs and fire. *Global Change Biology* **23**, 3249–3258. doi:10.1111/gcb.13614.

Camarero JJ, Gutiérrez E (2004) Pace and Pattern of Recent Treeline Dynamics: Response of Ecotones to Climatic Variability in the Spanish Pyrenees. *Climatic Change* **63**, 181–200. doi:10.1023/B:CLIM.0000018507.71343.46.

Cansler CA, Mckenzie D, Halpern CB (2016) Area burned in alpine treeline ecotones reflects region-wide trends. 1209–1220.

Carr DJ, Jahnke R, Carr SGM (1984) Initiation, development and anatomy of lignotubers in some species of *Eucalyptus*. *Australian Journal of Botany* **32**, 415–437.

Chhetri PK, Cairns DM (2018) Low recruitment above treeline indicates treeline stability under changing climate in Dhorpatan Hunting Reserve , Western Nepal. *Physical Geography* **3646**, 1–14. doi:10.1080/02723646.2018.1428266.

Coates F (2015) Comparative changes in *Eucalyptus pauciflora* (*Myrtaceae*) stand structure after bushfires in Victoria. *Cunninghamia* **15**, 1–12. doi:10.7751/cunninghamia.2015.15.001.

Colombaroli D, Henne PD, Kaltenrieder P, Gobet E, Tinner W (2010) Species responses to fire , climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. *Journal of Ecology* **98**, 1346–1357. doi:10.1111/j.1365-2745.2010.01723.x.

Compostella C, Caccianiga M (2017) A comparison between different treeline types shows contrasting responses to climate fluctuations. *Plant Biosystems* **3504**, 1–14. doi:10.1080/11263504.2016.1179695.

Condit R, Sukumar R, Hubbell SP, Foster RB, Condit R, Sukumar R, Hubbell SP, Foster RB (1998) Predicting Population Trends from Size Distributions : A direct test in a tropical tree community. *The American Naturalist* **152**, 495–509.

Connell J, Slatyer R (1977) Mechanisms of succession in natural communities and their role in community stability adn organisation. *American Naturalist* **111**, 1119–1144. doi:10.1086/283241.

Coop JD, Givnish TJ (2007) Spatial and temporal patterns of recent forest encroachment in montane grasslands of the Valles Caldera, New Mexico, USA. *Journal of Biogeography* **34**, 914–927. doi:10.1111/j.1365-2699.2006.01660.x.

Cuevas J. (2000) Tree Recruitment at the *Nothofagus pumilio* Alpine Timberline in Tierra del Fuego, Chile. *Journal of Ecology* **88**, 840–855.

Cuevas JG (2002) Episodic regeneration at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego. *Journal of Ecology* **90**, 52–60.

Cullen LE, Stewart GH, Duncan RP, Palmer JG (2001) Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *Journal of Ecology* **89**, 1061–1071.

Cutler S (2002) Floristic composition and stability of the high-mountain vegetation of the Mount Hotham region. La Trobe University.

Daniels LD, Veblen TT (2003) Regional and Local Effects of Disturbance and Climate on Altitudinal Treelines in Northern Patagonia. *Journal of Vegetation Science* **14**, 733–742.

Daniels LD, Veblen TT (2004) Spatiotemporal Influences of Climate on Altitudinal Treeline in Northern Patagonia. *Ecology* **85**, 1284–1296.

Dovčiak M, Hrivnák R, Ujházy K, Gömöry D (2015) Patterns of grassland invasions by trees: insights from demographic and genetic spatial analyses. *Journal of Plant Ecology* **8**, 468–479.

Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze : altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* **13**, 265–272. doi:10.1890/140231.

Fairman TA, Bennett LT, Tupper S, Nitschke CR, Ward D (2017) Frequent wildfires erode tree persistence and alter stand structure and initial composition of a fire-tolerant sub-alpine forest. *Journal of Vegetation Science* **28**, 1151–1165. doi:10.1111/jvs.12575.

Ferrar PJ, Cochrane PM, Slatyer RO (1988) Factors influencing germination and establishment of *Eucalyptus pauciflora* near the alpine tree line. *Tree physiology* **4**, 27–43.

Gehrig-Fasel J, Guisan A, Zimmermann N. (2007) Tree line shifts in the Swiss Alps : Climate change or land abandonment ? *Journal of Vegetation Science* **18**, 571–582.

Germino MJ, Smith WK, Resor AC (2002) Conifer Seedling Distribution and Survival in an Alpine-Treeline Ecotone. *Plant Ecology* **162**, 157–168.

Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL, Ezcurra E (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *Journal of Vegetation Science* **16**, 191–198.

Good RB (1982) The impacts of prescribed burning on subalpine woodlands. University of New South Wales.

Grace J, Berninger F, Nagy L (2002) Impacts of Climate Change on the Tree Line. *Annals of Botany* **90**, 537–544. doi:10.1093/aob/mcf222.

Green K (2009) Causes of stability in the alpine treeline in the Snowy Mountains of Australia – a natural experiment. *Australian Journal of Botany* **57**, 171–179.

Green K, Venn S (2012) Tree-Limit Ribbons in the Snowy Mountains , Australia : Characterization and Recent Seedling Establishment. *Arctic, Antarctic and Alpine Research* **44**, 180–187.

Hacket-pain AJ, Friend AD, Lageard JGA, Thomas PA (2015) The influence of masting phenomenon on growth – climate relationships in trees : explaining the influence of previous summers climate on ring width. *Tree Physiology* **35**, 319–330. doi:10.1093/treephys/tpv007.

Halpern CB, Antos JA, Rice JM, Haugo RD, Lang NL (2010) Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. *Journal of Vegetation Science* **21**, 717–732. doi:10.1111/j.1654-1103.2010.01183.x.

Harsch MA, Bader MY (2011) Treeline form – a potential key to understanding treeline dynamics. *Global Ecology and Biogeography* **20**, 582–596. doi:10.1111/j.1466-8238.2010.00622.x.

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* **12**, 1040–1049. doi:10.1111/j.1461-0248.2009.01355.x.

Harvey BJ, Donato DC, Turner MG (2016) High and dry : post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography* **55**, 655–669. doi:10.1111/geb.12443.

Harvey B, Holzman B, Forrestel A (2014) Forest resilience following severe wildfire in a semi-urban National Park. *Fremontia* **42**, 14–18.

Harwood C. (1976) Ecological studies of timberline phenomena. Australian National University, Canberra.

Hemp A (2005) Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Global Change Biology* **11**, 1013–1023. doi:10.1111/j.1365-2486.2005.00968.x.

Hennessy J., Whetton PH, Walsh K, Smith I., Bathols JM, Hutchinson M, Sharples J (2008) Climate change effects on snow conditions in main-land Australia and adaptation at ski resorts through snowmaking. *Cliamte Research* **35**, 255–270. doi:10.3354/cr00706.

Holtmeier F, Broll G (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography* **14**, 395–410. doi:10.1111/j.1466-822x.2005.00168.x.

Holtmeier F, Broll G (2007) Treeline advance – driving processes and adverse factors. *Landscape Online* **1**, 1–33. doi:10.3097/LO.200701.

Howard T, Ashton DH (1967) Studies of Soil Seed in Snow Gum Woodland (*E. pauciflora*) Sieb. ex Spreng var. alpina (Benth.) Edwart. *The Victorian Naturalist* **84**, 331–335.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (Eds TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex, PM Midgley) p. 1535. (Cambridge University Press: Cambridge) doi:10.1017/CBO9781107415324.

Jacobs MR (1955) Growth habits of the E*ucalypts*. (Canberra)

Johnson JS, Gaddis KD, Cairns DM, Krutovsky KV (2017) Seed dispersal at alpine treeline : an assessment of seed movement within the alpine treeline ecotone. *Ecosphere* **8**, 1–15. doi:10.1002/ecs2.1649.

Kambo D, Danby RK (2017) Constraints on treeline advance in a warming climate : a test of the reproduction limitation hypothesis. **11**, 411–422. doi:10.1093/jpe/rtx009.

Kane J, A Meinhardt K, Chang T, L Cardall B, Michalet R, G Whitham T (2011) Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecology* **212**, 733–741.

Keeley JE, Fotheringham CJ, Morais M (1999) Re-examining Fire Suppression Impacts on Brushland Fire Regimes. *Science* **284**, 1829–1832.

Klasner F., Fagre D. (2002) A half century of change in alpine treeline patterns at Glacier National Park, Montana, U.S.A. *Arctic, Antarctic and Alpine Research* **34**, 49–56.

Körner C (1998) International Association for Ecology A Re-Assessment of High Elevation Treeline Positions and Their Explanation. *Oecologia* **115**, 445–459.

Körner C (2003) Alpine treelines. ‘Alp. Plant Life’. pp. 77–100. (Springer: Berlin, Heidelberg) doi:10.1007/978-3-642-18970-8.

Körner C (2007) The use of ‘altitude’ in ecological research. *Trends in ecology & evolution*

22, 569–574.

Körner C (2012) High elevation treelines. ‘Alp. Treelines Fuctional Ecol. Glob. High Elev. Tree Limits’. pp. 1–4. (Springer: Basel) doi:10.1007/978-3-0348-0396-0.

Kullman L, Öberg L (2009) Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *Journal of Ecology* **97**, 415–429. doi:10.1111/j.1365-2745.2009.01488.x.

Lawrence R (1999) Vegetation changes on the Bogong High Plains from the 1850s to 1950s. *Transactions of the Royal Society of Victoria* **111**, xxix–lii.

Li C, Barclay HJ (2000) Fire disturbance patterns and forest age structure. *Natural Resource Modeling* **14**, 495–521. doi:10.1111/j.1939-7445.2001.tb00071.x.

Liang E, Wang Y, Piao S, Lu X, Camarero JJ, Zhu H, Zhu L, Ellison AM, Ciais P, Peñuelas J (2016) Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **113**, 4380–4385. doi:10.1073/pnas.1520582113.

Loehle C (2000) Strategy Space and the Disturbance Spectrum: A Life-History Model for Tree Species Coexistence. *The American Naturalist* **156**, 14–33. doi:10.1086/303369.

Loranger H, Zotz G, Bader MY (2017) Competitor or facilitator? The ambiguous role of alpine grassland for the early establishment of tree seedlings at treeline. *Oikos*. doi:10.1111/oik.04377.

Loveys BR, Egerton JJG, Bruhn D, Ball MC (2010) Disturbance is required for CO^2 -dependent promotion of woody plant growth in grasslands. *Fuctional Plant Biology* **37**, 555–565.

Maher EL, Germino MJ (2006) Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Écoscience* **13**, 334–341. doi:10.2980/i1195-6860-13-3-334.1.

van Mantgem PJ, Nesmith JCB, Keifer M, Knapp EE, Flint A, Flint L, Penuelas J (2013) Climatic stress increases forest fire severity across the western United States. *Ecology Letters* **16**, 1151–1156. doi:10.1111/ele.12151.

McDougall K. (2003) Aerial photographic interpretation of vegetation changes on the Bogong High Plains, Victoria, between 1936 and 1980. *Australian Journal of Botany* **51**, 251–256.

Meshinev T, Apostolova I, Koleva ES (2000) Influence of warming on timberline rising: A case study on Pinus peuce Griseb. in Bulgaria. *Phytocoenologia* **30**, 431–438.

Moore RM, Willaims J. (1976) A study of a subalpine woodland-grassland boundary. *Australian Journal of Ecology* **1**, 145–153.

Neuschulz EL, Merges D, Bollmann K, Gugerli F, Böhning-gaese K (2017) Biotic interactions and seed deposition rather than abiotic factors determine recruitment at elevational range limits of an alpine tree. *Journal of Ecology* **0**, 1–12. doi:10.1111/1365-2745.12818.

Noble IR (1980) Interactions between tussock grass (*Poa spp*.) and *Eucalyptus pauciflora* seedlings near treeline in south-eastern Australia. *Oecologia* **45**, 350–353.

Noble JC (2001) Lignotubers and meristem dependence in mallee (*Eucalyptus spp.*) coppicing after fire. *Australian Journal of Botany* **49**, 31–41.

Paton DM, Slattery HD, Willing RR (1979) Low Root Temperature Delays Dehardening of Frost Resistant Eucalyptus Shoots. *Annals of Botany* **43**, 123–124. doi:10.1093/oxfordjournals.aob.a085606.

Paulsen J, Korner C (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* **31**, 713–732.

Paulsen J, Weber UM, Korner C (2000) Tree Growth near Treeline : Abrupt or Gradual Reduction with Altitude? *Arctic, Antarctic and Alpine Research* **32**, 14–20.

Pickering CM, Barry K (2005) Size / age distribution and vegetative recovery of *Eucalyptus niphophila* (snowgum , *Myrtaceae*) one year after fire in Kosciuszko National Park. *Australian Journal of Botany* **53**, 517–527.

Rupp TS, Chapin FS, Starfield AM (2001) Modeling the Influence of Topographic Barriers on Treeline Advance at the Forest-Tundra Ecotone in Northwestern Alaska. *Climatic Change* **48**, 399–416. doi:10.1023/A:1010738502596.

Sakai A, D. M. Paton, P.Wardle (1981) Freezing Resistance of Trees of the South Temperate Zone, Especially Subalpine Species of Australasia. *Ecology* **62**, 563–570.

Shankman D, Daly C (1988) Forest Regeneration Above Tree Limit Depressed by Fire in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* **115**, 272–279. doi:10.2307/2996159.

Slattery D (2015) Soils. ‘Aust. Alps Kosciuszki, Alp. Namadgi Natl. Park.’ (Ed PSE Services) pp. 53–57. (CSIRO Publishing: Melbourne)

Slatyer RO (1989) Alpine and valley bottom treelines. ‘Sci. Significance Aust. Alps’. (Ed R Good) pp. 169–184. (Australian Alps Liaison Committee: Canberra)

Slatyer R, Morrow PA (1977) Altitudinal Variation in the Photosynthetic Characteristics of Snow Gum , *Eucalyptus pauciora* Sieb . ex Spreng . I Seasonal Changes under Field Conditions in the Snowy Mountains Area of South-eastern Australia. *Australian Journal of Botany* **25**, 1–20.

Slatyer RO, Noble IR (1992) Landscape Boundaries. (Ed AJH et Al) pp. 346–359. (Springer-Verlag: New York)

Slot M, Wirth C, Schumacher J, Mohren GMJ, Shibistova O, Lloyd J, Ensminger I (2005) Regeneration patterns in boreal Scots pine glades linked to cold-induced photoinhibition. *Tree Physiology* **25**, 1139–1150.

Smith WK, Germino MJ, Hancock TE, Johnson DM (2003) Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology* **23**, 1101–1112. http://dx.doi.org/10.1093/treephys/23.16.1101.

Stevens-Rumann C, Morgan P (2016) Repeated wildfires alter forest recovery of mixed-conifer ecosystems. *Ecological Applications* **26**, 1842–1853. doi:10.1890/15-1521.1.

Stueve KM, Cerney DL, Rochefort RM, Kurth LL (2009) Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA. *Journal of Vegetation Science* **20**, 107–120. doi:10.1111/j.1654-1103.2009.05437.x.

Szeicz JM, MacDonald GM (1995) Dendroclimatic Reconstruction of Summer Temperatures in Northwestern Canada since A.D. 1638 Based on Age-Dependent Modeling. *Quaternary Research* **44**, 257–266.

Tamme R, Gotzenberger L, Zobel M, Bullock J., Hooftman DA., Kaasik A, Partel M (2014) Predicting species' maximum dispersal distances from simple plant traits. *Ecology* **95**, 505–513.

Terando AJ, Youngsteadt E, Meineke EK (2017) Ad hoc instrumentation methods in ecological studies produce highly biased temperature measurements. *Ecology and Evolution* 1–15. doi:10.1002/ece3.3499.

Walsh NG, McDougall K. (2004) Progress in the recovery of teh flora of treeless subalpine vegetation in Kosciuszko National Park after the 2003 fires. *Cunninghamia* **8**, 439–452.

Walther G (2003) Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* **6**, 169–185.

Wardle P, Coleman MC (1992) Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany* **30**, 303–314. doi:10.1080/0028825X.1992.10412909.

Wearne L (1998) The floristic composition and stability of subalpine grasslands in the Mount Hotham. La Trobe University.

Wearne LJ, Morgan JW (2001) Recent Forest Encroachment into Subalpine Grasslands near Mount Hotham , Victoria , Australia. *Arctic, Antarctic and Alpine Research* **33**, 369–377.

Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences* **108**, 13165–13170. doi:10.1073/pnas.1110199108.

Williams R, Papst W, McDougall K, Al E (2014) Alpine ecosystems. ‘Biodivers. Environ. Chang. Monit. Challenges Dir.’ (Eds D Lindenmayer, E Burns, N Thurgate, A Lowe) pp. 167–212. (CSIRO Publishing: Melbourne, Australia) doi:10.1111/1745-5871.12077.

Williams R, Wahren C, Bradstock R, Muller W (2006) Does alpine grazing reduce blazing? A landscape test of a widely-held hypothesis. *Austral Ecology* **31**, 925–936. doi:10.1111/j.1442-9993.2006.01655.x.

Williams R, Wahren C, Tolsma A, Sanecki G, Papst W, Myers B, Mcdougall K, Heinze D, Green K (2008) Large fires in Australian alpine landscapes : their part in the historical fire regime and their impacts on alpine biodiversity. *International Journal of Wildland Fire* **17**, 793–808.

Wimbush D., Forrester RI (1988) Effects of Rabbit Grazing and Fire on a Subalpine Environment . II *. Tree Vegetation. *Australian Journal of Botany* **36**, 287–298.

Winkler DE, Chapin KJ, Kueppers LM (2016) Soil moisture mediates alpine life form and community productivity responses to warming. *Ecology* **97**, 1553–1563.

Woldendorp G, Hill M., Doran R, Ball MC (2008) Frost in a future climate : modelling interactive effects of warmer temperatures and rising atmospheric [CO 2] on the incidence and severity of frost damage in a temperate evergreen (Eucalyptus pauciflora). *Global Change Biology* **14**, 294–308. doi:10.1111/j.1365-2486.2007.01499.x.

Zylstra P (2012) The historical influence of fire on the flammability of subalpine Snowgum forest and woodland. *Contributions The Victorian Naturalist* **130**, 232–239.

