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Title:
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Date:
2024-02-01

Citation:
Duivenvoorden, E., Wagner, B., Nitschke, C. R. & Kasel, S. (2024). Short-interval, high-severity wildfires cause declines in soil seed bank diversity in montane forests of south-eastern Australia. Forest Ecology and Management, 553, https://doi.org/10.1016/j.foreco.2023.121627.

Persistent Link:
https://hdl.handle.net/11343/339452

Forest Ecology and Management 553 (2024) 121627

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Short-interval, high-severity wildfires cause declines in soil seed bank diversity in montane forests of south-eastern Australia

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ARTICLE INFO

Keywords:
Plant diversity
Understorey
Obligate seeder
Resprouter
Fire
Disturbance
Eucalyptus
Plant functional traits
Storage effect

ABSTRACT

Wildfires in forested ecosystems are increasing in severity and extent. The adaptations many plants have acquired in response to their natural fire regime may not be sufficient to allow some species to persist. This could impact the forest understorey and its seed bank, which are vital reservoirs of biodiversity, and forest resilience in the face of global change. We present a case study of the montane forests of south-eastern Australia, an area subjected to an increase in frequency and severity of fires. We utilise field surveys and a soil seed bank germination study to investigate if short-interval, high-severity wildfires affect the understorey diversity in montane forests, and if the extant vegetation and the soil seed bank exhibit contrasting responses. We consider species diversity and plant functional traits to explore plant diversity in long unburned sites, and sites with one, two or three short-interval, high-severity fires in the past 25 years. With increasing fire frequency, we found a decrease in total species richness, Shannon's diversity, and the richness of resprouters in the soil seed bank, contrasting a lack of response in the extant vegetation. Increased fire frequency shifted the species composition and the frequency of plant functional groups of both extant vegetation and soil seed bank towards a decrease in clonal resprouters and increase in grasses and other upright herbs. The frequency of wind-dispersed perennials and short-lived seeders and exotics increased sharply following single high severity burn, particularly in the soil seed bank, and remained elevated relative to long unburnt with subsequent fire. The combined species (extant vegetation plus soil seed bank) pool mirrored shifts in the frequency of functional groups in extant vegetation and soil seed bank. These findings highlight the importance of considering the soil seed bank when examining the effects of fire on fire-prone forests. Although a lack of response in the extant vegetation may be a buffering effect of the soil seed bank, the shift in the frequency of plant functional groups in the combined species pool suggests this cannot be maintained indefinitely. The increase in frequency and abundance of species characteristic of early successional states has implications for increased flammability and potential positive feedbacks between past fire and future fire, especially in a warming and drying climate. These shifts were independent of the fire response strategy of eucalypt canopy species raising significant questions of whether artificial re-seeding programs should extend beyond the current focus on obligate seeding forests and an obligate seeding tree.

1. Introduction

Wildfires are a fundamental natural process in many ecosystems (Bowman et al., 2009; Pausas and Keeley, 2009). Co-evolution of plants with wildfire means that many species are well-adapted to historical regional fire regimes (Bowman et al., 2009). Of particular interest is the mode of regeneration after fire, whether by seed ("obligate seeders"), by resprouting ("obligate resprouters") or both ("facultative resprouters", Gill, 1981b; Bond and Midgley, 2001). Resprouters persist after fire, with regeneration occurring via basal or epicormic shoots (Clarke et al., 2015). Obligate seeders are typically killed by fire and rely on the germination of serotinous or soil-stored seed for their persistence.

Shifts in the frequency, seasonality, extent, and severity of the fires (i.e., altered fire regimes) could however put the long-term survival of many plant species at risk (Pausas and Keeley, 2009; Enright et al., 2015; Shinneman et al., 2021). Obligate seeders are typically favoured in environments where fire regimes are predictable, within the bounds of maturity age, plant longevity, seed bank longevity, and in places with a

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https://doi.org/10.1016/j.foreco.2023.121627
Received 18 October 2023; Received in revised form 29 November 2023; Accepted 30 November 2023

seasonal climate where post-fire environmental conditions are favourable for germination and growth (Pausas and Keeley, 2014). This strategy involves an "immaturity risk" (Zedler, 1995; Pausas and Keeley, 2014), as too frequent fire may kill juvenile individuals before they are able to set seed.

The vulnerability of obligate seeders to short-interval wildfire raises questions about their persistence, and that of the plant communities they support where fire becomes too frequent (Fairman et al., 2016). Enright et al. (2015) coined the term "interval squeeze" to refer to the compounding effects of more frequent fire, reduced growth and fecundity, and reduced seedling survival with climate change. Together, these interacting factors can make the persistence of the population more unlikely. We are already seeing examples where key species are in decline following fire frequencies that exceed the historical norm (Arroyo-Vargas et al., 2022).

The understorey can be impacted directly by fire, via mortality, or indirectly through fire-induced changes to the canopy which increases light availability and alters microclimate. This multi-pronged impact can stimulate change in understorey community composition that is less noticeable in the tree community's response to fire (Kasel et al., 2017; Swan et al., 2018). Understanding how changing fire regimes impact the understorey is critical given the importance of this community in regulating forest regeneration, nutrient and water cycling, and providing habitat and biodiversity (Gupta et al., 2015; Landuyt et al., 2019; Balandier et al., 2022). Floristic or structural simplification of the understorey may cause a loss of many of these roles, and threaten the stability and resilience held by a functionally diverse ecosystem (Coverdale and Davies, 2023).

The soil seed bank is a vital extension of aboveground plant diversity. The forest soil seed bank buffers the community against change (Vandvik et al., 2016; Plue et al., 2017, 2021; Kasel et al., 2022). This "rescue effect" can facilitate the persistence of plant species through unfavourable environmental conditions and stochastic disturbances (Van der Veken et al., 2007). Some plants employ a "bet-hedging" strategy, where some seed will remain in the soil after an initial flush of germination post-fire, allowing for regeneration after a potential second disturbance (Santana et al., 2014; Palmer et al., 2018). The soil seed bank may however also facilitate the incursion of invasive species (Vandvik et al., 2016), and face declines in seed viability and disrupted germination with climate change (Ooi, 2012). A holistic examination of understorey species including both extant vegetation and the soil seed bank allows for such dynamics to be explored (Plue et al., 2017).

Unprecedented wildfire seasons have increased in occurrence due to hot and dry conditions made more likely by climate change (Enright et al., 2015; Harrison et al., 2021) in South America, the Mediterranean, western North America, and Australia in the last decade (Bowman et al., 2020; Harrison et al., 2021). In Australia's "Black Summer" wildfires of 2019–2020, an estimated 21% of the temperate forest biome across the continent was burned (Le Breton et al., 2022). In Australia's montane forests, fire frequency and severity has increased over the last two decades (Bowman et al., 2014; Zylstra, 2018). Theoretical and field-based studies indicate obligate seeder forests are at risk of decline and potential forest-type conversion with shortening fire intervals (Bowman et al., 2014; Bassett et al., 2015; Fairman et al., 2016; McColl-Gausden et al., 2020). High elevation mixed species forests in contrast contain a variety of resprouting species and are thought to be more resilient to frequent severe fire (Burrows, 2013; Clarke et al., 2015; Fairman et al., 2017; Collins et al., 2021).

