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Frequent wildfires erode tree persistence and alter stand structure and initial composition of a fire-tolerant sub-alpine forest

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Abstract

Question

Frequent severe wildfires have the potential to alter the structure and composition of forests in temperate biomes. While temperate forests dominated by resprouting trees are thought to be largely invulnerable to more frequent wildfires, empirical data to support this assumption is lacking. Does frequent fire erode tree persistence by increasing mortality and reducing regeneration, and what are the broader impacts on forest structure and understorey composition?

Location

Sub-alpine open *Eucalyptus pauciflora* ('snow gum') forests, Australian Alps, Victoria, Australia.

Methods

We examined tree persistence and understorey composition of *E. pauciflora* open forests that were unburned, burned once, twice or three times by high-severity wildfires between 2003 and 2013. At each of 20 sites (5 per fire frequency class) we assessed extent of top-kill and mortality of eucalypt clumps, spatial configuration of surviving and dead clumps, densities of new and lignotuberous eucalypt seedlings, and shrub and grass cover.

Results

At least two years after the last wildfire, proportions of top-killed *E. pauciflora* stems were significantly greater, and densities of live basal resprouts significantly lower, at sites burned two or three times compared to once burned or unburned sites. Clump death increased to 50% of individuals at sites burned by three short-interval wildfires, which led to changes in live tree patchiness as indicated by nearest-neighbour indices. Increased tree mortality was not offset by seedling recruitment, which was significantly lower at the twice and thrice-burned sites relative to single-burn sites – although seedling recruitment was also influenced by topography and coarse woody debris. In addition to changes in the tree-layer, the prominence of understorey shrubs was substantially reduced, and the frequency of grasses markedly increased, after two, and particularly three wildfires.

Conclusions

Our study provides strong empirical evidence of ecologically significant change in *E. pauciflora* forests after short-interval severe wildfires, namely, erosion of the persistence niche of resprouting trees, and a shift in understorey dominance from shrubs to grasses. Our findings highlight the need to consider the impacts of compounded perturbation on forests under changing climates, including testing assumptions of long-term persistence of resprouter-dominated communities.

Keywords: alternative stable states; compounded disturbances; cumulative impacts; eucalypt; *Eucalyptus pauciflora*; fire regimes; fire frequency; forest degradation; sub-alpine forest; temperate forest; wildfire

Nomenclature: Costermans (2009) for vascular plants

Running head: Frequent fire erodes resprouter persistence

Introduction

Globally, fire is a key factor influencing ecosystem composition and change (Bowman *et al.*, 2009). Trends in global temperature and assessments of changes in fire weather under recent and projected climate change indicate likely increases in fire activity for many forested regions of the world (Nitschke & Innes, 2008; Liu *et al.*, 2010). Increased fire activity increases the potential for shorter fire intervals, and for increased extent of more frequently burned forest (Nitschke & Innes, 2013). Repeated short-interval fires can be viewed as 'compounded perturbations' (Paine *et al.*, 1998), which can have negative impacts not only on forest structure and composition, but also forest-dependent species (Jones *et al.*, 2016). The prospect of such impacts has inspired analysis of forest and fire management (Adams, 2013; Bowman *et al.*, 2013; Stephens *et al.*, 2013), and intensified concerns for forest health during an 'era of emerging mega-disturbance' (Millar & Stephenson, 2015).

The persistence of forests after disturbances largely depends on plant traits such as resprouting and reseeding (Enright *et al.*, 2014; Pausas & Keeley, 2014); however, changing disturbance regimes can reduce trait effectiveness. For example, in obligate-seeder communities, shortening of the interval between disturbances (such as fire) can lead to extirpation of dominant tree species (Bowman *et al.*, 2014a). The vulnerability of obligate seeders to changing fire conditions has underpinned emerging concepts like 'interval squeeze', where a combination of climate-change factors – more frequent fire, warmer and drier environments – can reduce the likelihood that woody species will persist within their current distributions (Enright *et al.*, 2015).

Resprouting has been recognised as a trait that ensures a plant's 'persistence niche' (Bond & Midgley, 2001) by allowing established individuals to survive and re-establish rapidly after disturbances, particularly fire (Burrows, 2013; Clarke *et al.*, 2013a). The ability of resprouters to withstand disturbances means they have been considered more resistant to transformational structural and compositional changes than fire-sensitive obligate-seeder forests that have long juvenile phases (Bowman *et al.*, 2013; Fairman *et al.*, 2016). Fire-tolerant resprouter forests have therefore been considered likely replacements – naturally, or artificially – for fire-sensitive forests under climate change (Colloff *et al.*, 2016). However, assumptions of persistence of fire-tolerant resprouters under emerging fire regimes have rarely been tested. Recent studies have indicated increased mortality of fire-tolerant resprouting trees under extreme fire conditions (Bennett *et al.*, 2016; Prior *et al.*, 2016a; Nicholson *et al.*, 2017); however, interactive effects of multiple fires, particularly under high-severity conditions, remain largely unquantified (Haslem *et al.*, 2016).

The role of changing fire regimes – particularly abrupt shifts in frequency – in the development and maintenance of alternative stable states (Scheffer & Carpenter, 2003) is increasingly being recognised in many biomes around the world (Warman & Moles, 2009; Hirota *et al.*, 2011; Scheffer *et al.*, 2012). Wildfires have been identified as a key driver of alternative states in woody communities, at times decoupling tree cover from the environmental variables that otherwise determine tree presence (Abis & Brovkin, 2017). Alternative states have been identified in tropical forest and savanna ecosystems (Murphy & Bowman, 2012) where grass-fire feedback cycles drive the elimination of fire-sensitive trees (Bowman *et al.*, 2014b). Similarly, conceptual models indicate the potential for fragmentation of the tree layer in temperate resprouter forests under repeat short-interval fires (Fairman et al 2016), as seen in tropical forests (Silvério *et al.*, 2013); however, contemporary empirical evidence to underpin such models is lacking (Fletcher *et al.*, 2014).

This study examines the effects of short-interval repeat wildfires on the structure and composition of a temperate forest ecosystem dominated by resprouter trees. Our focal ecosystem is open forest in the Australian Alps dominated by *Eucalyptus pauciflora* Sieber ex Spreng (‘snow gum’) – a long-lived tree that vigorously resprouts from a partially buried lignotuber in response to partial or complete top-kill (death of above-ground stems) by fire (Coates, 2015). The understorey of this ecosystem is characterised by a variety of shrubs and grasses with obligate seeder and resprouter fire response traits (Williams & Costin, 1994). As such, like many other open eucalypt forests of temperate southern Australia, the structure of *E. pauciflora* dominated communities has invariably been shaped by the presence and frequency of fire (Barker, 1988). However, the nature of *E. pauciflora* community interactions with fire seem set to change given expectations of more frequent and severe fire weather in south-eastern Australia based on recent observations (Clarke et al., 2013b; Sharples et al., 2016) and future predictions (Clarke *et al*, 2011). Large mixed-severity fires in 2003, 2007, and 2013 burned a cumulative area of ~2.3 x 10^6 hectares in the Australian Alps (Williams *et al.*, 2014), meaning that sections of *E. pauciflora* open forest were burned once, twice, and three times between 2003 and 2013 – notably shorter intervals than the historic norm of once every 50-100 years (Williams *et al.*, 2008). This natural experiment provided an opportunity to examine the impacts of short-interval wildfires on the initial structure and composition of fire-tolerant temperate forests, by examining effects on a) potential erosion of the dominant tree's persistence niche via increased mortality and decreased regeneration (both vegetative and seed-based); b) changes in stand structure; and c) changes in the understorey composition as indicated by the balance of shrubs to grasses. Our overarching objective was to improve the empirical basis for assumptions about the limits to tolerance of fire-tolerant forests, particularly those at or near the tree-line in temperate biomes.

Methods

Study area

Our study encompasses an area of ~250 km^2 in the sub-alpine and alpine regions of Victoria, south-eastern Australia (37°01' 147°08'). The present climate is characterised by low temperatures (mean annual maximum 8.0°C; mean annual minimum 1.9°C), and high precipitation (mean annual total 1421 mm), the majority falling as winter snow (Williams & Costin, 1994), which typically persists from June until October (1990–2016, Bureau of Meteorology, Mt. Hotham, VIC Australia; http://www.bom.gov.au). Soils throughout the Victorian alpine region are variable with climate, parent material, topography, and vegetation type all influencing soil type (Kirkpatrick *et al.*, 2014), although shallow friable brown gradational soils are predominant at higher elevations (Land Conservation Council, 1977).

Sub-alpine forests are dominated by *E. pauciflora* and its subspecies, which occurs between 1400 and 1900 m ASL at the altitudinal tree limit in Australia, covering approximately 300,000 ha of mountainous terrain (Ferrar *et al.*, 1988; Slatyer & Noble, 1992; Costermans, 2009; Green & Venn, 2012). *E. pauciflora* stands are generally classified as open forests, reaching maximum heights of 20-30 m with 30-70% foliage projective cover, although they also often form sparser (10-30% cover) low open woodlands at higher elevations (Specht, 1970; Williams & Costin, 1994; Costermans, 2009). The understorey of *E. pauciflora* forests can be grassy (*Poa hothamensis* Vickery or *P. hiemata* Vickery) with a shrub stratum to 3 – 5 m of species such as *Prostanthera cuneata* Benth., *Bossiaea foliosa* A.

