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# The effect of species, size, and fire intensity on tree mortality within a catastrophic bushfire complex

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Running head: Estimating fire-related tree mortality

# Abstract

Infrequent, high-intensity disturbances can have profound impacts on forested landscapes, changing forest structure and altering relative species abundance. However, due to their rarity and the logistical challenges of directly observing such extreme events, both the spatial variability of disturbance intensity and the species-specific responses to this variability are poorly understood. We used observed patterns of mortality across a fire severity gradient following the 2009 Black Saturday fires in southeastern Australia to simultaneously estimate 1) species- and size-specific susceptibility to fire-induced mortality and 2) fire intensity. We found broad variation in patterns of fire susceptibility among the 10 tree species (five eucalypts and five non-eucalypts) sufficiently abundant for analysis. Among the eucalypts, *Eucalyptus obliqua* was the most resistant to fire-induced mortality, with trees of $\sim$25 cm DBH having a 50% probability of surviving even the most intense fires. In contrast, *E. regnans* had 100% mortality across all size classes when subjected to high intensity fire. Basal resprouting occurred in six of the study species and, when accounted for, fundamentally changed the mortality profile of these species, highlighting the importance of resprouting as an adaptation to fire in these landscapes. In particular, the two iconic cool temperate rainforest species (*Nothofagus cunninghami* and *Atherosperma moschatum*) were strong resprouters ($\sim$ 45% of individuals were able to resprout after being top-killed by fire). We also found evidence for compositional shifts in regeneration above threshold values of fire intensity in cool temperate rainforest and mixed forest sites, both of which have important conservation values within these landscapes. The observed patterns of species- and size-specific susceptibility to fire-induced mortality may be used to anticipate changes in forest structure and composition in the future. In addition, they may also help guide forest management strategies that reduce the length of time individual trees are exposed to potentially lethal fires, thereby increasing the resilience of these forests to future fires.

**Keywords:** Atherosperma moschatum, Bayesian hierarchical modelling, Black Saturday fire, Disturbance ecology, Eucalyptus, Fire severity, Latent variables, Mountain ash, Nothofagus cunninghamii, Size-related mortality, South-eastern Australia, Wildfire.

# Introduction

Fire is the dominant natural disturbance across many regions of the world, impacting native ecosystems from the tropics to the tundra (Bowman *et al.* 2009, McLauchlan *et al.* 2020). While fires are important drivers of many processes in forested ecosystems, such as nutrient dynamics, carbon fluxes, and biodiversity dynamics, they also generate great destructive forces that can dramatically alter the structure, composition, and developmental trajectory of entire forested landscapes (Moritz *et al.* 2014). However, fire is an inherently complex, partially stochastic phenomenon that varies in its impacts across spatial and temporal scales (Turner *et al.* 1989, Agee 1993, McLauchlan *et al.* 2020). In forested ecosystems the energy of a fire per unit time—its *intensity*—is primarily influenced by environmental conditions and fuel availability. The impact of a fire—its *severity*—reflects the interaction between 1) fire intensity and 2) the susceptibility of the trees at a site to fire-induced mortality. Both species- and size-specific differences in fire susceptibility interact to modulate fire severity. Tree species with adaptations such as thick bark or vigorous resprouting are more likely to survive a fire than tree species that lack such adaptations. Within a species, larger trees are more likely to survive fire than smaller trees as they tend to have thicker bark, which delays and reduces heat penetration to the cambium (Gill and Ashton 1968, Agee 1993, Baker and Bunyavejchewin 2006, Keyser *et al.* 2006, Ryan *et al.* 1988). As a consequence, two stands subjected to fires of the same intensity may show distinctly different patterns of mortality if they differ in species composition, tree size distribution, or both (Agee 1993). In complex landscapes in which topography, soils, and vegetation structure and composition may vary widely, complex patterns of fire behaviour may result in heterogeneous patterns of tree mortality across the landscape (Lertzman *et al.* 1998).