Here, we examine the response of montane forest understorey communities to short-interval, high severity wildfire through plant species and trait diversity metrics. Our research questions and associated hypotheses were:

1. Do more frequent wildfires affect the diversity of the understorey? We expect to find (i) an increase in diversity after a single high-severity fire, due to the emergence of early seral species and obligate seeder species stored in the soil seed bank, but a loss of diversity after two or three high severity fires, as the species assemblage simplifies, and some species and traits are filtered out; and (ii) an increase in the relative proportion of short-lived seeders with increase with in frequency.
2. Does the soil seed bank demonstrate the same response to more frequent fire as the extant vegetation? We expect a depletion of the seed bank with more frequent fires, with a "buffering effect" becoming evident.
3. Does the response of the understorey to frequent fire differ between forest types? We expect more prevalent fire frequency effects on understorey diversity in obligate seeding alpine ash forest than in mixed species forest with a greater abundance of resprouter species that can survive multiple severe fires.

2. Methods

2.1. Study area

The study area comprised of forested montane environments across south-eastern, Australia, with site clusters around the Carey and Hotham regions in Victoria (Fig. 1). These regions are part the Great Dividing Range, north-west from Bairnsdale, and predominantly fall within or near the Alpine National Park. The area has historically been subject to infrequent, high severity fire, on the scale of decades to centuries (~50–100 years, Gill, 1981a; Williams et al., 2008). However, between 1998 and 2020, six high-severity fires have occurred across the extent of the Victorian alps with a majority burnt at least once and other areas experiencing two, three and even four fires (DEECA, 2023a). We sampled across two forest types with contrasting fire response strategies – alpine ash (*Eucalyptus delegatensis*) dominated, and high elevation mixed-species forests, dominated by resprouting eucalypts such as mountain gum (*E. dalrympleana*) and snow gum (*E. pauciflora*). *Eucalyptus delegatensis* is an iconic obligate seeding tree species, requiring 15–20 years to reach reproductive maturity (Fairman et al., 2016); however, 8–9 year old trees have been found to produce viable seed (Doherty et al., 2017a). The region is a temperate montane environment with mild summers and cold winters. May and October-November typically experience the highest rainfall levels, with a maximum monthly rainfall of 224 mm. The mean annual precipitation is 1315 mm and mean monthly temperatures range from a minimum of − 2.3 degrees in July to a maximum of 22.2 degrees in January (Fick and Hijmans, 2017).

2.2. Site selection

Site selection was based on published spatial data of fire severity and extent (see Collins et al., 2018, 2020), as well as on-ground validation in the field. We selected sites that were either long unburned ("LUB"), which had not burned at high severity since 1939, or sites with one (single high severity, "SHS"), two (double high severity, "DHS") or three (triple high severity, "THS") high-severity fires between 1998 and 2020 (Fig. 1, Table S1).

Sites were located within the "Victorian Alps" and "Highlands – Northern Fall" bioregions, in Ecological Vegetation Classes (EVCs) known locally as Montane Woodland, Montane Grassy Woodland and Montane Damp Forest (DEECA, 2023b) and ranged in elevation from 1089 to 1561 m above sea level. Forests were eucalypt-dominated, with tree heights between 10 and 30 m and tree density of eucalypts in the overstorey of 200–400 trees per hectare in long unburnt sites, and up to 3000 in double burnt sites with subsequent reduction to 500–1000 stems in triple burnt sites (Table S2). Understorey strata ranged from dense shrubs to grassy ground cover, generally depending on level of exposure, fire frequency and moisture availability (Table S3).

Eucalyptus delegatensis closely resembles the iconic mountain ash (*E. regnans*); it is tall and straight with fibrous bark on the lower part of

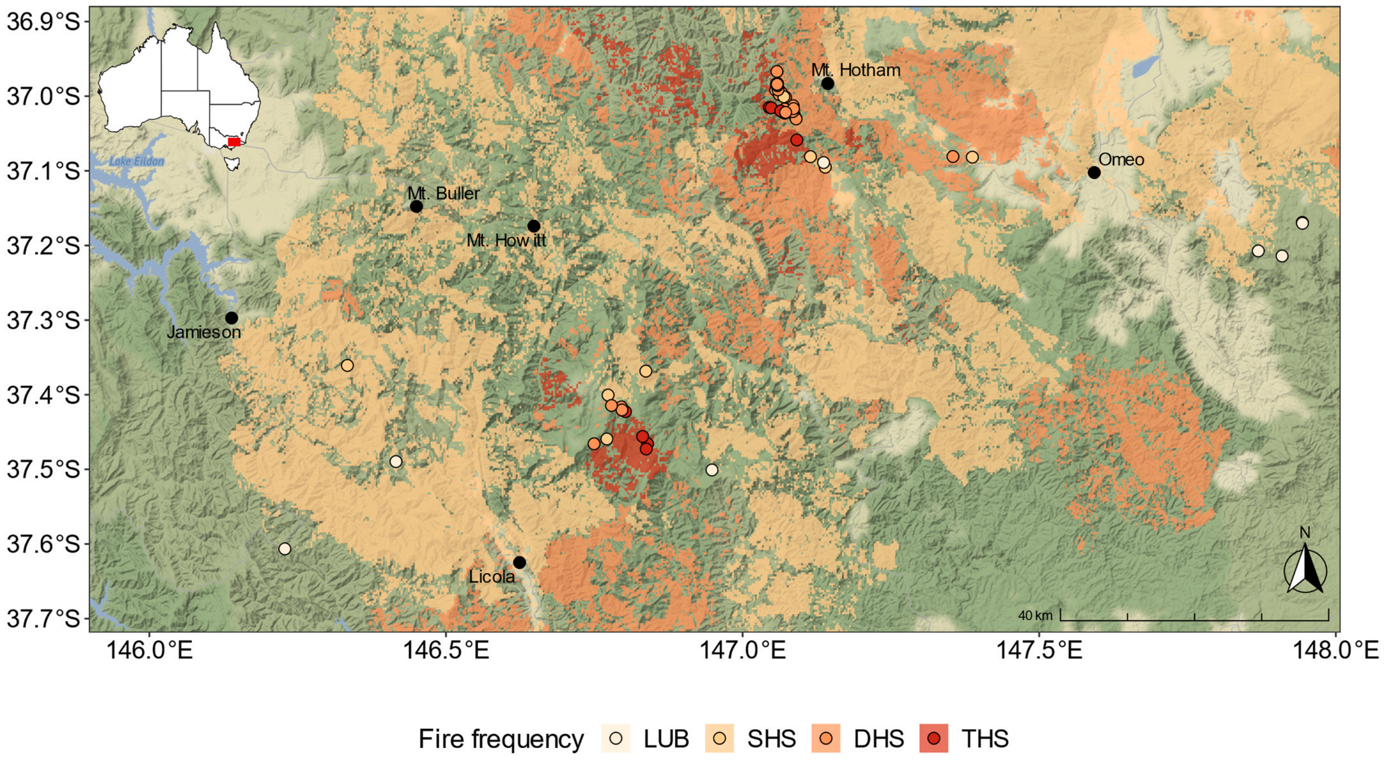

Fig. 1. Site locations in the Victorian alps, south-eastern Australia, with fire frequency of the region and terrain (source: STAMEN terrain) shown as base layers and major towns (black dots). LUB = long unburnt (n = 8), SHS = single high severity (n = 9), DHS = double high severity (n = 24), THS = triple high severity (n = 9) fires between 1998 and 2020. LUB areas on the map have been left transparent.

