Future fire regimes increase risks to obligate-seeder forests

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Abstract
Aim: Many species are adapted to a particular fire regime and major deviations from that regime may lead to localized extinction. Here, we quantify immaturity risks to an obligate-seeder forest tree using an objectively designed climate model ensemble and a probabilistic fire regime simulator to predict future fire regimes.

Location: Alpine ash (Eucalyptus delegatensis) distribution, Victoria, south-eastern Australia.

Methods: We used a fire regime model (FROST) with six climate projections from a climate model ensemble across 3.7 million hectares of native forest and non-native vegetation to examine immaturity risks to obligate-seeder forests dominated by alpine ash (Eucalyptus delegatensis), which has a primary juvenile period of approximately 20 years. Our models incorporated current and future projected climate including fuel feedbacks to simulate fire regimes over 100 years. We then used Random Forest modelling to evaluate which spatial characteristics of the landscape were associated with high immaturity risks to alpine ash forest patches.

Results: Significant shifts to the fire regime were predicted under all six future climate projections. Increases in both wildfire extent (total area burnt, area burnt at high intensity) and frequency were predicted with an average increase of up to 110 hectares burnt annually by short-interval fires (i.e., within the expected minimum time to reproductive maturity). The immaturity risk posed by short-interval fires to alpine ash forest patches was well explained by Random Forest models and varied with both location and environmental variables.

Main conclusions: Alpine ash forests are predicted to be burned at greater intensities and shorter intervals under future fire regimes. About 67% of the current alpine ash distribution was predicted to be at some level of immaturity risk over the 100-year modelling period, with the greatest risks to those patches located on the periphery of the current distribution, closer to roads or surrounded by a drier landscape at lower elevations.

Keywords: climate change, Eucalyptus, fire management, fire regime, risk, wildfire
1 | INTRODUCTION

Interactions between climate and fire have substantial impacts on vegetation communities at landscape scales (Collins et al., 2007; Loehman et al., 2020). Climate is central to the four conditions of fire occurrence, namely, sufficient fuel (as live and dead plant mass), availability of fuel (dryness), fire weather and an ignition source (Archibald et al., 2009; Bradstock, 2010; Clarke et al., 2020). Therefore, climate has a strong influence on the spatial and temporal distribution of fires across landscapes. For example, during a fire there are immediate impacts of local weather on fire activity (mostly via wind; Coen et al., 2018). In the months preceding a fire, low precipitation can lower the fuel moisture content of both live and dead fuels increasing the likelihood of ignition (Abatzoglou et al., 2018; Nolan et al., 2016) and the connectivity of available fuels (Caccamo et al., 2012; Nolan, Boer, et al., 2020). In the years before a fire, prolonged drought conditions may also increase flammability at certain thresholds when leaf cavitation and shedding turns live fuels into dead fuels, which are easier to ignite (Nolan, Blackman, et al., 2020). Conversely, increased precipitation may increase plant productivity and associated biomass particularly where grass is the dominant fuel type, therefore increasing the subsequent likelihood of ignition and fire spread (Westerling et al., 2002). Over longer time periods, climate is a key driver of biome distributions including through feedbacks with changing fire regimes and vegetation–community attributes (Archibald et al., 2018; Bowman et al., 2020; Murphy et al., 2013). These complex feedbacks are unlikely to play out evenly across a landscape, with, for example, topographic position influencing vegetation traits and flammability, as well as fire exposure (Hoecker et al., 2020; Holden & Jolly, 2011; Wood et al., 2011). Probabilistic landscape-level models are therefore useful tools to understand the drivers of vegetation change within and between communities.

Fire-dependent plant species, such as obligate seeders (i.e., species that are killed by fire and recruit from seed), are particularly vulnerable to altered fire frequencies (Pausas & Keeley, 2014). They require specific fire-free intervals for post-fire regeneration to reach maturity (Keith, 1996). Shortening fire-return intervals may lead to the loss of these species from some landscapes (Johnstone & Chapin, 2006; Westerling et al., 2011) with flow-on impacts to forest composition and habitat for dependent fauna species (Jones et al., 2016). Globally, many forests are dominated by obligate seeders including boreal and subalpine forests of Eurasia and North America (Turner et al., 2019), conifer forests in Mediterranean regions (Núñez & Calvo, 2000), and the wet eucalypt forests of temperate Australia (Bowman et al., 2016). A shortening of inter-fire intervals increases plant “immaturity risk” whereby species are less likely to reach reproductive maturity before the next fire (Enright et al., 2015). This risk can be exacerbated by warmer and drier climates where they reduce species recruitment, growth and survival, and increase the likelihood of regeneration failure (Harvey et al., 2016; Stevens-Rumann et al., 2018). Such demographic changes coupled with more frequent fire could narrow the interval for plant reproductive maturity and survival (“interval squeeze”; Enright et al., 2015), leading to decreased chances of population persistence and increased likelihood of extinction (Enright et al., 2015; Hoecker et al., 2020). Ecosystem-level changes arising from too frequent fire can cause shifts from forest to non-forested states (Bowman, 2000) or change forest structure and function (Hayes & Buma, 2021) with evidence that frequent fire favours grass over shrub species in some forest understoreys (Andersen et al., 2005; Watson et al., 2009; Murphy & Bowman, 2012; Hammill et al., 2016; Fairman et al., 2017). Understanding where such forest changes are most likely to occur could be used to prioritize management and resource allocation for activities such as fire suppression, pre-emptive management and post-fire restoration.

Recent evidence suggests that forests dominated by obligate-seeder trees in temperate Australia may be at risk of landscape-wide state conversions if high-intensity, short-interval fires become more widespread (Bowman et al., 2014). Management interventions in the form of aerial seed sowing (Bassett et al., 2015) have already been implemented to contain the effects of recent short-interval fires on the distribution of alpine ash (Eucalyptus delegatensis R.T. Baker subspecies delegatensis), an obligate-seeder tree that dominates single-species forests in the montane zone of south-eastern Australia. Alpine ash can live for over 200 years and reach up to 90 m in height (Boland et al., 2006). Alpine ash is particularly vulnerable to shortening fire intervals through immaturity risk and associated regeneration failure as it requires 15–20 years to reach reproductive maturity (Boland et al., 2006). Two fires within a period of less than 20 years resulted in alpine ash forest conversion to acacia shrublands in isolated locations in the central highlands of Victoria in the 1990s and the 2000s (Bassett et al., 2015; Costermans, 2009), and more broadly across the Australian Alps bioregion in the south-east of Australia (Bowman et al., 2014). Similar conversions of forests to shrublands are known for other obligate-seeder forests in temperate Australia dominated by mountain ash (E. regnans; McKimm & Flinn, 1979; Ashton, 2000). The alpine nature of the alpine ash potentially compounds its risk of regeneration failure with the additional stressor of a changing climate as indicated in Europe for alpine forest species, which were adversely affected by 2°C of warming (Albrich et al., 2020).