Appendix

Appendix A: Environmental variables – Soil properties

Methods

To quantify differences in environmental conditions below and above treeline soil depth, pH and Electrical Conductivity (EC) were measured, and soil moisture was recorded throughout the growing season (November 2017 to March 2018) at two representative alpine (Mount Hotham and Mount McKay) and subalpine sites (Green Gables and Paw Paw Plain). Measurements were made at ~40 m below treeline, at the treeline and ~40 m above treeline. Soil depth was measured by pushing a metal probe into the ground until bedrock was reached, or depth exceeded 40 cm. This was conducted five times at each position to produce a mean. A representative soil sample of the top 10 cm was taken. Soils were air dried and sieved (2 mm) to give the fine earth fraction. A 5 g soil sample was mixed 1:5 with distilled water and placed on a rotating agitator for one hour. pH and EC were then measured using an electronic pH/EC meter (Dane and Hopmans 2002). Soil moisture was measured within the top 10 cm of soil. Measurements were recorded with a HOBO Micro Station Data Logger and one 10HS Soil Moisture Smart Sensor per location and recorded at two-hour intervals. Sensors were placed in close proximity to temperature logger stations in representative vegetation. Soil moisture was used to calculate the difference in soil moisture content above and below treeline during rain events (peaks in soil moisture) and drying events (troughs in soil moisture) to determine differences in wetting and drying of the soil. T-tests were used to determine differences above and below treeline during rain and drying events.

Results

There were no clear trends of soil depth, pH or EC between alpine or subalpine sites, or between locations across the treeline boundary (Table 1). Soil moisture was similar across alpine and subalpine sites, and between above and below treeline (Figure 1,2). There was no significant difference in soil moisture content between above treeline and below treeline during dry periods or rain events at either alpine (P-value= 0.5837) or subalpine (P-value= 0.5677) sites (Table 2).

Table 1 Soil depth (cm ± standard deviation), pH and EC (µs) for Mount Hotham and Mount McKay alpine sites and Paw Paw Plain and The Lanes subalpine sites measured 40 m above treeline, at treeline and 40 m below treeline.

Treeline Form	**Site**	**Measurement**	**Location**		
			Above Treeline	**At Treeline**	**Below Treeline**
Alpine	Mount Hotham	Soil Depth (cm)	18 (±6.94)	22(±3.12)	24(±2.87)
		pH	4.9	4.8	4.6
		EC(µs)	71.6	78.8	134.4
	Mount McKay	Soil Depth (cm)	28.6(±5.08)	11.8(±3.61)	27.4(±6.9)
		pH	4.9	4.2	4.6
		EC(µs)	76.1	93.9	89.3
Subalpine	Paw Paw Plain	Soil Depth (cm)	40(±0.83)	28(±6.70)	24.2(±8.90)
		pH	4.9	4.7	5.2
		EC(µs)	150.8	93.9	85.1
	The Lanes	Soil Depth (cm)	24.8(±1.79)	37.7(±2.77)	40(±1.96)
		pH	5.2	5.3	4.7
		EC(µs)	91.4	95.8	118.5

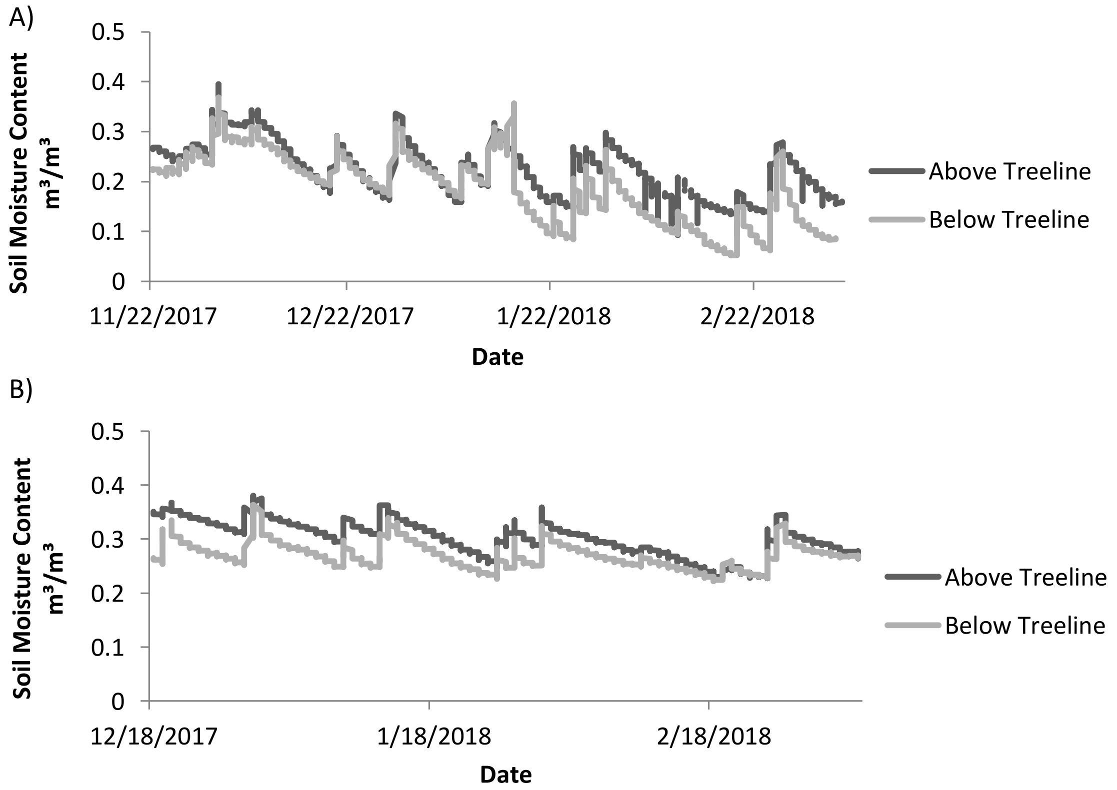


Figure 1 Mean soil Moisture content recorded Above Treeline and Below Treeline combined for Mount Hotham and McKay alpine sites (A) and Paw Paw Plain and The Lanes subalpine sites (B). Misreading's were removed from the graph. Alpine sites recorded from 22nd November 2017 to 6th March 2018. Subalpine sites recorded from 18th December 2017 to 6th march 2018 due to logger failure.

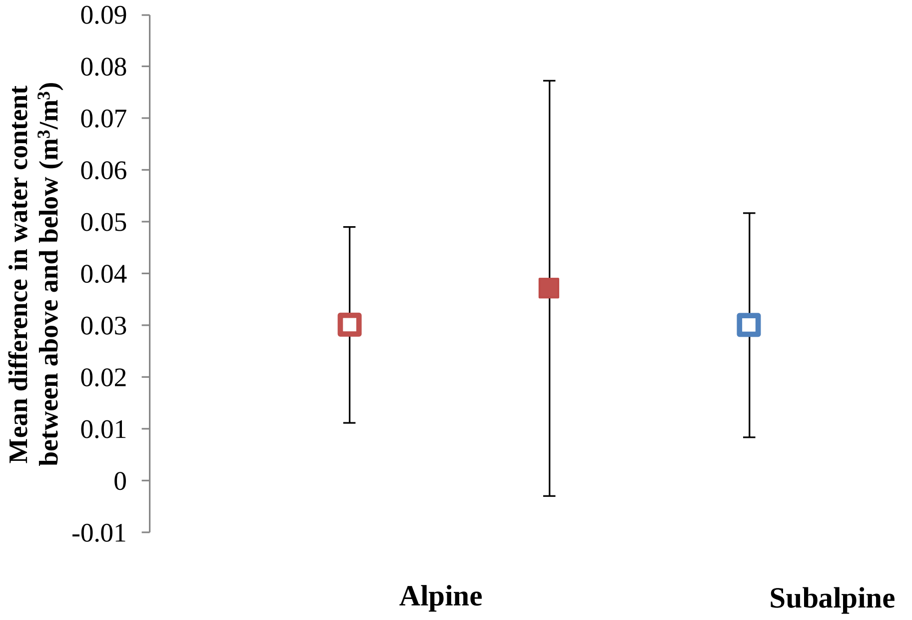


Figure 2 Mean (+/- standard deviation) soil moisture content difference between above and below treeline during rainfall events (peaks)(open square) and drying events (troughs)(closed square) at alpine (red) and subalpine (blue) sites. Means averaged across 2 alpine and 2 subalpine sites.

Table 2 Results of a two-sample t-test of mean difference in soil water content above treeline and below treeline during rain and dry events averaged across alpine and subalpine sites. * = P<0.05.

Treeline Form	**t**	**df**	**p-value**
Alpine	-0.559	16.246	0.584
Subalpine	-0.582	17.901	0.568

Appendix B: Assessment of landscape scale changes in treelines across the Victorian Alps through repeat photography

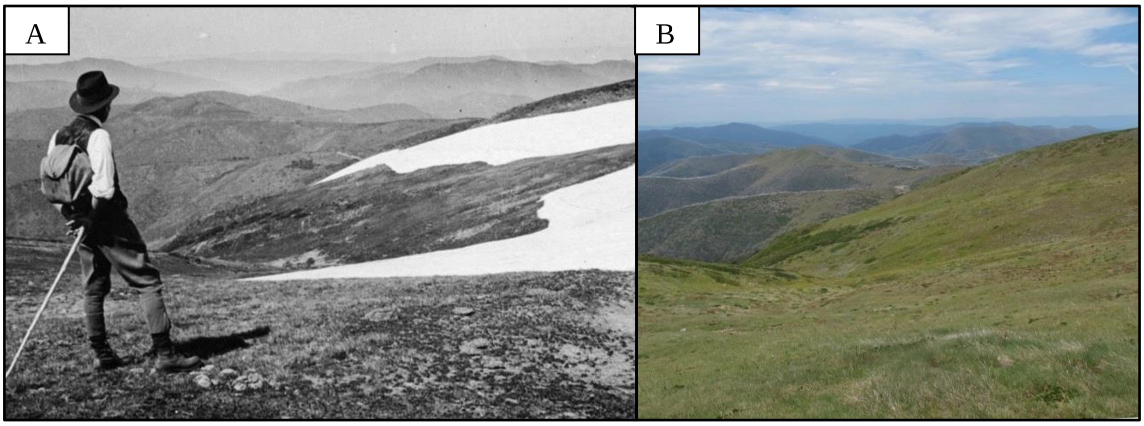


Figure 1 Historical (1920) (A) and modern (2015) (B) photographs looking north-east towards Mount Loch, Hotham, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by Z. Walker (2015).

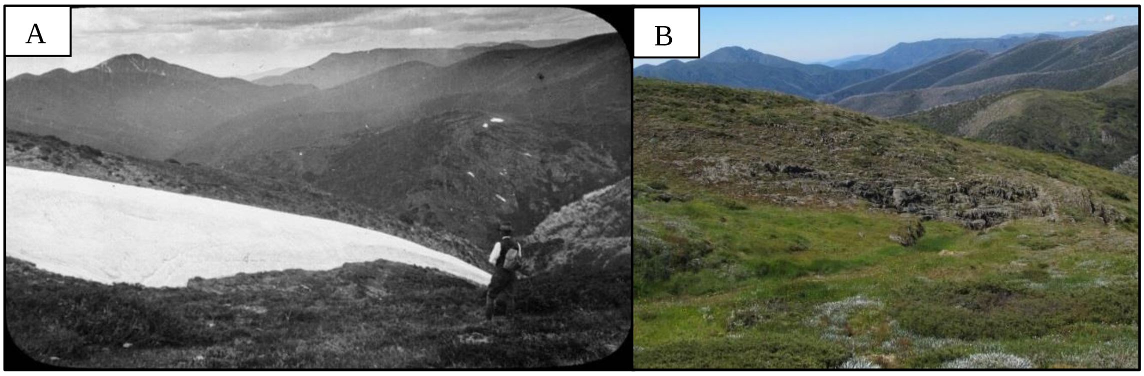


Figure 2 Historical (1920) (A) and modern (2015) (B) photographs looking west towards Mount Feathertop, Hotham, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by Z. Walker (2015).

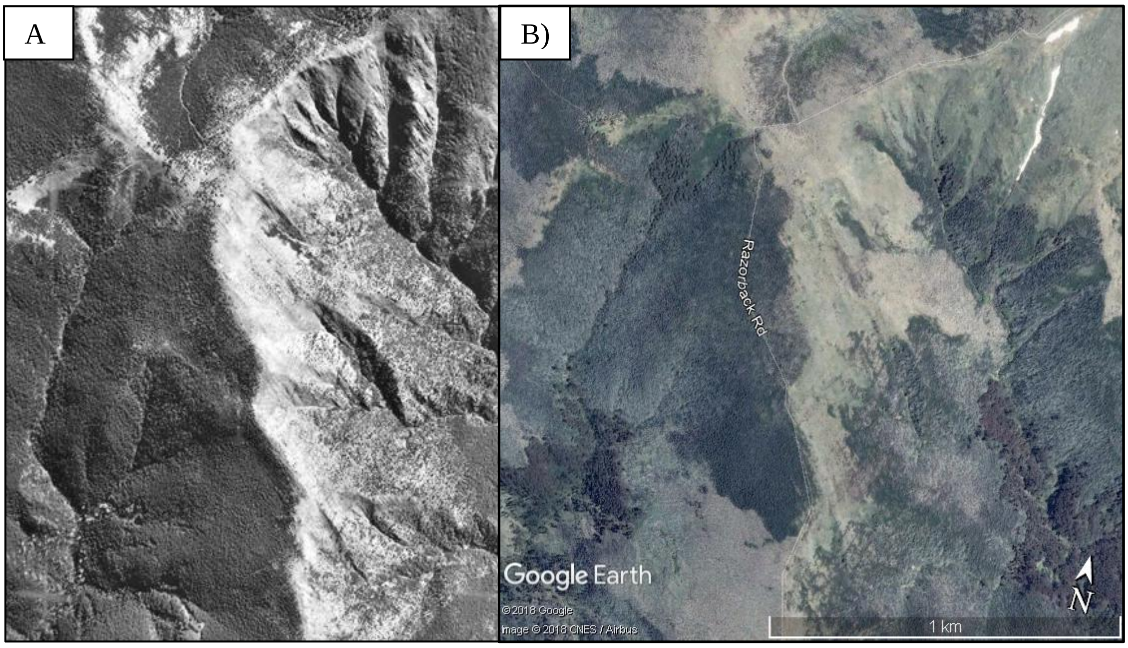


Figure 3 Historical (1961) (A) and modern (2017) (B) aerial photographs of Razorback trail towards Mount Feathertop Victoria, Australia. Historical photographed sourced from Soil Conservation Authority courtesy of Keith McDougall private collection. Modern photograph sourced from Google Earth (2017).

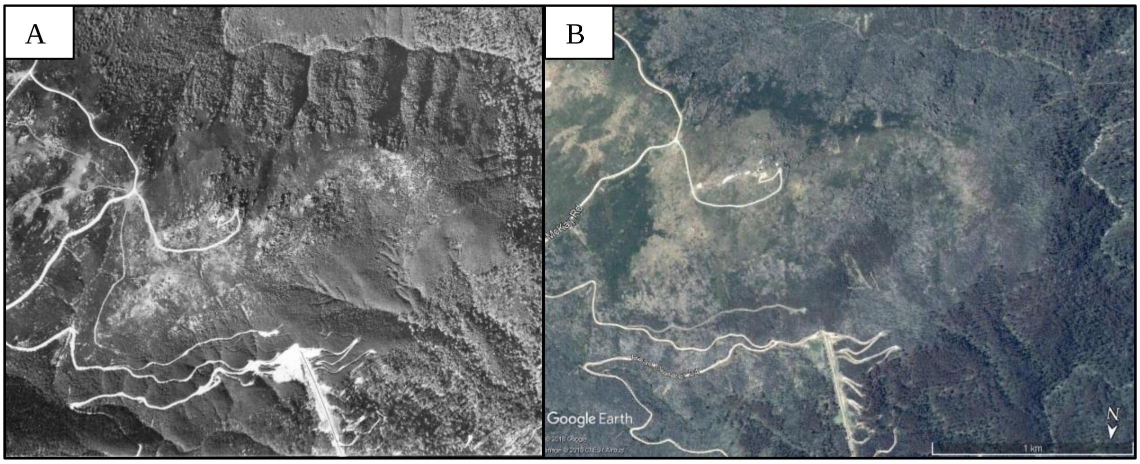


Figure 4 Historical (1961) (A) and modern (2017) (B) aerial photographs of Mount McKay, Falls Creek, Victoria, Australia. Historical photographed sourced from soil Conservation Authority courtesy of Keith McDougall private collection. Modern photograph sourced from Google Earth (2017).

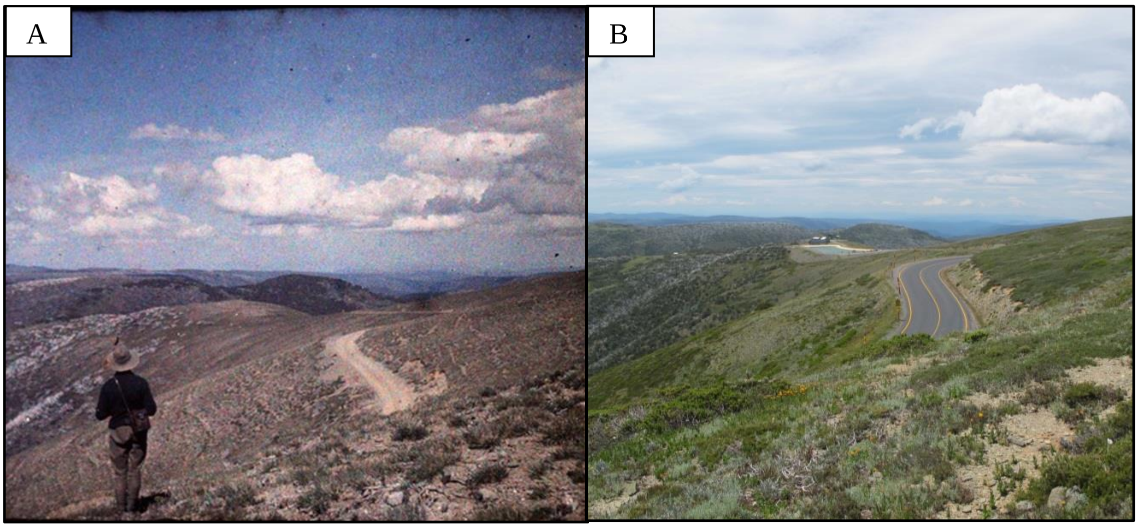


Figure 5 Historical (1927-1930) (A) and modern (2015) (B) photographs looking north-east towards Loch Dam, Hotham, Victoria, Australia. Historical photograph sourced from Trove. Modern photograph taken by Z. Walker (2015).

Appendix C: Assessment of the current state of alpine and subalpine treelines through re-visitation surveys

Table 1 Location of alpine and subalpine transects. Latitude and longitude presented in GDA94/ MGA zone 55. Coordinates refer to; alpine sites = treeline position centre, Paw Paw, JB, Precipice Plains = lower transect point at treeline on northern side, Green Gables and The Lanes = start (southern side) to end (northern side) transect post point.