the trunk, and canopy-stored seed. The high elevation mixed species canopy (dominated by *Eucalyptus dalrympleana* and *E. pauciflora*) sometimes included *E. delegatensis*, *E. dives* (broad-leaved peppermint), or *E. radiata* (narrow-leaved peppermint, Table S2). Because this forest type is dominated by canopy species that can recover via resprouting, it often has mature trees which survived multiple severe fires (Fairman et al., 2019). A total of 50 sites were selected across the study region, based on forest type (alpine ash n = 33, mixed n = 17), and fire frequency (Fig. 1). Some alpine ash sites (n = 14) were sown with *E. delegatensis* seed within 12 months of a fire occurring in 2013 to aid in forest recovery (Table S2). The occurrence of *E. delegatensis* stems in sowed plots is unlikely to have a significant impact on the understorey or soil seed bank composition. Singh et al. (2023b) found that the density of *E. regnans* regrowth (functionally and morphologically similar) had no significant effect on the community composition of aboveground or soil seedbank pools in lower elevation temperate wet forest sites.

2.3. Survey methods

Field surveys were conducted in two field campaigns between October 2020 to March 2021 and in January and February 2022. At each site, a 50 × 10 m survey plot was established and divided into five 10 × 10 m subplots where a range of measurements on the effects of increased fire frequency and severity on montane forest structure and ecosystem values (Fig. S1). Plots were located at least 60 m from roadsides and orientated to follow the contour of the landscape. Plot location, slope, aspect, and elevation were recorded at the origin point of plot establishment (0,0, see Fig. S1). Within five floristics sub-quadrats (10 × 2 m along one edge of each subplot), all observed vascular species were recorded, providing a plot-level frequency of 0–5 per species. This formed the dataset for the “extant vegetation” pool. Soil samples for soil seed bank trials were also retrieved from these floristics quadrats, using a bulb corer (6.84 cm diameter). Following the removal of the litter layer, six samples were taken randomly to a depth of 5 cm from each of the five quadrats, totalling a surface area of 1102 cm^2 per site. These were bulked to provide a single composite soil sample per site.

2.4. Soil seed bank greenhouse trial

Soil seed bank samples were air-dried at ambient temperature and sieved to pass an 8 mm screen to concentrate the seed in a smaller volume of soil (Bossuyt et al., 2000). Soils underwent cold-moist stratification at 4 °C for two weeks. Each sample was divided into four equal samples and treated with smoke (with or without heat treatments) or left untreated (control). The “low” heat treated soils reached 40–50 °C in an oven for approximately 30 min, while the “high” heat treated soils reached 90 °C for 60 min. The smoke treatment consisted of vermiculite infused with concentrated smoke extract (Regen 2000 germinator, Grayson Trading Australia, Bayswater) and applied at the recommended concentration of 100 ml m^{-2}. Treatments were applied to simulate the range of natural post-fire germination conditions and achieve as close to a complete picture of the germinable soil seed bank as possible (Younis and Kasel, 2023). Samples were spread to a maximum depth of 2 cm in seed-germination trays over sterilised pine bark. Four control trays were also prepared, two with only pine bark, and two with pine bark and smoke treatment, for an assessment of potential glasshouse contaminants. Trays were placed in a climate-mediated glasshouse (16 °C at night and 22 °C during the day) with automatic irrigation. As seedlings emerged, their species was identified, or (in few cases), to genus level, and removed from the trays. When germination appeared to have ceased, gibberellic acid (200 mg l^{-1}) was applied at a rate of 30 ml per tray for five days (Hoyle et al., 2013) to stimulate further seedling emergence (Vandvik et al., 2016). The soil seed bank trial was split across two periods that reflected the two field campaigns. The first trial was conducted from September 2021 to January 2023 (17 months) and the second from February 2022 to March 2023 (13 months). There was no attempt to account for any ungerminated seed at the end of each trial.

2.5. Species and trait data preparation

To identify key plant functional groups (PFGs), we first sourced trait information for each species identified in the extant vegetation and soil seed bank. We extracted trait information from government databases, published literature, and the AusTraits database (Kasel et al., 2017, 2022; Falster et al., 2021). Traits included fire response, dispersal mode, life form, plant growth form, life history, species origin, clonal spread, and nutrient uptake strategy (Tables S3, S4). Traits were chosen to capture response to disturbance, including fire tolerance/post-fire recolonisation, structural changes, successional processes, and the identification of incursions of exotic species. Where species were only identified to genus (37 in total), attributes common to all likely species of the genus were assigned, or otherwise left blank where trait information was missing. Here, we define the understorey species very broadly as any species which were not part of the *Eucalyptus* canopy. We excluded eight species of eucalypts from analysis, and for the traits analysis, excluded 13 species with missing trait information (Table S3). We acknowledge that *Acacia* can form part of the overstorey in eucalypt forest. However, as we were interested in potential changes in *Acacia* dominance with fire frequency (Colloff et al., 2016; Fairman et al., 2017; Bowd et al., 2021a, 2023), they were retained in the data.

2.6. Statistical analyses

We examined fire frequency (four categories: long unburnt, single high-, double high- and triple high severity) and forest type (two categories: alpine ash, mixed) effects on three levels of data aggregation: (i) all species; (ii) fire response strategy; and (iii) plant functional groups. Analysis considered three species pools: (i) extant vegetation, (ii) soil seed bank; and (iii) the combined pool (extant vegetation plus the soil seed bank). Analysis of fire response and functional groups considered both presence-absence and abundance data. Analysis of the combined species pool was limited to presence-absence data to avoid problems commonly associated with different sampling techniques and measures of abundance for extant vegetation and the soil seed bank (Vandvik et al., 2016). For extant vegetation, abundance was represented by frequency of occurrence in the five sub-plots per site. For the soil seed bank, the abundance measure was standardised (division by the total) and count of germinants were log-transformed log $(x + 1)$ (Anderson et al., 2005; Burrows et al., 2019). All analyses were conducted in R version 4.2.2 (R Core Development Team, 2022) with the packages *cluster*, *pariwiseAdonis* and *vegan* (Martinez Arbizu, 2017; Oksanen et al., 2020; Maechler et al., 2021). We utilised the standard significance level of $\alpha = 0.05$.

2.6.1. Plant species diversity

Two-way ANOVAs were used to test for significant differences in species richness and diversity as a function of fire frequency and forest type. For significant relationships, Tukey Honest Significant Differences were applied to examine pairwise differences. Diversity (*H*) was calculated using Shannon's diversity index (Shannon, 1948). We also tested for significance of effects of time since last (high severity) fire (TSF) on species richness and *H*' to account for possible confounding effects of TSF on fire frequency given differences in TSF with fire frequency (Table S1). We employed general linear models and considered an interaction between TSF and forest type or fire frequency.

