1 **Recovery of subalpine grasslands 15 years after landscape level fires**

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8 **Abstract**

9 As conditions warm, previously rare landscape level fires are more likely to affect vegetation in the
10 Australian Alps including in subalpine grasslands. The recovery of this community was assessed using
11 paired unburnt and burnt plots (30 x 20 m) at ten sites 15 years after largescale fires that burnt >70%
12 of the subalpine zone in Kosciuszko National Park. There were few significant differences found:
13 higher cover of shrubs (17.8% burnt vs 11.3% unburnt plots), and taller vegetation (22.6 vs 19 cm).
14 However, vegetation cover (97%), species richness (38 taxa), composition and limited presence of
15 invasive plants (10 species, 8.5% cover) were not significantly different. This differs from results six
16 weeks and one-year post-fire, when there were clear differences in the cover and composition of
17 vegetation. The results indicate subalpine grasslands recover from single fires, but with warmer and
18 drier conditions more common, and repeat fires in some areas, the distribution, structure and
19 composition of this and other communities in the Australian Alps will change.

20

21 **Key Words:** fire ecology; vegetation recovery; vegetation cover; Kosciuszko National Park;
22 Australian Alps

23 **Introduction**

24 Fire is an important type of disturbance in many Australian ecosystems, shaping the composition
25 of much of the flora (Gill 1981; Gill and Zylstra 2005; Mooney *et al.* 2011; Miller and Murphy 2017).
26 It can result in reductions in vegetation cover and biomass, changes in composition and nutrient levels,
27 with exposed soils and erosion (Wahren *et al.* 2001; Bond and Keely 2005; Fairman *et al.* 2016;
28 Murphy *et al.* 2019). A plant community's ability to recover from fire is affected both by the extent
29 and severity of the original fire, as well as by species traits affecting survival, recovery and/or
30 recolonising post-fire (Gill 1975, 1981; Walsh and McDougall 2004; Bowman *et al.* 2014; Miller and
31 Murphy 2017). However, in ecosystems where landscape level fires are less common (less than every
32 50-100 years), such as the subalpine and alpine zones in the Australian Alps (Good 1982; Mooney
33 2004; Zylstra 2006; Williams *et al.* 2008; Zylstra 2018), plants tend to have fewer adaptations to fire
34 than in other warmer areas where fires are more common (Billings 1974; Körner 2003; Grime 2006;
35 Tolsma *et al.* 2007; Venn *et al.* 2014).

36 When largescale fires do occur in the Australian Alps, they tend to be under exceptional conditions,
37 such as during sustained periods of drought and then only on hot dry days, when there are strong winds
38 and often multiple sources of ignition (Wahren *et al.* 2001; Leaver and Good 2004; Mooney 2004;
39 Zylstra 2018). In January and February 2003, much of the Australian Alps burnt when fires were
40 ignited by dry electrical storms amidst one of the driest periods in 100 years (Worboys 2003; Cary
41 2005). Over 70% of the subalpine zone of Kosciuszko National Park burnt (Worboys 2003; Wales
42 2006) with the loss of large areas of vegetation and increased soil exposure, including areas of
43 subalpine grasslands, heaths in valley floors and subalpine woodlands (Scherrer *et al.* 2004; Walsh
44 and McDougall 2004; McDougall *et al.* 2005; Bear and Pickering 2006; Williams *et al.* 2008).

45 Fires are predicted to become more common as the climate of the Australian Alps continues to
46 become warmer and drier in summer (Hennessy *et al.* 2008; Mooney *et al.* 2011; Green and Osborne
47 2012; Zylstra 2018), with conditions already changing over the last few decades. Since 1950, the mean

48 annual temperature has risen by 0.74°C at elevations above 1500 m (Gallagher *et al.* 2009), a 6%
49 reduction in annual precipitation (Wahren *et al.* 2013), and a consequent reduction in snowpack depth
50 and persistence (Sánchez-Bayo and Green 2013). These changes are likely to have enhanced the
51 intensity and severity of fires in the Australian Alps (Mooney *et al.* 2011; Zylstra 2018), with a
52 substantial increase in fire frequency over the past two decades (Fairman *et al.* 2016). Several
53 subalpine areas in the Australian Alps affected by the 2003 fires were burnt again in 2006-2007
54 (Williams *et al.* 2008; Bradstock *et al.* 2014; McDougall *et al.* 2015). Prior to 2003, most areas of
55 subalpine grasslands within Kosciuszko National Park had remained unburnt for several decades, as
56 deliberate burning related to grazing ceased by the 1950s and episodic fuel reduction burns were
57 abolished as a fire management tool in the 1970s (Leaver and Good 2004; McDougall *et al.* 2015).
58 These low-intensity fuel reduction burns promoted shrub dominance, resulting in a counterintuitive
59 increase in fuel loads in the years following fire (Good 1982).

60 There is over 100 years of research on the distribution and dynamics of plant communities in the
61 Australian Alps (e.g. Helms 1893; Gandoger 1899; Barrow *et al.* 1968; Costin 1954, 1959; Carr and
62 Turner 1959; McVean 1969; Barlow 1986; Williams and Costin 1994; Kirkpatrick and Bridle 1998;
63 Costin *et al.* 2000; Pickering *et al.* 2002; Williams and Wahren 2005; McDougall and Walsh 2007;
64 Pickering *et al.* 2008; Venn *et al.* 2017), but as fire was infrequent, there was limited research on its
65 effects on vegetation. There has been some research on short-term recovery of subalpine grasslands
66 from fire (Leigh *et al.* 1987; Williams 1990; Wahren and Walsh 2000; Bridle *et al.* 2001; Wahren and
67 Papst 2001; Kirkpatrick *et al.* 2002), including the 2003 fires (Growcock *et al.* 2004; Scherrer *et al.*
68 2004; Walsh and McDougall 2004; Bear and Pickering 2006), but research on the longer-term effects
69 of fire on this community is scarce (but see: McDougall *et al.* 2015). The 2003 fires resulted in the
70 near complete loss of existing vegetation, with estimates six weeks post-fire of as little as 1.5% cover
71 of vegetation in areas of burnt subalpine grasslands (Growcock *et al.* 2004), and one-year post-fire
72 there were still differences between burnt and unburnt grasslands (Bear and Pickering 2006). By 10