Cunn., *Phebalium squamulosum* Vent. and *Orites lancifolia* F. Muell (Williams & Costin, 1994). The composition of understorey species reflects site attributes & past disturbance history, such as fire and cattle grazing (Williams & Ashton, 1987; Wahren et al., 1994), and are comprised of both obligate seeders (e.g. *Acacia* sp.) and resprouters (e.g. *Bossiaea foliosa*) (Kasel *et al.*, 2017).

Our study sites were *E. pauciflora* open forests within or near the boundaries of single and multiple recent wildfires in two areas of the Victorian Alps: Mount Hotham and Mount Useful (*Figure S1 & S2*). Here, combinations of large, mixed-severity megafires (>100 000 ha) between 2003 and 2013 created mosaics of *E. pauciflora* forests that were either unburned, or burned once (254,775 ha), twice (32,548 ha), or three times (3,622 ha) in that decade (**Figure 1;** *Figure S1*).

Site selection

Site selection was based on spatial data sets that indicated the vegetation was *E. pauciflora* open forest, and that the area had been burned once, twice, or three times by high-severity wildfire between 2003 and 2013. Wildfire severity was as indicated by 1:25000 digital maps that were produced within two months of each wildfire, based on changes in the Normalised Burn Ratio as estimated from pre- and post-fire SPOT images in combination with Landsat and high resolution aerial imagery (DSE 2009, P. Black pers. comm., 2015). 'High severity' sites were burned by an intense overstorey fire that consumed 70 to 100% of both *E. pauciflora* and understorey crowns. After in-field verification of vegetation type and recent wildfire (indicated by tree charring and regeneration as relevant), five sites were selected to represent each fire frequency class ('Unburned', once burned 'Single', twice burned 'Double', and thrice burned 'Triple'), to give a total of 20 study sites. Sites of the same fire history were located at least 2.5 km apart, and sites of differing fire history were located as close as possible (*Figure S2*). Our study sites were selected if a) their fire history was unambiguous; b) they were clearly dominated (prior to fire) by *E. pauciflora*; c) they represented a continuous patch >3 ha of *E. pauciflora* forest; d) did not include or cross the tree line; and e) there was no evidence of other anthropogenic disturbances, such as firewood removal. Triple sites were burned by wildfires in 2003, 2007, and 2013, but the distribution and overlap of these wildfires constrained the choice of wildfire years in the Single and Double fire history classes, meaning that fire history varied slightly (see *Table S1*). Unburned sites were selected for similar vegetation type and structure, even distribution around the burned sites, and no evidence of fire (no stem charring, live overstorey canopy) since 1994 (one site) or 1939 (four sites).

E. pauciflora survival and regeneration assessment

All sites were assessed between February and May 2015, approximately two years after the last wildfire – an adequate interval for recovery and establishment of eucalypts and associated understorey in comparable forest types elsewhere (Prior *et al.*, 2016a). At each site, a fixed area plot (10 x 50 m^2, 0.05 ha) was randomly positioned to be entirely within the *E. pauciflora* patch, at least 50 m from the patch edges, and with the length of the plot running along the contour. All 'large' eucalypt stems >10 cm diameter at breast height overbark (dbhob, 1.3 m height) were assessed within the 0.05 ha plot, whereas 'small' eucalypt stems (2.5 – 10 cm dbhob), and eucalypt regeneration (<2.5 cm basal diameter), which both occurred at higher densities, were assessed within two embedded sub-plots of 10 x 10 m^2 (0.02 ha total area).

The design of our within-plot measurements was informed by our understanding of *E. pauciflora* habit, particularly its post-fire regeneration. *E. pauciflora* is a thin-barked eucalypt species that is typically top-killed after complete canopy combustion or scorch. Individuals typically recover after top-kill through basal resprouting from the lignotuber. This means that *E. pauciflora* often form a 'woody clump' habit (i.e. multiple stems arising from a single lignotuber; Lacey & Johnston 1990). Accordingly, we assessed each stem as either a singular stem, or part of a larger 'clump' of multiple stems arising from a single lignotuber, which was confirmed by physically checking the base of the tree for lignotuber presence. The following attributes of all large and small eucalypt stems were then recorded: dbhob (cm); dead or alive as indicated by the total absence or presence of live foliage at or above height 1.3 m; single or clumped with other stems; number of post-fire basal (lignotuber) resprouts; and number and location of post-fire epicormic resprouts. By assessing the extent of live foliage above and below 1.3m, we were able to assess the extent of a) stem death (top-kill) and b) clump mortality, where all stems and the lignotuber had died (for further information on assessment of resprouting and top-kill/clump mortality, see *Supporting Information*).

Eucalypt regeneration (<2.5cm basal diameter) that was not clearly sprouting from 'large' (>10 cm dbhob) stems was assessed in two ways. Firstly we counted 'lignotuberous seedlings' as comprising of one or a clump of stems (all <2.5 cm basal diameter) arising from a detectable lignotuberous swelling, which also had evidence of charring or the remains of a small burned stem. We grouped these individuals on the basis that it was highly likely they were present prior to the most recent fire. In contrast, individual seedlings without any significant signs of a lignotuberous swelling or charring that were predominantly single stemmed were counted as ‘new seedlings’ and were assumed to have established after the most recent fire.

Fallen wood and understorey composition

Coarse woody debris (CWD), defined as fallen dead woody material >2.5 cm in minimum cross-sectional diameter, was assessed as an integrated indicator of fire effects on woody fuel consumption and tree collapse. Individual CWD pieces were assessed using the line-intercept method (Van Wagner (1968) along two parallel 50-m transects defining the plot boundary (total transect length of 100 m per site) and following the protocols of Aponte *et al.* (2014).

Shrubs and grasses were assessed to evaluate the effects of wildfire frequency on vegetation composition. Shrubs were defined as woody single or multi-stemmed species, excluding *E. pauciflora*, and were counted by genus along two 10-m transects starting at 10 and 30 m along a 50-m line that bisected the plot. In addition, shrub cover was assessed by estimating the proportion of each 1-m portion of the 10-m transects covered by a vertical projection of the shrub crown. This was expressed as a percentage of the total transect length (20 m) by genus. For analysis, frequency and cover data were converted to prominence values (PV) following Douglas & Bliss (1977).

Grasses were defined as any non-woody plant species, predominantly *Poa spp.*, and were assessed as either present (1) or absent (0) for each 1-m portion of the 10-m transect. These values were then summed and divided by 20 to provide an indication of grass frequency per site, expressed as a propotion.

Statistical Analyses

Effects of wildfire frequency (Unburned, Single, Double, Triple) on percentage tree stem death (‘top-kill’), percentage clump mortality, number of live basal clumps (stems < or >10cm dbhob) per hectare, resprouting counts, seedling and lignotuberuous seedling regeneration counts, coarse woody debris piece counts, shrub prominence values, and grass frequencies were evaluated using one-way ANOVA, followed by post-hoc Tukey’s HSD test. Distributions of response variables were assessed for normality, and were square-root transformed where necessary. Where transformation did not improve the distribution, a Kruskal-Wallis test for non-parametric data was used followed by Dunn's Test for pairwise comparisons using a Bonferroni correction. In addition, we used a two-sample Kolmogorov-Smirnov test, to compare size-class distributions of sound and rotten CWD across the different wildfire frequencies.

Random Forest analyses (Breiman, 2001) were used to identify explanatory variables that were most important in explaining plot-level *E. pauciflora* mortality and regeneration. A total of 15 explanatory variables were considered, although this was reduced to 11 for analysis after removal of highly correlated variables (Pearson's correlation coefficient scores >0.9; *Table S2*). Landscape and topographic data (elevation at plot centre, predominant aspect and slope) were measured in-field using a compass and Garmin GPS 62s, and basal area of trees >10 cm was derived from stand-level measures. Aspect was transformed into Cosine of aspect (*COSα = Northness*; 1 = Northward, -1 = Southward, 0 = either East or Westward) and Sin of aspect (*SINα = Eastness*; 1 = Eastward, -1 = Westward, 0 = either North or South; Roberts, 1986). Fire history attributes (e.g. frequency of fires since 2000; time since last fire) were extracted from the Victorian State Government data. Annual mean temperature data were sourced from Stewart & Nitschke (2017), and annual precipitation from WorldClim grids (http:www.worldclim.org). All Random Forest models were run using the statistical package "rfPermute" (Archer, 2016).

We used a non-metric multi-dimensional scaling ordination (NMDS, R Vegan package, "metaMDS" function with Bray-Curtis similarity matrix and 3 dimensions) to examine whether the composition of shrubs and grasses differed among wildfire frequencies. Species of the same genera were pooled, and ordinations were based both on presence/absence data of shrub (11 genera) and grass (1 genera), and on shrub prominence values and grass frequencies per site. Ellipses estimating standard error were drawn around each fire frequency using the "ordiellipse" function (Oksanen, 2011), and similarity percentages analyses (SIMPER; Clarke, 1993) were used to quantify degrees of dissimilarity among wildfire frequencies.

To compare the impact of wildfire frequency on the within-plot spatial configuration of *E. pauciflora* clumps, we calculated Nearest Neighbour Index (NNI) and mean Nearest Neighbour Distance (mNND) (CrimeStat IV program; Levine, 2015). NNI is a continuous, unitless metric that provides an estimate of the degree of spatial aggregation, where scores close to 0 indicate a tendency towards a clustered spatial pattern, those approaching 1 a random dispersed pattern, and those approaching 2.15 a more regular or uniform pattern (Levine, 2015). In contrast, mNND provides an estimate of the average distance between neighbours, presented here as the distance (metres, *m*) between live tree clumps (For additional information on assumptions as part of Nearest Neighbour analysis, see *Supplementary Material*). Effects of wildfire frequency on NNI and mNND were then assessed using a one-way ANOVA. Statistical analyses were undertaken using the R statistical software package (R Core Team, 2016), except for the SIMPER analysis, which used the PRIMER statistical software (v6; Clarke & Gorley, 2006).