2.6.2. Species composition

PERMANOVA tested for fire frequency and forest type effects on species composition utilising Bray-Curtis dissimilarity of the species presence-absence and abundance matrices (999 permutations, Bray and Curtis, 1957). Where significant, we further tested for differences using pairwise PERMANOVA. In the case of a statistically significant interaction term between fire frequency and forest type, we considered fire frequency effects within each forest type using one-way PERMANOVA. SIMPER analyses produced pairwise dissimilarity percentages for significant pairwise effects and identified species which contributed most strongly to the dissimilarity.

2.6.3. Fire response strategy

Significance of effects of forest type and fire frequency on the frequency and abundance of species within each fire response strategy (resprouters, seeders, and facultative resprouters), followed the approach used for plant species diversity.

2.6.4. Plant functional groups

We used cluster analyses to identify key plant functional groups. Flexible beta clustering (Sneath and Sokal, 1973; Meers et al., 2010) of a Bray-Curtis dissimilarity matrix of species versus traits was used to produce an optimal cluster solution. Selection was based on examination of the fusion levels, Calinski-Harabasz indices and visual screening of the clusters. Significance of effects of forest type and fire frequency on the frequency and abundance of plant functional groups followed the approach used for species composition.

3. Results

3.1. Plant species diversity

We identified a total of 253 species from 61 plant families across all fire frequencies and forest types (Table S3). There were 133 species unique to the extant vegetation, 47 species unique to the soil seed bank, and 82 species shared between soil seed bank and extant vegetation (Fig. S2). A total of 6223 germinants emerged from the soil seed bank. There was no significant difference in species richness between forest types ($F = 0.44$, $P > 0.5$) and no significant change in the species richness of the extant vegetation or combined pool with fire frequency. In the soil seed bank, richness declined significantly with more frequent fire across both forest types, reducing from a mean of 19.1–10.7 species per site (Fig. 2). *H*' and species richness in the soil seed bank increased significantly with time since last (high severity) fire (TSF, Table S5, Fig. S3). There was no significant interaction of TSF with forest type or fire frequency, and no significant effects of TSF on richness or *H*' of extant vegetation or the combined species pool (Table S5).

Shannon's diversity (*H'*) did not differ significantly between forest types for both the extant vegetation and the soil seed bank. *H'* of the extant vegetation was non-responsive to frequent fire across both forest types, while *H'* of the soil seed bank pool reduced significantly with fire occurrence regardless of forest type (Fig. 3).

3.2. Species composition

There was a shift in species composition across all three species pools with fire frequency and forest type but there were no interaction effects (Tables 1, S6). SIMPER analyses identified species which contributed most to the between-site dissimilarity. For extant vegetation, this included an increase in *Cassinia aculeata*, *Viola betonicifolia* and *Acacia obliquinervia* and decrease in *Polystichum proliferum* and *Tasmannia lanceolata* in burnt relative to LUB sites (Table 1). Abundance data mirrored these trends with a decline however in *Viola betonicifolia* in THS relative to LUB (Table S6). For the soil seed bank and combined species pools, there was a decline in *Hydrocotyle hirta* and *Geranium potentilloides* and an increase in *Poa hothamensis* var. *hothamensis* and *Poa ensiformis* in burned sites relative to LUB (Table 1). This was consistent with abundance values in the soil seed bank (Table S6). Dissimilarities between fire frequency classes averaged 70% in extant vegetation and 75% in the soil seed bank and for all species' pools and were greatest in comparisons between the long unburnt and burnt assemblages and lowest between burnt classes (Tables 1, S7).

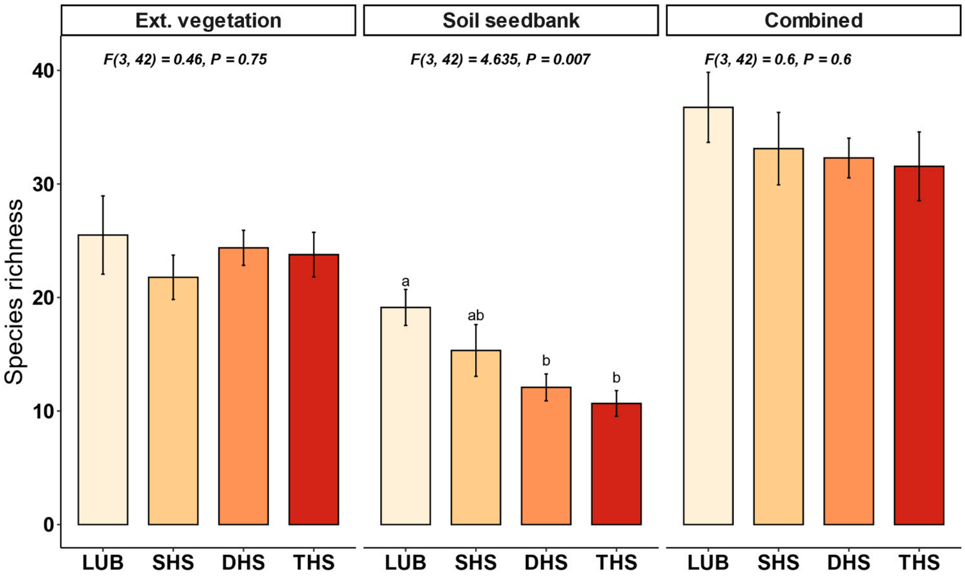

Fig. 2. Mean site species richness by fire frequency class, within the extant vegetation, the soil seed bank, and combined understory pool. Error bars indicate standard error. Letters indicate significant differences between fire frequency classes ($P \leq 0.05$), from a two-way ANOVA considering fire frequency and forest type. There were no statistically significant relationships with forest type, or interactions between forest type and fire frequency. *F* and *P* values for fire frequency effects are provided for each pool. LUB = long unburnt, SHS = single high severity, DHS = double high severity, THS = high severity fires between 1998 and 2020.

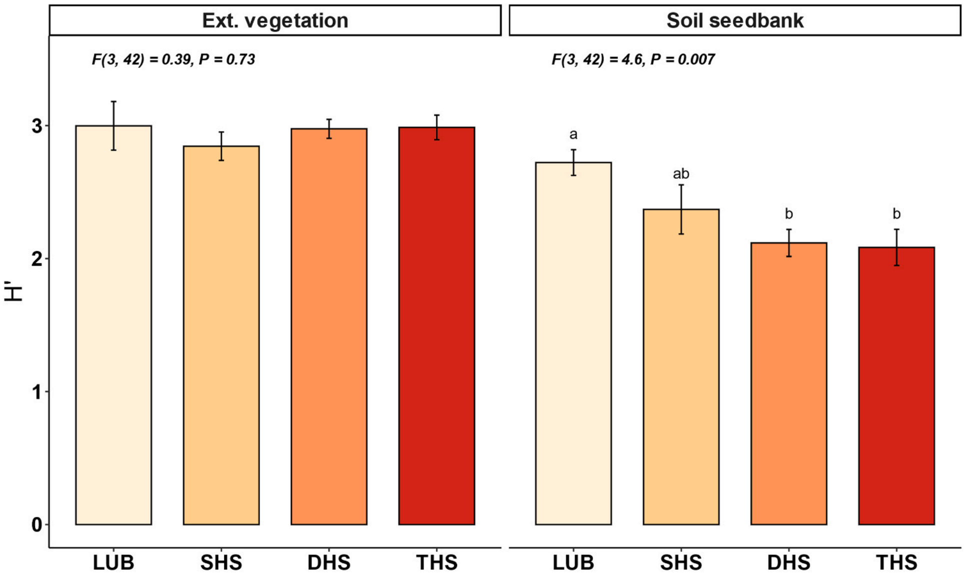

Fig. 3. Mean Shannon's diversity (***H'***) by fire frequency class, within the extant vegetation and the soil seed bank. Error bars indicate standard error. Letters indicate significant differences between fire frequency classes ($P \leq 0.05$), from a two-way ANOVA considering fire frequency and forest type. There was no statistically significant relationship with forest type, or interaction between forest type and fire frequency. *F* and *P* values for fire frequency effects are provided for each pool. LUB = long unburnt, SHS = single high severity, DHS = double high severity, THS = high severity fires between 1998 and 2020.