Treeline Form	Site	Transect	Transect Length (m)	Latitude, Longitude
Alpine	Mount Feathertop	1	42.00	-36.88759302, 147.1391903
		2	54.80	-36.88763299, 147.1390171
		3	40.60	-36.89706216, 147.1338984
		4	45.15	-36.89755056, 147.1327111
	The Razorback	1	46.10	-36.94537817, 147.1275696
		2	40.20	-36.96569269, 147.1209398
	Mount Hotham	1	41.80	-36.97785379, 147.1242343
		2	59.48	-36.97524903, 147.1266789
		3	45.31	-36.97644968, 147.1254575
		4	74.02	-36.97892085, 147.1247683
		5	86.80	-36.97884944, 147.1246779
	Mount McKay	1	82.95	-36.87497290, 147.2393232
		2	46.16	-36.87724029, 147.2410168
		3	43.40	-36.87746503, 147.2379679
		4	52.27	-36.87462649, 147.2407710
	The Twins	1	40.00	-37.02337328, 147.0592530
		2	40.00	-37.02341110, 147.0599431
		3	42.85	-37.02392545, 147.0616333
		4	40.00	-37.02306921, 147.0567063
		5	40.00	-37.02291647, 147.0568966
		6	40.45	-37.02308836, 147.0565635
Subalpine	Paw Paw Plain	1(Upper)	240.00	-37.01926612, 147.1904912
		2(Middle)	156.00	-37.02166842, 147.1917584
		3(Lower)	169.50	-37.02330920, 147.1919292
	Precipice Plain	1(Upper)	154.30	-37.03065954, 147.2225553
		2(Middle)	185.50	-37.03050568, 147.2231975
		3(Lower)	117.15	-37.03052315, 147.2240544
	JB Plain	1(Upper)	164.00	-37.02660580, 147.2167603
		2(Middle)	198.20	-37.02753684, 147.2189287
		3(Lower)	184.00	-37.02892832, 147.2197419
	The Lanes	1	170.20	Start: -36.88462155,147.3984184 End: -36.88334066, 147.3991244
		2	151.00	Start: -36.88427959, 147.3979652 End: -36.88330305, 147.3989579
		3	154.60	Start: -36.88412756, 147.3977744 End: -36.88412756, 147.3977744
	Green Gables	1	166.92	Start: -36.88529382, 147.391037 End: -36.88371501, 147.3909281
		2	171.60	Start: -36.88529382, 147.391037 End: -36.88367361, 147.3912051

Table 2 Results of two way ANOVAs on the effect of height (60, 30, 0, -10 cm) and Location (Above, at, below treeline) on weekly accumulated GDDs. df=degrees of freedom. p=p-value. *=P<0.05.

		df	**Sum sq**	**Mean sq**	**F value**	**p**
Alpine	Height	3	0.29	0.10	15.11	<0.001*
	Location	2	0.03	0.02	2.43	0.091
Subalpine	Height	3	0.14	0.45	7.25	<0.001*
	Location	2	0.03	0.015	2.43	0.092
	Height: Location	6	0.09	0.016	2.50	0.024*

Table 3 Results of a Tukey HSD test on the effect of height on GDD at alpine sites. Diff=Difference between means of months. Lwr CI= the lower 95% confidence interval of the differences in means. Upr CI= the upper 95% confidence interval of the differences in means. If the confidence interval crosses over zero it is not certain that the difference between the means is not equal to zero. * = P<0.05.

	diff	**lwr**	**upr**	**P adj**
10-60	-0.87	-0.13	-0.04	<0.001*
30-60	-0.20	-0.02	0.06	0.638
0-60	-0.30	-0.07	0.01	0.286
30-10	0.11	0.06	0.14	<0.001*
0-10	0.57	-0.01	0.10	0.004*
0-30	-0.05	-0.09	0.01	0.018*

Table 4 Results of a Tukey HSD test on the effect of height on GDD at subalpine sites. Diff=Difference between means of months. Lwr CI= the lower 95% confidence interval of the differences in means. Upr CI= the upper 95% confidence interval of the differences in means. If the confidence interval crosses over zero it is not certain that the difference between the means is not equal to zero. * = P<0.05.

	diff	**lwr**	**upr**	**P adj**
10-60	-0.05	-0.09	-0.00	0.041*
30-60	0.03	-0.02	0.08	0.319
0-60	-0.00	-0.05	0.04	0.999
30-10	0.08	0.03	0.12	<0.001*
0-10	0.04	-0.00	0.09	0.034*
0-30	-0.03	-0.07	0.01	0.242

Table 5 Results of a Tukey HSD test on the effect of height interacting with location on GDD at subalpine sites. Diff=Difference between means of months. Lwr CI= the lower 95% confidence interval of the differences in means. Upr CI= the upper 95% confidence interval of the differences in means. If the confidence interval crosses over zero it is not certain that the difference between the means is not equal to zero. * = P<0.05. Not significant values are excluded from the table.

	diff	**lwr**	**upr**	**P adj**
10:Below-30:Above	-0.13	-0.22	-0.03	0.001*
10:Below-0:Above	-0.13	-0.23	-0.04	<0.001*
10:Below-30:At	-0.11	-0.21	0.02	0.009*
10:Below-0:At	-0.11	-0.20	-0.13	0.013*
10:Below-60:Below	-0.11	-0.20	-0.01	0.017*
30:Below-10:Below	0.15	0.05	0.24	<0.001*
0:Below-30:Below	-0.10	-0.19	-0.00	0.043*

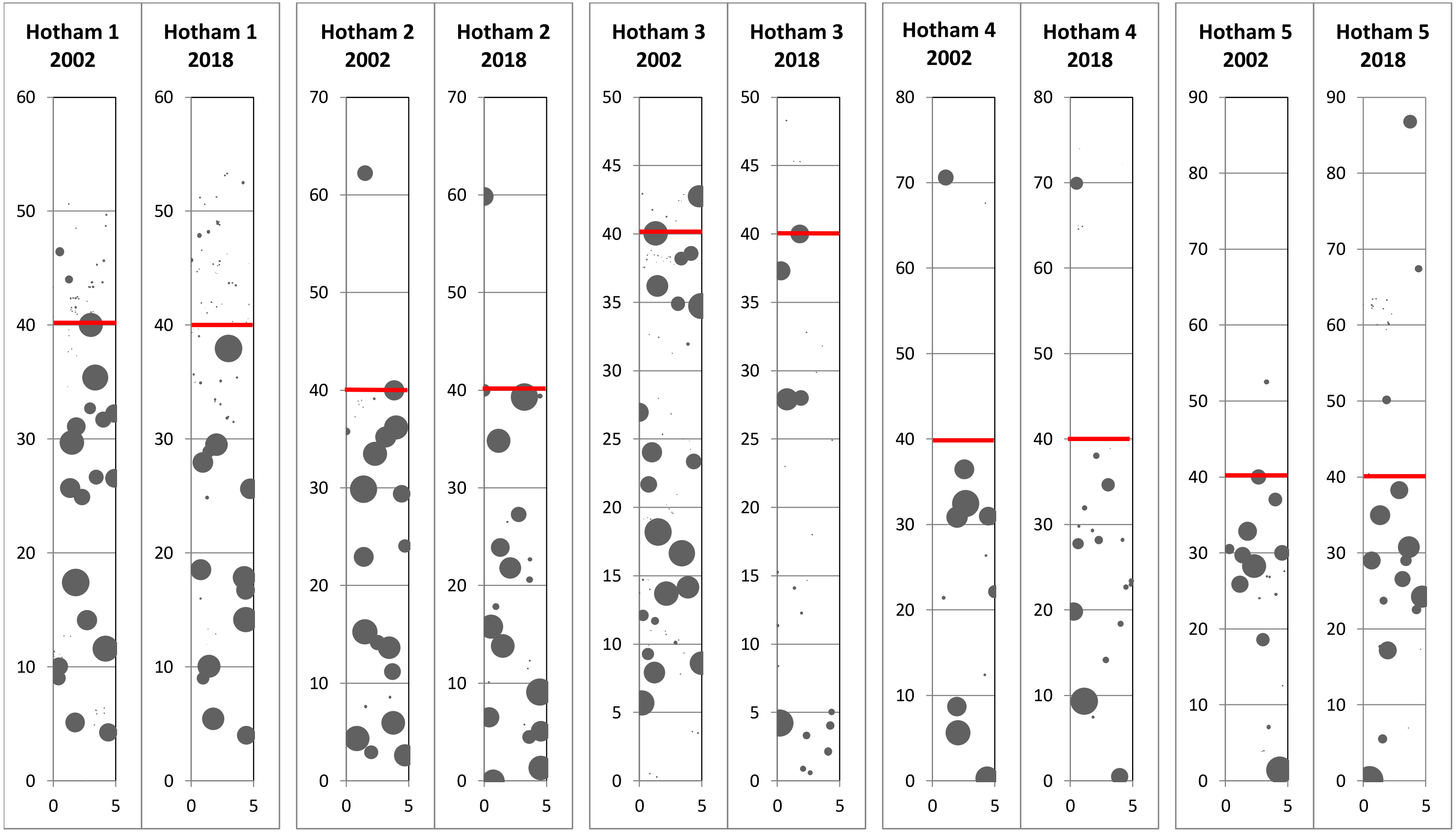


Figure 1 Visual representation of *E. pauciflora* individuals across transects at Mount Hotham in 2002 and 2018. Transects were unburnt in recent bushfires. Transect Aspects are as follows: Transect 1 = W, Transect 2 = W, Transect 3 = NW, Transect 4 = SW, Transect 5 = SW. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

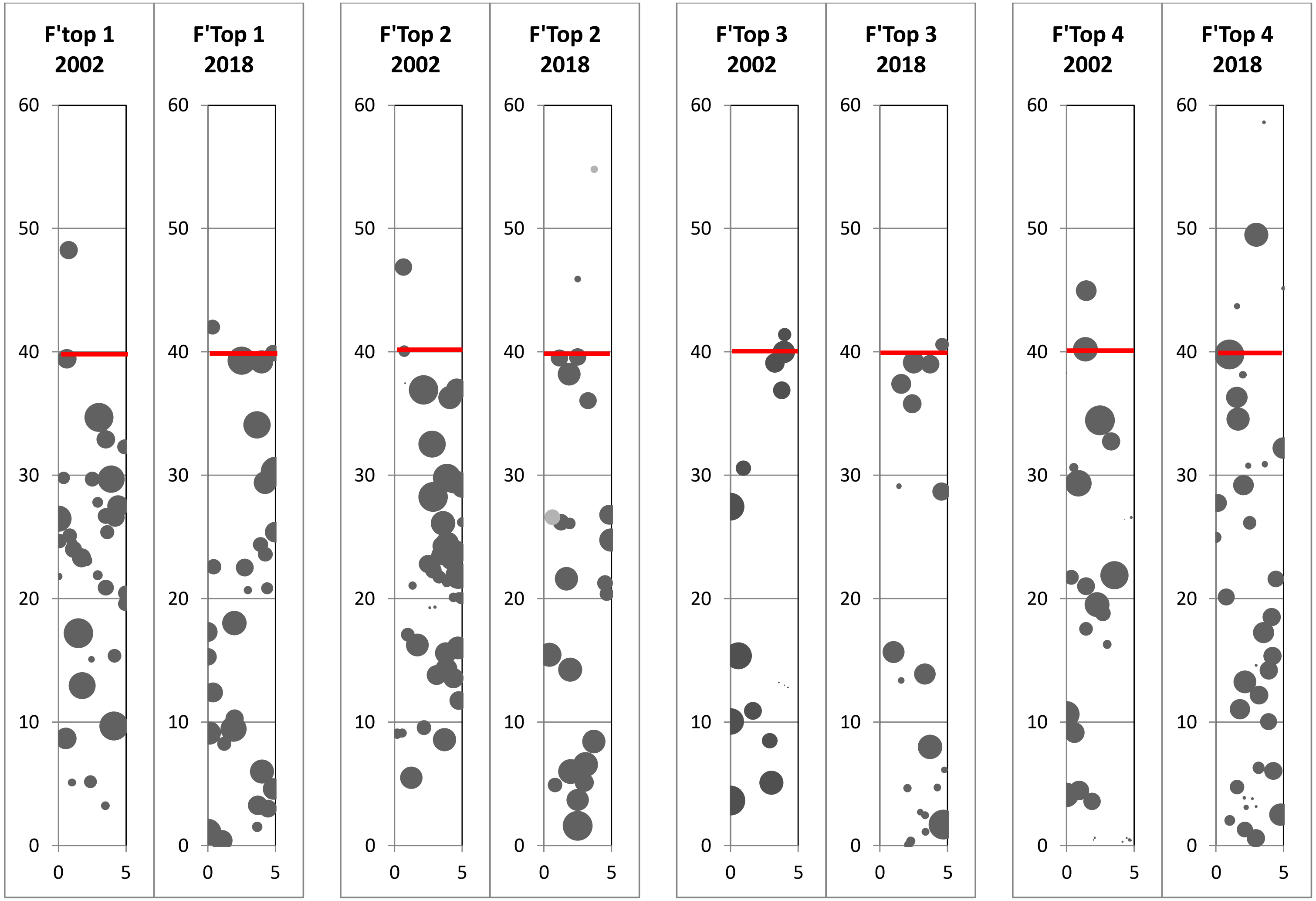


Figure 2 Visual representation of *E. pauciflora* individuals across transects at Mount Feathertop in 2002 and 2018. Transects were burnt once in recent bushfires. Transect Aspects are as follows: Transect 1 aspect = N. Transect 2 aspect = NW. Transect 3 aspect = W. Transect 4 aspect = W. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

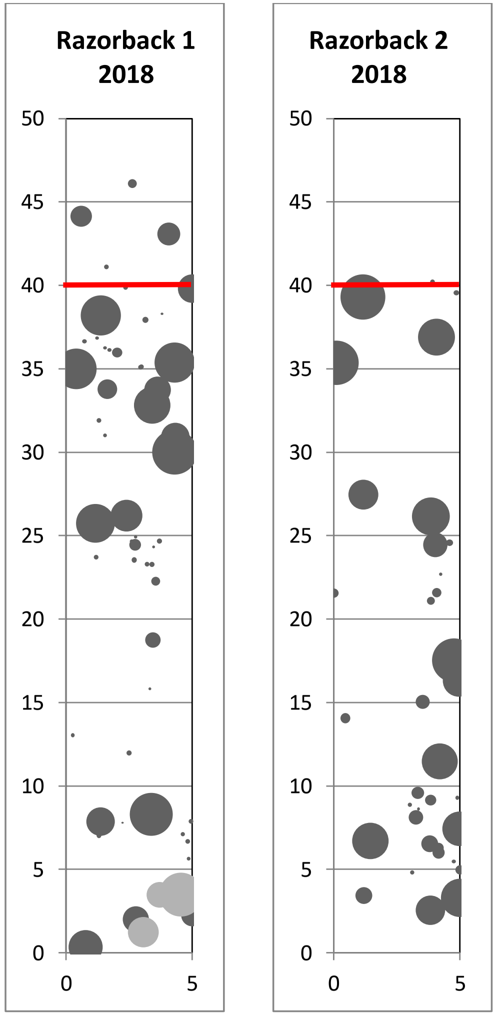


Figure 3 Visual representation of *E. pauciflora* individuals across transects at The Razorback in 2018. Transects were burnt twice in recent bushfires. Transect Aspects are as follows: Transect 1 aspect = E. Transect 2 aspect = W. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

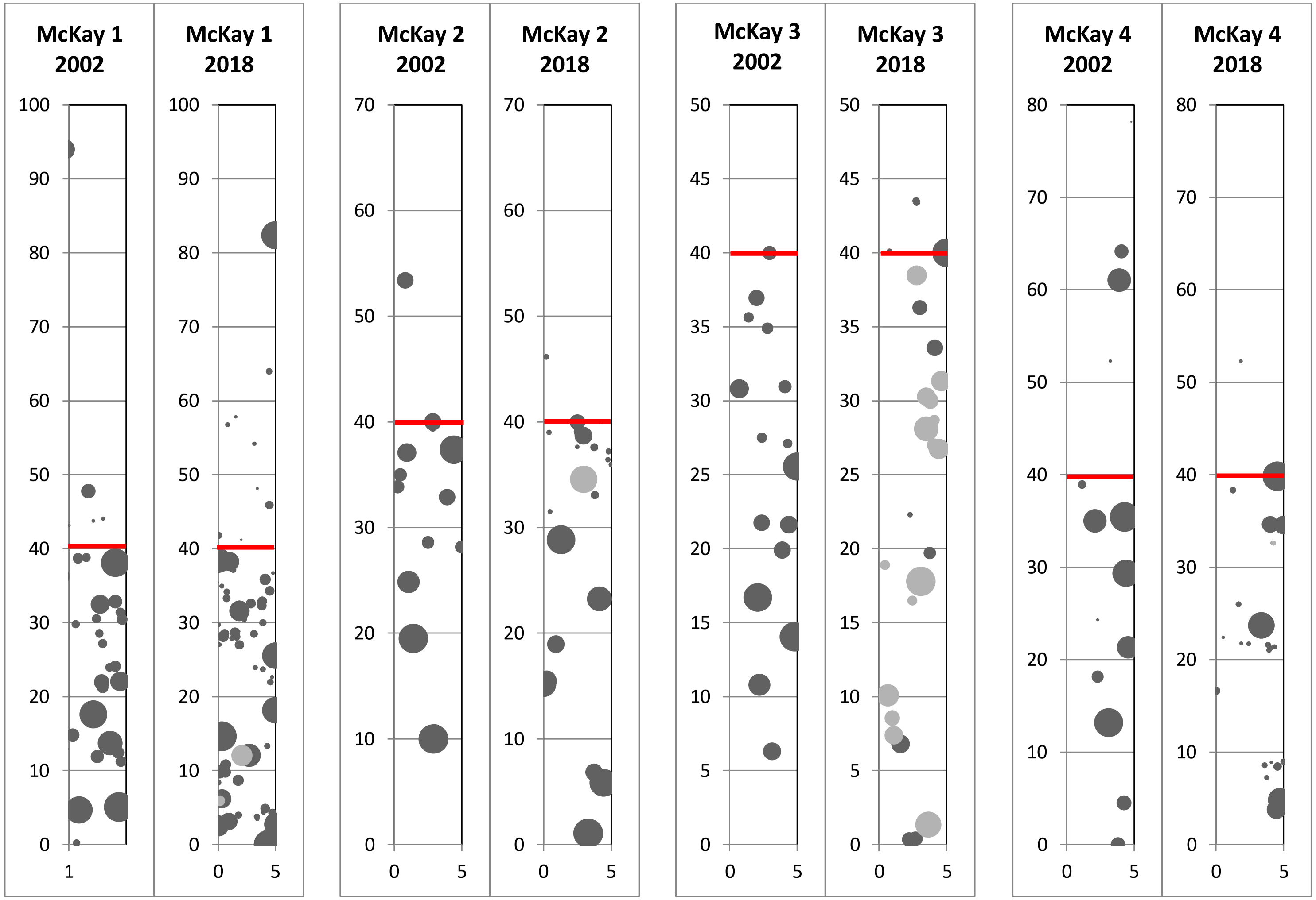


Figure 4 Visual representation of *E. pauciflora* individuals across transects at Mount McKay in 2002 and 2018. Transects were burnt once in recent bushfires. Transect Aspects are as follows: Transect 1 aspect = NW. Transect 2 aspect = S. Transect 3 aspect = S. Transect 4 aspect = NW. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