Previous fire research in alpine ash forests has focussed on empirical investigations of seed dispersal after fire (Morgan et al., 2017), effects of fire severity and wildfire interval on regeneration and fuel characteristics (Bowman et al., 2014; Rodríguez-Cubillo et al., 2020; Gale & Cary, 2021), vegetation structure and fauna (O’Loughlin et al., 2020) and post-fire management (Bassett et al., 2015; Bowman & Kirkpatrick, 1986; Fagg et al., 2013; Grose, 1960). Although some work has considered the direct effects of climate change on the survival of alpine ash (Morgan et al., 2017), no studies have used a multidecadal landscape fire simulation framework to examine effects of changing fire regimes with changing climates on the persistence of alpine ash, despite the acknowledged threat posed by more frequent and severe wildfires (Morgan et al., 2017).

To assess the future fire risks of alpine ash forests, we used a landscape-scale fire regime simulation with six climate projections.
from a climate model ensemble to predict the effects of climate change on fire regimes and to estimate immaturity risks across the alpine ash distribution on mainland Australia. We aimed to provide a stronger basis for identifying those alpine ash forests most at risk under future fire regimes so that they can be prioritized for active management. Specifically, we aimed to:

- Provide spatially explicit predictions of future fire risk to alpine ash using a probabilistic landscape-scale fire regime simulator and alternate climate scenarios.
- Identify those alpine ash patch and landscape features associated with the greatest risks of changing fire regimes.

2 METHODS

2.1 Study area

Our study focussed on the distribution of eucalypt forests dominated by alpine ash (Eucalyptus delegatensis) on public land in the state of Victoria, south-eastern Australia, which equates to approximately 283,000 hectares. Alpine ash occurs on mountain slopes from 900 to 1,450 m above sea level and is primarily found within the Victorian Alps bioregion of Victoria (Department of Environment Land Water & Planning, 2020). Alpine ash tends to dominate subalpine areas of Tall Mist, Moist and Forby forests (Table S1). Vegetation at higher elevations is dominated by alpine treeless meadows and shrublands. The surrounding vegetation at lower elevations is varied, with a dominance of dry forest types (Grassy/Heathy Dry Woodland, Tall Mixed and Foothills forests) and non-native vegetation including plantations and agriculture (Figure 1). These broad vegetation types represent ecological fire groups (Cheal, 2010), classified according to: (a) the ecological characteristics of the vegetation (e.g., dominant species, community structure); (b) physiographic variables (e.g., soil type, annual rainfall); and (c) the dominant fire-adapted traits (Table S1).

2.2 Fire scenario modelling

We simulated fire regimes over decades to centuries using a probabilistic fire regime simulation framework, FROST (Fire Regime and Operations Simulation Tool), that combines fire behaviour simulation with BN (Bayesian network) models to capture the uncertainty around fire regimes (Penman, Chong, et al., 2015). The major components of FROST are three “machines” (subsystems): the weather machine, ignition machine and fuel machine. The weather machine uses daily weather to determine the daily number of ignitions, and hourly or half-hourly weather to simulate fire behaviour when ignitions occur (see below for weather data details). The ignition machine uses Bayesian Networks to incorporate ignition probability based on Clarke, Gibson, et al. (2019) where weather, proximity to

![Figure 1](image-url)
human settlements and infrastructure are the key drivers of ignitions. The ignition machine predicts the number and time of ignitions for each day across the simulation area. The fuel machine predicts the spatial patterns of fuel hazard for each fuel stratum (a combined measure of surface and near-surface fuel, elevated and bark). For native vegetation, this prediction is based on the empirical models of McColl-Gausden et al. (2020). These models predict fuel as a function of soils, climate and time since fire. As such, they are independent of vegetation class and therefore allow for the prediction of fuel hazard under future climates. For non-native vegetation, fuel hazard is based on fire agency-derived fuel accumulation curves based on a negative exponential equation for the particular fuel type (Olson, 1963). These “machines” provide the input data for PHOENIX RapidFire (the underlying fire event simulator) to run fires each day throughout a simulation period. Details of PHOENIX RapidFire are presented in Cirulis et al. (2020); Penman et al. (2020), and details of FROST are presented in Penman, Chong, et al. (2015).

As the simulation polygon must be rectangular, and consistent data across state borders was not available, three rectangles were used to capture as much of the alpine ash distribution as possible while minimizing areas that do not influence the fire regime. This was done for computational efficiency.

### 2.3 Climate model selection

We used weather/climate data created as part of the NARClim project (Evans et al., 2014). The NARClim project provides dynamically downscaled climate projections for south-east Australia at a 10-km resolution. The data include standard bioclimatic variables (BIOCLIM; Busby, 1991) as well as hourly weather data required for fire behaviour simulations: surface air temperature, surface specific humidity, near-surface wind speed and direction, surface wind speed and surface pressure. NARClim uses the SRES A2 emissions scenario (IPCC, 2007), which projects a warming of the planet by approximately 3.4°C by 2100 and is similar to the new scenario RCP8.5 (Moss et al., 2010). NARClim uses four global climate models (GCMs), which were selected for their accuracy and independence, and provide equally plausible, alternate climate scenarios (Evans et al., 2014). Similar criteria were used to select three regional climate models (RCMs), which were used to downscale the four GCMs, providing a better representation of features important for local and regional climate such as topography and coastlines. The resulting 12-member NARClim ensemble has been extensively evaluated and used by managers and policymakers (Clarke, Tran, et al., 2019; Di Luca et al., 2016; Evans et al., 2017; Fita et al., 2017; Olson et al., 2016). The NARClim project currently produces three 20-year time series (epochs) of data. We used the current epoch (1990–2009), and the far future epoch (2060–2079).