3.3. Fire response strategy

There was significant decline in the richness of resprouters and seeders with increasing fire frequency in the soil seed bank, but no change for extant vegetation or the combined species pool (Fig. 4). Forest type and the interaction between forest type and fire frequency did not affect richness of fire response traits across pools. There was no change in the abundance of fire response strategies between forest types, with fire frequency effects limited to extant vegetation in alpine ash, following significant forest type by fire frequency interaction effects (Table S8). For alpine ash, the abundance of seeders and facultative resprouters increased with fire frequency with THS significantly greater than LUB (Fig. S4).

3.4. Plant functional groups

Cluster analysis identified seven plant functional groups (Fig. S5) with groups containing between seven and 52 species (Tables 2, S3). Groups were named according to the most prevalent attributes or those that distinguished them from other groups (Table 2). For each species pool, there was no significant difference in the composition of plant functional groups between forest types and no interaction with fire frequency (Table 3). Across all species pools, clonal resprouters, upright herbs, shrubs and trees and wind-dispersed perennials made the greatest contributions to differences with fire frequency. The frequency of clonal resprouters decreased with increasing fire frequency while the frequency of upright herbs increased with this trend consistently across all

Table 1

Significance of forest type (FT), fire frequency (FF) and interaction effects on species composition in the soil seed bank, extant vegetation, and combined species pool based on presence/absence data. Significant pairwise differences ($P \leq 0.05$) are provided for fire frequency effects along with the top three species contributing to dissimilarity following SIMPER analysis.

Fire frequency comparison	Dissimilarity (%)	Species	Contribution to dissimilarity (%)	Change in mean frequency with increase in fire frequency (%)
Extant vegetation				
Forest type $F(1, 42) = 3.14$, $P = 0.002$; Fire frequency $F(3, 42) = 2.43$, P 0.001; FT × FF $F(3, 42) = 1.27$, $P = 0.147$				
LUB vs. SHS*	74.1	*Tasmannia lanceolata*	1.7	-62
		Stellaria spp.	1.5	+41
		Acacia obliquinervia	1.4	+30
		Viola betonicifolia	1.3	+43
LUB vs. DHS***	77.5	*Cassinia aculeata*	1.8	+66
		Tasmannia lanceolata	1.6	-62
		Polystichum proliferum	1.5	-64
		Acacia obliquinervia	1.3	+37
LUB vs. THS**	76.8	*Viola betonicifolia*	1.9	+76
		Cassinia aculeata	1.7	+64
		Arthropodium milleflorum	1.7	+64
		Acacia obliquinervia	1.6	+64
Soil seed bank				
Forest type $F(1, 42) = 2.9$, $P = 0.001$; Fire frequency $F(3, 42) = 2.31$, $P = 0.001$; FT × FF $F(3, 42) = 1.29$, $P = 0.11$				
LUB vs. SHS**	76.8	*Geranium potentilloides*	3.0	-75
		Poa ensiformis	2.5	+51
		Carex breviculmis	2.5	-41
		Hydrocortyle hirta	2.5	-52
LUB vs. DHS***	75.7	*Poa hothamensis* var. *hothamensis*	3.7	+83
		Carex breviculmis	3.0	-54
		Geranium potentilloides	3.0	-58
		Hydrocotyle hirta	2.9	-63
LUB vs. THS**	78.1	*Geranium potentilloides*	3.4	-75
		Hydrocotyle hirta	2.9	-63
		Carex breviculmis	2.8	-53
		Poa hothamensis var. *hothamensis*	2.7	+54
SHS vs. DHS*	73.8	*Poa ensiformis*	3.1	-43
		Euchiton involucratus	3.0	+32
		Gonocarpus montanus	2.9	-22
		Luzula meridionalis var. *flaccida*	2.5	-18
Combined pool				
Forest type $F(1, 42) = 3.47$, $P = 0.002$; Fire frequency $F(3, 42) = 2.465$, $P = 0.001$, FT × FF $F(3, 42) = 1.24$, $P = 0.133$				
LUB vs. SHS*	71.5	*Coronidium monticola*	1.4	+77
		Hydrocotyle hirta	1.3	-64
		Geranium potentilloides	1.3	-75
		Tasmannia lanceolata	1.3	-62
LUB vs. DHS***	71.2	*Poa hothamensis* var. *hothamensis*	1.6	+83
		Hydrocotyle hirta	1.4	-71
		Acacia dealbata	1.3	-67
		Geranium potentilloides	1.2	-58
LUB vs. THS***	71.5	*Hydrocotyle hirta*	1.5	-76
		Viola bentonicifolia	1.4	+76
		Geranium potentilloides	1.3	-75
		Arthropodium milleflorum	1.3	+62

Fire frequency classes: LUB = long unburnt, SHS = single high severity, DHS = double high severity, THS = high severity fires between 1998 and 2020. (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

pools. The frequency of wind-dispersed perennials and short-lived seeders and exotics increased sharply following a single fire (SHS) and, particularly in the soil seed bank, remained elevated relative to LUB with subsequent fires (Table 3, Fig. S6). There was a decline in frequency of shrubs and trees following SHS, with some recovery with subsequent fire (Table 3). Analysis of abundance data mirrored that for frequency in both extant vegetation and the soil seed bank, although significant differences were limited to the extant vegetation (Table S10).

4. Discussion

Consistent with our hypotheses there was a decline in plant diversity with frequent high severity fire. However, this decline was limited to the soil seed bank that buffered potential effects of increased fire frequency on extant vegetation via their rescue effect. We did not find an increase in diversity following single high-severity fire, contrary to our expectations, although the relative proportion of short-lived seeders increased rapidly following SHS fire. Contrary to our hypothesis, fire frequency effects on understorey diversity were largely consistent among forest types, with differences limited to increases in abundance of seeders and facultative resprouters with increased fire frequency in alpine ash stands.