73 years post-fire, recovery of subalpine grasslands (e.g. non-groundwater dependent grassland) had
74 occurred although in wetter areas, the cover of the dominant snow-grass, *Poa costiniana*, was still
75 lower than pre-fire (McDougall *et al.* 2015). The response of vegetation to fire as well as warming in
76 the Australian Alps will be complicated with different responses of shrubs, forbs and graminoids
77 including regeneration strategies (Walsh and McDougall 2004; McDougall *et al.* 2015; Camac *et al.*
78 2017). For example, in the short-term, fires in the subalpine zone can favour species that resprout post-
79 fire including the dominant *Poa* grasses in subalpine grasslands (Bear and Pickering 2006), but over
80 longer periods, fire and warming may favour some species of shrubs (McDougall *et al.* 2015) that have
81 higher germination rates post-fire and when conditions are warmer, faster growth rates, strengthening
82 a positive feedback between alpine shrubs and fire (Camac *et al.* 2017). Therefore, the future of
83 subalpine grasslands in the Australian Alps will be complex in response to fire and warming, as well
84 as other factors such as spread of invasive plants, and damage from feral animals and disease
85 (McDougall *et al.* 2015; Camac *et al.* 2017). However, these interactions will be difficult to
86 comprehend without baseline knowledge regarding the longer-term recovery of subalpine grasslands
87 after a single fire.

88 This study assesses the recovery of subalpine grasslands 15 years post-fire. Specifically, differences
89 in vegetation structure (height and biomass), cover and composition were compared between paired
90 unburnt and burnt plots at 10 subalpine grassland sites in Kosciuszko National Park. The results are
91 then compared with other research in the same area six weeks (Growcock *et al.* 2004; Scherrer *et al.*
92 2004) and one-year post-fire (Bear and Pickering 2006) to assess the rate and extent of recovery of this
93 community from a single large fire event.

94

95 **Materials and Methods**

96 *Study site*

Subalpine grasslands are a widespread and diverse plant community found between the upper limits of montane vegetation (~1370 m a.s.l) and the treeline (~1850 m a.s.l) in the Australian Alps (Costin *et al.* 2000; Walsh and McDougall 2004; McDougall and Walsh 2007). They occur mainly on deep, well-drained humus soils on transitional slopes and valley bottoms, where cold air drains from the surrounding ridges to form frost hollows, inhibiting the establishment of trees (Paton 1988; Williams and Costin 1994). Subalpine grasslands above ~1500 m a.s.l (winter snowline – see Happold 1998) experience continuous snow cover from around June to October, and temperatures are low throughout winter (average 0 °C, range -5 °C to 2 °C). By comparison, summers are relatively warm, where the average monthly temperatures vary from 9 °C to 12 °C (Paton 1988; Happold 1998; Williams and Costin 1994). Approximately half of the annual 1950 mm precipitation is in the form of snow in winter with the other half as rain in the warmer months, while mist and dew are important for reducing the risk of fires in summer (Good 1982; Happold 1998; Zylstra 2016, 2018).

Subalpine grasslands are a highly diverse community, supporting 170 species with tussock-forming snow grasses (*Poa* spp.) dominant, while perennial forbs colonise areas between the tussocks but there is limited shrub cover (Williams and Costin 1994; Pickering *et al.* 2002; McDougall and Walsh 2007). There is near complete vegetation cover, although some areas have been disturbed in the past by grazing, anthropogenic fires, the construction of tourism facilities and feral animals (pigs, horses and more recently, deer) (Costin *et al.* 2000; Hone 2002, 2012; Green and Osbourne 2012; Davis *et al.* 2016). Associated with areas of disturbance are a range of invasive plants, with more than 100 species recorded in the subalpine zone of Kosciuszko National Park (McDougall *et al.* 2005; Bear *et al.* 2006; Doherty *et al.* 2015).

Experimental Design

Vegetation cover, composition and structure were assessed at 10 subalpine grassland sites in Kosciuszko National Park in December 2017 (Figure 1), 15 years after the January-February 2003 fires. Six of the sites were the same as those used to assess recovery of vegetation one-year post-fire

122 (Bear and Pickering 2006), with four more sites added to increase the number of replicates and the size
123 of the plots increased to deal with the high variability in this community. Suitable locations for the
124 four new sites were identified using fire severity mapping (Leaver and Good 2004; NPWS 2018) and
125 photo evidence combined with on-ground assessment. However, it was difficult to find continuous,
126 adjacent unburnt and burnt areas of subalpine grasslands because so much of the subalpine zone had
127 burnt during the 2003 fires (~70%) (Worboys 2003).

128 At each site, two 30 x 20 m plots were randomly located, with the burnt plot in areas affected by
129 the 2003 fires and the unburnt plot in adjacent unburnt grasslands, with plots no more than 250 m
130 apart. The sites were away from roads and walking tracks, and the plots were located where there was
131 no evidence of damage by feral animals to limit the effects of other types of disturbance. Repeat
132 sampling from 2003 was not possible as the plots in 2003 were not permanently marked, and a larger
133 plot size with different dimensions was used in 2017 to minimise edge effects and deal with the high
134 variability within the community.

135 *Assessment of vegetation*

136 In each plot average vegetation height, above ground biomass, vegetation cover, composition and
137 diversity were measured. Vegetation height per plot was the average of the maximum height of
138 vegetation at 40 randomly located points in each plot. If no vegetation was present at a sampling point
139 (i.e. vegetation height was zero), the value was excluded from the average. Above ground biomass
140 consisted of the dry weight of all graminoids and forbs in four randomly located 10 x 10 cm sub-
141 quadrats in each plot, with values converted to kg m⁻². Shrubs were not harvested due to the difficulty
142 of sampling these growth forms within the relatively small quadrats, and to minimise damage to the
143 sites.