Due to computational constraints, we selected six of the twelve NARClim ensemble members based on independence, performance (minimizing errors) and spread of future climate change. The six ensemble members deriving from the ECHAM5 and CSIRO Mk3 GCMs were selected, as these have been found to best simulate observed mean and extreme fire weather conditions in south-eastern Australia as represented by FFDI (Forest Fire Danger Index; Clarke & Evans, 2019). FFDI incorporates many important fire weather components including temperature, windspeed, relative humidity and a component representing fuel dryness called Drought Factor (Griffiths, 1999). Drought Factor is computed using the Keetch–Byram Drought Index (Keetch & Byram, 1968) based on total daily rainfall over the previous 20 days. Across our study area, the CSIRO-Mk3 RCMs project a ~100 mm decrease in average annual rainfall and an increase of ~1.5°C average annual temperature by 2070, and the ECHAM5 RCMs project a larger increase in temperature (~2.0°C) and little change in precipitation (Figure S1). While the selected NARClim ensemble members are on the drier end of the spectrum and have larger increases in fire danger compared to the omitted ones, none of the NARClim ensemble members project substantial decreases in fire danger (Clarke, Gibson, et al., 2019). We did not select the GCM with the biggest rainfall increase (MIROC3.2) as this GCM was the lowest performing GCM for simulating FFDI (Clarke, Gibson, et al., 2019). Our selection could be viewed as the upper end of change in fire weather relative to current conditions, which allows exploration of the potential upper limits of changed fire behaviour across the study area.

### 2.4 Simulation modelling design

A diagram (Figure 2) is provided to illustrate our overall modelling process, starting with the selection of climate models and using FROST to generate fire regime data before using Random Forest modelling to evaluate the patterns of immaturity risk.

Our simulation modelling first tested the effects of climate change on the fire regime across the distribution of alpine ash. The climate epochs were as follows:

- Current climate (1990–2009) influencing fuel and fire behaviour (current)
- Future climate (2060–2079) influencing fuel and fire behaviour (future)

These two climate epochs were run for each of the six climate model ensemble members, yielding 12 scenarios in total (Figure 2). FROST was run for 120 years under each scenario to simulate effects of the set of climate and fuel conditions on the fire regime. The first 20 years of data are not used in further analysis but are run to allow for the fire regime to stabilize under the set conditions. Because the climate data contain 20 years of climate time series data, these data were looped five times to cover the 100-year simulation period. Each scenario was replicated 50 times to represent uncertainty in the fire simulations given that many conditions were probabilistic.

Outputs from FROST include local and landscape fire impacts. Local impacts record values for each cell (180m cell, 3.24 ha) in a fire.
These values include the following: fire intensity, flame height, flame depth, ember density, convection, fire weather and rate of spread. Landscape level impacts include data for the start and end time of each individual fire, and the burnt area. The simulation area covered a total area of 3,704,943 hectares of which 282,797 hectares were alpine ash-dominated forests.

2.5 Data analysis

Fire-behaviour metrics were calculated to compare the effects of current weather and fuel conditions to those predicted in the future. Annual area burnt was calculated for the alpine ash-dominated forests as the average area burned across each of the 100-year simulations. Box plots with notches were used, where non-overlapping notches are indicative of a 95% confidence interval for comparing medians (Krzywinski & Altman, 2014; McGill et al., 1978).High-intensity fire was defined as cells burnt at >5,000 kW/m (Murphy et al., 2013).

The juvenile period is where the greatest risk to alpine ash occurs. Therefore, all other aspects of alpine ash demography were held constant as it has been hypothesized that the indirect effects of a changing fire regime will pose a more immediate threat to alpine ash than the direct effects of climate change (Morgan et al., 2017). We used three different juvenile periods, encompassing the potential continuum of stand-level reproductive maturity for alpine ash, to examine effects of short-interval fires: 15, 20 and 25 years. While some individual alpine ash trees have been noted to exhibit early flowering as young as 6 years (Doherty et al., 2017), <5% of individuals exhibited early maturation in Kosciusko National Park ten years after stand-replacing fire (Doherty et al., 2017). The threshold value of 20 years to bear effective quantities of seed to achieve stand-level regeneration is widely supported (Bassett et al., 2015; Fagg et al., 2013); however, there is probably more of a continuum (Gale & Cary, 2021). Here, we are modelling stand-level reproductive maturity, not the primary juvenile period of an individual (von Takach Dukai et al., 2018). Short-interval fires were recorded as present in a cell if two fires occurred within each of the three tested juvenile periods (i.e., within the expected minimum time to reproductive maturity for an alpine ash stand). The number of 50 replicate runs per cell that included at least one short-interval fire was then used as a measure of immaturity risk within each juvenile period.
Finally, to better understand patterns of alpine ash immaturity risk, we used Random Forest models to examine associations of simulated future immaturity risk with 15 variables representing both alpine ash patch features and landscape features (Figure 2). Variables were selected on the basis of: patch-level features (area, P/A ratio, BDW, CLY, pH, bio1, bio18, canopy top height and elevation); landscape context (aridity, amount of dry forest and non-native vegetation area within a 1-km buffer); and location (distance to houses, to roads and to other patches of alpine ash; Table 1). The climate variables (bio1, bio18) were the average annual values as projected in each of the six future climate models. Our study excluded variables with a pairwise Pearson correlation higher than 0.8 (Figure S2). This analysis only used immaturity risk based on a juvenile period of 20 years as the results for 15 and 25 years were highly correlated (>0.98; Table S2). All variables were calculated in QGIS 3.6.1 or ArcGIS desktop 10.7.1 using built-in functions to calculate landscape metrics.

Random Forests (RF; Liaw & Wiener, 2002), including all 15 predictors with simulated future immaturity risk as the response variable (20-year juvenile period only, as above), were implemented for each of the six future climate models using the "randomForest" package in the R computing language (Liaw & Wiener, 2002; R Core Team, 2018). We used the RF algorithm to fit 500 regression trees per climate model with all other parameters set to default. The full dataset (2047 patches) was spatially blocked using the R package BlockCV (Valavi et al., 2019) to account for spatial autocorrelation. Block size was calculated using existing autocorrelation in the predictors as an indication of landscape spatial structure. Block size was 30 km and was divided into 10 randomly assigned folds. A training and testing fold were used for each Random Forest run. Model fit was assessed using mean square error (MSE) and R-squared (Rsq). We used permutation feature importance to determine variable importance. Higher values indicated variables were more important to the RF regression model ("varImpPlot" in R package "randomForest"; Liaw & Wiener, 2002). We used partial dependence plots in the R package "pdp" to visualize the relationship between the simulated immaturity risk and individual predictor variables (Greenwell, 2017).

3 | RESULTS

3.1 | Changes in the fire regime

Annual area burnt, high-intensity fire area and the prevalence of short-interval fires all increased across the alpine ash distribution under the six-member climate ensemble. Fire simulations showed significant increases in average annual area burnt under future climates with increases ranging from an average of 97 hectares per annum for CSIRO R1 to 345 hectares per annum for ECHAM R3 (Figure 3a). In areas dominated by alpine ash, a significant increase in the average area burnt by high-intensity fire (fire intensity > 5,000 kW/m) was also predicted (Figure 3b). Similar patterns were seen in the increase of short-interval fires under the three juvenile periods tested with average increases of up to 110 hectares burnt annually (Figure 3c). All six climate models showed significant increases in the three fire regime attributes tested, with non-overlapping notches indicating 95% confidence intervals when comparing the medians (Krzywinski & Altman, 2014).