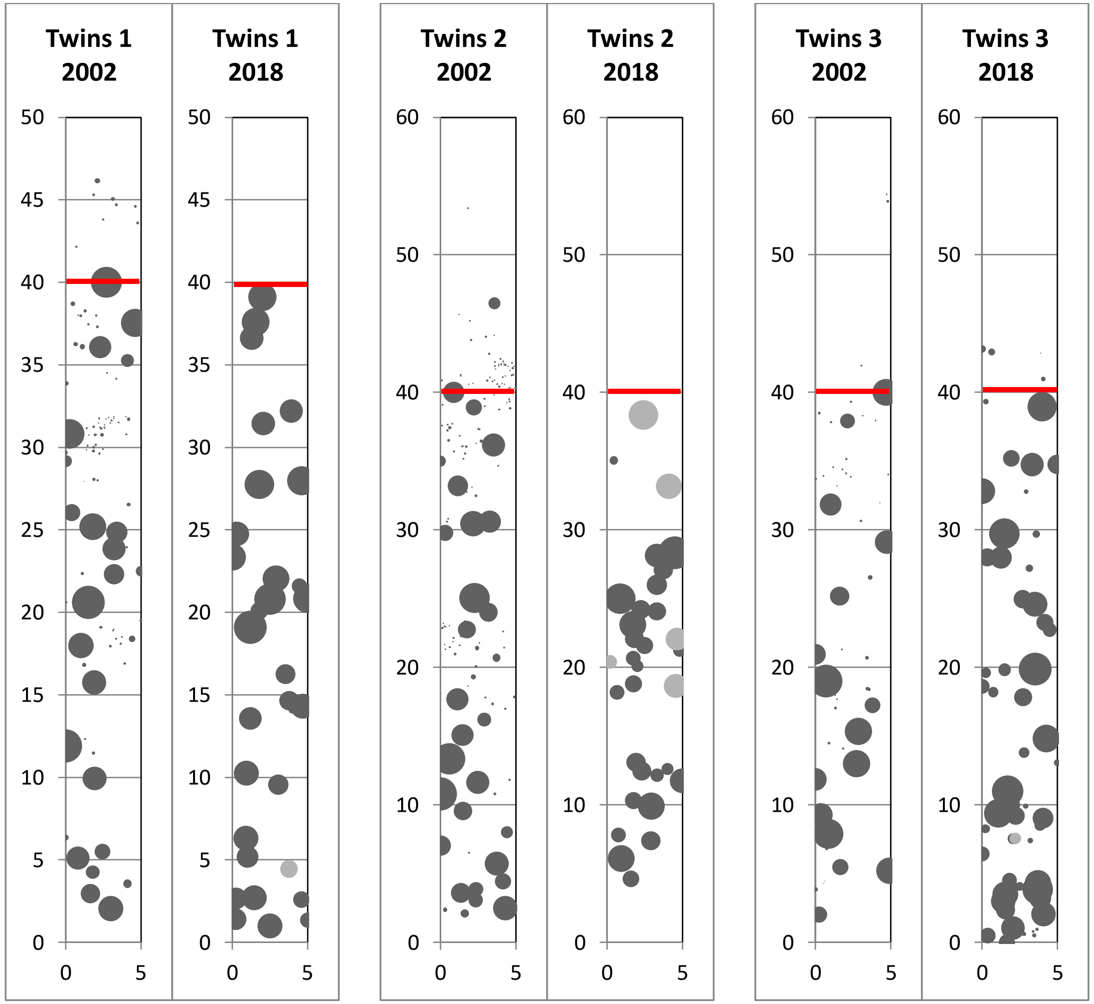


Figure 5 Visual representation of *E. pauciflora* individuals across transects 1, 2 and 3 at The Twins in 2002 and 2018. Transects were burnt twice in recent bushfires. Transect Aspects are as follows: Transect 1 aspect = N. Transect 2 aspect = N. Transect 3 aspect = N. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

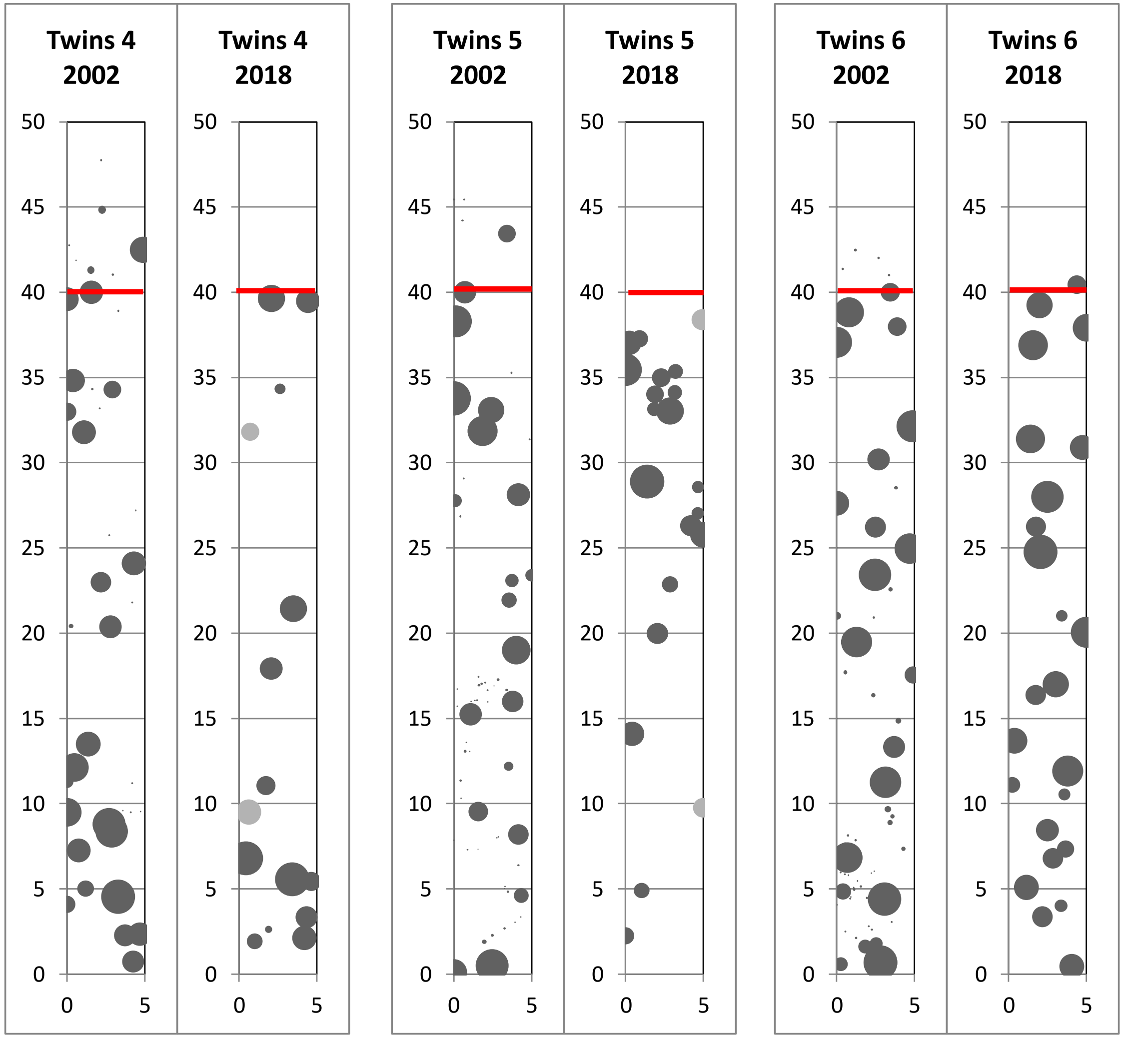


Figure 6 Visual representation of *E. pauciflora* individuals across transects 4, 5 and 6 at The Twins in 2002 and 2018. Transects were burnt twice in recent bushfires. Transect Aspects are as follows: Transect 4 aspect = W. Transect 5 aspect = W. Transect 6 aspect = W. X and Y axes indicate exact meter locations across the transect. Circle size indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<40 within the woodland, y>40 above treeline.

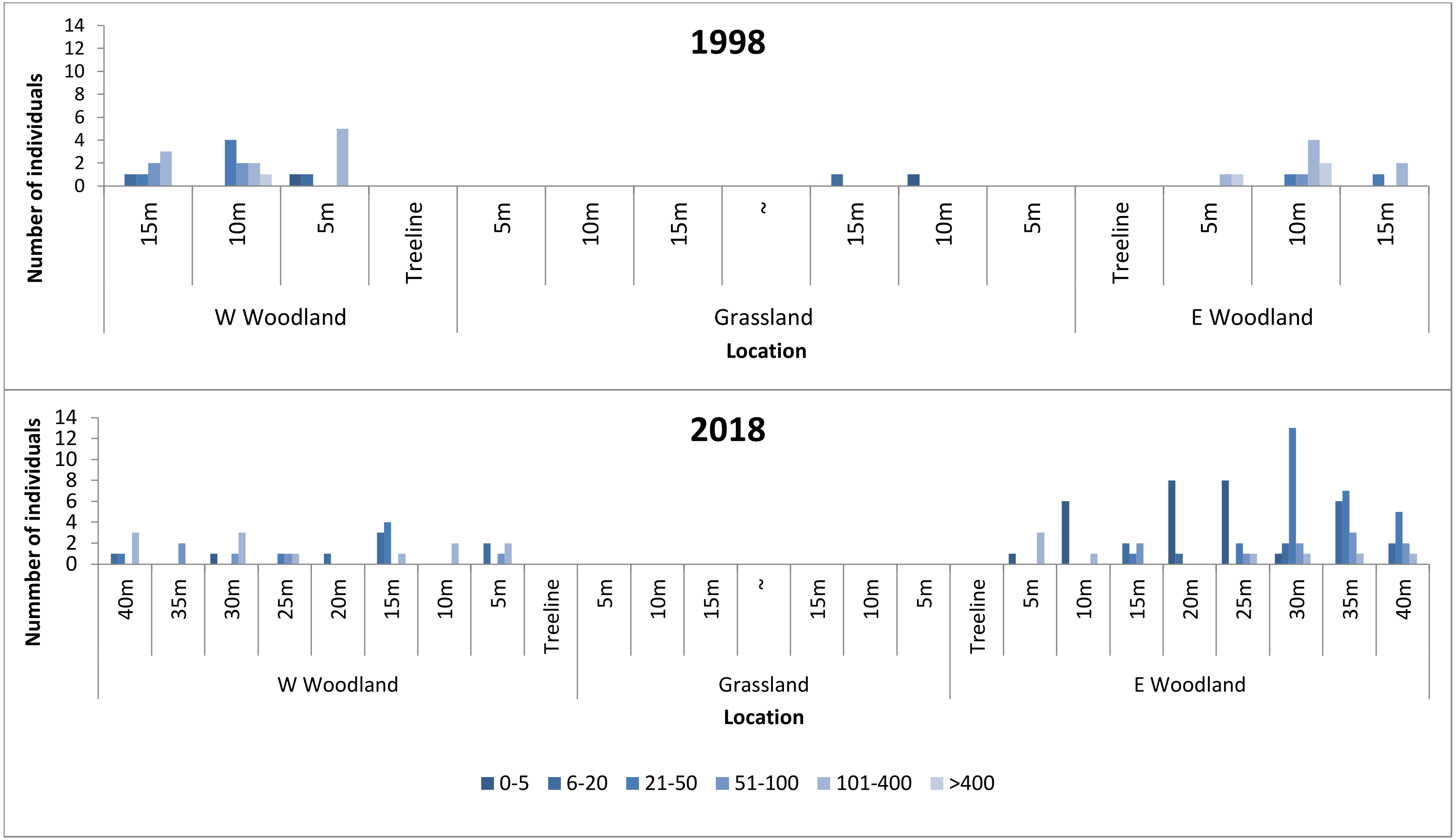


Figure 7 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 1 (upper position) at JB Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

1597

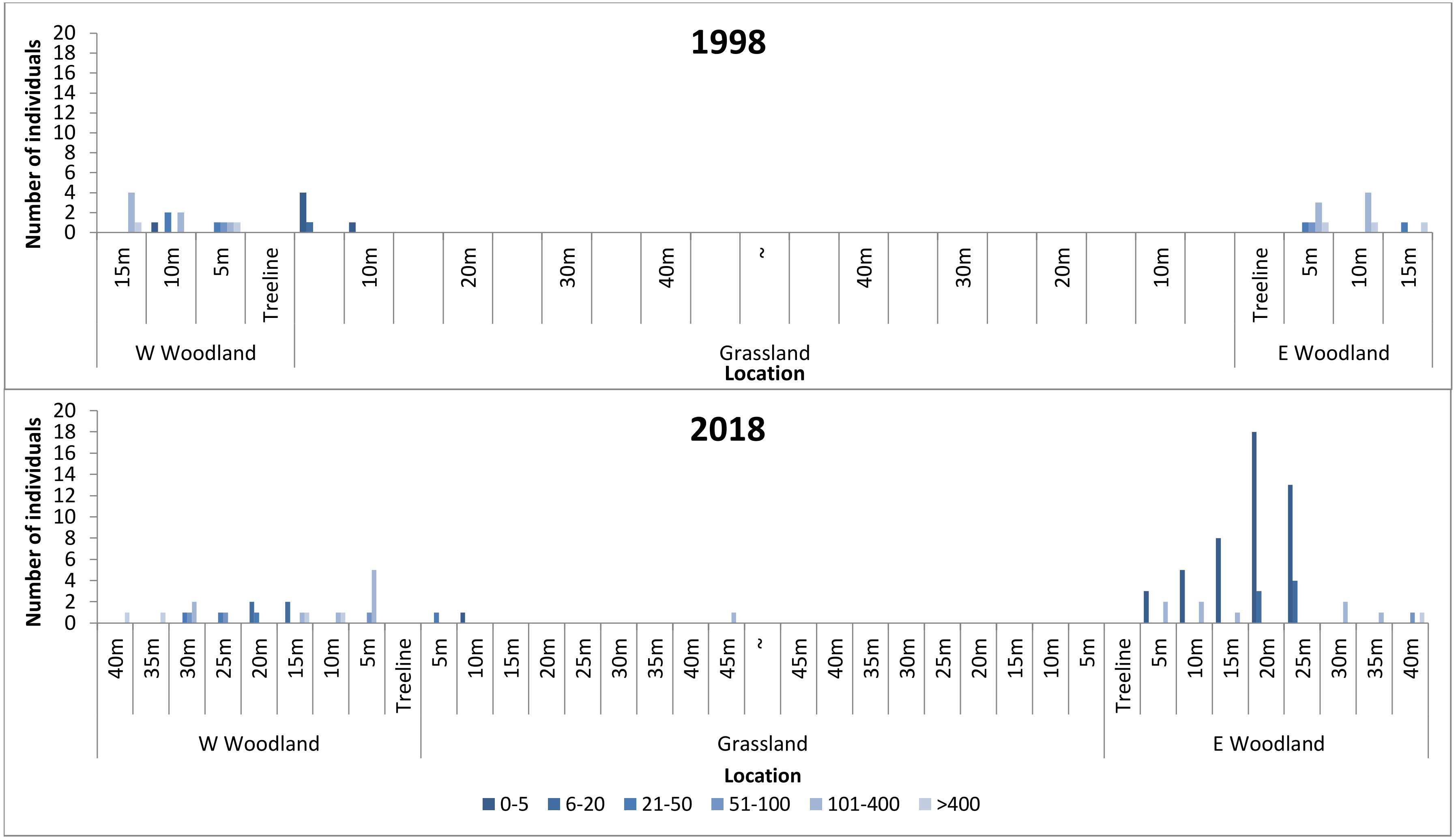


Figure 8 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 2 (middle position) at JB Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

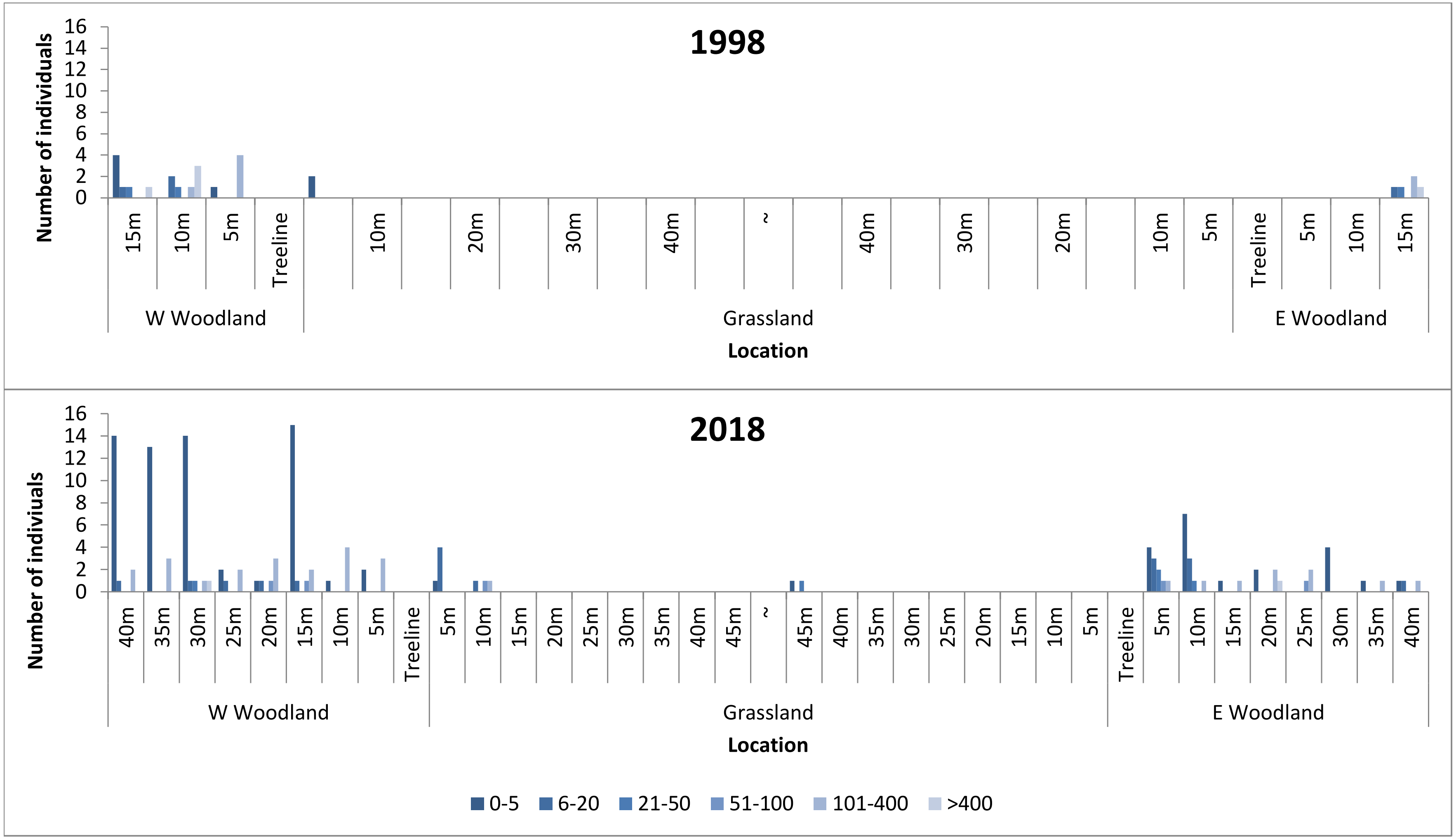


Figure 9 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 3 (lower position) at JB Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