4.1. Fire frequency effects on species diversity

A major finding of our study is the loss of species richness and complexity in the soil seed bank, with increasing frequency of severe

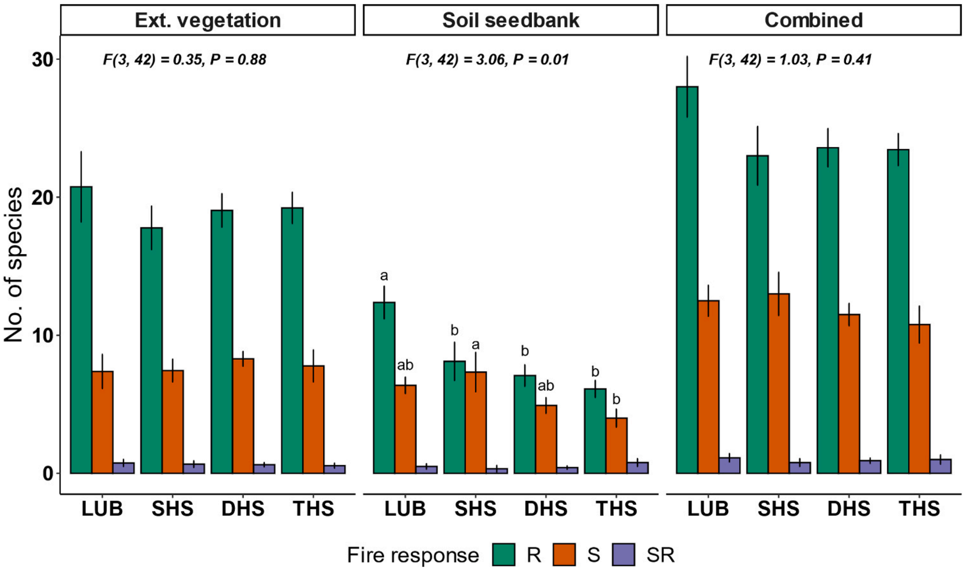

Fig. 4. Fire frequency effects on the mean number of species per site, according to fire response strategy. Values are mean number of species (R = resprouter; S = seeder; SR = facultative resprouter) for extant vegetation, soil seed bank and combined species pools. Error bars indicate standard error. Letters indicate significant pairwise differences between fire frequency classes ($P \leq 0.05$) within each fire response strategy. The two-way ANOVA found no statistically significant relationship with forest type, or interaction between forest type and fire frequency. *F* and *P* values for fire frequency effects are provided for each pool. LUB = long unburnt, SHS = single high severity, DHS = double high severity, THS = high severity fires between 1998 and 2020.

Table 2
Characteristics plant traits of the identified plant functional groups. Values represent the proportion of the most characteristic attribute within each group.

	Shrubs and trees	Clonal resprouters	Partial rosette seeders	Upright herbs	Short-lived seeders and exotics	Wind-dispersed perennials	Orchids
Number of species	40	56	17	52	34	34	7
Dispersal mode	myr (0.42)	bar (0.39)	bar (0.35)	bar (0.46)	ane (0.59)	ane (0.91)	**mob (1.0)**
Life form	**P (1.0)**	HPr (0.29)	**HPr (0.71)**	HE (0.73)	**T (0.70)**	P (0.56)	**G (1.0)**
Nutrient uptake strategy	AM (0.30)	AM (0.89)	AM (0.64)	AM (0.81)	**AM (0.88)**	**AM (0.97)**	**OM (1.0)**
Fire response	R (0.67)	**R (0.93)**	**S (0.94)**	**R (0.87)**	**S (1.0)**	R (0.53)	**R (1.0)**
Clonal spread	**NC (0.97)**	**C (0.93)**	NC (0.64)	**NC (0.92)**	**NC (1.0)**	**NC (0.94)**	C (0.85)
Life history	**P (1.0)**	**P (0.98)**	**P (0.71)**	**P (1.0)**	A (0.47)	**P (1.0)**	P (1.0)
Species origin	**N (1.0)**	**N (0.96)**	**N (0.76)**	**N (0.92)**	N (0.50)	**N (0.94)**	N (1.0)
Growth form	S (0.52)	H (0.39)	H / LH (0.41)	MTG (0.27)	H (0.50)	H (0.35)	H (0.43)
Most representative species	*Coprosma hirtella* *Acacia obliquinervia* *Podolobium alpestre*	*Dianella tasmanica* *Poa ensiformis* *Stellaria pungens*	*Acetocella vulgaris* *Wahlenbergia capillaris* *Galium gaudichaudii*	*Poa hothamensis* var. *hothamensis* *Luzula meridionalsi* var. *flaccida* *Gonocarpus montanus*	*Senecio linearifolius* *Poranthera microphylla* *Senecio linearifolius* var. *denticulatus*	*Cassinia aculeata* *Cassinia longifolia* *Senecio prenanthoides*	*Chiloglottis valida* *Caladenia alpina* *Microtis* spp.

Dispersal mode: ane, anemochory; bar, barochory; mob, mobile seed; myr, myrmecochory. Nutrient uptake strategy: AM, arbuscular mycorrhizal; OM, orchid mycorrhizal. Fire response: R, resprouter; S, seeder. Clonal spread: C, clonal; NC, non-clonal. Species origin: N, native. Growth form: S, shrub; H, herb; LH, large forb/herb; MTG, medium tufted grass/sedge. Definitions are provided in Table S4. The four traits making the greatest contributions to within group similarity are bolded (as determined via SIMPER analysis). Most representative species defined as those most frequent across the combined species pool (see also Table S3).

wildfires, while the species diversity of the extant vegetation was unaffected. The relative consistency of the plant diversity in the extant vegetation and combined pools may indicate a balancing effect between resource availability and competition (Chesson, 2000). High levels of disturbance have been found to have divergent impacts on species diversity. For Californian shrublands, Keeley et al. (2005) reported an increase in species richness with fire. Zou et al. (2021) found soil seed bank diversity was greatest in both old-growth forest and early successional stages in subtropical forests of China and Sanou et al. (2018) observed that greater levels of disturbance due to grazing led to reduced plant diversity in riverbank communities in Burkina Faso. Differences in responses may be due to the presence or absence of storage effects that influence diversity patterns (Chesson, 2000). The positive effect on time since last fire on soil seed bank richness and *H*' suggests many of the species rely on germination from a long-term soil seed bank for persistence (Gill, 1981b). The depletion in richness and *H*' under frequent fire suggests germination is promoted via heat shock and/or chemicals in smoke (Keeley and Fotheringham, 2000), or postfire conditions of increased resource (e.g., light, water, nutrients) availability (Pausas and Keeley, 2014; Vivian and Cary, 2012).

The lack of response in species richness in the extant vegetation and combined pools may be attributed to the soil seed bank functioning as a buffer to change, maintaining alpha diversity in the aboveground assemblage through disturbances (Vandvik et al., 2016; Plue et al., 2021). However, the decline in Shannon's diversity in the soil seed bank suggests this buffering capacity is likely unsustainable in the longer term and we may have observed an example of the concept of a "resilience debt" (Johnstone et al., 2016), where the repercussions of an intolerable shift in disturbances are not immediately apparent, and the plant community may appear more resilient than it actually is. If the current

Table 3

Significance of forest type and fire frequency effects on plant functional groups in extant vegetation, the soil seed bank and the combined species pool. Values represent the mean proportion of species. There was no significant ($P > 0.05$) interaction between forest type and fire frequency. SIMPER tests provided the mean contribution to dissimilarity for significant pairwise comparisons. Bold values indicate the three functional groups that contributed most strongly to dissimilarity for each pairwise comparison.