3.2 | Spatial distribution of immaturity risk

The number of fires across the landscape varied between climate models but consistently increased in at least some areas under future climate projections (Figure 4, Figure S3, Figure S4). The simulated average number of fires in an individual cell (180 m²) across the 100-year simulation varied with a maximum of six under CSIRO R1 current to 13 under ECHAM R2 future. The majority of fires under current projections occurred in the northern portion of the simulation area, within either non-native vegetation or drier forest types such as Grassy/Heathy Dry forests or Forby forests. Under future climates, the projected number of fires increased across higher-elevation areas and the northern portion of the simulation area (Figure 4).

The simulated immaturity risk for alpine ash was not evenly distributed across the landscape and changed over time (Figure 5; future immaturity risk and standard deviations by six climate models, Figures S5-S9). Predictions of the number of short-interval fires over the 100-year period were highly correlated among the three alpine ash juvenile periods (Pearson's correlation coefficient >0.9; Table S2). Short-interval fires were most prevalent in the northern distribution of alpine ash (Figures S5-S7), with increasing immaturity risk under climate change (Figure 5). The central highlands region, the most westerly alpine ash distribution, was also an area of high predicted immaturity risk (Figures S5-S7). Between 53 and 82% of the alpine ash distribution experienced some level of immaturity risk. While there were localized differences in predicted changes to the number of short-interval fires among the six climate models, the majority indicated the potential for increased immaturity risk across the alpine ash distribution particularly on the margins of the distribution (Figure 5). The central distribution of alpine ash was consistently predicted to have little change in immaturity risk.

3.3 | Risk pattern evaluation

RF models explained 54 (CSIRO R2) to 69% (ECHAM R1) of the variation in simulated immaturity risk to alpine ash patches (20-year juvenile period) in the training set, and 13 (CSIRO R1) to 52% (CSIRO R3 and ECHAM R1) of variation in the test set (Table 2; Figure S10). Distance to roads, precipitation in the warmest quarter (bio18) and annual mean temperature (bio1), had the strongest associations with immaturity risk across the six future climate models (Figure 6). The next strongest associations were with % clay content, canopy top height and soil bulk density (Figure 6). Partial dependencies were
| Group                  | Variable (abbreviation in brackets) | Description                                                                 | Units   | Resolution (m) | Source                                                                 |
|------------------------|--------------------------------------|------------------------------------------------------------------------------|---------|----------------|------------------------------------------------------------------------|
| Patch level            | Alpine ash patch area (area_patch)   | A patch was defined as any area of alpine ash separated by at least 1 km from another vegetation type to represent the maximum seed dispersal distance (Cremer, 1977) | Hectares| NA             | (Department of Environment Land Water & Planning, 2021a)               |
|                        | Perimeter/area ratio (P/A_ratio)      | Ratio of the perimeter (km) to area (hectares) of each alpine ash patch       | NA      | NA             | data.vic.gov.au                                                        |
|                        | Mean elevation (ele_mean)             | Mean elevation of the patch                                                   | metres  | 30             | data.vic.gov.au                                                        |
|                        | Canopy top height (canopy_top_height) | Mean canopy top height in the patch                                           | metres  | 180            | DELWP                                                                  |
|                        | Annual mean temperature (bio1)        | Predicted average annual mean temperature across the 20-year epoch in the patch for each climate model | °C      | 250            | https://climatechange.environment.nsw.gov.au/Climate-projections-for-NSW/Download-datasets |
|                        | Precipitation in the warmest quarter (bio18) | Predicted precipitation in the warmest quarter across the 20-year epoch in the patch for each climate model | mm      | 250            | https://climatechange.environment.nsw.gov.au/Climate-projections-for-NSW/Download-datasets |
|                        | Soil clay content (CLY)               | Mean soil clay content in the patch                                           | %       | 90             | https://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html         |
|                        | Soil Bulk Density (BDW)               | Soil Bulk Density in the patch                                                | g/cm³   | 90             | https://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html         |
|                        | Soil pH CaCl₂ (PHC)                   | Mean pH of the soil in the patch                                              | NA      | 90             | https://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html         |
| Landscape context      | Mean aridity (aridity_mean)           | Mean aridity index in the patch and 1-km buffer. Aridity data was a non-dimensional measure of the long-term balance between rainfall and net radiation (Nyman et al., 2014) | NA      | 20             | Nyman et al. (2014)                                                   |
|                        | Dry forest area in buffer (area_dry)  | Area of dry forests in the 1-km buffer. Dry forests were defined as Grassy/Heathy dry forest, Tall mixed forest and Foothills forest (Figure 1, Table S1). | m²      | NA             | (Department of Environment Land Water & Planning, 2021b)               |
|                        | Non-native area in buffer (Area_non_native) | Area of non-native vegetation in the 1-km buffer. Non-native vegetation was defined as any area without an ecological vegetation class. | Hectares| NA             | (Department of Environment Land Water & Planning, 2021b)               |
| Location               | Distance to houses (dist_houses)      | Distance to nearest address point from nearest patch edge                     | metres  | NA             | data.vic.gov.au                                                        |
|                        | Distance to roads (dist_roads)        | Distance to nearest road from nearest patch edge                             | metres  | NA             | data.vic.gov.au                                                        |
|                        | Distance to alp ash (dist_alp_ash)    | Distance to another patch of alpine ash from edge to edge                     | metres  | NA             | data.vic.gov.au                                                        |
used to evaluate the influence each variable had on the immaturity risk (Figure 7). Of the most important variables, immaturity risk in all models decreased to an asymptote with increasing distance to roads, annual mean temperature and clay content, and increased with increasing precipitation in the warmest quarter (>200 mm; Figure 7). Consistent responses of immaturity risk across models were also indicated for mean aridity and the area of dry forest in the patch and 1km buffer (positive to asymptote), soil bulk density (positive), canopy top height (negative beyond 15 metres) and elevation (negative beyond 1,000 m; Figure 7).