Fire intensity, particularly in extreme fire conditions, is difficult to measure. As a consequence, fire severity—typically a measure of the proportion of individual trees killed or canopy area lost—is more commonly measured in the wake of a fire (Turner and Dale 1998, Keeley 2009). While disturbance intensity and severity are related, the relationship between the two is rarely a simple, linear one (Lentile *et al.* 2006, Keeley 2009). Disentangling the roles of fire intensity and tree and stand susceptibility presents a challenge because the observed pattern of fire severity is influenced by both. For example, an area of forest that had high levels of mortality may have experienced a high-intensity fire or it may have been dominated by tree species or size classes that were particularly susceptible to fire-induced mortality (even from low-intensity fires). Canham *et al.* (2001) proposed a method for simultaneously estimating disturbance intensity and species- and size-specific susceptibility to wind disturbance that takes advantage of variability in wind damage and species-specific responses to wind damage. Their approach is readily generalised to other types of disturbances with spatially variable impacts. Here we adapt it to disentangle various underlying drivers of fire-induced mortality during the 2009 Black Saturday fires—one of the most extreme fire events in the history of southeastern Australia prior to the 2019/20 fire season.

As the climate in many regions of the world becomes hotter and drier, extreme fire conditions are expected to become more frequent, more extensive, and potentially more severe. Unprecedented fire events, like those of the 2017, 2018, and 2020 Californian fires or the 2019-20 Australian fire season, that burn hundreds of thousands to millions of hectares of forest may become more common in the coming decades. If they do, it will be critically important to anticipate how they will impact and potentially alter forest communities. This requires understanding how different tree species are impacted by fire and whether there are particular combinations of stand structures or composition that are more resistant or resilient to future fires (Lavorel *et al.* 2014, Doherty *et al.* 2016, Tepley *et al.* 2017, Koontz *et al.* 2020, Trouvé *et al.* 2020). In this study we addressed two specific questions to explore this issue across a range of species and forest types:

1. How do species and size influence fire-induced mortality in a large, heterogeneous bushfire complex?
2. How does fire intensity vary across a landscape subjected to a catastrophic fire?

# Methods

## Study area, fire and forest types

On 7 February 2009, after nearly a decade of drought conditions (Palmer *et al.* 2015), the area around Melbourne, Victoria, had experienced three consecutive days of extreme fire conditions with temperatures >43°C, relative humidity $<10\%$, and wind speeds of 65 km $h^{-1}$, gusting to 90 km $h^{-1}$. The Australian Fire Danger Rating (AFDR) system (Noble *et al.* 1980) classifies days with Forest Fire Danger Index ratings $>100$ as Catastrophic fire conditions—on 7 February 2009 the FFDI was 103. Nearly 600 fires started across the state with a complex of four particularly large fires initiating within 100 km of Melbourne (Teague *et al.* 2010). The Murrindindi fire, which burned through the Central Highlands east of Melbourne, spread rapidly during the day moving nearly 40 km to the small township of Narbethong. In the late afternoon a cold front brought strong southwesterly winds that turned the flanking fires into the main fire line, and increased the size of the fire-affected area dramatically. However, the cooler temperatures and increased relative humidity that accompanied the cold front meant that the fire conditions eased over the course of the night.

This led to a complex mosaic of different fire impacts that reflected the interactions of weather, topography, and vegetation on fire behaviour.

We conducted our study at six sites that burned in the Murrindindi fire: Acheron Way, Marysville, and Mount Margaret in the Marysville State Forest; the Beeches Rainforest and Cambarville in the Yarra Ranges National Park; and Cathedral Ranges State Park. Study sites were chosen to collectively represent the full range of fire severity (*i.e.*, unburnt, understorey burn, crown scorch, and crown fire) across the four major forest types in the area: dry sclerophyll forest, cool temperate rainforest, tall open forest, and cool temperate mixed forests. Dry sclerophyll forest (DSF) typically occurs on drier, north-facing slopes at elevations <600 m.a.s.l. (Ashton and Attiwill 1994). This forest type is typically characterised by an overstory of *Eucalyptus* species (predominantly *E. obliqua* [messmate], *E. radiata* [narrow-leaf peppermint], and *E. dives* [broad-leaf peppermint]), and a midstory of *Acacia* species (predominantly *A. dealbata* [silver wattle] and *A. melanoxylon* [blackwood]). Cool temperate rainforest (CTR) is restricted to cool, moist gullies and riparian areas typically on southeastern-facing slopes (Busby and Brown 1994). It is characterised by a dense, closed canopy dominated by *Nothofagus cunninghamii* (myrtle beech) and *Atherosperma moschatum* (southern sassafras) and typically has a sparse and heavily shaded understory (Busby and Brown 1994). Tall open forest (TOF) occurs at elevations above 400 m in cooler, moister areas than dry sclerophyll forests (Ashton and Attiwill 1994). These forests have a tall overstory of *Eucalyptus* species (dominated by *E. regnans* [mountain ash] below 900m elevation and *E. delegatensis* [alpine ash] above 900m elevation), a mid-story of *Acacia* (*A. dealbata*, *A. melanoxylon*, and *A. obliquinervia* [mountain hickory wattle]), and a dense understory of small trees and shrubs (predominantly *Pomaderris aspera* [hazel pomaderris], *Olearia argophylla* [musk daisy-bush], *Lomatia fraseri* [forest lomatia], and *Bedfordia arborescens* [blanket-leaf]) (Ashton 2000). In the heavily dissected topography of the Central Highlands, TOF on midslope sites often grades into CTR in the gullies (Ashton and Attiwill 1994, Simkin and Baker 2008). The transition from TOF to CTR is readily distinguished due to the presence of eucalypts in the overstorey and rainforest species in the understorey. These ecotones are known as cool temperate mixed forest (MF). Because they have high conservation value within the Central Highlands landscape and are readily identifiable in the field, we included MF as a distinct forest type in this study.