Results

Tree stem and coarse woody debris size distributions

Mean numbers of total live and dead standing eucalypt stems were highest at Double burned sites (2,816 stems ha^{-1} ± 1384 SE), followed by Single (2,000 stems ha^{-1} ± 474), Unburned (1,416 stems ha^{-1} ± 159), and finally Triple burned sites (1,362 stems ha^{-1} ± 662), though there were no significant differences among wildfire frequencies. The majority of stems (≥95%) were ≤35 cm dbhob at all sites irrespective of wildfire frequencies (**Figure 2**). Live stem densities were relatively even across size classes at Unburned, Double and Triple burned sites, but skewed towards the smallest size classes at Single burned sites**.** Mean densities of standing dead eucalypt stems did not differ among wildfire frequencies (**Figure 2**). However, proportions of top-killed stems were significantly greater at Double (98.8% ± 0.8) and Triple burned sites (98.2% ± 1.8) than Single burned (55.0% ± 11.1) and Unburned (36.8% ± 10.8) sites.

Mean total numbers of CWD pieces and mean numbers of sound CWD pieces did not vary significantly among wildfire frequencies. However, mean numbers of rotten CWD pieces were significantly greater at Unburned (20.6 ± 8.3 pieces ha^{-1}) than Triple (4.2 ± 1.8) and Double burned sites (3.4 ± 1.8), but not Single burned sites (8.2 ± 3.1). Kolmogorov-Smirnov Tests (D = 0.14, 0.17, 0.15; $P<0.05$) indicated significant differences in the size-class distribution of sound CWD pieces between Double sites and Unburned, Single, and Triple sites, quite likely due to the absence of large sound CWD at Double burned sites (**Figure 2**). Similarly, there were significant differences in the size-class distribution of rotten CWD between the Unburned and Double burned sites ($P \leq 0.02$; **Figure 2**).

Clump mortality and regeneration

Mortalities of *E. pauciflora* clumps were significantly affected by wildfire frequency ($P<0.01$; **Figure 3A**). Total clump mortality at any one site varied from 0% (Single burned site) to 84% (Triple burned site), reflecting considerable variation in the numbers of live clumps per hectare particularly those comprised of 'small' stems (<10 cm dbhob; **Figure 3B**). Mean total clump mortality was greatest at the Triple burned sites (50% ± 9%), which was significantly greater than mean mortalities at the Single burned sites (9% ± 7%), but not Double burned (19% ± 8%) and Unburned sites (25% ± 9%; **Figure 3A**). However, while relatively high mean clump mortalities at Triple burned sites reflected significantly greater mortality of clumps comprised of at least one large stem (>10 cm dbhob; 56%), mean mortality patterns at Unburned sites were dominated by relatively high mortality of clumps of small stems (67%; **Figure 3A**)

The mNND of live *E. pauciflora* clumps was greatest at the Triple burned sites (2.7 m ± 0.43), which was significantly different from the Unburned (1.65 m ± 0.12; **Figure 3C**). In contrast, the mean NNI of live clumps was significantly lower at the Triple burned (0.69 ± 0.04) than Unburned sites (0.84 ± 0.05; **Figure 3C**), indicating stronger spatial clustering at the Triple burned sites. Numbers of new seedlings were significantly greater at Single than Double and Triple burned sites, although there were no differences among wildfire frequencies in the numbers of lignotuberous seedlings (**Figure 3D**). Similarly, mean basal resprouts on remaining live clumps were significantly greater at Single (13.4 ± 0.92) than both Double (8.6 ± 0.40) and Triple (9.3 ± 0.90) burned sites (**Figure 3E**), leading to the greatest numbers of basal resprouts per hectare at Single (6064 ± 1968 ha^{-1}) and Double (10038 ± 3989) burned sites **(Figure 3F).**

Most important explanatory variables for clump mortality, top-kill and seedlings

The Random Forest analyses confirmed the overriding influence of wildfire frequency on tree mortality, with the frequency of fires in the 2000 – 2013 period having a positive relationship with both percentage clump mortality and top-kill, explaining 20% and 26% of the variation respectively. Time since fire was also important in explaining percentage top-kill (24% variance explained, negative relationship; **Table 1**).

Fire-history variables were not the most important variables for explaining seedling counts. The volume of coarse woody debris and slope explained 14 and 13% of the variation in new seedling counts respectively, while the most influential fire-history variable (Time Since Wildfire) explained only 8% (all negative relationships; **Table 1**). Similarly, “Eastness” was identified as the most important variable in explaining counts of lignotuberous seedlings (24%, positive relationship; **Table 1**).

Understorey Composition

Wildfire frequency significantly affected both shrub prominence values ($P < 0.001$) and grass occurrence ($P < 0.05$). Mean shrub prominence values increased after a single fire (65.1 ± 15.4) relative to the Unburned (40.9 ± 11.7) sites, but then were dramatically reduced with subsequent fires, particularly in the Triple burned sites (1.05 ± 0.45; **Figure 4a**). In contrast, the mean frequency of grasses increased with the number of wildfires to be significantly greater at Triple (0.83 ± 0.04) than Single (0.18 ± 0.11) and Unburned (0.22 ± 0.1) sites (**Figure 4b**).

Shrub genera varied in their persistence with fire frequency. *Olearia* and *Acacia* species (resprouter and obligate seeder, respectively) were present at Unburned sites, and persisted after three wildfires although with decreasing prominence (**Figure 4c**). In contrast, other genera were either absent after one fire (*Leucopogon*, *Podocarpus*; resprouter and obligate seeder respectively), or were eliminated by two (*Prostanthera*, *Tasmannia*; both obligate seeders), or three (*Cassinia*, *Pimelia*; both obligate seeders) wildfires (**Figure 4c**). Still others were only evident after one fire but decreased with fire frequency to either be absent after three wildfires (*Polycias*, *Bossiaea*, both resprouters) or to persist with decreased prominence (*Podolobium*, resprouter).

NMDS ordinations and SE-ellipses based on presence/absence data, clearly indicated differences in shrub and grass composition among wildfire frequencies (**Figure 5a**). Each of the wildfire frequencies occupied a distinct NMDS space, except for the Double burned sites, which supported an intermediate composition between Single and Triple burned sites. Similarity percentage analysis of presence-absence data supported these observations, indicating the greatest dissimilarity between Unburned and Single burned sites (73.0%), followed by Unburned and Double (69.6%), Single and Triple (65.9%), Single and Double (60.7%), Unburned and Triple (58.2%), and finally Double and Triple burned sites (43.6%; data not shown). Separation of wildfire frequencies was also evident in the NMDS ordination of shrub prominence values and grass frequencies (**Figure 5b**), although with greater differentiation of the Single and Triple burned sites. Similarity percentages were higher than those for the presence/absence NMDS, and indicated greatest dissimilarity between Single and Triple burned sites (97.5%), and least dissimilarity between Double and Triple burned sites (82.7%; data not shown).

Discussion

Clump mortality increased by short-interval wildfires

This study has illustrated that, after three successive fires in a decade, the ability of resprouting *E. pauciflora* to persist and survive is severely curtailed to such an extent that on average 50% of clumps died compared to 25% in long unburned forests, with mortality rates as high as 80% on some Triple burned sites. The rates of death are substantially higher than mortality rates after high-severity fire in resprouter dry eucalypt forests (25%; Prior *et al.*, 2016a), in forest (8%) and savanna ecosystems (7%; Hoffmann *et al.*, 2009), or following extreme drought in other eucalypt forests in southern Australia (26%; Matusick *et al.*, 2013).

Mean clump mortalities among wildfire frequencies reflected contrasting trends in clump mortality by size class. Comparatively high mean clump mortalities at Unburned sites (25%) were largely due to high percentage mortalities in the smaller size classes (67%). Coates (2015) measured a mean stand density of 665 trees ha^{-1} for *E. pauciflora* forests 70 years after wildfire elsewhere in the Australian Alps, which was markedly lower than the 1072 trees ha^{-1} measured 23 years after wildfire by Ashton and Hargreaves (1983). This suggests potential for ongoing self-thinning of *E. pauciflora* forests decades after fire, which might be exacerbated by overstorey suppression of smaller size classes (Barker, 1988; Stoneman et al. 1994). Other disturbances such as drought (in particular, a ‘very long’ rainfall deficit from 1996 to 2010 in south-east Australia; BOM, 2010) could have contributed to seemingly high percentage clump mortalities and top-killed stems (37%) at Unburned sites, as has been recently recorded for other resprouter forests in southern Australia (Prior *et al.*, 2016a). In contrast to Unburned sites, high overall percentage clump mortalities at Triple burned sites (50%) reflected elevated mortalities of ‘large’ clumps (56%). This portends significant potential for structural change of *E. pauciflora* open forests after three short-interval fires.

Tree regenerative capacity eroded by two and three short-interval wildfires

Our study confirms that *E. pauciflora* can regenerate from both resprouts and seeds after a single fire (Green, 2009; Coates, 2015), making it a ‘facultative seeder’ functional type (Pausas *et al.*, 2016). However, we detected a significant decrease in the number of basal resprouts per surviving tree after two and three successive wildfires compared with just one wildfire. While the magnitude of the change was not particularly large, and lignotuberous resprout numbers are known to vary widely in eucalypts (Noble, 2001), a reduction in resprouting may indicate a depletion of viable buds, suggesting a physiological limitation to the persistence niche of *E. pauciflora*. We also detected a significant decrease in the total number of basal resprouts per hectare between Double and Triple burned sites, reflecting decreases in the number of resprouts and in the number of living clumps at Triple burned sites due to elevated mortality.