4 | DISCUSSION

Our projections reveal climate-mediated changes in the fire regime will have negative implications for alpine ash persistence. Fire
FIGURE 4 The average number of fires across the 100-year simulation under: (a) current ECHAM R3; (b) current CSIRO R3; (c) future ECHAM R3; (d) future CSIRO R3; and (e) the difference between future and current ECHAM R3; and (f) difference between future and current CSIRO R3. (a–d) Yellow colours indicate small number of fires, purple colours indicate higher number of fires. (e–f) Blue colours indicate a decrease or little change in the number of fires and orange colours indicate an increase in the number of fires. Dark grey outline is the simulation area. Grey polygons are the distribution of alpine ash.
FIGURE 5 Change in the number of simulations that contained at least one short-interval fire (two fires within 20 years) between current and future conditions for each of the six climate models in alpine ash dominated forests. Results for juvenile periods of 15 and 25 years were very highly correlated (Pearson's correlation coefficient >0.9; Table S2). No change (i.e., values of 0) were removed from the colour scale for clarity and are shown in purple. Blue colours indicate a decrease in immaturity risk and orange colours indicate an increase in immaturity risk. Light grey outline is the simulation area.
regimes in some alpine ash-dominated landscapes will be characterized by more frequent fire across larger areas. The key implication is the increased immaturity risk for alpine ash forests driven by more frequent short-interval fires. Importantly, simulated immaturity risk was spatially variable with increased risk most closely associated with patches located closer to human features such as roads, on the periphery of the current distribution (i.e., at lower elevations), and in drier, warmer parts of the landscape. These results on the relative risk provide insights for managers to develop spatially explicit strategies to assist the landscape-level persistence of the species.

Species persistence is driven by global change, including changes in the fire regime, climate, biotic invasions and land use (Steffen, 2005). Research forecasting plant community responses to global change is beginning to incorporate a wider range of feedbacks, including disturbance regimes, shifting ecological niches and population dynamics (Franklin et al., 2016). The treatment of fire regimes in research varies, with some including fire as an aspatial element (i.e., the probability of fire in one grid cell not affected by the probability of fire in adjacent cells; Penman, Keith, et al., 2015) while others use landscape-scale process models (Loehman et al., 2020). However, many miss the feedback between climate, fuels and future fire regimes (Franklin et al., 2014). There is also the potential for interacting and synergistic impacts, with shifts in fire regimes occurring alongside shifts in demographic traits and or climate change, which may increase extinction risk (Enright et al., 2015), cause shifts in forest composition (Hayes & Buma, 2021), and reduce biodiversity or ecosystem resilience (Stevens-Rumann et al., 2018). Further work will concentrate on combining powerful fire regime simulations with population-level demographic data to explore these complex feedbacks with greater realism.

4.1 Changes to the fire regime

Significant changes to the fire regime were predicted with increases in the extent (total area burnt, and area burnt at high intensity) and in the frequency of fire. This combination increased the likelihood of areas being burned at short intervals with serious implications for the longevity of alpine ash populations. The related obligate seeder, mountain ash (*E. regnans*) requires a mean fire frequency of between 37 and 75 years to avoid local extinction (McCarthy et al., 1999). Increased fire frequency has been identified as one of the key drivers of species compositional changes (Fairman et al., 2019; Syphard et al., 2019; Watson & Wardell-Johnson, 2004). Localized extinction from changing fire frequencies have already been seen in southeastern Australia and around the world (Bassett et al., 2015; Brown & Johnstone, 2012; Holz et al., 2015) with more predicted to occur (Esther et al., 2010; Henzler et al., 2018).
Fire seasons in temperate Australia are predicted to lengthen and increase in severity; therefore, we may expect a greater extent of fire across the landscape (Clarke et al., 2011; Collins et al., 2021; Jolly et al., 2015; Moritz et al., 2012). However, the relationship between extent and fire frequency cannot increase indefinitely, with the growth of biomass eventually limiting fire spread for some systems (Archibald et al., 2013; Clarke et al., 2020). Nevertheless, our simulations, which incorporate climate influences on fuel growth, indicate there will be enough fuel in the landscape to support an increase in both extent and frequency of fire in alpine ash-dominated stands under the climate scenarios tested. It has been suggested that regenerating stands of alpine ash have increased flammability, with well-aerated and greater vertical and horizontal continuity of fuel than mature stands (Bowman et al., 2014; Zylstra, 2018; Gale & Cary, 2021). Evidence of this relationship has been found in other subalpine ecosystems (Cawson et al., 2017; Turner et al., 2019). However, these relationships have not been incorporated explicitly into the modelling. Therefore, our results may in fact underestimate the risk of high-intensity fire in vulnerable regenerating stands compared to neighbouring mature stands. Conversely, our modelling currently relies on historical relationships between fuel, climate and soil and therefore does not model the potential for vegetation state changes and the associated changes in fuel and fuel structure.

4.2 | Characterizing the patterns of immaturity risk

Anthropogenic and environmental features such as roads, amount of summer rainfall and %clay content were associated with high immaturity risk of alpine ash. Distance to a road was the most influential variable in our model. As distance increased, immaturity risk to an alpine ash patch decreased until about 500 metres. This lower simulated risk to patches with distance from human access/activity was potentially driven by fewer ignitions with distance from human caused ignitions (Syphard et al., 2009, 2019; van Wilgen et al., 2010).
In addition, patches remote from human activity might burn less frequently than closer patches because the conditions required to carry fires across greater distances from ignition sources might occur less frequently. Fire locations can also be influenced by interactions between human activity and prevailing weather. For example, high fire danger days often coincide with strong north-westerly winds with south-westerly changes (Harris et al., 2017; Long, 2006) potentially also driving the higher immaturity risk on the western and northern edges of the study area.

Multiple other predictor variables indicated the importance of the environment to future alpine ash immaturity risk. For example, immaturity risk decreased with increasing % soil clay content and elevation and increased with increasing summer rainfall (bio18). Both % clay content and bio18 have been shown to be influential in predicting fuel components in south-eastern Australia (McColl-Gausden et al., 2020) and may therefore be capturing some aspects of fuel important for predicting fire behaviour. Other climate-related variables indicated greater immaturity risk in drier (aridity index) parts of the landscape, particularly for fire regime projections based on ECHAM R3. The influence of climatic factors suggests that local fire management may not be able to mitigate all future immaturity risks to alpine ash-dominated forests in these landscapes.

Our Random Forest models captured much of the spatial variation in alpine ash immaturity risk. While there is remaining uncertainty around the exact drivers of fire in the landscape due to variability and interactions among environmental and human activity variables, the shapes of relationships of immaturity risk with predictor variable were often consistent across all six climate projections. This suggests that the general patterns in risk are congruent and can be used to identify priority locations and practices, and to focus future research.