A map of the study area and plot location is shown in figure 1.

## Data collection

To characterise the impacts of, and species-specific responses to, the 2009 bushfire, we established 53 circular plots of 20 m radius (0.125 ha) between October 2012 and January 2013. Plots were distributed every 300-600 m along transects in forested areas along minor roads or walking tracks. Transects varied in length from 1.5 to 4 km depending on the length of available roads and tracks. Consequently, the number of plots per transect varied from 2 to 10. The number and location of available sites were constrained by the many roads and forested areas that 3.5 years after the fire were still either inaccessible or unsafe due to the extensive damage caused by the bushfire. Topography and site conditions were highly variable among study locations, from cool moist gullies in Acheron Way and The Beeches Rainforest to steep dry slopes in the Cathedral Ranges. In all, we established 18 plots in DSF, 9 plots in CTR, 16 plots in TOF, and 10 plots in MF.

Within each plot we sampled every tree with a diameter at breast height (DBH) >10 cm. Each tree was identified to species, measured for DBH, and tallied as dead or alive. Mortality was determined for all trees rooted within the plot and for recently fallen trees showing evidence of fire damage. We distinguished between trees that had been top-killed but were resprouting from the base and those that were completely killed (*i.e.*, no evidence of basal resprouting; Hoffmann and Solbrig (2003)). The former was recorded as top-kill; the latter as full-kill. Dead trees with all bark removed and showing burnt wood uncharacteristic of the damage to the plot were considered to have died before the 2009 fires and were not recorded. Table 1 shows a breakdown of the experimental design by species. The diameter distributions per species per plot as well as tree status (live and top-kill) in our experimental design are shown in Appendix S1: Figs. S1 and S2. Importantly, there was sufficient overlap of species mixture between the different forest type and plots (Appendix S1: Figs. S1 and S2) to provide some link between the estimates of latent relative fire intensity of each plot in Eq. 1.

Within each study plot a central 5-m radius sub-plot (78.5 $m^2$) was established to characterise recruitment patterns. For seedlings of large shrubs and trees, each individual was identified to species and the height of the tallest shoot measured. This allowed us to assess how species diversity and seedling density and size correlated with fire intensity, as well as the potential filtering effect of fire intensity on post-fire regeneration.

## Data analyses

We adapted the approach proposed by Canham *et al.* (2001, 2010) that uses spatial variability in disturbance-induced mortality to simultaneously estimate plot-level disturbance intensity and species- and size-specific susceptibility to disturbance-induced mortality. They used a logistic regression model, in which the probability of mortality is a logistic function of tree species, individual tree size, and plot-level disturbance intensity. We modified their approach by using a hierarchical Bayesian framework to fit the model. The hierarchical approach allows for partial pooling of information among species and better estimates of parameter values and their associated uncertainties (Gelman and Hill 2008). We first focus on the top-kill model, which considers a tree to be have been top-killed in the fire if the aboveground woody stem was dead, irrespective of the tree's resprouting status. The top-kill model takes the form:

$$
\begin{aligned}
y_{ijk} &= Bernoulli(p_{ijk}) \qquad (1)\\
p_{ijk} &= \frac{1}{1+exp(-logit_{ijk})}\\
logit_{ijk} = log\left(\frac{p_{ijk}}{1-p_{ijk}}\right) &= \alpha_j + \beta_j \times I_i \times D_{ijk}^{\gamma_j}, where\\
\alpha_j &\sim \alpha_0 + N(0,\sigma_\alpha)\\
\beta_j &\sim \beta_0 + N(0,\sigma_\beta)\\
\gamma_j &\sim \gamma_0 + N(0,\sigma_\gamma)
\end{aligned}
$$