144 Vegetation cover and composition were assessed using 200 randomly located points per plot, with
145 a 2 mm diameter rod lowered vertically at each point and all species touching the rod recorded. Species
146 nomenclature, growth form and status as native or invasive were based on Costin *et al.* (2000) and

147 Harden (1992). If no vegetation was present at the point, then it was recorded as bare ground,
148 rock/scree or litter. The point data were used to calculate overlapping cover for species (number of hits
149 for species / 200 points * 100). Total vegetation cover was calculated as 100 minus the values for bare
150 ground, rock/scree and litter. The overlapping cover of growth form/status (graminoids, forbs, shrubs
151 and invasive plants) was calculated as the sum of all the species with that growth form/status. A
152 thorough search of each plot was made after the point sampling, and any additional species found that
153 were not recorded at any point were noted as present in the plot and allocated a nominal low cover of
154 0.002%.

155 *Statistical Analysis*

156 To determine if unburnt and burnt plots differed, paired *t*-tests were performed in SPSS (version
157 23) (IBM 2016), with assumptions of homogeneity of variance and normality checked prior to analysis.
158 Dependent variables of this study were: (1) vegetation height, (2) biomass, (3) total cover of vegetation,
159 (4) overlapping cover of graminoids, forbs, shrubs and invasive plants, (5) overlapping cover of each
160 of the 12 most common species, (6) species richness, (7) heterogeneity (Shannon-Weiner Index) and
161 (8) evenness (Simpsons Index). Measures of diversity (i.e. Shannon-Weiner and Simpsons Index) were
162 calculated using the DIVERSE feature in the statistical package Primer (version 6) (Clarke and Gorley
163 2006). To satisfy assumptions of normality, vegetation height and biomass values were $\log(x + 1)$
164 transformed while cover values were arcsine square-root transformed.

165 To assess differences in growth form and species composition between plots, Bray-Curtis
166 dissimilarity matrixes were calculated in the statistical package Primer (version 6) (Clarke and Gorley
167 2006). Non-metric multidimensional scaling (NMDS) ordinations were then generated from the Bray-
168 Curtis dissimilarity matrices. This type of analysis is a commonly used technique for comparing
169 ecological compositional data. The resulting ordinations provide a visual representation of variances
170 in composition between the unburnt and burnt plots (McCune and Grace 2002). The SIMPER function
171 was applied to the matrices to identify species driving variances between the unburnt and burnt plots,

172 with the most influential species represented using a Pearson correlation co-efficient. One-way
173 Analysis of Similarity with replicates (ANOSIM) was conducted on dissimilarity matrixes using 999
174 random permutations in Primer (version 6) (Clarke and Gorley 2006). The ANOSIM test statistic (Rho)
175 is a measure of variation between unburnt and burnt plots compared to variation among unburnt plots
176 and among burnt plots using ranked differences among replicates (Clarke 1993) and is scaled between
177 ± 1 , with values closer to + 1 indicating greater differences among samples (Chapman and Underwood
178 1999).

179

180 **Results**

181 There were few differences between the unburnt and burnt plots in structure and cover. Vegetation
182 was, on average, 3.6 cm shorter in unburnt plots than in burnt plots (19.0 vs 22.6 cm, $P < 0.001$). There
183 was no difference found for average biomass of vegetation (1.21 vs 1.03 kg m⁻²) including graminoid
184 biomass (1.12 vs 1.0 kg m⁻²) in unburnt plots compared to burnt plots. Forb biomass was low in both
185 unburnt and burnt plots with some plots with no measurable forb biomass (0.05 kg m⁻² in unburnt vs
186 0.04 kg m⁻²). Although the cover of vegetation (97%), forbs (11 vs 10%) and invasive plants (10 vs
187 8%) were similar in unburnt and burnt plots, there was significantly less shrub cover in unburnt plots
188 (11 vs 18%, $P = 0.033$) and a trend for more graminoid cover (73 vs 67% cover) (Table 1). There was
189 limited bare ground, rock/scree and litter in any of the 20 plots, and no significant difference between
190 unburnt and burnt plots.

191 There was some variation among plots in the relative proportions of graminoids, forbs and shrubs
192 reflecting the high level of variability in this plant community, but no clear separation between unburnt
193 and burnt plots (Figure 2a). This was confirmed by a One-way ANOSIM ($R = 0.029$, $P = 0.269$), with
194 an average similarity in growth form composition between unburnt and burnt plots of 86.6%.

195 There was high diversity within plots (38 species) with a total of 124 species/taxa recorded across
196 the 20 plots, with the native snow grass *Poa fawcettiae* (52%) and the invasive grass *Anthoxanthum*

197 *odoratum* (Sweet Vernal Grass, 7%) with the highest cover (Table 1). There were no significant
198 differences in the cover of any of the most common taxa, although a trend for higher cover of
199 *Anthoxanthum odoratum* in unburnt plots (8.7 vs 5.4%).

200 Although there was variation in composition among all the plots, there was no clear separation
201 between unburnt and burnt plots in the ordination of overall species composition (One-way ANOSIM
202 ($R = 0.086$, $P = 0.987$) (Figure 2b). Reflecting the high diversity and variability of this community,
203 average species composition similarity between unburnt and burnt plots was only 57.6%, with the
204 separation of plots due to differences in the cover of species such as the shrub *Epacris glacialis* in one
205 burnt plot (bottom of ordination), the Rope Rush *Empodisma minus* (mainly three unburnt plots,
206 bottom right of ordination) and Sweet Vernal Grass *Anthoxanthum odoratum** (two burnt and two
207 unburnt plots to left of ordination) (Figure 2b).