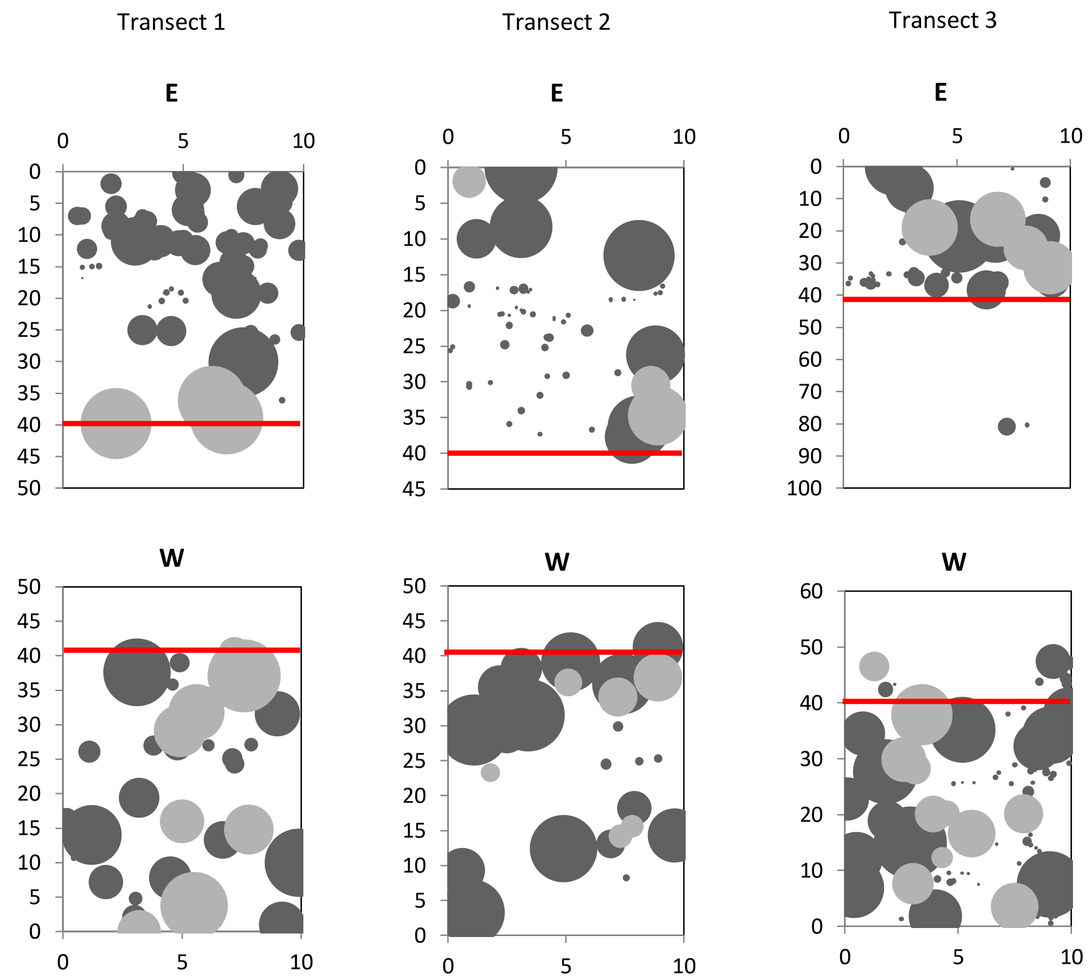


Figure 10 Visual representation of *E. pauciflora* individuals across transect 1, 2 and 3 at JB Plain in 2018.Transects were burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the x and y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline.

1605

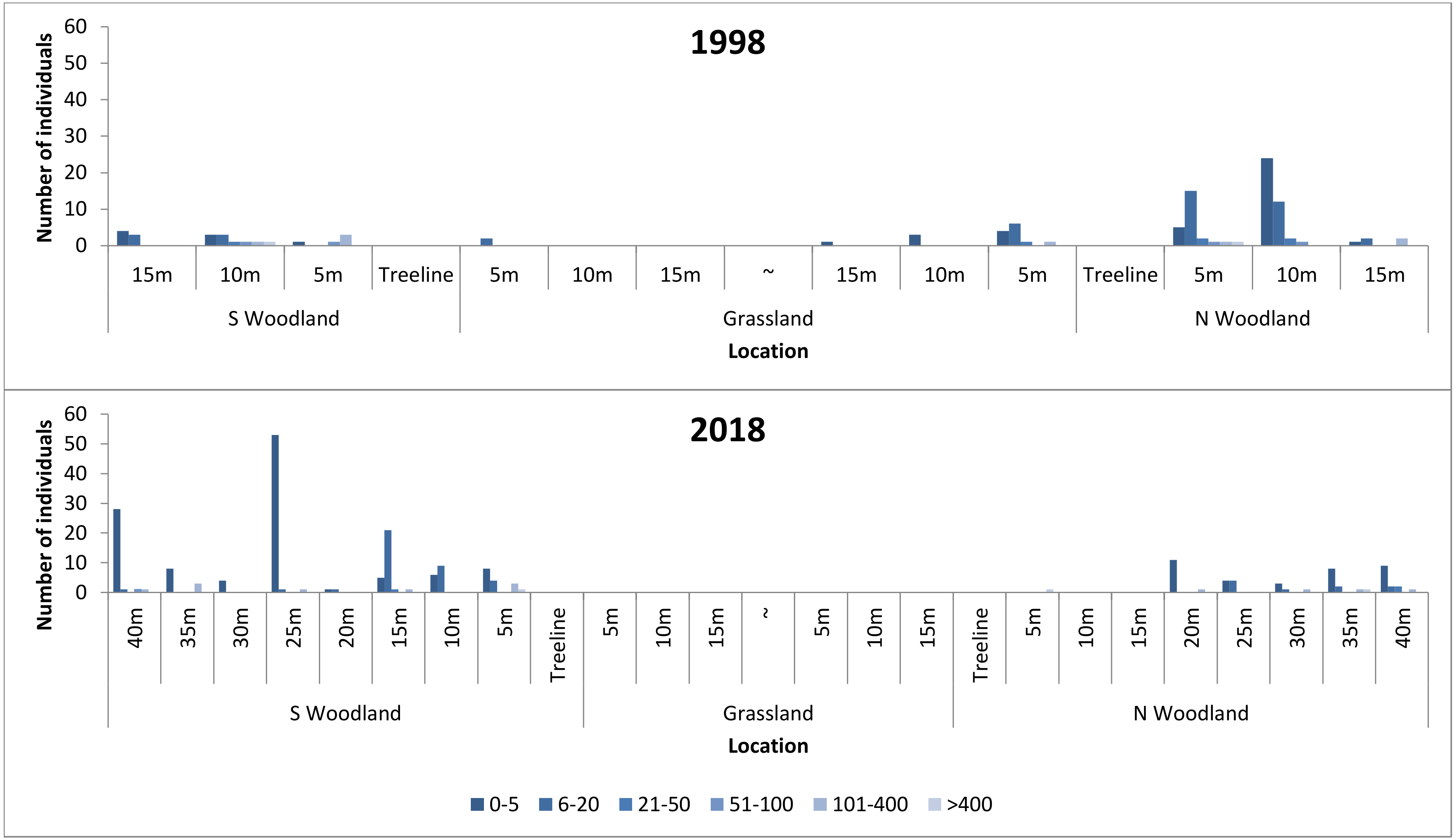


Figure 11 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 1 (upper position) at Precipice Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

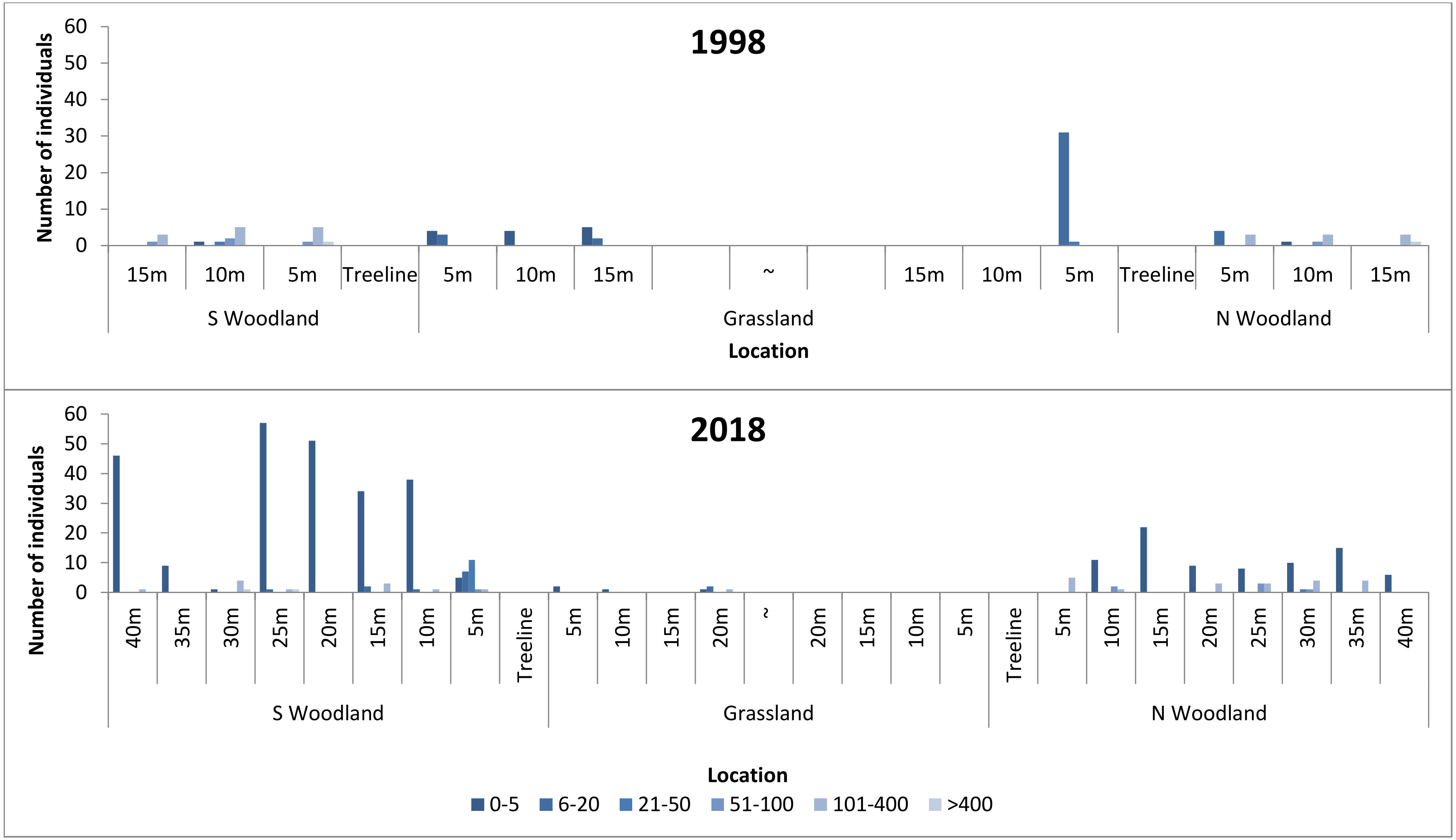


Figure 12 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 2 (middle position) at Precipice Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

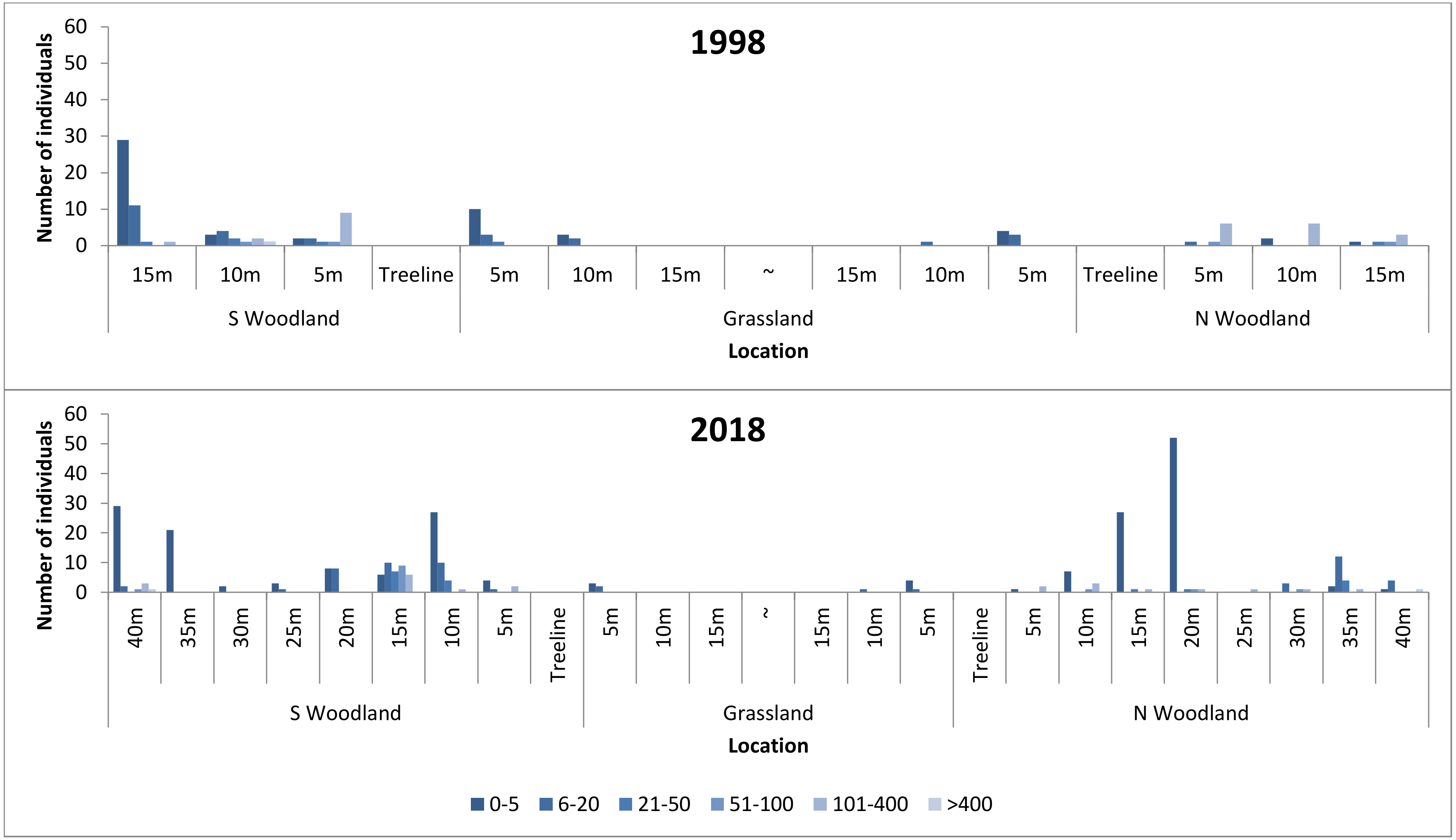


Figure 13 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 3 (lower position) at Precipice Plain in 1998 and 2018. The transect was burnt once in recent bushfires

1609

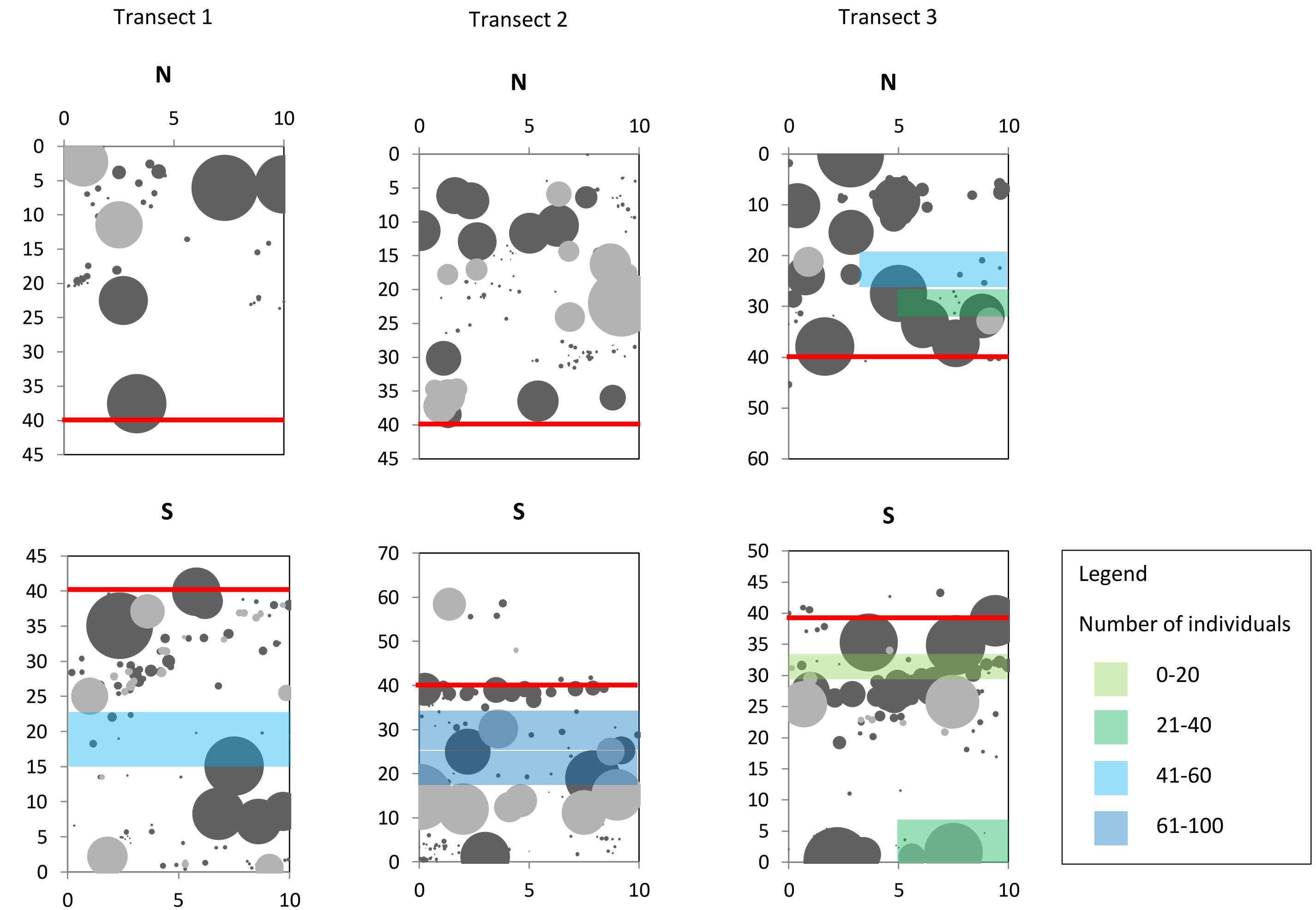


Figure 14 Visual representation of *E. pauciflora* individuals across transects 1, 2 and 3 at Precipice Plain in 2018.Transects were burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Coloured areas represent areas of high seedling (<25 cm basal girth) density.