	Forest type		Fire frequency^A				Dissimilarity %				
Species pool/ Functional group	Alpine ash	Mixed species	LUB	SHS	DHS	THS	LUB vs. SHS	LUB vs. DHS	LUB vs. THS	SHS vs. DHS	SHS vs. THS
Extant vegetation	*F(1, 42) = 0.99, P = 0.41*		*F(3, 42) = 2.31, P = 0.017*				33.3 *	33.5 * *	34.2 * *	n.s.	26.3 *
Clonal resprouters	30.0	29.4	42.2	32.1	27.2	22.6	**34.1**	**33.8**	**35.4**	-	**23.1**
Orchids	0.4	1.9	2.5	0.5	0.5	0.9	4.0	3.8	3.9	-	2.5
Partial rosette seeders	3.4	1.4	1.0	3.6	2.9	2.8	5.5	4.8	4.2	-	6.8
Short-lived seeders and exotics	6.7	5.9	3.9	8.2	6.3	7.5	9.3	8.0	8.4	-	12.7
Shrubs and trees	20.2	21.3	23.0	19.4	20.2	20.3	**17.6**	**15.3**	14.1	-	14.7
Upright herbs	19.0	21.3	15.2	16.8	20.5	25.0	11.7	15.2	**18.3**	-	**19.8**
Wind-dispersed perennials	20.4	18.7	12.3	19.4	22.3	20.8	**17.8**	**19.0**	**15.5**	-	**20.4**
Soil seed bank	*F(1, 42) = 2.0, P = 0.11*		*F(3, 42) = 3.3, P = 0.001*				40.2 * *	42.0 * **	42.0 * **	41.0 *	40.0 *
Clonal resprouters	28.5	30.2	43.1	27.0	24.7	22.9	**21.6**	**43.6**	**47.2**	21.8	**21.6**
Orchids	0.0	0.9	0.7	0.7	0.0	0.0	0.8	0.9	1.0	0.8	0.8
Partial rosette seeders	10.2	12.0	10.5	8.0	11.5	13.5	10.6	7.8	8.5	9.0	10.6
Short-lived seeders and exotics	8.5	9.3	4.6	14.6	9.0	6.2	16.2	6.1	3.4	**16.7**	16.2
Shrubs and trees	8.2	9.3	9.2	7.3	9.0	8.3	8.4	**11.2**	**11.2**	9.3	8.4
Upright herbs	30.5	27.6	23.5	24.8	33.0	35.4	**22.7**	**20.4**	**16.5**	**26.0**	**22.7**
Wind-dispersed perennials	14.0	10.7	8.5	17.5	12.8	13.5	**19.5**	10.0	12.2	**16.3**	**19.5**
Combined pool	*F(1, 32) = 0.44, P = 0.8*		*F(3, 42) = 2.37, P = 0.008*				28.0 * *	27.3 * *	26.7 * *	n.s.	24.5 *
Clonal resprouters	28.5	28.7	39.2	28.6	26.4	22.9	**31.1**	**37.2**	**43.5**	-	**20.5**
Orchids	0.3	1.7	2.0	0.7	0.4	0.7	3.7	3.8	4.0	-	2.2
Partial rosette seeders	6.0	5.4	5.6	5.2	6.1	5.7	6.1	6.0	6.5	-	7.5
Short-lived seeders and exotics	7.8	8.0	4.9	12.4	7.7	7.2	12.5	8.8	7.0	-	16.6
Shrubs and trees	16.2	17.2	18.0	14.1	16.6	17.6	**16.0**	13.7	**12.9**	-	13.6
Upright herbs	23.6	22.8	19.0	20.7	24.4	28.0	**15.6**	**15.7**	**14.4**	-	**22.2**
Wind-dispersed perennials	17.6	16.0	11.4	18.3	18.4	17.9	15.0	**14.8**	11.9	-	**17.3**

PERMANOVA tested for differences in Bray-Curtis distance between forest type, fire frequency, and their interaction based on presence/absence data. Significant pairwise comparisons are indicated (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, **** $P \leq 0.0001$, n.s. not significant). ^{A} Fire Frequency: LUB = long unburnt, SHS = single high severity, DHS = double high severity, THS = high severity fires between 1998 and 2020.

increase in the fire frequency in the Australian temperate montane regions continues as forecasted (Enright et al., 2015; Harrison et al., 2021), there may be losses in the aboveground plant diversity due to soil seed bank depletion and loss of the storage effect (Chesson, 2000; Angert et al., 2007).

Despite the lack of fire frequency effects on alpha diversity in the extant vegetation and combined understorey pools, there was evidence of species compositional change (i.e., beta diversity) across pools. The long-unburned sites were particularly different in species assemblage compared to burnt forests which is not unexpected. Fire is known to rapidly change the resource availability and competition dynamics of forests, the high frequency of fire may be holding the post-fire species assemblages at earlier successional stages (Halpern and Antos, 2022), with shade- and moisture-dependent species (e.g., *Tasmannia lanceolata*) relegated to long unburned sites (Fairman et al., 2017; Kasel et al., 2022). Our findings of the impact of increased fire frequency on beta diversity is consistent with changes in plant composition reported in the region. Chick et al. (2018) found that fire frequency had an influence on species turnover in the soil seedbank in coastal woodlands in Victoria. Fairman et al. (2017) found that an increase in the number of short-interval fires changed plant composition in subalpine woodlands sites which occur at higher-elevations in our study area. These results highlight that too frequent fire in the region's forests can drive changes in species composition in both below and aboveground pools.

4.2. *Fire frequency effects on diversity of plant functional groups*

We found the greatest diversity of resprouting species in the soil seed bank in long unburnt sites, with richness declining with each subsequent fire. This loss of richness was more pronounced in the clonal resprouters plant functional group, which for all understorey pools, were consistently among the greatest contributors to dissimilarities among the fire frequency classes. This is contrary to relationships found in other studies, which suggest that resprouting and clonal species may be at an advantage when it comes to post-fire recovery (Halpern and Antos, 2022). Resprouters can persist in situ, which gives them a competitive advantage over seeders, which must establish themselves to benefit from the increase in resources after fire (Falster and Westoby, 2005). However, this is often observed in the case of low-severity or patchy fires (Ooi et al., 2006). During high-severity fires, resprouters and clonal species may be killed outright depending on the type and depth of species' perennating structures (Chapman and Crow, 1981; Halpern and Antos, 2022). For example, the abundance of species with exposed stolons (e.g., *Hydrocotyle hirta*, *Geranium potentilloides*) declined with fire frequency while those with deeply buried rhizomes (e.g., *Rubus* spp., *Pteridium esculentum* subsp. *esculentum*) contributed little to changes in species composition. Resprouters may also be at a competitive disadvantage in recolonising a burned area due to their more limited capacity for dispersal than seeders (Nelson et al., 2007; Halpern and Antos, 2022) and lower expected seed production due to trade-off in allocating resources to resprouting over seed production (Bond and Midgley, 2001; Clarke and Dorji, 2008).