Significant decreases in the densities of both new seedlings, in addition to reduced basal resprouts, could portend reduced *E. pauciflora* regenerative capacity and decreased potential to compensate for increased tree mortality. The potential vulnerability of *E. pauciflora* seedlings to high-intensity fire has been considered for some time; for example Jacobs (1955) suggested a seedling's developing lignotuber could be less protected by soil than older stems. Our analyses indicated that site-level factors could also play a role in *E. pauciflora* seedling dynamics. While not significantly different among wildfire frequencies (data not shown), our model indicated a negative relationship between CWD volume and new seedling abundance, reflecting lower seedling counts and marginally higher CWD volumes at both Unburned and Triple burned sites. This finding is counter-intuitive, as sheltering has been shown to benefit *E. pauciflora* seedlings (Egerton *et al.*, 2000), although CWD might act as a barrier to seedling establishment by physically obstructing substrate, and/or the relationship could be associative (low seedling numbers reflecting an absence of fire at Unburned sites, and too much fire at Triple burned sites) rather than causative. Slope and aspect were identified as important site variables in explaining new and lignotuberuous seedling densities, respectively. There were fewer new seedlings on steeper slopes, which may be related to less available water in the soil profile, as indicated for seedling establishment of *E. pauciflora* (Ferrar *et al.*, 1988) and other eucalypt species (Bailey et al., 2012). Lignotuberous seedlings were more abundant on easterly slopes, which may be related to greater protection. These two findings suggest reduced snow gum regeneration on steep, unprotected sites, and illustrate that several interactive factors (including post-fire drought; Harvey et al., 2016) will likely determine seedling abundance in sub-alpine forests in addition to fire effects.

Indications of reduced resprouter and seedling regeneration after two and particularly three wildfires could have serious ramifications for the future formation and persistence of *E. pauciflora* open forests. Our findings suggest that *E. pauciflora* seedlings in certain landscape positions may be prone to the 'immaturity risk' that characterises obligate seeder communities (Keeley *et al.*, 1999), where young stems are more vulnerable than mature stems to the return of disturbance before they have developed regenerative capacity (whether that is via seeds or, in our example, the ability to resprout from a fully developed or protected lignotuber).

Signs of altered structure and understorey composition with repeated short-interval wildfires?

Elevated clump mortalities after three short-interval wildfires indicate potential disruption to the canopy structure of these sub-alpine ecosystems, including significant changes in the spatial configuration of surviving clumps. Analyses based on distances between surviving clumps and their spatial aggregation indicate an 'opening up' of the tree canopy after short-interval fires, suggesting a shift from a forest to a woodland- or savanna-like vegetation structure.

In addition to an opening-up of the canopy layer, we detected a general trend in the understorey away from shrub- to grass-dominance following frequent fire. Decreased shrub dominance was not solely due to elimination of seeder shrubs, since some resprouting shrub species were also absent after three (*Cassinia*, *Pimelia*, *Polyscias*, and *Bossiaea*) and in some cases two (*Leucopogon*, *Prosthanthera*, *Tasmannia*) fires. This contrasts with findings elsewhere of greater resilience of resprouter than seeder shrubs to changing fire regimes (Enright *et al*, 2014), and implies that frequent fire may test the persistence niche of the broader ecosystem, and not just the overstorey trees.

Frequent fires also reduced the number of shrub genera present – after three wildfires, only three genera of shrubs were detected (*Olearia*, *Acacia* and *Podolobium*); compared with eight, nine and six genera in Unburned, Single and Double burned sites respectively. In addition, some shrubs that were only detected after a single fire (*Bossiaea* and *Polycias*) – implying a dependence on fire for regeneration from the seedbank (Camac et al, 2017) – were then eliminated after subsequent short-interval fires. This indicates that frequent fires will not only rearrange the structure of the understorey – encouraging grasses at the expense of shrubs – but also alter the initial composition of the understorey following disturbances. In southeast

Australia, vegetation communities typically adhere to the Initial Floristics model (Egler, 1954) where species are re-established soon after fire through soil-stored seed, serotiny or resprouting, allowing persistence over time (Cremer & Mount, 1964; Purdie & Slatyer, 1976). Whether subalpine woodland ecosystems adhere to this model after a single fire remains unclear, although our results indicate potential for new floristic pathways in the first decade after multiple short-interval wildfires. Similarly, whether relay floristics (Egler, 1954) allow species extirpated from some sub-alpine forests after frequent fires to recolonise after long fire-free intervals remains to be seen, though some of the species found in our study sites are known for their limited dispersal capacity (Morgan & Venn, 2017).

Our study indicates that more frequent fires could add to the complexity of expected vegetation dynamics in temperate treeline communities under climate change. It is generally expected that, depending on the type of vegetation community, tree- (and shrub-) lines will either entirely advance upslope; shift upslope but only within the species existing range; or collapse and recede as climates warm (Breshears *et al.*, 2008; Kelly & Goulden, 2008). Global meta-analysis of treelines over the last 100 years found that there were substantially more instances of treelines advancing (52% of surveyed studies) than receding (1%); however, those receding showed evidence of disturbances (Harsch *et al.*, 2009). Indeed, *E. pauciflora* forests are known to expand into non-tree alpine areas under long fire-free intervals (c. > 40 years) in favourable environmental conditions (Wearne & Morgan, 2001; McDougall, 2003). Our study illustrates the possibility that climate change-associated changes in large-scale disturbance regimes (such as fire) could override the putative effects of increased CO_2 and temperature on vegetation composition in alpine and sub-alpine environments (Jarrad *et al.*, 2008; Camac *et al.*, 2017), leading to 'ecological surprises' (Noble, 1993; Paine *et al.*, 1998; Kim & Lee, 2015) such as a relative increase in the proportion of receding treelines. There is, therefore, a need to acknowledge and incorporate the effects of stochastic wildfires with short return intervals into predictive models of future vegetation structure and composition.

Changing trajectories or state shifts for E. pauciflora forests?

Our findings indicate a multitude of ways in which multiple short-interval wildfires can impact on the structure and composition of *E. pauciflora* open forests, including: a) increased clump mortality; b) increased spatial clustering of surviving clumps; c) decreased numbers of new seedlings; and d) compositional change in the understorey from shrub- to grass-dominance. Together these structural and compositional changes indicate that frequent fires may act to fragment and to change the recovery trajectories of our sub-alpine forests ecosystems, leading to more open structures reminiscent of 'sub-alpine savannas' (*Figure S3*).

Whether our different post-fire states translate to 'state shifts' (Scheffer & Carpenter 2003) towards more open and potentially more flammable communities cannot yet be determined. Burning experiments on alpine shrub and grasses have indicated that shrub species are generally more flammable than densely-packed grasses, which tend to retain moisture more effectively than aerated shrubs species (Fraser *et al.*, 2016); however, these field experiments did not address whether increased curing rates – the annual grass death and drying cycle, expected to be amplified by climate change – would increase the relative flammability of grasses in alpine areas, making them similarly flammable to other grasslands in Australia (Prior *et al.*, 2016b). Other studies of *E. pauciflora* sub-alpine forests have indicated that burned *E. pauciflora* forest is more likely to burn again, and more extensively, in subsequent fires (Zylstra, 2013). This has analogies with the 'landscape trap' hypothesis for other montane ecosystems of southern Australia (Lindenmayer *et al.*, 2011), where fire severity is arguably higher in younger stands (Taylor *et al.*, 2014); however, this hypothesis is contested in tall montane forest ecosystems, with evidence that extrinsic factors such as fire weather and climate override intrinsic stand age factors when it comes to determining area burned (Bowman *et al.*, 2016). Thus, whether the extent of double- and triple- burned forest is likely to increase, or exist as a historic landscape anomaly, is likely to be a complex interplay between stand-level changes and extrinsic factors like fire weather and climate.

Numerous conceptual models are being developed to identify the impacts of frequent disturbances (Enright *et al.*, 2015) and to build ecosystem resilience into the future adaptive management of many ecosystems (Johnstone *et al.*, 2016), including our study region (Colloff *et al.*, 2016; Doherty et al., 2017). Many of these frameworks, particularly in the Australian context, are predicated on a limitless resilience of resprouter-type forests to rebound from single and compounded disturbances. Our study, combined with recent evidence of increased mortality of resprouter eucalypts after single high-severity wildfires (Bennett *et al.*, 2016; Fairman *et al.*, 2016; Prior *et al.*, 2016a), suggests that even comparatively hardy forests dominated by strong resprouters cannot safely be assumed to be invulnerable to emerging fire regimes.

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References

Abis, B., & Brovkin, V. 2016. Environmental conditions for alternative tree cover states in high latitudes. *Biogeosciences Discussions* 14: 1–22.

Adams, M.A. 2013. Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. *Forest Ecology and Management* 294: 250–261.

Aponte, C., Tolhurst, K.G., & Bennett, L.T. 2014. Repeated prescribed fires decrease stocks and change attributes of coarse woody debris in a temperate eucalypt forest. *Ecological Applications* 24: 976–989.