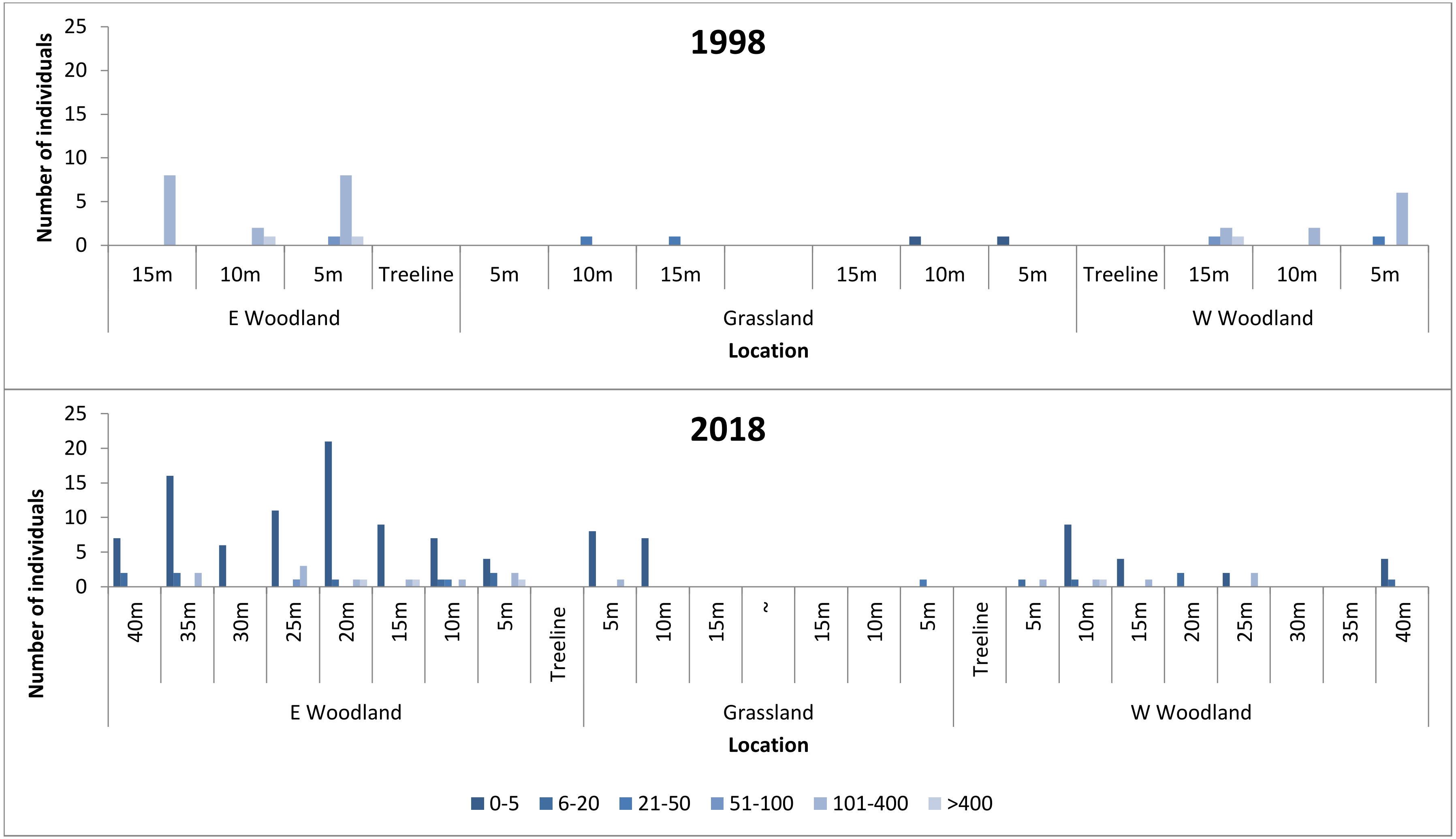


Figure 15 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 1 (upper position) at Paw Paw Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

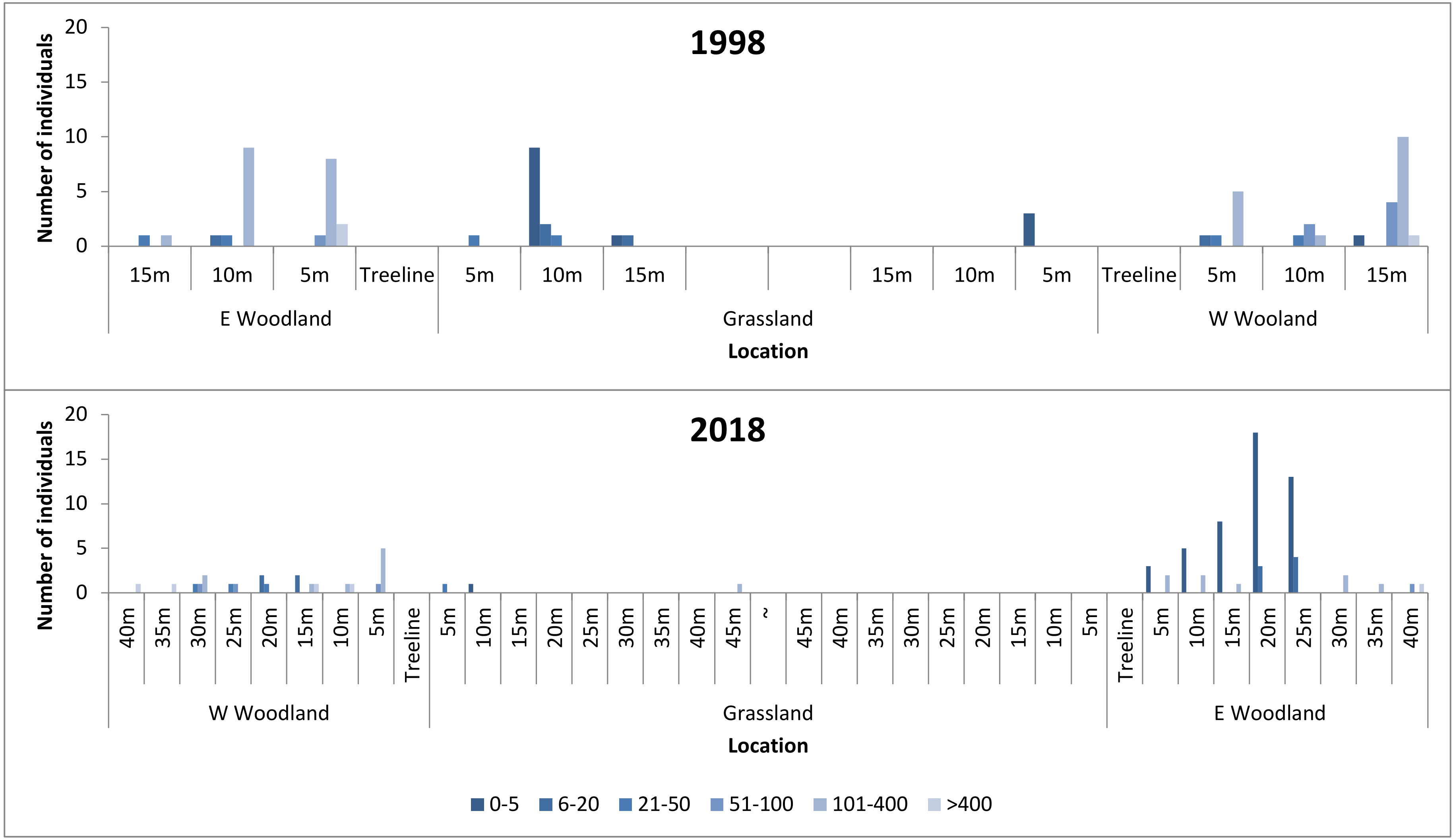


Figure 16 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 2 (middle position) at Paw Paw Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

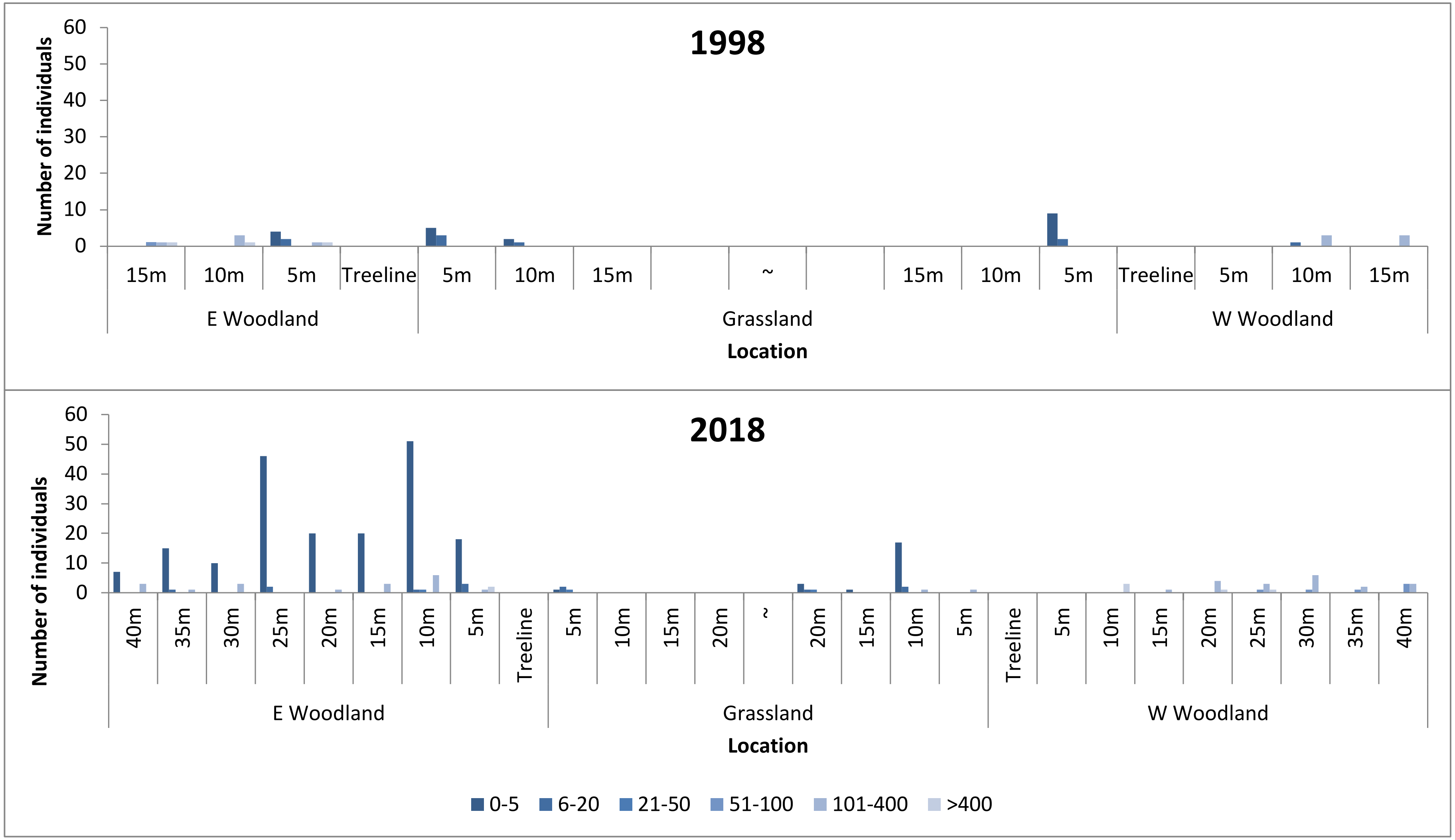


Figure 17 The number of *E. pauciflora* individuals per basal girth class (cm) across Transect 3 (lower position) at Paw Paw Plain in 1998 and 2018. The transect was burnt once in recent bushfires.

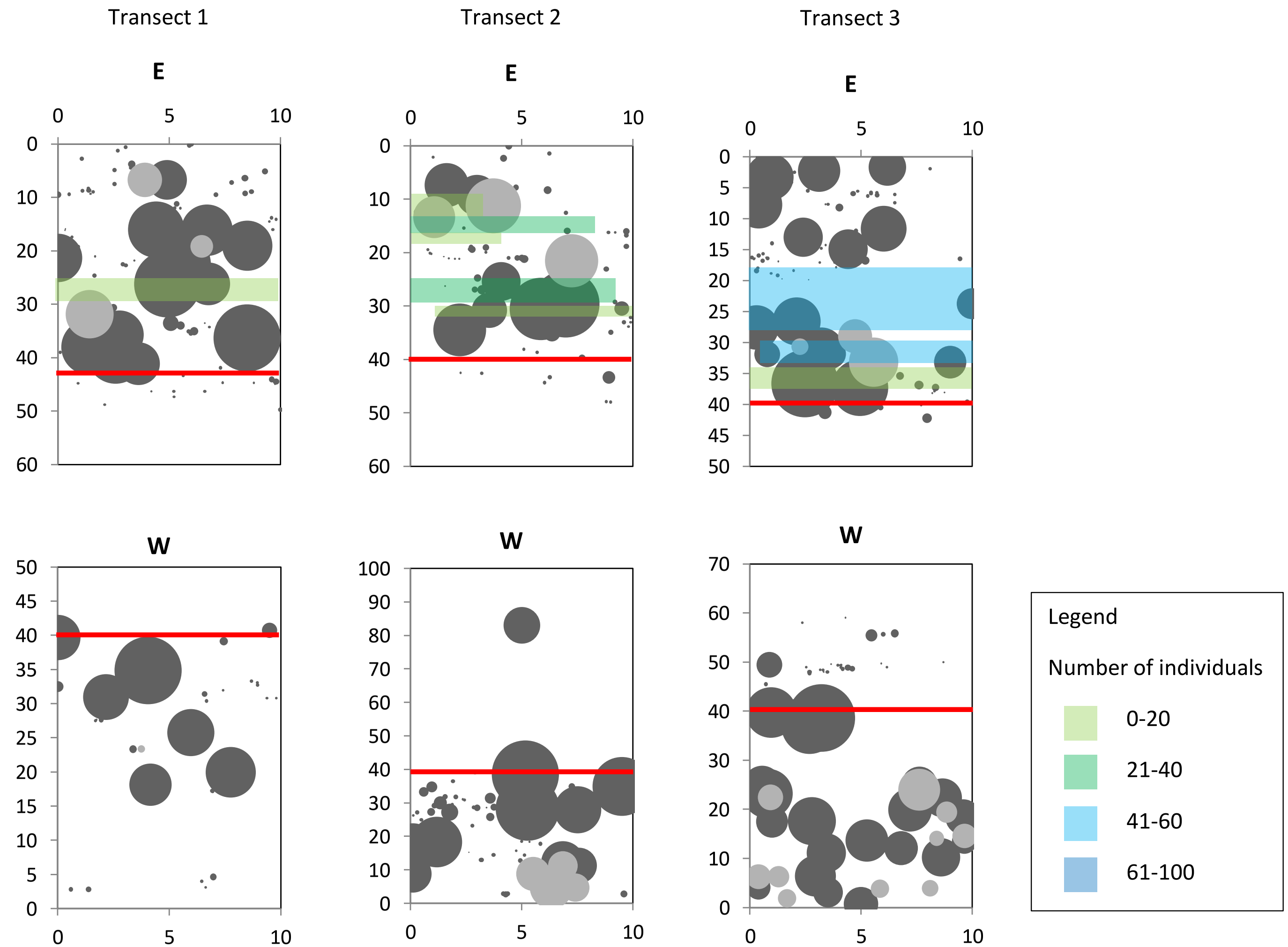


Figure 18 Visual representation of *E. pauciflora* individuals across transects 1, 2 and 3 at Paw Paw Plain in 2018.Transects were burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Coloured areas represent areas of high seedling (<25 cm basal girth).density.