The left-hand term $y_{ijk}$ is the observed mortality status (0 = alive, 1 = top-kill) of the *k*th individual of species $j$ in plot $i$, which is assumed to be sampled from a Bernoulli distribution with probability of top-kill $p_{ijk}$. The probability of top-kill per individual $p_{ijk}$ is modelled on the logit scale and depends on latent (*i.e.*, unobserved) relative fire intensity, tree diameter, and species. On the right-hand side of the equation, $I_i$ is the relative fire intensity for plot $i$ (on a scale of 0-1, with 0 being undisturbed and 1 being the most intensely disturbed plot measured), modelled as a latent (i.e., unobserved) random variable with a prior uniformly distributed between 0 and 1, $D_{ijk}$ is the DBH (in cm) of the *k*th individual of species $j$ in plot $i$, and $\alpha_j$, $\beta_j$, and $\gamma_j$ are species-specific parameters to be estimated. $\alpha$ can be interpreted as the baseline top-kill rate (*i.e.*, when relative fire intensity equals zero), $\beta$ represents the effect of fire intensity and the effect of DBH, and $\gamma$ affects the shape of the top-kill-DBH relationship.

To explore the effect of resprouting on our estimates of species- and size-specific susceptibility to fire, we refitted Eq. 1 using full-kill as a response variable. We refer to this as the full-kill model where we only considered a tree to be dead if the aboveground parts of the tree were killed *and* there was no evidence of basal resprouting. Those trees that were top-killed, but resprouting from their base, were treated as alive. For the full-kill model, we used the plot-level estimates of $I_i$ from the top-kill model as a predictor instead of re-estimating it as a latent variable.

To assess the predictive ability of our top-kill model, we plotted the observed proportion of top-killed trees per plot against the predicted proportion of top-killed trees per plot. Well-calibrated curves should fall along a 1:1 line; that is, the predicted and observed top-killed rates should be roughly the same.

## Fire intensity, top-kill patterns, and regeneration

We used univariate linear regression to check whether the estimated values of latent relative fire intensity ($I$) per plot were associated with landscape attribute details extracted from GIS layers (*i.e.*, elevation, slope, aspect, and topographic wetness index, Gallant and Austin 2012).

We also explored the effect of fire intensity on the proportion of top-killed trees per forest type and post-fire forest regeneration patterns. To visualise the relationship between the proportion of top-killed trees (both by number of trees and basal area of trees) and relative fire intensity per forest type, we plotted and fitted a separate general additive model (GAM) with a Beta error distribution and a logit link to each forest type. We used the plot-level latent relative fire intensity estimate to determine if regeneration patterns were associated with fire intensity across the plots. To determine if there was any indication of directional changes in species composition, we visually inspected whether there was a change in the dominant forest type of the seedling community vs. the pre-fire adult trees forest type community. All data analyses were conducted in the R statistical package (Version 3.6.0, R core development team, 2019) and the top-kill and full-kill models were fitted using the Stan software (Carpenter *et al.* 2017, Stan Development Team 2020).

# Results

We sampled 2863 trees >10cm DBH (including both living and dead trees) across the 53 plots. Ten species (*Acacia dealbata*, *Acacia melanoxylon*, *Atherosperma moschatum*, *Eucalyptus dives*, *Eucalyptus obliqua*, *Eucalyptus radiata*, *Eucalyptus regnans*, *Eucalyptus viminalis*, *Nothofagus cunninghamii*, and *Olearia argophylla*) were sufficiently abundant (>15 individual trees in total) across enough plots and had a sufficiently broad DBH range (> 20 cm) for analysis. These 10 species comprised 97% of all trees recorded in the study plots. Other species present but not included in the analyses due to insufficient numbers or DBH range were *Bedfordia arborescens* (17), *Eucalyptus cypellocarpa* (6), *Eucalyptus delegatensis* (134), *Hedycarya angustifolia* (5), *Kunzea ericoides* (4), *Lomatia fraseri* (24), *Pomaderris aspera* (45), and *Tasmannia lanceolata* (8). It is worth noting that *Eucalyptus delegatensis* was not included in the analyses despite being relatively abundant because every tree found in the study plots had been killed in the fires.