4.3 | Applications and future directions

Fire regime modelling is a crucial tool in examining the impacts of future fire regimes on social, economic and environmental values. Here, we used a new fire regime modelling approach focussed on one geographic region and species. However, the methods could be applied more broadly, allowing a range of possible fire futures in different fire-prone ecosystems to be explored. The modelling framework can be applied to any species and location assuming a similar level of data are available. Further, integrating fire simulation modelling with adaptive management can help land managers identify key areas where management is required to reduce fire occurrence (e.g., ignition awareness and suppression, prescribed fire in nearby fire-tolerant vegetation communities), and where the ecosystem is most likely to shift to a changed state under future fire regimes (and thus potentially a lower priority for restoration to an alpine ash forest). While we have a limited capacity to change fire patterns at landscape scales and may be unable to change some of the predicted outcomes from fire regime modelling, adaptive management could improve the resilience of the ecosystem in its new state.

4.4 | Limitations

The role of demographic variability in species persistence can be incorporated into dynamic population models, linking environmental stochasticity with demographic stochasticity (Visintin et al., 2020). Research into the relationship between changing climate and demographic parameters has indicated some concerns where demographic changes and changes to the fire regime interact to reduce species persistence (Enright et al., 2015). This approach was not taken in our study as variation in juvenile period, the time of greatest risk to species persistence for alpine ash, did not change overall risk between the shortest (15 years) and longest (25 years) tested juvenile periods. This suggests that the role of climate change on fire regimes poses a far greater threat to alpine ash than the effects of climate change on alpine ash demography. Due to computational constraints, we were only able to select six of the 12-member NARClim ensemble. While more climate models will provide broader scope to examine uncertain climate futures, we selected the drier and warmer ensemble members as they were most robust in terms of current performance and also allowed for an exploration of the greatest predicted changes in fire weather, which may be important for exploring the limits of fire regime changes. Due to the inherent uncertainty of climate projections, it may be advisable for future research and managers to acknowledge the range of risk, and plan accordingly.

5 | CONCLUSIONS

Projections of future fire regimes indicate increased immaturity risk for the obligate seeding species alpine ash. The ecological implications of a shift in the fire regime are likely to mean a reduction in the distribution of alpine ash. The spatial distribution of risk was not uniform across the landscape with those closer to roads, at lower elevations and in drier, warmer parts of the landscape more likely to experience the short-interval fires that can cause localized extinc-
tion. These patterns will guide future research and provide spatially explicit information to examine and develop management practices that acknowledge changing risks created by climate-mediated shifts in fire regimes across landscapes.

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**PEER REVIEW**

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**DATA AVAILABILITY STATEMENT**

All environmental data used are cited within the main body of this manuscript. Regional climate data were provided by the NARClIM project and are freely available: https://climatechange.environment.nsw.gov.au/Climate-projections-for-NSW. The FROST data that support the findings of this study are available in figshare at http://doi.org/10.26188/16458132.

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**REFERENCES**

Abatzoglou, J. T., Williams, A. P., Boschetti, L., Zubkova, M., & Kolden, C. A. (2018). Global patterns of interannual climate–fire relationships. *Global Change Biology*, 24, 5164–5175. https://doi.org/10.1111/gcb.14405

Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, 26, 4013–4027. https://doi.org/10.1111/gcb.15118

Andersen, A. N., Cook, G. D., Corbett, L. K., Douglas, M. M., Eager, R. W., Russell-Smith, J., Setterfield, S. A., Williams, R. J., & Woinarski, J. C. Z. (2005). Fire frequency and biodiversity conservation in Australian tropical savannas: Implications from the Kapalga fire experiment. *Austral Ecology*, 30, 155–167. https://doi.org/10.1111/j.1442-9993.2005.01441.x

Archibald, S., Lehmann, C. E. R., Belcher, C. M., Bond, W. J., Bradstock, R. A., Daniuia, A.-L., Dexter, K. G., Forrestel, E. J., Greve, M., He, T., Higgins, S. I., Hoffmann, W. A., Lamont, B. B., McGlinn, D. J., Moncrieff, G. R., Osborne, C. P., Pausas, J. G., Price, O., Ripley, B. S., ... Zanne, A. E. (2018). Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters*, 13, 033003. https://doi.org/10.1088/1748-9326/aa9ead

Archibald, S., Lehmann, C. E. R., Gómez-Dans, J. L., & Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6442–6447. https://doi.org/10.1073/pnas.1211466110

Archibald, S., Roy, D. P., Van Wilgen, B. W., & Scholes, R. J. (2009). What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology*, 15, 613–630. https://doi.org/10.1111/j.1365-2486.2008.01754.x

Ashton, D. H. (2000). The Big Ash forest, Wallaby Creek, Victoria—changes during one lifetime. *Australian Journal of Botany*, 48, 1–26. https://doi.org/10.1071/BT98045

Bassett, O. D., Prior, L. D., Slijkerman, C. M., 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 and Management*, 342, 39–48. https://doi.org/10.1016/j.foreco.2015.01.008

Boland, D., Brooker, I., & McDonald, M. W. (2006). *Forest trees of Australia*. CSIRO Publishing.

Bowman, D. M. J. S. (2000). *Australian rainforests. [Electronic resource]: Islands of green in a land of fire*. Cambridge University Press.

Bowman, D., & Kirkpatrick, J. (1986). Establishment, Suppression and Growth of Eucalyptus delegatensis R.T. Baker in Multiaged Forests. I. The Effects of Fire on Mortality and Seedling Establishment. *Australian Journal of Botany*, 34, 63–72. https://doi.org/10.1071/BT9860063

Bowman, D. M. J. S., Kolden, C. A., Abatzoglou, J. T., Johnston, F. H., van der Werf, G. R., & Flannigan, M. (2020). Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment*. https://doi.org/10.1038/s43017-020-0085-3

Bowman, D. M. J. S., Murphy, B. P., Neyland, D. I. J., Williamson, G. J., & Prior, L. D. (2014). Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Global Change Biology*, 20(3), 1008–1015. https://doi.org/10.1111/gcb.12433.

Bowman, D. M. J. S., Williamson, G. J., Prior, L. D., Murphy, B. P., & Poulter, B. (2016). The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Global Change Biology and Biogeography*, 25, 1166–1172. https://doi.org/10.1111/gcb.12484

Bradstock, R. A. (2010). A biogeographic model of fire regimes in Australia: Current and future implications. *Global Ecology and Biogeography*, 19, 145–158. https://doi.org/10.1111/j.1466-8238.2009.00512.x

Brown, C. D., & Johnstone, J. F. (2012). Once burned, twice shy: Repeat fires reduce seed availability and alter subalpine constraints on *Picea mariana* regeneration. *Forest Ecology and Management*, 266, 34–41. https://doi.org/10.1016/j.foreco.2011.11.006

Busby, J. R. (1991). BIOCLIM: A bioclimate analysis and prediction system. *Plant Protection Quarterly*, 6, 8–9.