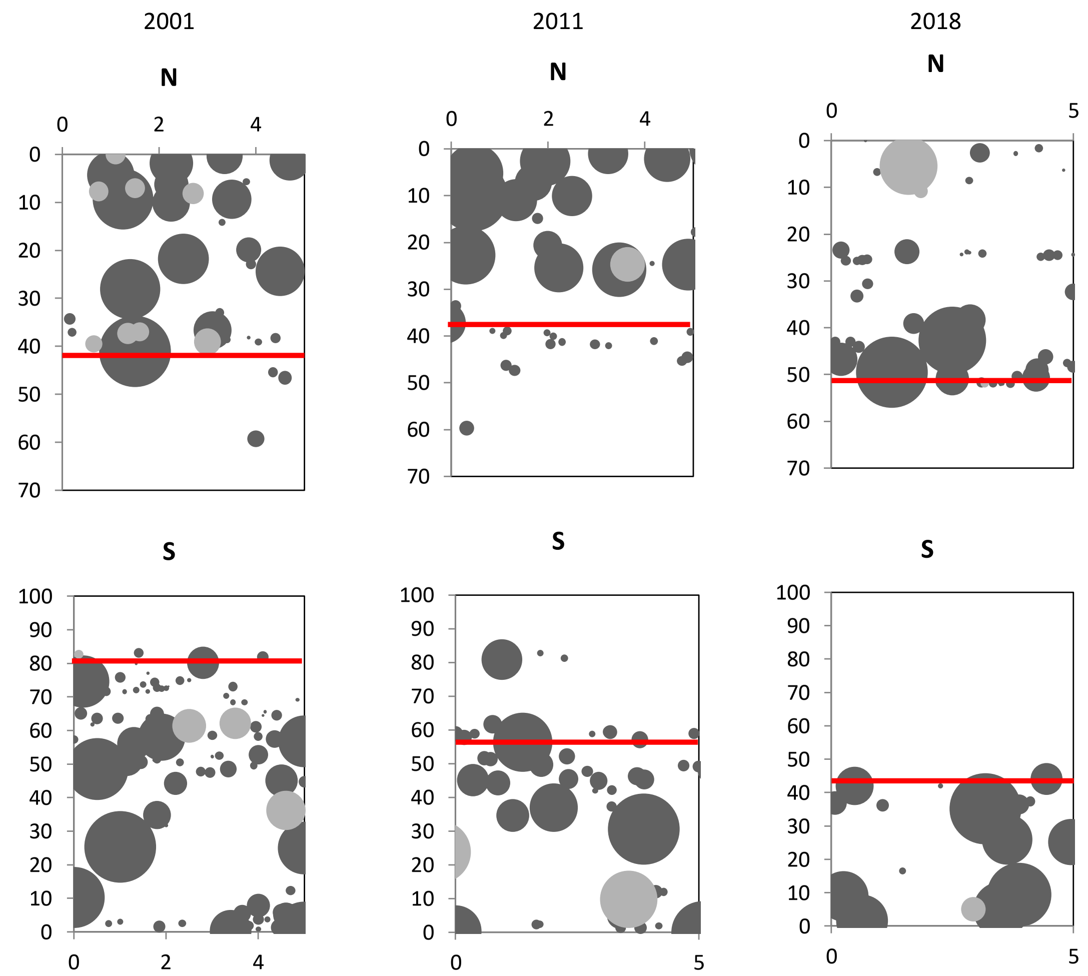


Figure 19 Visual representation of *E. pauciflora* individuals across transect 1 at Green Gables Plain in 2001, 2011 and 2018. The transect was burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline position for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

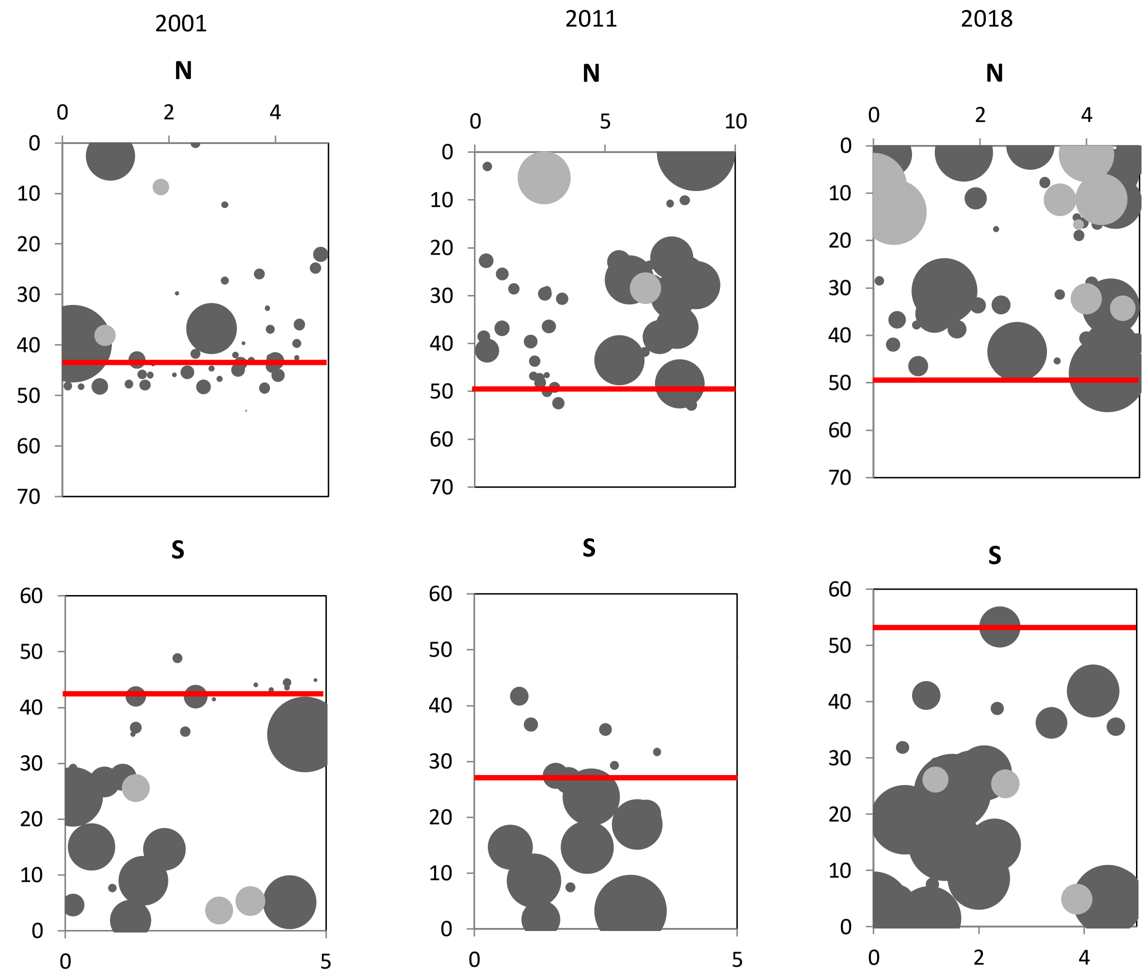


Figure 20 Visual representation of *E. pauciflora* individuals across transect 2 at Green Gables Plain in 2001, 2011 and 2018. The transect was burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline positions for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

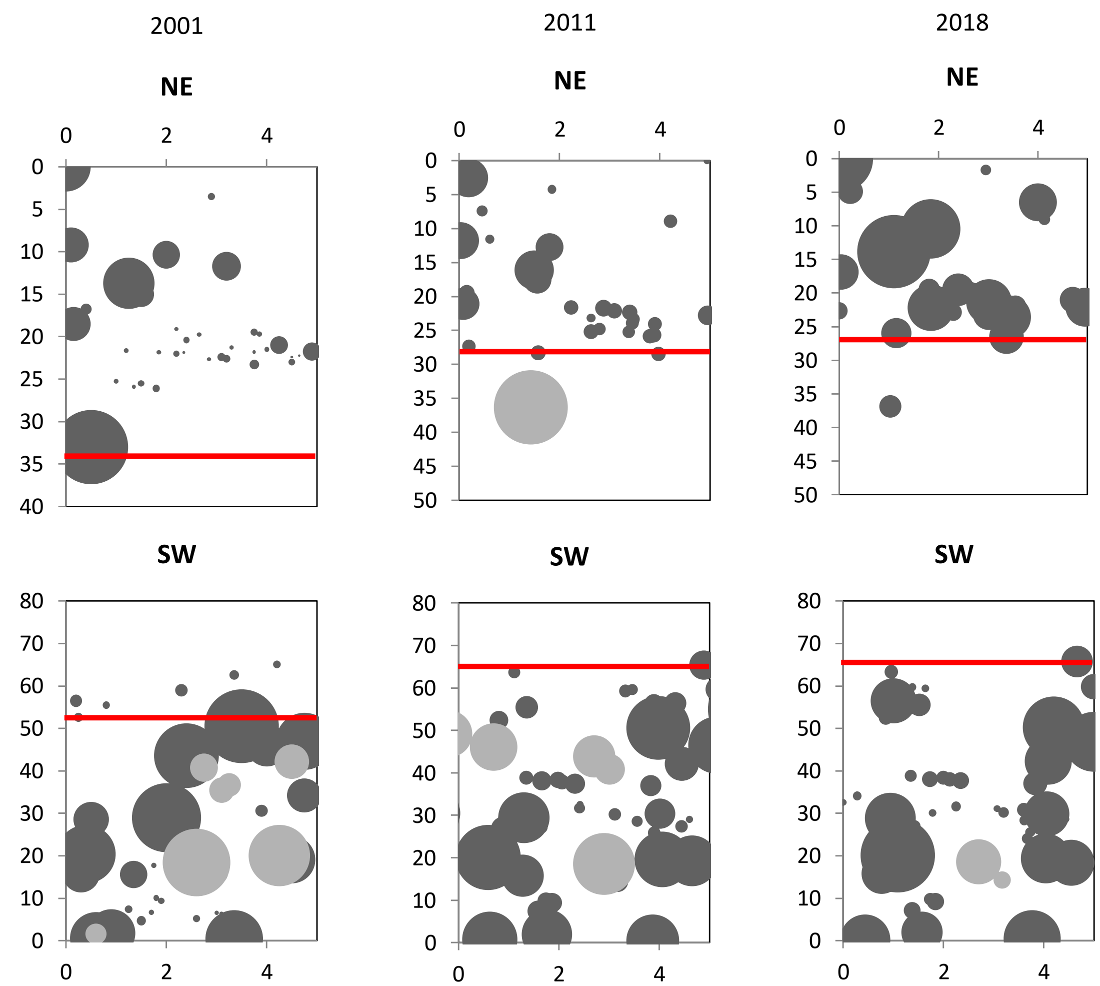


Figure 21 Visual representation of *E. pauciflora* individuals across transect 1 at The Lanes Plain in 2001, 2011 and 2018. The transects was burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline positions for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

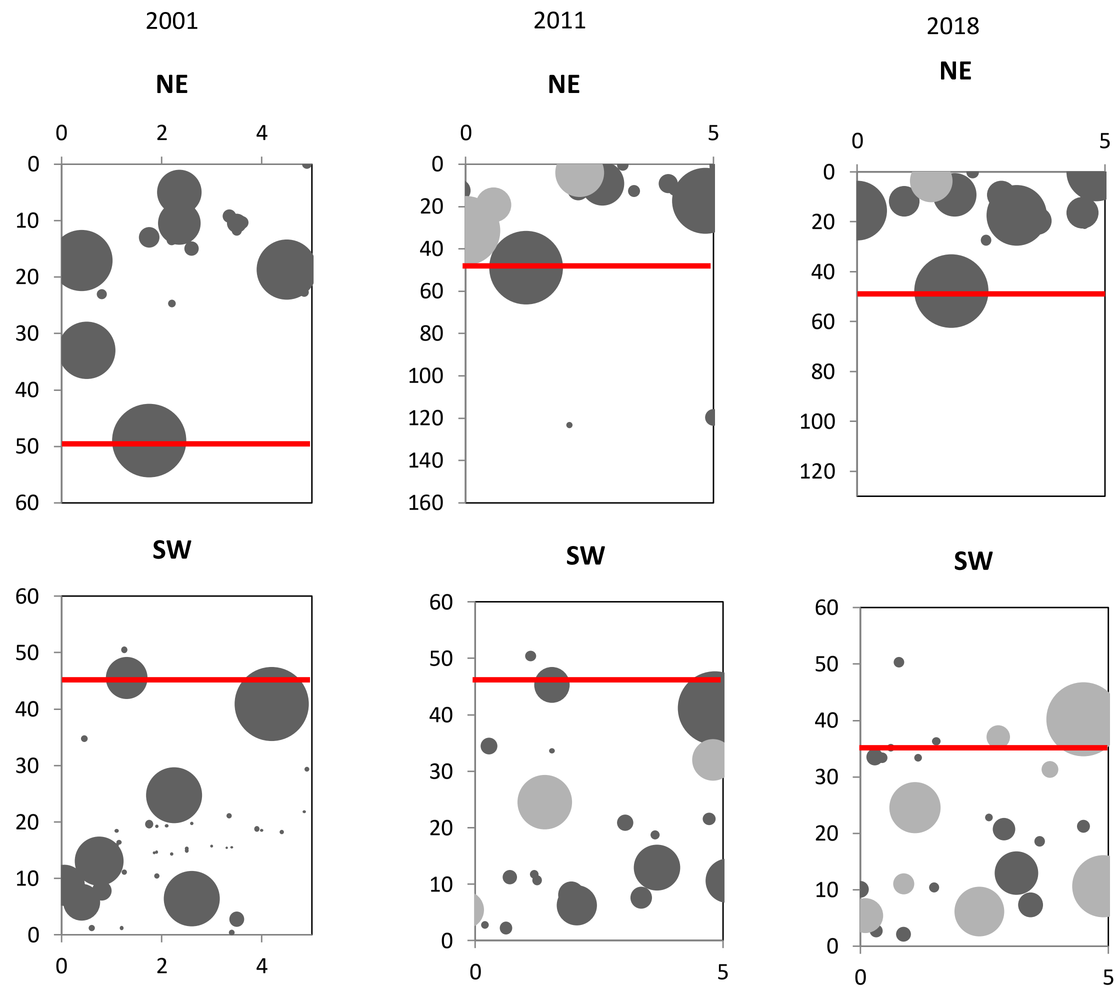


Figure 22 Visual representation of *E. pauciflora* individuals across transect 2 at The Lanes Plain in 2001, 2011 and 2018. The transect was burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline position for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

Figure 23 Visual representation of *E. pauciflora* individuals across transect 3 at The Lanes Plain in 2001, 2011 and 2018. The transects was burnt once in recent bushfires. X and Y axes indicates exact meter locations across the transect. Circle circumference indicates basal circumference in relative proportions to the X and Y axes. Grey = dead individuals. Black = alive individuals. Treeline is represented by the red line at y=40m, y<red line within the woodland, y>red line above treeline. Treeline position for 2001 and 2011 are estimates based on the distribution of large mature trees at treeline.

Table 6 Results of a fisher exact test of seedlings counts above treeline per site between 2002 and 2018 survey period. P=p-value.* = P<0.05.

Site	P
Mount McKay	0.442
Mount Hotham	<0.001*
Mount Feathertop	NA
The Twins	0.008*

Table 7 Results of a Pearson's correlation test and linear regression of the number of individuals above treeline against year of establishment combined for each aspect for alpine sites. North, South and E aspects were excluded due to the lack of data points. P=value.* = P<0.05

Treeline Form	Aspect	Pearson's correlation coefficient	Estimate	Std. Error	t-value	P
Alpine	W	0.825	0.055	0.011	5.048	<0.001*
	NW	0.548	0.028	0.013	2.175	0.052
	SW	0.267	0.042	0.062	0.679	0.522

Table 8 Results of a fisher exact test of seedlings counts above treeline per site between 2002 and 2018 survey period. P=p-value.* = P<0.05.

Site	P
Green Gables	<0.001*
The Lanes	<0.001*
JB Plain	<0.001*
Paw Paw Plain	0.004*
Precipice Plain	0.010*

Table 9 Results of a Pearson's correlation test and linear regression of the number of seedlings above treeline against year of establishment combined for each aspect subalpine sites. NE and SW aspects were excluded due to the lack of data points. P=value.* = P<0.05

Treeline Form	Aspect	Pearson's correlation coefficient	Estimate	Std. Error	t-value	P
Subalpine	N	0.359	0.013	0.013	1.021	0.341
	S	-0.107	-0.004	0.015	-0.424	0.819
	E	0.578	0.019	0.009	2.242	0.049*
	W	0.805	0.025	0.005	5.070	<0.001*

Appendix D: Dispersal limitation in *Eucalyptus pauciflora* and other global treeline forming species

Table 1 Information of species used in dispersal modelling and data source.

Species	Family	Genus	Dispersal Syndrome	Mean Seed Mass (mg)	Reference (seed mass)
Abies balsamea	*Pinaceae*	*Abies*	wind	7.622	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Walters and Reich 2000; Royal Botanic Gardens Kew 2018
Abies georgei	*Pinaceae*	*Abies*	wind	0.345	Wang *et al.* 2016)
Abies lasiocarpa	*Pinaceae*	*Pinus*	wind	10.154	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Knapp and Smith 1982; Greene and Johnson 1993; Li *et al.* 1994; Veech *et al.* 2000; Royal Botanic Gardens Kew 2018
Alnus incana	*Betulaceae*	*Alnus*	wind	0.996	'Baker Seed Herbarium'; Jones and Earle 1966; Forest Service 1974; FAO 1975; Cromarty *et al.* 1982; Mazer 1989; Royal Botanic Gardens Kew 2018
Betula pubescens	*Betulaceae*	*Betula*	wind	0.297	Hutchinson 1967; Forest Service 1974; Grime *et al.* 1981; Royal Botanic Gardens Kew 2018
Eucalyptus pauciflora	*Mrytaceae*	*Eucalyptus*	none	7.917	Cromarty *et al.* 1982; Turnbull and Doran. 1987; von Carlowitz *et al.* 1991; Royal Botanic Gardens Kew 2018
Fagus sylvatica	*Fagaceae*	*Fagus*	animal	236.916	Salisbury 1942; Forest Service 1974; FAO 1975; Cromarty *et al.* 1982; Bouman *et al.* 2000; Ammer *et al.* 2002; Rose *et al.* 2009; Royal Botanic Gardens Kew 2018
Juniperus communis	*Cypress*	*Thuja*	animal	18.311	'Baker Seed Herbarium'; Barclay and Earle 1974; Forest Service 1974; FAO 1975; Houle and Babeux 1993; Veech *et al.* 2000; Royal Botanic Gardens Kew 2018
Larix decidua	*Pinaceae*	*Pinus*	wind	5.671	Baldwin 1942; Simak 1967; Forest Service 1974; Felfoldi 1980; Cromarty *et al.* 1982
Larix gmelinii	*Pinaceae*	*Pinus*	wind	3.222	Forest Service 1974; Lukkarinen *et al.* 2009; Barchenkov 2011; Royal Botanic Gardens Kew 2018
Larix sibirica	*Pinaceae*	*Pinus*	wind	10.222	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Lukkarinen *et al.* 2009; Royal Botanic Gardens Kew 2018