208

209 Discussion

210 Subalpine grasslands appear to have nearly completely recovered from the 2003 fires, with few
211 differences in vegetation, mainly consisting of an increase in shrub cover and vegetation height in
212 burnt plots compared to unburnt plots. These results differ to those six weeks post-fire when there was
213 nearly no vegetation in similar areas of subalpine grasslands (Growcock *et al.* 2004; Scherrer *et al.*
214 2004). Even a year post-fire there were still many differences between unburnt and burnt subalpine
215 grasslands including in vegetation height, biomass, the cover of graminoids and forbs (Bear and
216 Pickering 2006, Table 2). The structure of the vegetation has changed since the fire, with vegetation
217 in burnt plots shorter one-year post-fire (5.6 cm, Bear and Pickering 2006), but 15 years post-fire it is
218 taller than unburnt grassland (3.6 cm, Table 1). Biomass in burnt plots was 9% of that in unburnt plots
219 one-year post-fire (Bear and Pickering 2006), but is now 85% of unburnt plots (Table 1). The recovery
220 of biomass is particularly important as previous research found that more than 1.0 kg m^{-2} of dry
221 graminoid and/or herbaceous biomass is required to reduce runoff and stabilise soils in subalpine

222 grasslands (Costin 1959; Leigh *et al* 1987). Several studies have found that biomass can take several
223 years to recover to levels that protected soils, let alone return to pre-fire levels. For example, the
224 recovery of biomass in subalpine grasslands in Victoria was still incomplete two and a half years post
225 the 2003 fires, with biomass still too low to provide sufficient soil protection (Wahren *et al.* 2001).
226 Research assessing previous fires demonstrated that biomass in lower altitude subalpine grasslands
227 (~1400 m a.s.l) recovered from fire after just four years (Leigh *et al.* 1987), but at higher elevations
228 subalpine grasslands took 12 years to recover to levels equivalent to unburnt areas (Costin 1959).

229 There is near complete vegetation cover in burnt plots (97.1%) 15 years post-fire, in contrast to just
230 after the fire, when it was between 1.5% and 10% cover (Growcock *et al.* 2004; Scherrer *et al.* 2004),
231 and 56% one-year post-fire (Bear and Pickering 2006). Again, this highlights how vegetation was
232 unlikely to have protected soils from erosion, with values above 60% vegetation cover required to
233 effectively safeguard soils from erosion (Bryant 1973; Wahren *et al.* 2001; Growcock *et al.* 2004).
234 Vegetation cover in unburnt subalpine grasslands also appears to have increased post-drought (97.4 vs
235 86.6%, see: Bear and Pickering 2006).

236 An important remaining difference is the higher shrub cover in burnt subalpine grasslands. Six
237 weeks post-fire there were very few, if any, shrubs that survived the fire (Scherrer *et al.* 2004), and
238 only limited shrub cover (6.1%) one-year post-fire (Bear and Pickering 2006). The shrubs in the 20
239 plots of subalpine grasslands were a mixture of species that re-establish via seed following fire
240 (obligate seeders), resprouters or both (see: McDougall and Walsh 2004). Increased shrub cover
241 following fire can result from heat scarification of seeds and increased germination and seedling
242 establishment (Camac *et al.* 2017), compounded by reduced competition from existing species
243 including graminoids (Williams and Ashton 1987; Kirkpatrick *et al.* 2002). There can also be faster
244 growth rates of shrubs in a warming climate (Camac *et al.* 2017), with shrub cover in unburnt subalpine
245 grasslands doubling from the 2004 assessment (11 vs 6%) (see: Bear and Pickering).

Graminoids can resprout following fire including the dominant *Poa* species in subalpine grasslands, resulting in rapid recovery with 10% graminoid cover six weeks post-fire (Scherrer *et al.* 2004) and 53% one-year post-fire (Bear and Pickering 2006). In some cases, this can result in equivalent cover as unburnt grasslands within as little as two and a half years post-fire (Leigh *et al.* 1987). Graminoid cover in unburnt subalpine grasslands also appears to have increased since the 2004 assessment (73 vs 61%, see: Bear and Pickering 2006).

Although some minor forbs benefited from reduced competition post-fire (Scherrer *et al.* 2004; Bear and Pickering 2006), in the longer term they tend to decline as graminoids and shrubs establish, with no difference in forbs in subalpine grasslands 15 years post-fire. This pattern of short term increases in forb cover and diversity occurs in response to a range of types of disturbance including fire, cattle grazing and insect herbivory that can reduce the near complete cover of the dominant snow grasses, but is not sustained (Bryant 1973; Wimbush and Costin 1979a,b; Leigh *et al.* 1987; Scherrer *et al.* 2004). In unburnt subalpine grasslands forb cover has been reduced by more than half since the 2004 assessment (22 vs 10%, see Bear and Pickering 2006) and there has been a corresponding increase in graminoid and shrub cover.

Overall, no difference was found for both growth form, species composition and species richness between unburnt and burnt subalpine grasslands 15 years post-fire. However, one-year post-fire there was a clear difference in species composition but not in growth forms or species richness (Bear and Pickering 2006). Reductions in the cover of dominant species such as *Poa* species in the Australian Alps, often result in increases in species with more ruderal functional traits compared to competitive traits (Pickering and Venn 2013). In some cases, this can result in short term increases in species richness, or, as appears to have occurred here, no change in total richness, just changes in composition. In other cases, fires have resulted in long-term shifts in growth form and species composition of subalpine grasslands following fires as has occurred in Tasmania (Kirkpatrick and Dickinson 1984;

270 Kirkpatrick *et al.* 2002; Kirkpatrick & Bridle 2013) and may occur in the Australian Alps with repeated
271 fires (McDougall *et al.* 2015).