Caccamo, G., Chisholm, L. A., Bradstock, R. A., & Puotinen, M. L. (2012). Using remotely-sensed fuel connectivity patterns as a tool for fire danger monitoring. *Geophysical Research Letters*, 39, L01302. https://doi.org/10.1029/2011GL050125

Cawson, J. G., Duff, T. J., Tolhurst, K. G., Baillie, C. C., & Penman, T. D. (2017). Fuel moisture in Mountain Ash forests with contrasting fire histories. *Forest Ecology and Management*, 400, 568–577. https://doi.org/10.1016/j.foreco.2017.06.046

Cheal, D. C. (2010). Growth stages and tolerable fire intervals for Victoria's native vegetation data sets. Fire and adaptive management. Department of Sustainability and Environment, Melbourne, Australia.

Cirulis, B., Clarke, H., Boer, M., Penman, T., Price, O., & Bradstock, R. (2020). Quantification of inter-regional differences in risk mitigation from prescribed burning across multiple management values. *International Journal of Wildland Fire*, 29, 414–426. https://doi.org/10.1071/WF18135

Clarke, H., & Evans, J. P. (2019). Exploring the future change space for fire weather in Southeast Australia. *Theoretical & Applied Climatology*, 136(1/2), 513–527. https://doi.org/10.1007/s00704-018-2507-4

Clarke, H., Gibson, R., Cirulis, B., Bradstock, R. A., & Penman, T. D. (2019). Developing and testing models of the drivers of anthropogenic and lightning-caused wildfire ignitions in south-eastern Australia. *Journal of Environmental Management*, 235, 34–41. https://doi.org/10.1016/j.jenvman.2019.01.055

Clarke, H., Penman, T., Boer, M., Cary, G. J., Fontaine, J. B., Price, O., & Bradstock, R. (2020). The proximal drivers of large fires: A pyrogeographic study. *Frontiers Earth Science*, 8. https://doi.org/10.3389/feart.2020.00090

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. https://doi.org/10.1071/WF10070

Clarke, H., Tran, B., Boer, M. M., Price, O., Kenny, B., & Bradstock, R. (2019). Climate change effects on the frequency, seasonality and interannual variability of suitable prescribed burning weather conditions
in South-Eastern Australia. *Agricultural and Forest Meteorology*, 271, 148–157. https://doi.org/10.1016/j.agrformet.2019.03.005

Coen, J. L., Stavros, E. N., & Fites-Kaufman, J. A. (2018). Deconstructing the King magafire. *Ecological Applications*, 28, 1565–1580. https://doi.org/10.1002/eco.1752

Collins, M. L., van Wagendonk, J. W., & Stephens, S. L. (2007). Spatial patterns of large natural fires in Sierra Nevada wilderness areas. *Landscape Ecology*, 22, 545–557. https://doi.org/10.1007/s10180-006-9047-5

Collins, L., Bradstock, R. A., Clarke, H., Clarke, M. F., Nolan, R. H., & Penman, T. D. (2021). The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters*, 16(4), 044029. https://doi.org/10.1088/1748-9326/abeb9e

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

Cremer, K. W. (1977). Distance of seed dispersal in eucalypts estimated from seed weights.

Department of Environment Land Water and Planning. (2020). *Bioregions and EVC benchmarks*. Retrieved from environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks

Department of Environment Land Water and Planning. (2021a). *Structural Vegetation*. Retrieved from discover.data.vic.gov.au/dataset/structural-vegetation-1995

Department of Environment Land Water and Planning. (2021b). *Native Vegetation - Modelled 2005 Ecological Vegetation Classes*. Retrieved from discover.data.vic.gov.au/dataset/native-vegetation-model led-2005-ecological-vegetation-classes-with-bioregional-conservation-sta

Di Luca, A., Argüeso, D., Evans, J. P., de Elia, R., & Laprise, R. (2016). Quantifying the overall added value of dynamical downscaling and the contribution from different spatial scales. *Journal of Geophysical Research: Atmospheres*, 121, 1575–1590. https://doi.org/10.1002/2015JD024009

Doherty, M. D., Gill, A. M., Cary, G. J., & Austin, M. P. (2017). Seed viability of early maturing alpine ash (*Eucalyptus delegatensis* subsp. *delegatensis*) in the Australian Alps, south-eastern Australia, and its implications for management under changing fire regimes. *Australian Journal of Botany*, 65, 517–523. https://doi.org/10.1071/BT17068

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. https://doi.org/10.1890/140231

Esther, A., Groeneveld, J., Enright Neil, J., Miller Ben, P., Lamont Byron, B., Perry George, L. W., Blank, F. K., & Jeltsch, F. (2010). Sensitivity of plant functional types to climate change: Classification tree analysis of a simulation model. *Journal of Vegetation Science*, 21, 447–461. https://doi.org/10.1111/j.1654-1103.2009.01155.x

Evans, J., Argüeso, D., Olson, R., & Di Luca, A. (2017). Bias-corrected regional climate projections of extreme rainfall in South-East Australia. *Theoretical & Applied Climatology*, 130(3–4), 1085–1098. https://doi.org/10.1007/s00704-016-1949-9

Evans, J. P., Ji, F., Lee, C., Smith, P., Argüeso, D., & Fita, L. (2014). Design of a regional climate modelling projection ensemble experiment - NARClim. *Geoscientific Model Development*, 7, 621–629. https://doi.org/10.5194/gmd-7-621-2014

Fagg, P., Lutze, M., Slijkerman, C., Ryan, M., & Bassett, O. (2013). Silvicultural recovery in ash forests following three recent large bushfires in Victoria. *Australian Forestry*, 76, 140–155. https://doi.org/10.1080/00049158.2013.848610

Fairman, T. A., Bennett, L. T., & Nitschke, C. R. (2019). Short-interval wildfires increase likelihood of respouting failure in fire-tolerant trees. *Journal of Environmental Management*, 231, 59–65. https://doi.org/10.1016/j.jenvman.2018.10.021

Fairman, T. A., Bennett, L. T., Tupper, S., & Nitschke, C. R. (2017). Frequent wildfires erode tree persistence and alter stand structure and initial composition of a fire-tolerant sub-alpine forest. *Journal of Vegetation Science*, 28, 1151–1165. https://doi.org/10.1111/jvs.12575

Fita, L., Evans, J. P., Argüeso, D., King, A., & Liu, Y. (2017). Evaluation of the regional climate response in Australia to large-scale climate modes in the historical NARClIM simulations. *Climate Dynamics*, 49, 2815–2829. https://doi.org/10.1007/s00382-016-3484-x

Franklin, J., Regan, H. M., & Syphard, A. D. (2014). Linking spatially explicit species distribution and population models to plan for the persistence of plant species under global change. *Environmental Conservation*, 41, 97–109. https://doi.org/10.1017/S0376892913000453

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 3725–3734. https://doi.org/10.1073/pnas.1519911113

Gale, M. G., & Cary, G. J. (2021). Stand boundary effects on obligate seedling *Eucalyptus delegatensis* regeneration and fire dynamics following high and low severity fire: Implications for species resilience to recurrent fire. *Austral Ecology*, 46, 802–817.