Nothofagus menziesii	*Nothofagaceae*	*Nothofagus*	wind	3.75	Ledgard and Cath 1983; Allen 1987; Wardle 1991; Moles and Westoby 2003
Nothofagus pumilio	*Nothofagaceae*	*Nothofagus*	wind	45.28	
Picea abies	*Pinaceae*	*Pinus*	wind	7.504	Jones and Earle 1966; Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Johnsen 1989; Oleksyn *et al.* 1998; Moles and Westoby 2003; Royal Botanic Gardens Kew 2018
Picea egalmannii	*Pinaceae*	*Larix*	wind	2.942	Felfoldi 1980; Cromarty *et al.* 1982; Knapp and Smith 1982; Greene and Johnson 1993, 1994; Royal Botanic Gardens Kew 2018
Picea glauca	*Pinaceae*	*Abies*	wind	2.442	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Greene and Johnson 1994; Li *et al.* 1994; Oleksyn *et al.* 1998; Royal Botanic Gardens Kew 2018
Picea mariana	*Pinaceae*	*Abies*	wind	1.198	Forest Service 1974; Felfoldi 1980; Cromarty *et al.* 1982; Greene and Johnson 1993, 1999; Oleksyn *et al.* 1998; Walters and Reich 2000; Campbell and Rochefort 2003
Picea obovata	*Pinaceae*	*Picea*	wind	4.843	Otoda *et al.* 2013; Royal Botanic Gardens Kew 2018
Picea pungens	*Pinaceae*	*Pinus*	wind	4.772	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Cram 1983; Veech *et al.* 2000
Picea schrenkiana	*Pinaceae*	*Picea*	wind	2.363	Royal Botanic Gardens Kew 2018
Pinus cembra	*Pinaceae*	*Tsuga*	animal	264.159	Forest Service 1974; FAO 1975; Cromarty *et al.* 1982; Keeley and Zedler. 1998; Grotkopp *et al.* 2002
Pinus contorta	*Pinaceae*	*Larix*	wind	4.008	Gifford 1987; Greene and Johnson 1993; Li *et al.* 1994; Veech *et al.* 2000; Moles and Westoby 2003
Pinus monophylla	*Pinaceae*	*Picea*	animal	464.247	'Baker Seed Herbarium'; Forest Service 1974; Keeley and Zedler. 1998; Veech *et al.* 2000
Pinus monticola	*Pinaceae*	*Picea*	wind	21.637	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Gifford 1987; Li *et al.* 1994; Keeley and Zedler. 1998; Veech *et al.* 2000; Royal Botanic Gardens Kew 2018
Pinus peuce	*Pinaceae*	*Picea*	animal	44.602	Forest Service 1974; FAO 1975; Cromarty *et al.* 1982; Royal Botanic Gardens Kew 2018
Pinus ponderosa	*Pinaceae*	*Abies*	wind	41.043	Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Gifford 1987; West and Lott 1993; Greene and Johnson 1994; Li *et al.* 1994; Keeley and Zedler. 1998; Veech *et al.* 2000; Grotkopp *et al.* 2002; Vander Wall 2003
Pinus sylvestris	*Pinaceae*	*Pinus*	wind	6.531	Salisbury 1942; Forest Service 1974; FAO 1975; Felfoldi 1980; Cromarty *et al.* 1982; Gifford 1987; West and Lott 1993; Oleksyn *et al.* 1998; Keeley and Zedler. 1998;

					Karlsson 2000; Escudero *et al.* 2002; Grotkopp *et al.* 2002; Moles and Westoby 2003; Tapias *et al.* 2004; Royal Botanic Gardens Kew 2018
Pinus uncinata	*Pinaceae*	*Pinus*	wind	10.3	Escudero *et al.* 2000; Tapias *et al.* 2004
Populus tremuloides	*Salicaceae*	*Populus*	wind	0.119	Forest Service 1974; FAO 1975; Felfoldi 1980; Oleksyn *et al.* 1998; Walters and Reich 2000
Sorbus aucuparia	*Rosaceae*	*Sorbus*	animal	3.375	'Baker Seed Herbarium'; Salisbury 1942; Forest Service 1974; FAO 1975; Grime *et al.* 1981; Cromarty *et al.* 1982; Barclay and Crawford 1984; Moles and Westoby 2003; Csonthos *et al.* 2007; Royal Botanic Gardens Kew 2018
Tsuga mertensiana	*Pinaceae*	*Pinus*	wind	3.39	Forest Service 1974; FAO 1975; Veech *et al.* 2000; Moles and Westoby 2003

Table 2 Species with observed treeline advance used to compare distance of advance with dispersal distance and data source.

Species	Mean modelled dispersal distance	Distance of advance	Time period of advance	Reference
Abies georgei	442.153	18.7-28.1m	100 years	Liang *et al.* (2016)
Abies lasiocarpa	380.972	40m	100 years	Koch *et al.* (2004)
Betula pubescens	324.145	315m	50 years	Kullman (2002)
Fagus sylvatica	256.447	70m	Since 1955	Peñuelas and Boada (2003)
Larix decidua	396.379	115m	1901-2000	Leonelli *et al.* (2011)
Larix gmelinii	411.924	30 -50m	last 100 years	Kirdyanov *et al.* (2011)
Larix sibirica	380.799	100-500m	since 1920	Shiyatov (1993, 2003)
Nothofagus menziesii	13.951	7-9m	60 years	Wardle and Coleman (1992)
Nothofagus pumilio	11.776	10m	since 1850	Cuevas (2000)
Picea abies	388.895	240m	50 years	Kullman (2002)
Picea glauca	419.766	10-20m	150 years	Szeicz and MacDonald (1995)
Picea mariana	440.616	12 km	Since late 1800s	Lescop-Sinclair and Payette (1995)
Picea obovata	400.658	60-80m	Last 70 years	Moiseev and Shiyatov (2003)
Picea pungens	401.062	up to 50m	1983-2004	Moore and Huffman (2004)
Pinus cembra	1170.092	65m	1850-1980	Nicolussi *et al.* (2005)
Pinus contorta	405.849	5831 ha	Last 110 years	Andersen and Baker (2006)
Pinus monophylla	1126.046	825 ha	30 years	Weisberg *et al.* (2007)
Pinus monticola	361.856	up to 250m	since 1935	Butler and DeChano (2001)
Pinus peuce	1320.645	130-340m	Since 1970	Meshinev *et al.* (2000)
Pinus ponderosa	346.431	2108.43ha	1935-1996	Coop and Givnish (2007)
Pinus sylvestris	392.587	340m	50 years	Kullman (2002)
Populus tremuloides	695.615	up to 50m	1983-2004	Moore and Huffman (2004)
Sorbus aucuparia	716.813	375m	50 years	Kullman (2002)
Tsuga mertensiana	410.501	40m	100 years	Koch *et al.* (2004)

References for treeline species used in dispersal modelling

Allen RB (1987) Ecology of *Nothofagus menziesii* in the catlins ecological region, South-east Otago, New Zealand (I) seed production, viability, and dispersal. *New Zealand Journal of Botany* **25**, 5–10. doi:10.1080/0028825X.1987.10409953.

Ammer C, Mosandl R, Kateb H El (2002) Direct seeding of beech (*Fagus sylvatica L.*) in Norway spruce (*Picea abies* [L.] Karst.) stands—effects of canopy density and fine root biomass on seed germination. *Forest Ecology and Management* **159**, 59–72. doi:https://doi.org/10.1016/S0378-1127(01)00710-1.

Andersen M, Baker D (2006) Reconstructing Landscape-scale Tree Invasion Using Survey Notes in the Medicine Bow Mountains, Wyoming, USA. *Landscape Ecology* **21**, 243–258.

Baker Seed Herbarium

Baldwin HI (1942) 'Forest tree seed of the north temperate regions with special reference to North America.' (Chronica Botanica Co.; Wm. Dawson & Sons, Ltd.: Waltham, Mass.; Lindon, W.1., USA; UK)

Barchenkov A (2011) Morphological variability and quality of seeds of *Larix gmelinii* (*Rupr.*) Rupr. *Contemporary Problems of Ecology* **4**, 327–333.

Barclay AM, Crawford RMM (1984) Seedling Emergence in the Rowan (*Sorbus Aucuparia*) from an Altitudinal Gradient. *Journal of Ecology* **72**, 627–636. doi:10.2307/2260072.

Barclay AS, Earle FR (1974) Chemical analyses of seeds III: oil and protein content of 1253 species. *Economic Botany* **28**, 178–236.

Bouman F, Boeswinkel D, Bregman R, Devente N, Oostermeijer G (2000) 'Verspreiding van Zaden.' (KNNV Uitgeverij: Utrecht)

Butler D., DeChano L. (2001) Environmental change in Glacier National Park, Montana: An assessment through repead photography from fire lookouts. *Physical Geography* **22**, 291–304.

Campbell D, Rochefort L (2003) Germination and seedling growth of bog plants in relation to the recolonization of milled peatlands. *Plant Ecology* **169**, 71–84.

von Carlowitz P, Wolf G V, Kemperman REM (1991) ‘Multipurpose tree and shrub database: an information and decision support system.’

Coop JD, Givnish TJ (2007) Spatial and temporal patterns of recent forest encroachment in montane grasslands of the Valles Caldera, New Mexico, USA. *Journal of Biogeography* **34**, 914–927. doi:10.1111/j.1365-2699.2006.01660.x.

Cram W (1983) Some effects of seld-, cross-, and open-pollination in *Picea pungens*. *Canadian Journal of Botany* **62**, 329–395.

Cromarty AS, Ellis RH, Roberts EH (1982) The Design of Seed Storage Facilities for Genetic Conservation. (Rome)

Csonthos P, Tamas J, Balogh L (2007) Thousand-seed weight records of species from the flora of Hungary, II. Dicotyledonopsida. *Studia bot.hung* **38**, 179–189.

Cuevas J. (2000) Tree Recruitment at the *Nothofagus pumilio* Alpine Timberline in Tierra del Fuego, Chile. *Journal of Ecology* **88**, 840–855.

Escudero A, Nunez Y, Perez-Garcia F (2000) Is fire a selective force of seed size in pine species? *Acta Oecologica* **21**, 4–5.

Escudero A, Perez-Garcia F, Luzuriaga A (2002) Effects of light, temperature and population variability on the germination of seven Spanish pines. *Seed Science Research* **12**, 261–271.

FAO (1975) Forest Tree Seed Directory. (Rome)

Felfoldi E (1980) Seed Counts (Numbers of Seeds Per Unit Weight). Technical Report Series, 32.

Forest Service (1974) Seeds of Woody Plants in the United States. 'Agric. Handb. Number 450.' (Forest Service, U.S. Department of Agriculture: Washington, D.C)

Gifford D (1987) An electrophoretic analysis of the seed proteins from *Pinus monticola* and eight other species of pine. *Canadian Journal of Botany* **66**, 1808–1812.

Greene DF, Johnson EA (1993) Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos* **67**, 69–74.

Greene DF, Johnson EA (1994) Estimating the mean annual seed production of trees. *Ecology* **75**, 642–647.

Greene D, Johnson E (1999) Modelling recruitment of *Populus tremeloides, Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. *Canadian Journal of Forest Research* **29**, 462–473.

Grime JP, Mason G, Curtis AA, Rodman J, Band SR, Mowforth MAG, Neal AM, Shaw S (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017–1059.

Grotkopp E, Rejmanek M, Rost T (2002) Toward a casual explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* **159**, 396–419.

Houle G, Babeux P (1993) Variation in rooting ability of cuttings and in seed characteristics of five populations of *Juniperus communis var. depressa* from subarctic Quebec. *Canadian Journal of Botany* **72**, 493–498.

Hutchinson TC (1967) Comparative studies of the ability of species to withstand prolonged periods of darkness. *Journal of Ecology* **55**, 291–299.

Johnsen O (1989) henotypic changes in progenies of northern clones of *Picea abies* (L) Karst. grown in a southern seed orchard. *Scandinavian Journal of Forest Research* **4**, 317–330.

Jones Q, Earle FR (1966) Chemical analyses of seeds II: oil and protein content of 759 species. *Economic Botany* **20**, 127–155.

Karlsson C (2000) Seed production of *Pinus sylvestris* after release cutting. *Canadian Journal of Forest Research* **30**, 982–989.

Keeley JE, Zedler. PH (1998) Evolution of life histories in *Pinus*. ‘Ecol. Biogeogr. Pinus’. (Ed .M.D Richardson) pp. 219–250. (Cambridge University Press: Cambridge)

Kirdyanov A V, HAGEDORN F, Knorre A, Fedotova E, Vaganov EA, M. NAURZBAEV M, Moiseev P, Rigling A (2011) 20th century tree-line advance and vegetation changes along an altitudinal transect in the Putorana Mountains, northern Siberia. *Boreas* **41**, 56–67.

Knapp A, Smith W (1982) Factors in uencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine (*Abies lasiocarpa*) in southeast Wyoming. *Can J Bot* **60**, 2753–2761.

Koch J, Menounos B, Clague JJ, Osborn GD (2004) Environmental change in Garibaldi provincial park, southern coast mountains, British Columbia. *Geoscience Canada* **31**, 127–135.

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* **90**, 68–77. doi:10.1046/j.0022-0477.2001.00630.x.

Ledgard N, Cath P (1983) Seed of New Zealand *Nothofagus* species: studies of seed weight, viability, shape, and the effects of varying stratification periods. *New Zealand Journal of Forestry* **28**, 150–162.

Leonelli G, Pelfini M, Morra di Cella U, Garavaglia V (2011) Climate Warming and the Recent Treeline Shift in the European Alps: The Role of Geomorphological Factors in High-Altitude Sites. *AMBIO* **40**, 264–273. doi:10.1007/s13280-010-0096-2.

Lescop-Sinclair K, Payette S (1995) Recent Advance of the Arctic Treeline Along the Eastern Coast of Hudson Bay. *Journal of Ecology* **83**, 929–936. doi:10.2307/2261175.

Li X, Burton P, Leadem C (1994) Interactive effects of light and stratification on the germinantion of some British Colombia conifers. *Canadian Journal of Botany* **72**, 1635–1646.

Liang E, Wang Y, Piao S, Lu X, Camarero JJ, Zhu H, Zhu L, Ellison AM, Ciais P, Peñuelas J (2016) Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **113**, 4380–4385. doi:10.1073/pnas.1520582113.

Lukkarinen AJ, Ruotsalainen S, Nikkanen T, Peltola H (2009) The growth rhythm and height growth of seedlings of Siberian (*Larix sibirica Ledeb.*) and Dahurian (*Larix gmelinii Rupr.*) larch provenances in greenhouse conditions. *Silva Fennica* **43**, 5–20.

Mazer S (1989) Ecological, taxonomic, and life history correlates of seed mass among Indiana dunes *Angiosperms*. Supplement: species list, untransformed seed mass, seed mass class and ecological data associated with each species. *Ecological Monographs* **59**,.

Meshinev T, Apostolova I, Koleva ES (2000) Influence of warming on timberline rising: A case study on *Pinus peuce* Griseb. in Bulgaria. *Phytocoenologia* **30**, 431–438.

Moiseev P, Shiyatov S (2003) Vegetation Dynamics at the Tree-Line Ecotone in the Ural

Highlands,Russia. *Ecol. Stud.* **167**,.

Moles A, Westoby M (2003) Latitude, seed predation and seed mass. *Journal of Biogeography* **30**, 105–128.

Moore M, Huffman D (2004) Tree encroachment on meadows of the north rim, Grand Canyon National Park, Arizona, U.S.A. *Arctic, Antarctic and Alpine Research* **36**, 474–483.

Nicolussi K, Kaufmann M, Patzelt G, Van derPlicht J, Thurner A (2005) Holocene tree-line variability in the Kauner Valley, Central Eastern Alps, indicated by dendrochronological analysis of living and subfossil logs. *Vegetation History and Archeobotany* **14**, 221–234.

Oleksyn J, Modrzynski J, Tjoelker M, Zytkowiak R, Reich P, Karolewski P (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology* **12**, 573–590.

Otoda T, Doi T, Sakamoto K, Hirobe M, Nachin B, Yoshikawa K (2013) Frequent fires may alter the future composition of the boreal forest in northern Mongolia. *Journal of Forest Research* **18**, 246–255. doi:10.1007/s10310-012-0345-2.

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* **9**, 131–140. doi:10.1046/j.1365-2486.2003.00566.x.

Rose L, Leuschner C, Kockemann B, Buschmann H (2009) Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research* **128**, 335–343.

Royal Botanic Gardens Kew (2018) Seed Information Database (SID). *Version 7.1. Wakehurst Place*. http://data.kew.org/sid/.

Salisbury EJ (1942) ‘The Reproductive Capacity of Plants.’ (G. Bell and Sons: London)

Shiyatov SG (1993) The upper timberline dynamics during the last 1100 years in the Polar Ural Mountains. ‘Oscil. Alp. polar tree limits Holocene.’ (Eds B Frenzel, M Eronen, B Glaser) pp. 195–203. (Gustav Fischer Verlag: Stuttgart, Germany)

Shiyatov SG (2003) Rates of Change in the Upper Treeline Ecotone in Polar Ural Mountains. *PAGES News* **11**, 8–10.

Simak M (1967) Seed weight of larch from different provenances (*Larix decidua* Mill.). *Stud For Suec* **57**,.

Szeicz JM, MacDonald GM (1995) Dendroclimatic Reconstruction of Summer Temperatures in Northwestern Canada since A.D. 1638 Based on Age-Dependent Modeling. *Quaternary Research* **44**, 257–266.

Tapias R, Climent J, Pardos J, Gil L (2004) Life histories of Mediterranean pines. *Plant Ecology* **171**, 53–68.

Turnbull LA, Doran. JC (1987) Species of Eucalyptus responding to cold-moist stratification (3-58C). ‘Germination Aust. Nativ. Plant Seed’. (Ed PJ Langkamp) p. 196. (Inkata Press Pty Ltd: Melbourne)

Veech JA, Charlet DA, Jenkins SH (2000) Interspecific variation in seed mass and the co-existence of conifer species: a null model test. *Evolutionary Ecology Research* **2**, 353–363.

Vander Wall S. (2003) Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* **100**, 25–34. doi:10.1034/j.1600-0706.2003.11973.x.

Walters MB, Reich PB (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* **81**, 1887–1901.

Wang J, Feng J, Chen B, Shi P, Zhang J, Fang J, Wang Z, Yao S, Ding L (2016) Controls of seed quantity and quality on seedling recruitment of smith fir along altitudinal gradient in southeastern Tibetan Plateau. *Journal of Mountain Science* **13**, 811–821. doi:10.1007/s11629-015-3761-x.

Wardle P (1991) 'Vegetation of New Zealand.' (Cambridge University Press: Cambridge)

Wardle P, Coleman MC (1992) Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany* **30**, 303–314. doi:10.1080/0028825X.1992.10412909.

Weisberg PJ, Lingua E, Pillai RB (2007) Spatial Patterns of Pinyon–Juniper Woodland Expansion in Central Nevada. *Rangeland Ecology & Management* **60**, 115–124. doi:https://doi.org/10.2111/05-224R2.1.

West MM, Lott JNA (1993) Studies of mature seeds of eleven *Pinus* species differing in seed weight. I. Element concentrations in embryos and female gametophytes. *Canadian Journal of Botany* **71**, 570–576.

Appendix E: Instructions for Authors

This thesis has been written in the form of a thesis as per the thesis guidelines of the Department of Ecology, Environment & Evolution, La Trobe University. The referencing style, illustration (centred with regard to proportions of the page, numbered sequentially and caption title below the figure), photograph (arrange photographs so that they abut each other without gaps, centred with regard to proportions of the page, numbered sequentially and caption title below the figure) and table (centred with regard to proportions of the page, numbered sequentially and caption title above the table) format follow the publishing conventions of the Australian Journal of Botany. The referencing style and formatting of the Australian Journal of Botany can be found in full at http://www.publish.csiro.au/bt/forauthors/AuthorInstructions. The formatting of page margins, line spacing and title page, and word limit follows the thesis guidelines. The word limit, of 12,000 words excludes figures, tables, references and appendices.