Archer, E. 2016. rfPermute: Estimate permutation p-values for random forest importance metrics, R Package version 2.1.5 http://CRAN.R-project.org/package=rfPermute

Ashton, D.H. & Hargreaves, G.R. 1983. Dynamics of sub-alpine vegetation at Echo Flat, Lake Mountain, Victoria. *Proceedings of the Ecological Society of Australia.* 12: 35–60.

Attiwill, P.M. 1994. Ecological disturbance and the conservative management of eucalypt forests in Australia. *Forest Ecology and Management* 63: 301–346.

Bailey, T.G., Davidson, N.J., & Close, D.C. 2012. Understanding the regeneration niche: Microsite attributes and recruitment of eucalypts in dry forests. *Forest Ecology and Management* 269: 229–238.

Ball, M.C., Egerton, J.J.G., Leuning, R., Cunningham, R.B., & Dunne, P. 1997. Microclimate above grass adversely affects spring growth of seedling snow gum (*Eucalyptus pauciflora*). *Plant, Cell and Environment* 20: 155–166.

Barker, S. 1988. Population structure of snow gum (*Eucalyptus pauciflora* Sieb. ex Spreng.) subalpine woodland in Kosciusko National Park. *Australian Journal of Botany* 36: 483.

Bassett, O.D., Prior, L.D., Slijkerman, C., Jamieson, D., & Bowman, D.M.J.S. 2015. Aerial sowing stopped the loss of alpine ash (*Eucalyptus delegatensis*) forests burnt by three short-interval fires in the Alpine National Park, Victoria, Australia. *Forest Ecology & Management* 342: 39–42.

Bennett, L.T., Bruce, M.J., MacHunter, J., Kohout, M., Tanase, M.A., & Aponte, C. 2016. Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire. *Forest Ecology and Management* 380: 107–117.

BOM (Bureau of Meteorology) 2010. Australia's wettest September on record but it is not enough to clear long-term rainfall deficits. *National Climate Centre: Special Climate Statement No. 22*. Bureau of Meteorology, Melbourne, Australia

Bond, W.J., & Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16: 45–51.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., & DeFries, R.S. 2009. Fire in the earth system. *Science* 324: 481–484.

Bowman, D.M.J.S., Murphy, B.P., Boer, M.M., Bradstock, R.A., Cary, G.J., Cochrane, M.A., Fensham, R.J., Krawchuk, M.A., Price, O.F., & Williams, R.J. 2013. Forest fire management, climate change, and the risk of catastrophic carbon losses. *Frontiers in Ecology and the Environment* 11: 66–68.

Bowman, D.M.J.S., Murphy, B.P., Neyland, D.L.J., Williamson, G.J., & Prior, L.D. 2014a. Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Global Change Biology* 20: 1008–1015.

Bowman, D.M.J.S., MacDermott, H.J., Nichols, S.C., & Murphy, B.P. 2014b. A grass-fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecology and Evolution* 4: 4185–4194.

Bowman, D.M.J.S., Williamson, G.J., Prior, L.D., & Murphy, B.P. 2016. The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Global Ecology & Biogeography* 25: 1166-1172

Breiman, L. 2001. Random Forests, *Machine Learning* 45: 5-32

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B., & Davison, J.E. 2008. Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11591–11592.

Brown, C.D., & Johnstone, J.F. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management* 266: 34–41.

Burrows, G.E. 2013. Buds, bushfires and resprouting in the eucalypts. *Australian Journal of Botany* 61: 331–349.

Camac, J.S., Williams, R.J., Wahren, C.-H., Hoffmann, A.A., & Vesk, P.A. 2017. Climatic warming strengthens a positive feedback between alpine shrubs and fire. *Global Change Biology* 23: 3249-3258

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117–143.

Clarke, K.R. & Gorley, R.N. 2006. PRIMER v6: User Manual/Tutorial, PRIMER-E, Plymouth, 192 pp.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., & Knox, K.J.E. 2013a. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19–35.

Clarke, H.G., Lucas, C., & Smith, P. 2013b. Changes in Australian fire weather between 1973 and 2010. *International Journal of Climatology* 33: 931–944.

Clarke, H.G., Smith, P.L., & Pitman, A.J. 2011. Regional signatures of future fire weather over eastern Australia from global climate models. *International Journal of Wildland Fire* 20: 550–562.

Coates, F. 2015. Comparative changes in Eucalyptus pauciflora (Myrtaceae) stand structure after bushfires in Victoria. *Cunninghamia* 15: 1–11.

Colloff, M.J., Doherty, M.D., Lavorel, S., Dunlop, M., Wise, R.M., & Prober, S.M. 2016. Adaptation services and pathways for the management of temperate montane forests under transformational climate change. *Climatic Change* 138: 267–282.

Costermans, L. 2009. *Native trees and shrubs of south-eastern australia*. New Holland Publishing, Melbourne, Australia.

Cremer, K.W. & Mount, A.B. 1965, Early stages of plant succession following the complete felling and burning of *Eucalyptus regnans* forest in the Florentine Valley, Tasmania. *Australian Journal of Botany* 13: 303-322.

Crisp, M.D., Burrows, G.E., Cook, L.G., Thornhill, A.H., & Bowman, D.M. 2011. Flammable biomes dominated by eucalypts originated at the Cretaceous-Palaeogene boundary. *Nature Communications* 2: 1–8.

Doherty, M.D., Lavorel, S., Colloff, M.J., Williams, K.J., & Williams, R.J. 2017. Moving from autonomous to planned adaptation in the montane forests of south-eastern Australia under changing fire regimes. *Austral Ecology* 42: 309–316.

Douglas, G.W., & Bliss, L.C. 1977. Alpine and high subalpine plant communities of the North Cascades Range, Washington and British Columbia. *Ecological Monographs* 47: 113–150.

Egerton, J.J.G., Banks, J.C.C., Gibson, A., Cunningham, R.B., & Ball, M.C. 2000. Facilitacion of seedling establishment: reduction in irradiance enhances winter growth of *Eucalyptus pauciflora*. *Ecology* 81: 1437–1449.

Egler, F.E. 1954. Vegetation science concepts 1. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4: 412-417.

Enright, N.J., Fontaine, J.B., Bowman, D.M., Bradstock, R.A., & Williams, R.J. 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.

Enright, N.J., Fontaine, J.B., Lamont, B.B., Miller, B.P., & Westcott, V.C. 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *Journal of Ecology* 102: 1572–1581.

Fairman, T.A., Nitschke, C.R., & Bennett, L.T. 2016. Too much, too soon? A review of the impacts of increasing wildfire frequency on tree demography and structure in temperate forests. *International Journal of Wildland Fire* 25: 831–848.

Ferrar, J., Cochrane, P.M., & Slatyer, R.O. 1988. Factors influencing germination and establishment of *Eucalyptus pauciflora* near the alpine tree line. *Tree Physiology* 4: 27–43.

Fletcher, M.-S., Wood, S.W., & Haberle, S.G. 2014. A fire-driven shift from forest to non-forest: evidence for alternative stable states? *Ecology* 95: 2504–2513.

Fraser, I.P., Williams, R.J., Murphy, B.P., Camac, J.S., & Vesk, P.A. 2016. Fuels and landscape flammability in an Australian alpine environment. *Austral Ecology* 41: 657–670.

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.

Harsch, M.A., Hulme, P.E., McGlone, M.S., & Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12: 1040–1049.

Harvey, B.J., Donato, D.C., & Turner. 2016. High and dry: Postfire drought and large stand-replacing burn patches reduce postfire tree regeneration in subalpine forests. *Global Ecology and Biogeography* 25: 655–669.

Haslem, A., Leonard, S.W., Bruce, M.J., Christie, F., Holland, G.J., Kelly, L.T., MacHunter, J., Bennett, A.F., Clarke, M.F., & York, A. 2016. Do multiple fires interact to affect vegetation structure in temperate eucalypt forests? *Ecological applications* 26: 2414-2432

Hirota, M., Holmgren, M., Van Nes, E.H., & Scheffer, M. 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* 334: 232–235.

Hoffmann, W.A., Adasme, R., Haridasan, M., de Carvalho, M.T., Geiger, E.L., Pereira, M., Gotsch, S.G., & Franco, A.C. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90: 1326–37.

Jacobs, M.R. 1955. *Growth Habits of the Eucalypts*. CSIRO Forestry & Timber Bureau, Canberra, Australia.

Jarrad, F.C., Wahren, C.H., Williams, R.J., & Burgman, M.A. 2008. Impacts of experimental warming and fire on phenology of subalpine open-heath species. *Australian Journal of Botany* 56: 617–629.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., (…) & Turner, M.G. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14: 369–378.

Jones, G.M., Gutiérrez, R.J., Tempel, D.J., Whitmore, S.A., Berigan, W.J., & Peery, M.Z. 2016. Megafires: an emerging threat to old-forest species. *Frontiers in Ecology and the Environment* 14: 300–306.

Kasel, S., Bennett, L.T., Aponte, C., Fedrigo, M., & Nitschke, C.R. 2017. Environmental heterogeneity promotes floristic turnover in temperate forests of south-eastern Australia more than dispersal limitation and disturbance. *Landscape Ecology*. 32: 1613-1629

Keeley, J.E., Ne'eman, G., & Fotheringham, C.J. 1999. Immaturity risk in a fire dependent pine. *Journal of Mediterranean Ecology* 1: 41–48.

Kelly, A.E., & Goulden, M.L. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11823–11826.

Kim, J.W., & Lee, J.S. 2015. Dynamics of alpine treelines: Positive feedbacks and global, regional and local controls. *Journal of Ecology and Environment* 38: 01–14.