The flush of nutrients, increase in light availability, reductions in herbivory, competition and seed predation that come with a severe burn, can aid recolonising species or those emerging from the seed bank (Neary et al., 1999; Wright and Clarke, 2009; Kasel et al., 2022). Severe fire can also cause the exposure of more mineral soil, which recolonising seeders can capitalise on (Halpern and Antos, 2022). This may explain the prominence of short-lived seeders and exotics, and wind-dispersed perennials in our study, which took up a greater proportion of the total species richness in burnt compared to long unburnt sites across all pools. In extensively burnt areas like the Victorian montane forests, wind dispersal is likely favoured as a mode of colonisation due to the distances that propagules can be carried (Kasel et al., 2017). While obligate seeding canopy species may be subject to immaturity risk (Doherty et al., 2017b; Chick et al., 2018) this is less likely for shorter-lived understorey species (Penman et al., 2008; Pausas and Keeley, 2014), especially when the minimum time between fires in our study was four years, and the mean time to reproductive maturity of the understorey species was about two years.

The increase in the abundance of upright herbs – particularly graminoids – in our study is not unexpected. In other south-east Australian montane forests, such as those dominated by *Eucalyptus regnans (*Blair et al., 2016*)* and *E. pauciflora* (Fairman et al., 2017), as well as *E. delegatensis* (Bowd et al., 2021b), graminoids often increased with fire frequency. Fairman et al. (2017) found that in *E. pauciflora* woodlands a change in dominance from shrubs to grasses occurred with increased frequency of high severity fire. Upright herbs were also the most abundant plant functional group in the soil seed bank. This readily available store of plant propagules, combined with the mechanisms mentioned above, particularly the increase in light availability, may be favouring these species (Blair et al., 2016).

Studies in Australia (Penman et al., 2008; Enright et al., 2015; Fairman et al., 2017; Bowd et al., 2023) and elsewhere (Vila-Cabrera et al., 2008) often observed a decrease in the abundance of shrubs and other woody species with increasing fire frequency. This was not the case for extant vegetation in our study, although there was some evidence for depletion in the soil seed bank. For extant vegetation, this trend was largely explained by the increase in abundance of *Acacia obliquinervia* and *Cassinia aculeata* in sites with more frequent fire. Both species are obligate seeders with short time to reproductive maturity (*C. aculeata* 3 years; *A. obliquinervia* 5–10 years) and long-term persistent soil seed banks (Falster et al., 2021). These observed responses for these obligate seeders and the above-mentioned short-lived seeders plant functional group align with the theoretical predictions from the model of Pausas and Keeley (2014) highlighting that frequent fire in temperate climates can favour obligate seeders where immaturity risk is low or non-existent.

Like many of the species in the shrubs and trees plant functional group, *Acacia* seed is ant-dispersed with seed burial by ants and hard seed coats providing for long-term persistent seed banks that accumulate over time and germinate in response to heat from fire (Berg, 1975; Auld and O'Connell, 1991; Palmer et al., 2018; Kasel et al., 2022). The poor representation of *Acacia obliquinervia* in the soil seed bank, and shrubs and trees more broadly (just 14 of 40 species), point to the dual effect of frequent plus high severity fire in limiting seed recruitment (Palmer et al., 2018). With fire regimes predicted to intensify across south-eastern Australia (McColl-Gausden et al., 2022), further depletion of already limited residual soil seed stores are likely to manifest in further changes to the occurrence and abundance of shrubs and trees in the extant vegetation.

4.3. Implications for forest management

Even with the lack of evidence provided by measures of species diversity in the extant vegetation, declines in soil seed bank richness and shifts in plant functional composition in both soil seed bank and extant vegetation provide clear indication of changes in understorey plant diversity due to emerging fire regimes. Despite differences in fire response strategies of dominant canopy species, the response of understorey plant diversity to frequent, high severity fire was largely consistent among forest types and apparent after a single high severity fire. These findings suggest that broad-scale classification of forests into fire response types do not provide a strong basis for supporting measures of plant diversity conservation.

Increases in abundance of *Acacia* spp. in response to shifts in disturbance regimes are well documented for obligate seeder forests, and typically characterised as a state change to "*Acacia* shrubland" (Colloff et al., 2016; Doherty et al., 2017b). Flow on effects to ecosystem services (Le Maitre et al., 2011) and understorey plant diversity, including decline in species richness and species turnover (Bowd et al., 2023; Singh et al., 2023a, 2023b, 2023c) are well documented. Significantly, our finding for increased potential for local extirpation of *Acacia* seed banks may further advance the shift to a more open and grass-dominated forest (McKimm and Flinn, 1979; Broadhurst and Young, 2006).

The shift in prevalence of species characteristic of early successional states (e.g., grasses) has likely implications for increased flammability of these forests, particularly in a warming and drying climate (Prior et al., 2017). Other work in sub-alpine *Eucalyptus pauciflora* forests point to greater potential for repeat and more extensive burns in forest that has previously been burnt (Zylstra, 2013) and for dry eucalypt forests, high severity fire high severity fire promotes further fire of high severity (Barker and Price, 2018). These intrinsic drivers of future fire are more contested for other forest types including montane obligate seeding forest where climate and fire weather dictate shifts to fire regimes (Bowman et al., 2016). More broadly, likely shifts in fire regime across a range of eucalypt forests are a product of aridity effects on potential availability of fuel to burn (McColl-Gausden et al., 2022). These potential positive feedbacks between past fire and future fire, in interaction with climate change suggest likely future fire for frequently burnt forests and increase in extent in areas burnt at even higher frequency (e.g., four to five times; Lindenmayer and Taylor, 2020). Our work demonstrates that resprouter forests are not immune to these changes and raises significant questions of whether artificial re-seeding programs should extend beyond the current focus on obligate seeding forests and an obligate seeding tree species.

Research permit

This research was conducted with an access agreement for parks and reserves from Parks Victoria and a research permit for state forests issued by the Victorian Department of Energy, Environment and Climate Action.

Funding statement

Funding for the Montane Values project was provided by the Victorian Government Department of Energy, Environment and Climate Action (DEECA), and as part of the Integrated Forest Ecosystem Research (IFER) program (Grants: C2019-22:03, S2020:06, S2020:08). BW and CRN acknowledge funding from the Australian Department of Climate Change, Energy, the Environment and Water (Grant: MSSPI000021). CRN and SK acknowledge funding through the Integrated Forest Ecosystem Research (IFER) program of DEECA.

CRediT authorship contribution statement

Kasel Sabine: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Supervision, Validation, Writing – review & editing. **Nitschke Craig R.:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Duivenvoorden Emily:** Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Wagner Benjamin:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

All authors contributed to the drafts and gave final approval for publication. There are no conflicts of interest or competing interests to declare.

Data availability

The codes and datasets supporting the findings of this research will be deposited onto a publicly accessible Github repository.

Acknowledgements

We recognize and acknowledge the traditional owners of the lands on which this research was conducted: The Wurundjeri, Gunaikurnai, Taungurung and Bidwell people. We pay our respects to their Elders, past, present, and emerging. This work was part of the broader Montane Values project, and we would like to gratefully acknowledge everyone who has contributed in the field and laboratory. Thanks to Ben Smith, David Lockwood, Bernard Gandy, Yogendra Karna, Bang Trang, Anu Singh, Kaitie Hammond, Jeremy Johnson, Claudia Giraldo, Emily McIntyre and Harry Barton for their work on the project. Further gratitude goes to Matthew Burns. We thank the two anonymous reviewers for their comments that improved our manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121627.

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