272 The 2003 fires were an extraordinary disturbance event that exposed soils in large areas of the
273 subalpine zone and there were concerns at the time that invasive plants may colonise these areas
274 (Johnston and Johnston 2003, 2004; Leaver and Good 2004) with the increase in soil nutrients and
275 reduced competition from native species post-fire (Leigh *et al.* 1987; Mallen-Cooper 1990; Scherrer
276 *et al.* 2004). But 15 years post-fire, invasive plant cover was similar between unburnt and burnt
277 subalpine grasslands (6.7 vs 10.3%) with *Anthoxanthum odoratum** (Sweet Vernal Grass) as the main
278 invasive species. Six weeks post-fire there was an increase in invasive plant cover in burnt subalpine
279 grasslands (Scherrer *et al.* 2004) with the cover of invasive plants comparable to that following other
280 types of disturbance events (i.e. cattle grazing) (Costin 1959; Bryant 1973). Yet, one-year post-fire
281 there was no difference in invasive plant cover between unburnt and burnt subalpine grasslands (Bear
282 and Pickering 2006). It should be kept in mind that the plots one-year post-fire and here 15 years post-
283 fire were specifically selected to avoid other types of disturbance including hiking trails, roadsides,
284 infrastructure and feral animal activity. Although ten invasive plant species were recorded, all had low
285 cover indicating that fire has not affected invasive plant distribution and abundance in subalpine
286 grasslands, but these results must be interpreted cautiously due to low number of replicates.

287 Some limitations with the sampling methods used need to be considered in interpreting the results.
288 As pre-fire data for the burnt plots were not available, this study compared unburnt and burnt areas to
289 gauge recovery. However, due to the mosaic of subalpine grasslands that burnt in the 2003 fires, it is
290 possible that the unburnt plots did not burn because of some characteristics of their vegetation, and
291 hence are not representative of the vegetation in the burnt plots pre-fire. Some species within subalpine
292 grasslands have been found to be fire retardant (Williams and Costin 1994), and therefore species
293 composition might have influenced how the fire spread. However, these factors may not have
294 influenced the results as there were several sources of ignition in the 2003 fires, with embers spread

295 by strong winds from the alpine ridgelines of the Main Range and fires were started by these embers
296 burning down-wind in the subalpine zone (Worboys 2003). Furthermore, low overnight temperatures,
297 weakening winds and dew in late January 2003 were thought to be the main factors extinguishing the
298 fires in the subalpine zone (Worboys 2003; Bear and Pickering 2006). Thus, these climatic factors may
299 account for clear fire boundary within homogeneous vegetation, rather than compositional differences
300 between tracts of unburnt and burnt subalpine grassland. Also, the current study used randomly located
301 points, increased plot size and included more replicates and compared results with unburnt plots
302 addressing some of the limitations associated with previous studies post-fire in subalpine grasslands
303 (Growcock *et al.* 2004; Scherrer *et al.* 2004; Bear and Pickering 2006; McDougall *et al.* 2015). The
304 increased number of replicates and plot size (120 m⁻² to 300 m⁻²) also decreased variability in the
305 estimates of vegetation cover with lower variance and standard error estimates for unburnt plots of
306 subalpine grasslands in this study compared to the 2004 assessment (Bear and Pickering 2006).

307 The results of the current study indicate that subalpine grasslands can recover from landscape-level
308 fires in less than 15 years. Other studies have found variation in the recovery rate, with some subalpine
309 grasslands recovering in as little as two to four years (Leigh *et al.* 1987), or by 10 years (McDougall *et*
310 *al.* 2015), while others found that recover may take longer depending on post-fire climate and the other
311 disturbance events during the recovery period (Costin 1959; Bridle *et al.* 2001; Wahren *et al.* 2001;
312 Kirkpatrick *et al.* 2002).

313 With fires predicted to become more frequent and increase in severity in the Australian Alps as the
314 climate continues to warm and become drier (Hennessy *et al.* 2008; Gallagher *et al.* 2009; Mooney *et*
315 *al.* 2011; Green and Osborne 2012; Zylstra 2018), longer periods (15 years plus) fire free may become
316 rarer. Already there has been repeated fire disturbance since the 2003 fire in some parts of the subalpine
317 zone of Victoria and New South Wales (Williams *et al.* 2008; Pickering and Venn 2013; McDougall
318 *et al.* 2015). Several studies highlight the effect of disturbance during the recovery of subalpine
319 grasslands from fire (Costin 1959; Leigh *et al.* 1987; Whelan *et al.* 2002), including how it can reduce

the capacity for the community to recover. Therefore, more research assessing the impact of multiple fires and of other types of disturbance, such as damage from feral animals including horses, pigs and deer in subalpine grasslands, is particularly important. It is also important to assess the flammability of post-fire vegetation and how feedback mechanisms may result in the replacement of vegetation communities over time because of fire as has been hypothesised for the Australian Alps (McDougall *et al.* 2015; Zylstra 2016; Camac *et al.* 2017; Zylstra 2018).

Conclusions

In summary, subalpine grasslands have largely recovered from the 2003 fires with vegetation cover, growth form cover and composition, species cover and composition, biomass and diversity in burnt subalpine grasslands similar to adjacent unburnt areas 15 years post-fire, although there was higher cover of shrubs and taller vegetation. However, with warmer and drier conditions the severity, scale and frequency of fires is likely to increase. Therefore, although this study contributes to knowledge regarding how subalpine grasslands recover from single largescale fires, the interactions of climatic warming and increased fire frequency pose serious threats to the conservation of many plant communities in the Australian Alps.

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Figure 1: Location of 10 sites where paired plots of unburnt (white triangles) and burnt (black triangles) subalpine grasslands were sampled in Kosciuszko National Park in December 2017.

(2a)

(2b)

559 **Figure 2:** Results of ordinations of (a) percent overlapping cover of growth forms (graminoid, forb,
560 shrub, stress = 0.04, $r = 0.029$, $P = 0.269$) and (b) percent overlapping cover of individual species
561 (stress = 0.1, $r = 0.086$, $P = 0.987$) in unburnt (white circles) and burnt (black circles) paired plots at
562 10 subalpine grassland sites in Kosciuszko National Park in December 2017. Left shows Pearson
563 correlations for the growth forms/species showing the strongest influences on the separation of plots
564 with strength of influence in brackets.