Kirkpatrick, J.B., Green, K., Bridle, K.L., & Venn, S.E. 2014. Patterns of variation in Australian alpine soils and their relationships to parent material, vegetation formation, climate and topography. *Catena* 121: 186–194.

Lacey, C.J., & Johnston, R.D. 1990. Woody clumps and clumpwoods. *Australian Journal of Botany* 38: 299–334.

Land Conservation Council 1977. *The Alpine Study Area*. 93-98 pp. State Government of Victoria, Melbourne, Victoria.

Levine, N. 2015. CrimeStat: A Spatial statistics program for the analysis of crime incident locations. Ned Levine & Associates. Houston, TX, USA.

Lindenmayer, D.B., Hobbs, R.J., Likens, G.E., Krebs, C.J., & Banks, S.C. 2011. Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences* 108: 15887–15891.

Liu, Y., Stanturf, J., & Goodrick, S. 2010. Trends in global wildfire potential in a changing climate. *Forest Ecology and Management* 259: 685–697.

Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B., & Hardy, G.S.J. 2013. Sudden forest canopy collapse corresponding with extreme drought and heat in a Mediterranean-type eucalypt forest in southwestern Australia. *European Journal of Forest Research* 132: 497–510.

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

Millar, C.I., & Stephenson, N.L. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349: 823–826.

Morgan, J.W., & Venn, S.E. 2017. Alpine plant species have limited capacity for long-distance seed dispersal. *Plant Ecology* 218: 813–819.

Murphy, B.P., & Bowman, D.M.J.S. 2012. What controls the distribution of tropical forest and savanna? *Ecology Letters* 15: 748–58.

Nicholson, A., Prior, L., Perry, G., & Bowman, D.M.J.S. 2017. High post-fire mortality of resprouting woody plants in Tasmanian Mediterranean-type vegetation. *International Journal of Wildland Fire* 26: 532–537.

Nitschke, C.R., & Innes, J.L. 2008. Climatic change and fire potential in south-central British Columbia, Canada. *Global Change Biology* 14: 841–855.

Nitschke, C.R., & Innes, J.L. 2013. Potential effect of climate change on observed fire regimes in the Cordilleran forests of south-central interior British Columbia. *Climatic Change* 116: 579–591.

Noble, I.R. 1993. A model of the response of ecotones to climate change. *Ecological Applications* 3: 396–403.

Oksanen, J. 2011. Multivariate analysis of ecological communities in R: Vegan tutorial. http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf

Paine, R.T., Tegner, M.J., & Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535–545.

Pausas, J.G., & Keeley, J.E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55–65.

Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I.N., & Davis, S.D. 2016. Towards understanding resprouting at the global scale. *New Phytologist* 209: 945–954.

Prior, L.D., Williamson, G.J., & Bowman, D.M.J.S. 2016a. Impact of high severity fire in a Tasmanian dry eucalypt forest. *Australian Journal of Botany* 64: 193–205.

Prior, L.D., Murphy, B.P., Williamson, G.J., Cochrane, M.A., Jolly, W.M., & Bowman, D.M.J.S. 2016b. Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity? *Journal of Biogeography* 44: 1225-1238

Purdie, R.W., & Slatyer, R.O. 1977. Vegetation succession after fire in sclerophyll woodland communities in south-eastern Australia. *Australian Journal of Ecology* 1: 223–236.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Roberts, D.W. 1986. Ordination on the basis of fuzzy set theory. *Vegetatio* 66: 123–131.

Scheffer, M., & Carpenter, S.R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* 18: 648–656.

Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H., & Chapin, F.S. 2012. Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences of the United States of America* 109: 21384–9.

Scholes, R.J., & Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517–544.

Sharples, J.J., Cary, G.J., Fox-Hughes, P., Mooney, S., Evans, P., Fletcher, M.-S., Fromm, M., Grierson, P.F., McRae, R., & Baker, P.J. 2016. Natural hazards in Australia: extreme bushfires. *Climatic Change* 139: 85–99.

Silvério, D.V., Brando, P.M., Balch, J.K., Putz, F.E., Nepstad, D.C., Oliveira-Santos, C., & Bustamante, M.M.C. 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philosophical transactions of Royal Society B* 368: 1-7.

Slatyer, R.O., & Noble, I.R. 1992. Dynamics of montane treelines. In Hansen, A.J. & di Castri, F. (eds.), *Landscape Boundaries*, pp. 346–359. Springer, New York.

Specht, R.L. 1970. Vegetation. In Leeper, G.W. (ed.) *The Australian Environment*, pp. 44–67. Melbourne University Press, Melbourne.

Stephens, S.L., Agee, J.K., Fule, P.Z., North, M.P., Romme, W.H., Swetnam, T.W., & Turner, M.G. 2013. Managing Forests and Fire in Changing Climates. *Science* 342: 41–42.

Stewart, S.B., & Nitschke, C.R. 2017. Improving temperature interpolation using MODIS LST and local topography: a comparison of methods in south east Australia. *International Journal of Climatology* 37: 3098-3110

Stoneman, G.L., Dell, B., & Turner, N.C. 1994. Mortality of *Eucalyptus marginata* (Jarrah) seedlings in Mediterranean-climate forest in response to overstory, site, seedbed, fertilizer application and grazing. *Australian Journal of Ecology* 19: 103–109.

Taylor, C., McCarthy, M.A., & Lindenmayer, D.B. 2014. Nonlinear effects of stand age on fire severity. *Conservation Letters* 7: 355–370.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. *Forest Science* 14: 20–26.

Wahren, C.-H., Papst, W., & Williams, R. 1994. Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: An analysis of vegetation records from 1945 to 1994. *Australian Journal of Botany* 42: 607–639.

Warman, L., & Moles, A.T. 2009. Alternative stable states in Australia's Wet Tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology* 24: 1–13.

Wearne, L.J., & Morgan, J.W. 2001. Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. *Arctic, Antarctic, and Alpine Research* 33: 369–377.

Williams, R.J., & Ashton, D.H. 1987. Effects of disturbance and grazing by cattle on the dynamics of heathland and grassland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* 35: 413–31.

Williams, R.J., & Costin, A.B. 1994. Alpine and subalpine vegetation. In Groves, R.H. (ed.), *Australian Vegetation*, pp. 467–500. Cambridge University Press, UK.

Williams, R.J., Papst, W.A., McDougall, K.L., Mansergh, I., Heinze, D.A., Camac, J.S., Nash, M.A., Morgan, J.W., & Hoffman, A. 2014. Alpine ecosystems. In Lindenmayer, D.B., Burns, E.L., Thurgate, N., & Lowe, A.J. (eds.), *Biodiversity & Environmental Change*, pp. 177–222. CSIRO Publishing, Melbourne, Australia.

Williams, R., Wahren, C.-H., Tolsma, A.D., Sanecki, G.M., Papst, W.A., Myers, B.A., McDougall, K.L., Heinze, D.A., & Green, K. 2008. Large fires in Australian alpine landscapes: their part in thehistorical fire regime and their impacts on alpine biodiversity. *International Journal of Wildland Fire* 17: 793–808.

Zylstra, P. 2013. The historical influence of fire on the flammability of subalpine snow gum forest and woodland. *Victorian Naturalist* 130: 232–240.

Appendix and Supporting Information

Appendix 1: Additional methodological information for assessment of resprouting, and nearest neighbour analyses.

Appendix 2: Additional Figures

Figure S1: Map of broader landscape and extent of recurrent wildfires 2003 – 2013

Figure S2: Map of plot locations, extent of E. pauciflora and Australian Alps bioregion

Figure S3: Stylised representation of changes in E. pauciflora open forest after recurrent fire.

Appendix 3: Additional Tables

Table S1: Plot data including fire history and site characteristics.

Table S2: Summary of explanatory variables used in Random Forests analysis

Table 1. Significant explanatory variables (p-value < 0.05) in order of importance from Random Forest models of clump mortality, stem top-kill, and new seedling and lignotuberous seedling counts. +/- indicates positive/negative relationship between explanatory and response variable.

Response variables	Most important explanatory variables	Variance explained (%)
Clump mortality (%)	+ Fire Frequency (0.02)	19.7
	- Time Since Fire (0.04)	12.0
Top-kill (%)	+ Fire Frequency (0.01)	25.5
	- Time Since Fire (0.01)	24.1
New seedlings (no. 0.01 ha^{-1})	- Coarse Woody Debris (0.05)	13.9
	- Slope (0.02)	13.4
	- Time Since Fire (0.05)	7.9
Lignotuberous seedlings (no. 0.01 ha^{-1})	+ Aspect (Eastness) (0.01)	23.7