The model estimation procedure produced an excellent fit of the model to the dataset. The predictions of our top-kill model were well calibrated as the observed and predicted proportion of top-kill per plot and per species were aligned with the 1:1 line (Figure 2).

## Variability in fire intensity

The plot-level estimates of fire intensity ($I$) were highly variable both within and among study locations, ranging from 0.05 (no fire) to 0.9 (highest observed intensity, resulting in all trees being top-killed) (Figure 3). The distribution of plot-level relative fire intensity scores was not uniform over the range of possible values. While 12 plots had $I < 0.2$ and nine plots had $I > 0.8$, there were clear peaks in relative fire intensity around $I$ = 0.25, 0.7, and 0.9. The Beeches, Cambarville, and Cathedral Ranges sites experienced the full range of fire intensities—in most cases within several hundred metres. A one-way ANOVA and *post-hoc* pairwise comparisons showed that there were significant differences among the sites in latent relative fire intensity ($F_{(5,47)} = 3.532$, $p = 0.009$). However, this was largely driven by differences between the Mt Margaret plots (mean $I = 0.69$) and the Acheron Way (mean $I = 0.275$) and Cathedral Ranges (mean $I = 0.32$) plots. Latent relative fire intensity was not associated with forest type ($F_{(3,49)} = 1.25$, $p = 0.302$). A comparison of plot-level relative fire intensity values to topographic variables (*i.e.*, elevation, aspect, slope, topographic wetness index) showed only weak positive relationship with elevation ($R^2 = 0.12$, $p = 0.007$) and negative relationship with topographic wetness index ($R^2 = 0.14$, $p = 0.007$). None of the other variables was correlated with relative fire intensity.

## Species-specific patterns of fire-induced top-kill and full-kill

We found distinct differences among the 10 study species in their susceptibility to fire-induced top-kill and full-kill. Figure 4 shows the size-specific probability of top-kill and full-kill for each tree species across a range of relative fire intensities. The model results show three distinct patterns among the tree species.

First, there is a distinct hierarchy of susceptibility to fire-induced top-kill among the eucalypt species. *Eucalyptus obliqua* is the most fire resistant of the eucalypts. Under the most intense fire conditions (*e.g.*, $I$=0.8, Figure 4), *E. obliqua* has a 50% probability of surviving once it reaches 25 cm DBH. In contrast, *E. regnans*, the least resistant of the eucalypts, has 100%

top-kill under similar high-intensity fire conditions regardless of tree size. The three other eucalypt species are intermediate in their responses, but notably all had probabilities of top-kill that were $<$100% under the most extreme fire conditions. They differed only in the probability of top-kill for a given size. The size-specific responses of the five eucalypt species were also strongly influenced by relative fire intensity. At low relative fire intensities all five of the eucalypt species had high top-kill survival rates. Even the relatively fire-sensitive *E. regnans* had a 50% probability of surviving a low intensity fire once individuals reached $\sim$25 cm DBH.

The second pattern that emerged from our analyses was that fire-induced top-kill of the five non-eucalypt species is primarily driven by relative fire intensity, not tree size. At low fire intensities, the probability of mortality is less than 100% for all non-eucalypt species with the exception of *Olearia argophylla*. However, once $I > 0.4$, the probability of mortality for all five species is 100%, irrespective of DBH. These results suggest a threshold response in fire mortality for the non-eucalypt species in these forests—in low-intensity fires, larger trees may survive (although typically with low to moderate probability), but in high-intensity fires, all of the trees are top-killed.

Third, accounting for basal resprouting (full-kill model) dramatically reduces estimated fire susceptibility for those species that are capable of resprouting. The most extreme example of this was *Olearia argophylla*, which experienced 100% top-kill under nearly all fire intensities, irrespective of stem size, but almost complete survival when basal resprouting was included (*i.e.*, full-kill was close to zero). The two cool temperate rainforest canopy dominants, *Atherosperma moschatum* and *Nothofagus cunninghamii*, were also exceptionally resilient to fire when basal resprouting was considered. Under the highest fire intensity *Atherosperma moschatum* and *Nothofagus cunninghamii* had 50% probabilities of full-kill survival for stems that were $\sim$6 and $\sim$20 cm DBH, respectively. All three of the dry sclerophyll forest eucalypt species were capable of basal resprouting, although *E. radiata* was the less vigorous of the three. For *E. obliqua* and *E. dives*, the combination of low probabilities of top-kill (even under high-intensity fire conditions) and the ability to resprout from the base following top-kill makes them extremely resilient to fires.