Appendix A. Mean $\pm$ standard errors of overlapping cover measured in unburnt and burnt paired plots at 10 subalpine grasslands sites in Kosciuszko National Park in December 2017. * denotes invasive plant taxa.

Taxa	Family	Common name	Growth form	% Overlapping cover	
				Unburnt	Burnt
<i>Acaena novae-zelandiae</i>	Rosaceae	Bidgee Widgee	Forb	0.03 $\pm$ 0.03	0.04 $\pm$ 0.04
<i>Acaena ovina</i>	Rosaceae	Downy Sheep Burr	Forb	0.12 $\pm$ 0.07	0.03 $\pm$ 0.03
<i>Acetosella vulgaris</i> *	Polygonaceae	Sheep Sorrel	Forb	0.60 $\pm$ 0.31	1.02 $\pm$ 0.34
<i>Achillea millefolium</i> *	Asteraceae	Common Yarrow	Forb	0.03 $\pm$ 0.03	0.03 $\pm$ 0.03
<i>Aciphylla simplicifolia</i>	Apiaceae	Mountain Aciphyll	Forb	1.12 $\pm$ 0.47	1.33 $\pm$ 0.98
<i>Acrothamnus montanus</i>	Ericaceae	Snow Beard-Heath	Shrub		0.03 $\pm$ 0.03
<i>Agrostis muelleriana</i>	Poaceae	Mueller's Bent	Graminoid		0.08 $\pm$ 0.06
<i>Ajuga australis</i>	Lamiaceae	Austral Bugle	Forb		
<i>Anthoxanthum odoratum</i> *	Poaceae	Sweet Vernal Grass	Graminoid	8.68 $\pm$ 4.11	5.37 $\pm$ 3.05
<i>Argyrotegium fordianum</i>	Asteraceae	Ford's Cudweed	Forb	0.06 $\pm$ 0.06	
<i>Arthropodium milleflorum</i>	Asaparagaceae	Pale Vanilla-Lilly	Forb		0.06 $\pm$ 0.04
<i>Asperula gunnii</i>	Rubiaceae	Mountain Woodruff	Forb	2.28 $\pm$ 1.22	1.96 $\pm$ 0.99
<i>Astelia alpina</i> var. <i>novae-hollandiae</i>	Asteliaceae	Silver Astelia	Forb	0.06 $\pm$ 0.06	
<i>Astelia psychrocharis</i>	Asteliaceae	Kosciuszko Pineapple Grass	Forb		
<i>Australopyrum velutinum</i>	Poaceae	Velvet Wheatgrass	Graminoid	0.30 $\pm$ 0.30	
<i>Baloskion australis</i>	Restionaceae	Mountain Cordrush	Forb	0.05 $\pm$ 0.05	0.58 $\pm$ 0.58
<i>Bossiaea foliosa</i>	Fabaceae	Leafy Bossiaea	Shrub		0.44 $\pm$ 0.31
<i>Brachyscome scapigera</i>	Asteraceae	Tufted Daisy	Forb		0.09 $\pm$ 0.09
<i>Brachyscome</i> sp. aff. <i>tadgelli</i>	Asteraceae	Creeping Daisy	Forb		
<i>Brachyscome spathulata</i>	Asteraceae	Spoon Daisy	Forb	0.03 $\pm$ 0.03	0.05 $\pm$ 0.04
<i>Caladenia alpina</i>	Orchidaceae	Alpine Caladenia	Forb		
<i>Cardamine lilacina</i>	Brassicaceae	Native Bitter-cress	Forb	0.03 $\pm$ 0.03	
<i>Carex apressa</i>	Cyperaceae	Tall Sedge	Graminoid		0.16 $\pm$ 0.16
<i>Carex breviculmis</i>	Cyperaceae	Short-stem Sedge	Graminoid	1.06 $\pm$ 0.30	1.40 $\pm$ 0.42
<i>Carex gaudichaudiana</i>	Cyperaceae	Tufted Sedge	Graminoid	0.61 $\pm$ 0.38	0.48 $\pm$ 0.35
<i>Carex hebes</i>	Cyperaceae	Dryland Sedge	Graminoid	0.03 $\pm$ 0.03	
<i>Celmisia costiniana</i>	Asteraceae	Silver Snow Daisy	Forb		0.03 $\pm$ 0.03
<i>Celmisia pugioniformis</i>	Asteraceae	Slender Snow Daisy	Forb	0.53 $\pm$ 0.32	0.12 $\pm$ 0.12
<i>Cerastium diffusum</i> *	Caryophyllaceae	Fourstamen Chickweed	Forb		
<i>Cerastium vulgare</i> *	Caryophyllaceae	Mouse-ear Chickweed	Forb		
<i>Chiloglottis cornuta</i>	Orchidaceae	Green Bird Orchid	Forb		