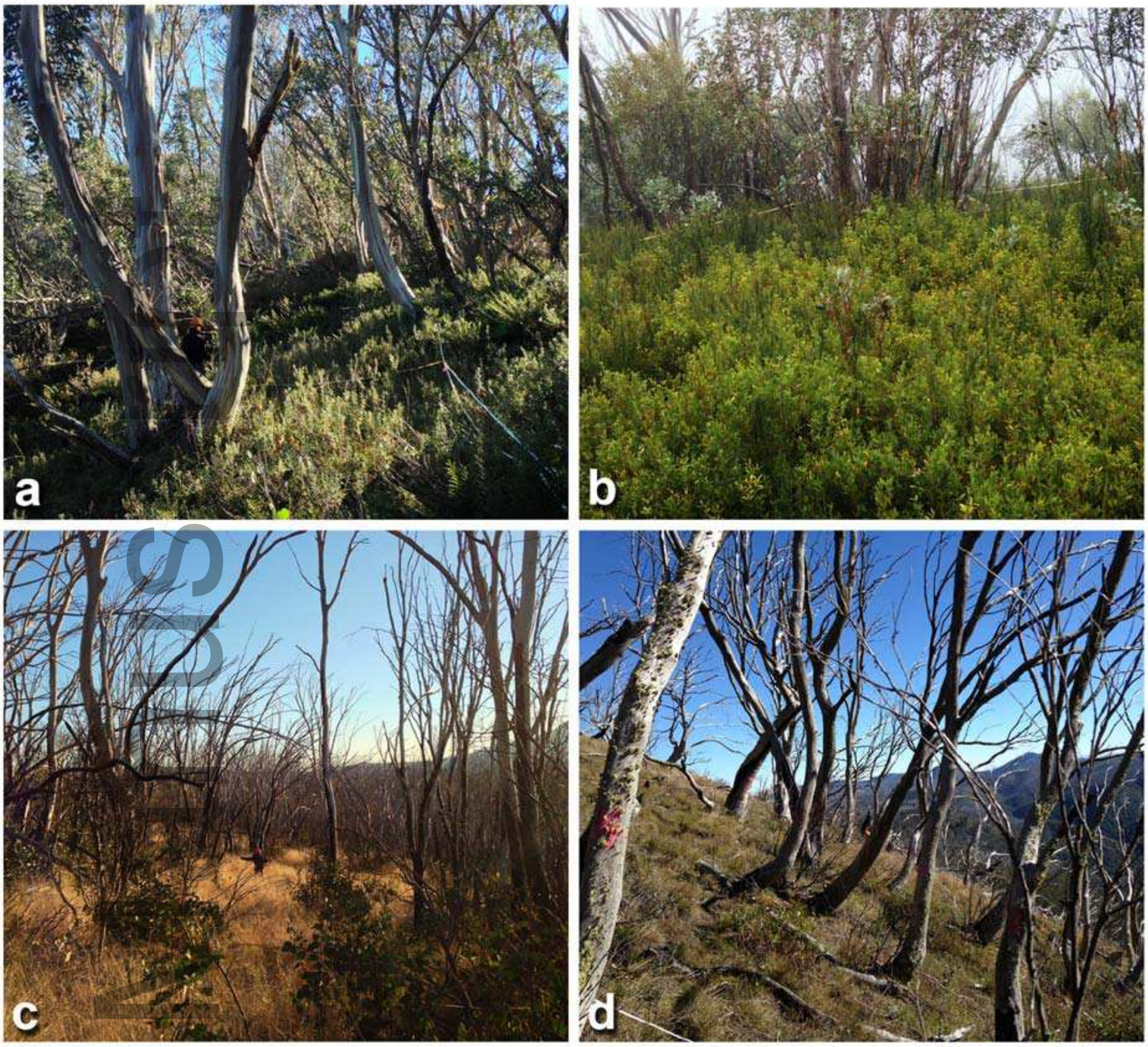

Figure 1. Examples of *E. pauciflora* forest in four fire history categories: a) unburned, showing live stems of mature overstorey *E. pauciflora* above a discontinuous and mixed understorey of shrubs and grasses; b) burned once, showing substantial development of shrub layer and regenerating *E. pauciflora* basal resprouts and seedlings; c) burned twice, showing reduced shrub cover amongst grasses and *E. pauciflora* basal resprouts; and d) burned three times, showing predominance of wholly-dead eucalypts and heavily reduced regeneration and shrub cover.

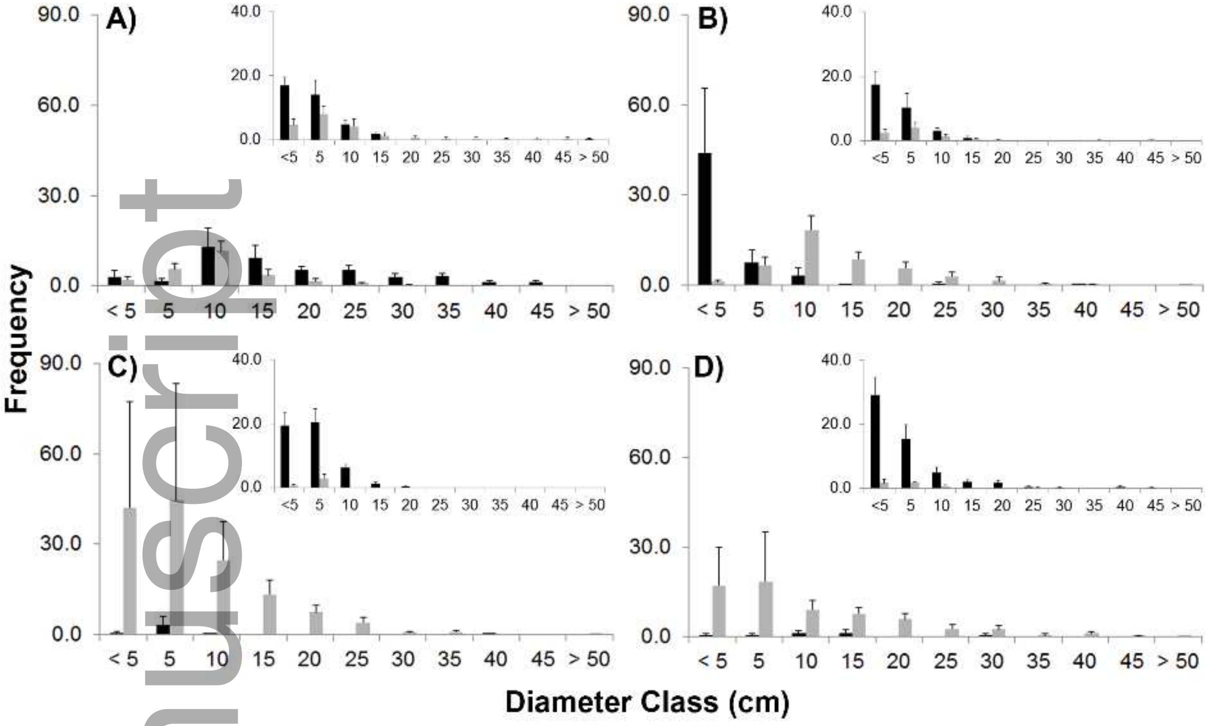

Figure 2. Mean numbers of live (black) and dead (grey) stems per dbhob class, and, as insets, mean number of sound (black) and rotten (grey) coarse woody debris (CWD) pieces per diameter class, across A) Unburned, B) Single, C) Double, and D) Triple wildfire frequencies. Values are the means (± SE) of five sites per wildfire frequency. Diameter intervals are 5 cm, except for the smallest size class, which spanned 2.5 to 5 cm. Note that 'dead' stems represent stems that were dead above breast height (1.3 m), but may have been resprouting from a basal lignotuber. Note for CWD, decay was scored a value between D1 – D5, where D1 – D3 represent 'sound', and D4 – D5 represent 'rotten'. Remaining cross-sectional area was to nearest 5% (assuming the piece was originally circular).