Greenwell, B. M. (2017). Pdp: An R package for constructing partial dependence plots. *The R Journal*, 9(1), 421–436.

Griffiths, D. (1999). Improved formula for the drought factor in McArthur’s Forest fire danger meter. *Australian Forestry*, 62, 202–206.

Grose, R. (1960). Effective seed supply for the natural regeneration of *Eucalyptus delegatensis* RT Baker syn. *Eucalyptus gigantea* Hook. F. *APPITA*, 13, 141–148.

Hammill, K., Penman, T., & Bradstock, R. (2016). Responses of resilience traits to gradients of temperature, rainfall and fire frequency in fire-prone, Australian forests: Potential consequences of climate change. *Plant Ecology*, 217, 725–741. https://doi.org/10.1007/s11258-016-0578-9

Harris, S., Graham, M., & Timothy, B. (2017). Variability and drivers of extreme fire weather in fire-prone areas of south-eastern Australia. *International Journal of Wildland Fire*, 26, 177–190. https://doi.org/10.1071/WF16118

Harvey, B. J., Donato, D. C., & Turner, M. G. (2016). High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography*, 25, 655–669. https://doi.org/10.1111/geb.12443

Hayes, K., & Buma, B. (2021). Effects of short-interval disturbances continue to accumulate, overwhelming variability in local resilience. *Ecosphere*, 12, e03379.

Henzler, J., Britta, T., Hanna, W., Neal, J. E., & Susanne, Z. (2018). A squeeze in the suitable fire interval: Simulating the persistence of fire-killed plants in a Mediterranean-type ecosystem under drier conditions. *Ecological Modelling*, 389, 41–49. https://doi.org/10.1016/j.ecolmodel.2018.10.010

Hoecker, T. J., Hansen, W. D., & Turner, M. G. (2020). Topographic position amplifies consequences of short-interval stand-replacing fires on postfire tree establishment in subalpine conifer forests. *Forest Ecology and Management*, 478, 118523. https://doi.org/10.1016/j.foreco.2020.118523

Holden, Z. A., & Jolly, W. M. (2011). Modeling topographic influences on fuel moisture and fire danger in complex terrain to improve wildland fire management decision support. *Forest Ecology and Management*, 262, 2133–2141. https://doi.org/10.1016/j.foreco.2011.08.002

Holz, A., Wood, S. W., Veblen, T. T., & Bowman, D. M. J. S. (2015). Effects of high-severity fire drove the population collapse of the subalpine Tasmanian endemic conifer *Athrotaxis cupressoides*. *Global Change Biology*, 21, 445–458.
Syphard, A. D., Brennan, T. J., & Keeley, J. E. (2019). Extent and drivers of vegetation type conversion in Southern California chaparral. *Ecosphere, 10*, e02796. https://doi.org/10.1002/ecs2.2796

Syphard, A. D., Radeloff, V. C., Hawbaker, T. J., & Stewart, S. I. (2009). Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conservation Biology, 23*, 758–769. https://doi.org/10.1111/j.1523-1739.2009.01223.x

Turner, M. G., Brazuiunas, K. H., Hansen, W. D., & Harvey, B. J. (2019). Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences of the United States of America, 116*, 11319–11328. https://doi.org/10.1073/pnas.1902841116

Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillera-Arroita, G. (2019). blockCV: An R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution, 10*, 225–232.

van Wilgen, B. W., Forsyth, G. G., de Klerk, H., Das, S., Khuluse, S., & Schmitz, P. (2010). Fire management in Mediterranean-climate shrublands: A case study from the Cape fynbos, South Africa. *Journal of Applied Ecology, 47*, 631–638. https://doi.org/10.1111/j.1365-2664.2010.01800.x

Visintin, C., Briscoe, N. J., Woolley, S. N. C., Lentini, P. E., Tingley, R., Wintle, B. A., & Golding, N. (2020). steps: Software for spatially and temporally explicit population simulations. *Methods in Ecology and Evolution, 11*, 596–603.

von Takach Dukai, B., Lindenmayer, D. B., & Banks, S. C. (2018). Environmental influences on growth and reproductive maturation of a keystone forest tree: Implications for obligate seeder susceptibility to frequent fire. *Forest Ecology and Management, 411*, 108–119. https://doi.org/10.1016/j.foreco.2018.01.014

Watson, P. J., Bradstock, R. A., & Morris, E. C. (2009). Fire frequency influences composition and structure of the shrub layer in an Australian subcoastal temperate grassy woodland. *Austral Ecology, 34(2)*, 218–232. https://doi.org/10.1111/j.1442-9993.2008.01924.x

Watson, P., & Wardell-Johnson, G. (2004). Fire frequency and time-since-fire effects on the open-forest and woodland flora of Girraween National Park, south-east Queensland, Australia. *Austral Ecology, 29*, 225–236. https://doi.org/10.1111/j.1442-9993.2004.01346.x

Westering, A. L., Gershunov, A., Cayan, D. R., & Barnett, T. P. (2002). Long lead statistical forecasts of area burned in western U.S. wildfires by ecosystem province. *International Journal of Wildland Fire, 11*, 257–266. https://doi.org/10.1071/WF02009

Westering, A. L., Turner, M. G., Smithwick, E. A. H., Romme, W. H., & Ryan, M. G. (2011). Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences of the United States Of America, 108*, 13165–13170. https://doi.org/10.1073/pnas.1110199108

Wood, S. W., Murphy, B. P., & Bowman, D. M. J. S. (2011). Firescape ecology: How topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area. *Journal of Biogeography, 38(9)*, 1807–1820. https://doi.org/10.1111/j.1365-2699.2011.02524.x

Zylstra, P. (2018). Flammability dynamics in the Australian Alps. *Austral Ecology, 43*, 578–591. https://doi.org/10.1111/aec.12594

**BIOSKETCH**

Sarah C. McColl-Gausden is a PhD candidate in the FLARE Wildfire Research group, School of Ecosystem and Forest Sciences, at the University of Melbourne. Her PhD investigates the implications for biodiversity under the joint threats of altered fire regimes and changing climate using fire simulation modelling.

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

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