Taxa	Family	Common name	Growth form	% Overlapping cover	
				Unburnt	Burnt
<i>Chionogentias muelleriana</i>	Gentianaceae	Mountain Gentian	Forb	0.13 ± 0.05	0.10 ± 0.05
<i>Cirsium vulgare</i> *	Asteraceae	Spear Thistle	Forb		0.04 ± 0.04
<i>Coronidium scorpioides</i>	Asteraceae	Button Everlasting	Forb	0.27 ± 0.27	0.28 ± 0.18
<i>Cotula alpina</i>	Asteraceae	Alpine Cotula	Forb		
<i>Craspedia costiniana</i>	Asteraceae	Hairy Billy-button	Forb		0.03 ± 0.03
<i>Craspedia lamicola</i>	Asteraceae	Bog Billy-button	Forb	0.42 ± 0.19	0.56 ± 0.23
<i>Derwentia nivea</i>	Plantaginaceae	Snow Speedwell	Shrub		
<i>Derwentia derwentiana</i>	Plantaginaceae	Derwent Speedwell	Shrub		0.07 ± 0.07
<i>Deyeuxia crassiuscula</i>	Poaceae	Coarse Bent Grass	Graminoid		0.04 ± 0.04
<i>Empodisma minus</i>	Restionaceae	Spreading Rope-rush	Graminoid	7.84 ± 3.12	5.67 ± 2.18
<i>Epacris glacialis</i>	Ericaceae	Bog Heath	Shrub	0.99 ± 0.77	1.82 ± 1.22
<i>Epacris paludosa</i>	Ericaceae	Swamp Heath	Shrub		0.56 ± 0.56
<i>Epacris petrophila</i>	Ericaceae	Snow Heath	Shrub	0.10 ± 0.10	0.13 ± 0.13
<i>Epilobium sarmentaceum</i>	Ongraceae	Mountain Willow-herb	Forb		
<i>Erigeron bellidioides</i>	Asteraceae	Violet Fleabane	Forb	0.04 ± 0.04	
<i>Erigeron nitidus</i>	Asteraceae	Sticky Fleabane	Forb	0.50 ± 0.50	
<i>Erigeron paludicola</i>	Asteraceae	Bog Fleabane	Forb	0.03 ± 0.03	
<i>Eucalyptus niphophila</i>	Myrtaceae	Snow Gum	Shrub	1.52 ± 0.73	1.58 ± 0.67
<i>Euphrasia collina</i> subsp. <i>diversicolor</i>	Scrophulariaceae	Variable Eyebright	Forb	0.10 ± 0.10	0.03 ± 0.03
<i>Festuca rubra</i> *	Poaceae	Red Fescue	Graminoid		
<i>Geranium antrorsum</i>	Geraniaceae	Rosetted Cranebill	Forb	0.06 ± 0.06	
<i>Geranium potentilloides</i>	Geraniaceae	Cinequefoil Geranium	Forb	0.05 ± 0.05	
<i>Gingidia harveyana</i>	Apiaceae	Slender Gingidia	Forb		0.02 ± 0.02
<i>Gonocarpus micranthus</i>	Haloragaceae	Creeping Raspwort	Forb		
<i>Grevillea australis</i>	Proteaceae	Alpine Grevillea	Shrub	2.44 ± 1.10	5.12 ± 1.53
<i>Herpolirion novae-zelandiae</i>	Anthericaceae	Sky Lily	Forb		0.04 ± 0.04
<i>Hovea montana</i>	Fabaceae	Alpine Hovea	Shrub	1.96 ± 1.05	3.06 ± 1.52
<i>Hydrocotyle algida</i>	Araliaceae	Mountain Pennywort	Forb		
<i>Hypochaeris radicata</i> *	Asteraceae	Catsear, Flatweed	Forb	0.38 ± 0.25	0.17 ± 0.13
<i>Isolepis montivega</i>	Cyperaceae	Mountain Club-rush	Graminoid		
<i>Kunzea muelleri</i>	Myrtaceae	Yellow Kunzea	Shrub	0.38 ± 0.33	0.03 ± 0.03
<i>Leptorhynchus squamatus</i> s.l.	Asteraceae	Scaly Buttons	Forb	0.24 ± 0.14	0.78 ± 0.57
<i>Linum marginale</i>	Linaceae	Wild Flax	Forb		
<i>Luzula altrata</i>	Juncaceae	Slender Woodrush	Graminoid		
<i>Luzula flaccida</i>	Juncaceae	Pale Woodrush	Graminoid		0.18 ± 0.13