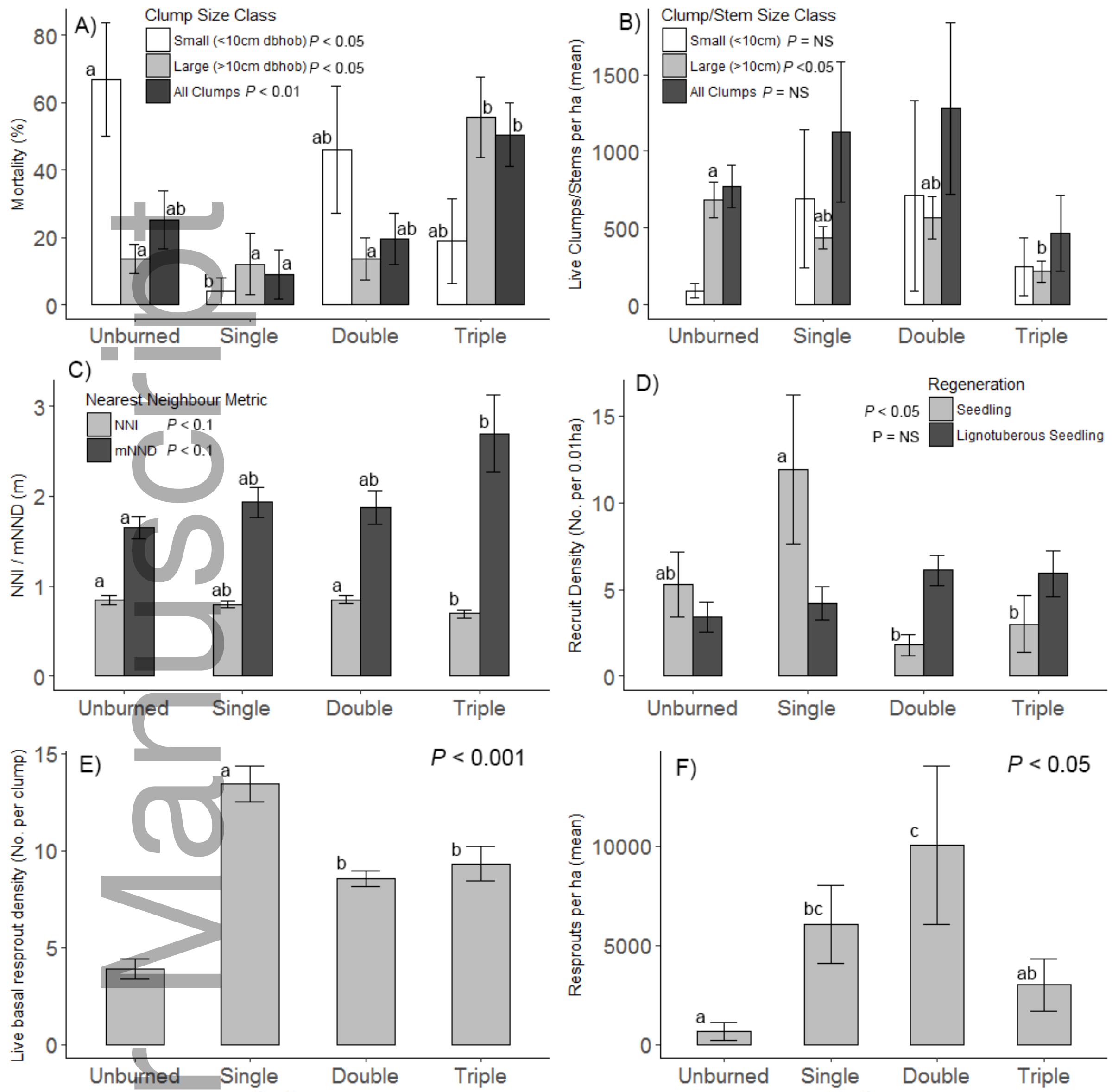

Figure 3. Effects of wildfire frequencies on **A)** percentage mortality (dead main stem, no signs of live leaves or resprouting) of ‘small’ *E. pauciflora* clumps (stem dbhob 2.5 cm – 10cm, white bar), ‘large’ *E. pauciflora* clumps (stem dbhob >10cm, light grey bar) and all *E. pauciflora* clumps combined (dark grey bar); **B)** number of live clumps and stems per hectare, as per aforementioned ‘small’ and ‘live’ definitions, and total number; **C)** nearest neighbour index (NNI; where scores close to 0 = clustered spatial pattern, 1 = random pattern, 2.15 = uniform pattern) and mean distance to nearest neighbour (mNND) of live *E. pauciflora* clumps; **D)** new seedling and lignotuberous seedling densities (only live individuals); **E)** number of live basal sprouts per live clump; and **F)** total number of live basal resprouts per hectare across fire frequencies. Note that for live basal sprouts (D), Unburned values are presented but were not included in the statistical analysis as our primary interest

was examining the patterns of fire-induced resprouting as it was influenced by fire frequency (not fire absence). Values are the mean of five sites (± SE), *P*-values are from one-way ANOVAs applied to transformed variables, with different letters indicating that wildfire frequencies were significantly different at P ≤ 0.05 (Tukey HSD); for non-parametric data, *P*-values are from Kruskal-Wallis tests with different letters derived from Dunn Tests.

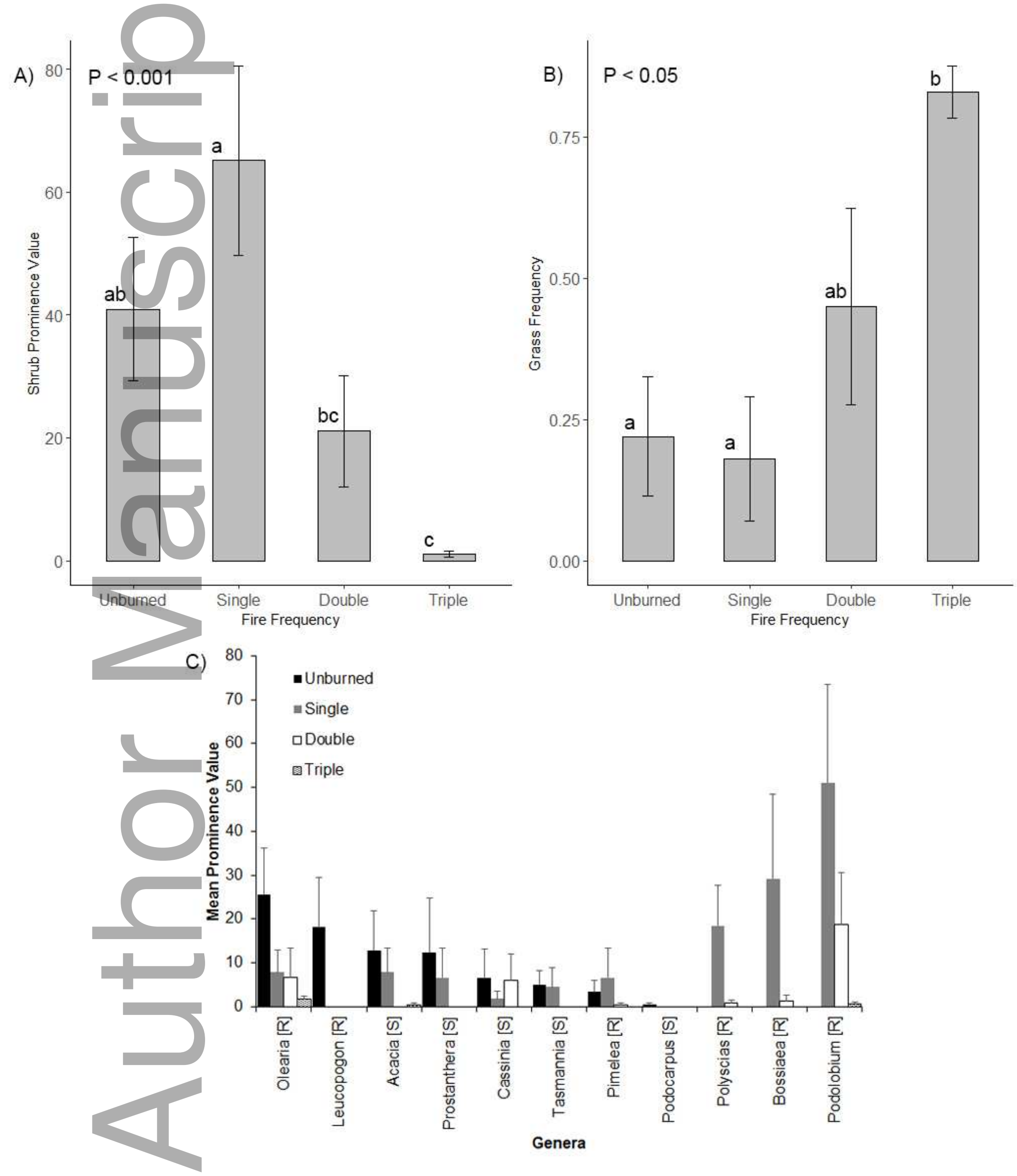

Figure 4. Changes in understorey composition among wildfire frequencies as a) mean shrub prominence values; b) mean grass frequencies (as a proportion from 0 - 1); and c)

prominence values of shrub genus groups. Values are the means of five sites (± SE), and in 4c) [R] indicates a fire response trait of resprouting, and [S] indicates seeding.

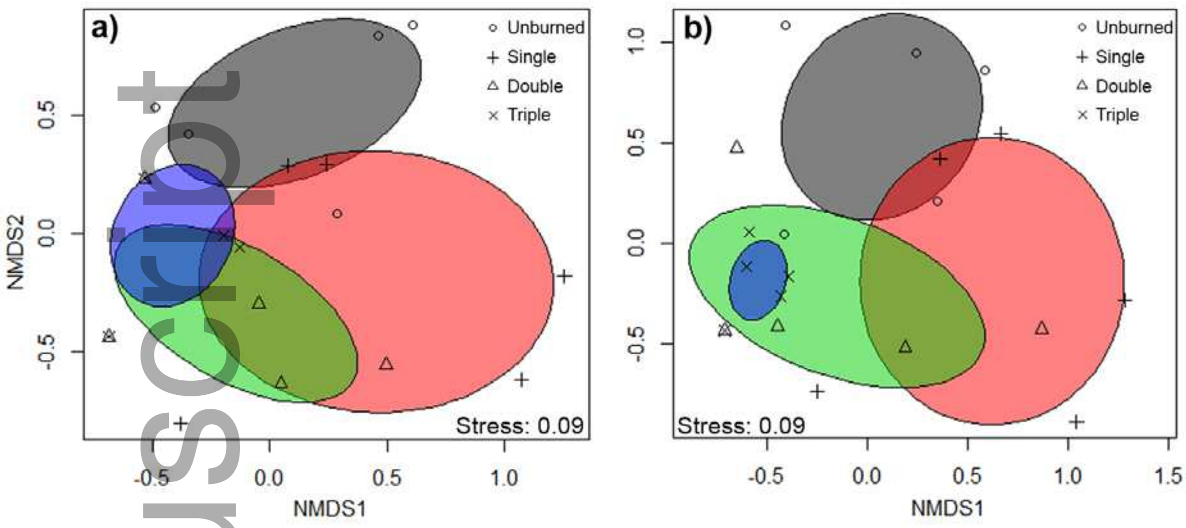

Figure 5. Shrub and grass compositions as influenced by wildfire frequency. Figures are non-metric multidimensional scaling (NMDS) ordinations (stress value = 0.09; dimensions = 3) based on **a)** shrub and grass genera presence/ absence data (11 shrub and 1 grass genera); and **b)** shrub prominence values and grass frequencies. Points represent individual sites, with the legend indicating wildfire frequency. Axis values are arbitrary and distances indicate similarity between points, as per the rank-based approach of the NMDS. Ellipses indicate standard error and shading indicates wildfire frequency – Unburned (grey); Single (red); Double (green); Triple (blue). Note some sites overlap so that not all sites are clearly visible.