Taxa	Family	Common name	Growth form	% Overlapping cover	
				Unburnt	Burnt
<i>Luzula modesta</i>	Juncaceae	Bog Woodrush	Graminoid	0.45 ± 0.26	0.39 ± 0.22
<i>Luzula novae-cambriae</i>	Juncaceae	Rock Woodrush	Graminoid		0.04 ± 0.04
<i>Lycopodium fastigiatum</i>	Lycopodiaceae	Mountain Clubmoss	Bryophyte	0.30 ± 0.17	0.03 ± 0.03
<i>Melicytus</i> sp. aff. <i>dentatus</i>	Violaceae	Woody Violet	Shrub	0.14 ± 0.14	0.30 ± 0.18
<i>Microseris lanceolata</i>	Asteraceae	Yam Daisy	Forb	0.06 ± 0.04	0.09 ± 0.09
<i>Myosotis australis</i>	Boraginaceae	Austral Forget-me-not	Forb		0.02 ± 0.02
<i>Myosotis discolor</i>	Boraginaceae	Changing Forget-me-not	Forb		
<i>Nematolepis ovatifolia</i>	Rutaceae	Ovate Nematolepis	Shrub	1.58 ± 1.06	0.23 ± 0.19
<i>Olearia algida</i>	Asteraceae	Alpine Daisy Bush	Shrub	0.80 ± 0.38	1.25 ± 0.57
<i>Olearia phlogopappa</i> subsp. <i>flavescens</i>	Asteraceae	Dusty Daisy-bush	Shrub	0.19 ± 0.11	0.74 ± 0.36
<i>Oreomyrrhis brevipes</i>	Apiaceae	Rock Carraway	Forb	0.93 ± 0.93	
<i>Oreomyrrhis ciliata</i>	Apiaceae	Bog Carraway	Forb	0.10 ± 0.10	0.10 ± 0.10
<i>Oreomyrrhis eriopoda</i>	Apiaceae	Australian Carraway	Forb	0.46 ± 0.27	0.75 ± 0.44
<i>Oschatzia cuneifolia</i>	Apiaceae	Wedge Oschatzia	Forb		
<i>Oxylobium ellipticum</i>	Fabaceae	Common Shaggy-pea	Shrub	1.04 ± 0.46	1.01 ± 0.41
<i>Ozothamnus alpinus</i>	Asteraceae	Alpine Everlasting	Shrub		0.38 ± 0.30
<i>Ozothamnus hookeri</i>	Asteraceae	Kerosine Bush	Shrub	0.05 ± 0.05	0.24 ± 0.20
<i>Ozothamnus rosmarinifolius</i>	Asteraceae	Silver Jubilee	Shrub	0.48 ± 0.33	0.87 ± 0.46
<i>Ozothamus secundiflorus</i>	Asteraceae	Cascade Everlasting	Shrub	0.05 ± 0.05	
<i>Pentachondra pumila</i>	Ericaceae	Carpet Heath	Shrub	0.03 ± 0.03	
<i>Pimelea alpina</i>	Thymelaeaceae	Alpine Rice-flower	Shrub	0.57 ± 0.35	1.28 ± 0.48
<i>Pimelea axiflora</i> subsp. <i>alpina</i>	Thymelaeaceae	Alpine Bootlace Bush	Shrub	0.05 ± 0.05	0.06 ± 0.06
<i>Pimelea biflora</i>	Thymelaeaceae	Matted Rice-flower	Shrub		0.07 ± 0.05
<i>Plantago euryphylla</i>	Plantaginaceae	Broad Plantain	Forb	0.03 ± 0.03	0.11 ± 0.08
<i>Plantago muelleri</i>	Plantaginaceae	Star Plantain	Forb		
<i>Poa fawcettiae</i>	Poaceae	Smooth Blue Snowgrass	Graminoid	52.60 ± 4.37	50.85 ± 3.68
<i>Poa saxicola</i>	Poaceae	Rock Poa	Graminoid	0.22 ± 0.22	
<i>Poa</i> sp. 1	Poaceae	Snow Grass	Graminoid		1.84 ± 1.37
<i>Podolepis robusta</i>	Asteraceae	Mountain Lettuce	Forb		0.06 ± 0.04
<i>Polystichum proliferum</i>	Dryopteridaceae	Mother Shield Fern	Pteridophyte		
<i>Polytrichum juniperinum</i>	Polytrichaceae	Juniper Haircap	Bryophyte		
<i>Poranthera microphylla</i>	Phyllanthaceae	Small Poranthera	Forb	0.08 ± 0.08	0.19 ± 0.19
<i>Prasophyllum alpestre</i>	Orchidaceae	Highland Leek-orchid	Forb	0.03 ± 0.03	
<i>Pratia</i> sp. A	Lobeliaceae	Mud Pratia	Forb	0.62 ± 0.62	
<i>Prostanthera cuneata</i>	Lamiaceae	Alpine Mint-bush	Shrub		0.04 ± 0.04

Taxa	Family	Common name	Growth form	% Overlapping cover	
				Unburnt	Burnt
<i>Ranunculus anemoneus</i>	Ranunculaceae	Anemone Buttercup	Forb		
<i>Ranunculus graniticola</i>	Ranunculaceae	Granite Buttercup	Forb	0.10 ± 0.05	0.15 ± 0.09
<i>Ranunculus gunnianus</i>	Ranunculaceae	Gun's Apple Buttercup	Forb	0.11 ± 0.11	0.12 ± 0.08
<i>Richea continentis</i>	Ericaceae	Candle Heath	Shrub	0.50 ± 0.34	0.08 ± 0.08
<i>Rytidosperma nudiflorum</i>	Poaceae	Alpine Wallaby Grass	Graminoid	0.69 ± 0.66	0.08 ± 0.08
<i>Schizeilema fragoseum</i>	Apiaceae	Alpine Pennywort	Forb		0.03 ± 0.03
<i>Schoenus calyptratus</i>	Cyperaceae	Alpine Bog-sedge	Graminoid		0.12 ± 0.09
<i>Scleranthus singuliflorus</i>	Caryophyllaceae	Mossy Knawel	Forb	0.26 ± 0.10	0.12 ± 0.09
<i>Senecio gunnii</i>	Asteraceae	Gunn's Groundsel	Forb		0.11 ± 0.05
<i>Senecio pinnatifolius</i> subsp. <i>pleiocephalus</i>	Asteraceae	Highland Groundsel	Forb		
<i>Sphagnum cristatum</i>	Sphagnaceae	Sphagnum	Bryophyte	0.26 ± 0.14	0.53 ± 0.35
<i>Stackhousia pulvinaris</i>	Stackhousiaceae	Alpine Candles	Forb		
<i>Stellaria pungens</i>	Caryophyllaceae	Prickly Starwort	Forb	0.08 ± 0.05	0.04 ± 0.04
<i>Stylidium graminifolium</i>	Stylidiaceae	Alpine Trigger-plant	Forb		0.09 ± 0.07
<i>Taraxacum officinale</i> *	Asteraceae	Dandelion	Forb	0.03 ± 0.03	
<i>Tasmannia xerophila</i>	Winteraceae	Alpine Pepperbush	Shrub	0.03 ± 0.03	
<i>Trifolium repens</i> *	Fabaceae	White Clover	Forb	0.28 ± 0.21	0.03 ± 0.03
<i>Trisetum spicatum</i>	Poaceae	Bristle Grass	Graminoid	0.79 ± 0.34	0.63 ± 0.24
<i>Viola betonicifolia</i>	Violaceae	Native Violet	Forb	0.02 ± 0.02	0.16 ± 0.09
<i>Viola fuscoviolacea</i>	Violaceae	Dusky Violet	Forb		
<i>Viola hederacea</i>	Violaceae	Ivy-Leaved Violet	Forb		
<i>Wahlenbergia ceracea</i>	Campanulaceae	Waxy Bluebell	Forb		
<i>Xerochrysum bracteatum</i>	Asteraceae	Golden Everlasting	Forb	0.05 ± 0.05	0.21 ± 0.14
Total Cover				97.4 ± 6.8	97.1 ± 0.7
Absolute taxa richness		124		104	108