### Patterns of fire-induced mortality among forest types

The amount of top-killed trees per plot, whether calculated as the proportion of individuals killed or the proportion of basal area (BA) killed, showed considerable variability when compared to the estimated relative fire intensities. An important component of this variability was differences among the four forest types in their response to fire intensity (Figure 5). For a given fire intensity, DSF sites had a smaller proportion of dead individuals and BA than the three other forest types. The relationships between top-kill and forest type differed for individuals top-killed and BA top-killed. When the number of individuals is considered, the proportion of trees top-killed by the fire was approximately linearly related with latent relative fire intensity in the DSF. However, in the three other forest types, the relationship was non-linear, with an apparent threshold effect. For values of $I > 0.35$, most individuals in CTR, MF, and TOF in our sample plots were top-killed. For stand BA, the proportion top-killed was approximately linearly related to fire intensity for DSF and CTR, although for a given relative fire intensity the proportion of BA top-killed was much lower in DSF than CTR. TOF and MF exhibited a threshold response between relative fire intensity and proportion of BA top-killed with complete loss of BA when $I > 0.6$.

### Post-fire regeneration and fire intensity

We compared various measures of regeneration performance (*i.e.*, species richness, maximum height, and density) to fire intensity across the 53 study plots. Neither species richness nor density of post-fire regeneration was correlated with fire intensity. However, maximum height of the regeneration was weakly, but significantly, correlated with fire intensity at the plot level ($\mathrm{Ht}_{max} = 1.89 + 1.91I$), d.f. = 49, $p < 0.001$, $R^2 = 0.19$).

There was some indication that fire intensity may have had a threshold effect on species composition in CTR and MF plots (Table 3). When $I < 0.5$, regeneration was dominated by rainforest species, but when $I > 0.5$ the regeneration was dominated by TOF species, particularly *Eucalyptus regnans*.

# Discussion

Fire is a complex, stochastic phenomenon influenced by a wide range of variables associated with weather, climate, topography, and vegetation (Agee 1993, Bradstock *et al.* 2002, Romme *et al.* 2016) that generates spatially variable patterns of fire damage across multiple scales (Turner *et al.* 1994, Schoennagel *et al.* 2008). Direct, high-resolution measurements of fire intensity are rarely available for active high-intensity fires. This makes it difficult to disentangle the various influences driving fire-induced damage and mortality in forested landscapes. By simultaneously estimating fire intensity and species- and size-specific susceptibility to fire mortality, we were able to identify interspecific differences in fire susceptibility and site-specific variability in relative fire intensity. These differences have important implications for understanding how these forests will respond to fires in the future and suggest forest management strategies to increase the resilience of these native forests to increased fire activity in the future.

## Spatial variability in fire intensity

Our latent-variable approach to estimating unobserved relative fire intensity highlighted the broad range of variability in fire intensity in the 2009 Black Saturday fires. Spatially heterogeneous canopy damage and mortality are a common feature of large disturbances, regardless of forest type (Foster *et al.* 1998, Lertzman *et al.* 1998, Halofsky *et al.* 2011). In extreme fires, such as the 1988 Yellowstone fires (Turner *et al.* 1994), the 2009 Black Saturday fires (Cruz *et al.* 2012), or the recent fires in southeastern Australia (NSW Google Earth Engine Burned Area Map (GEEBAM)), large areas within the fire complex experience low- to moderate-severity impacts. In these areas even relatively fire-sensitive trees or tree species may be able to survive, creating a heterogeneous post-fire landscape composed of a mosaic of patches with different forest structures and species. Turner *et al.* (1994) found that the spatial variability in damage after the 1988 Yellowstone fires often occurred over small distances. Our estimates of fire intensity for the 2009 Black Saturday fires showed similar patterns, with areas of low-intensity fire ($I < 0.25$) occurring within several hundred metres of high-intensity fires ($I > 0.75$). This spatial heterogeneity has important consequences for forest recovery and potential management because it will generate a diverse set of stand development trajectories across the broader landscape (Tepley *et al.* 2013, Romme *et al.* 2016). At the broader landscape scale, the spatial arrangement of stands with different developmental trajectories can also have important consequences for habitat connectivity and metapopulation dynamics (Levey *et al.* 2008, Brudvig and Damschen 2009), particularly of species associated with specific structural features such as dead trees (Gibbons and Lindenmayer 1996) or specific developmental stages such as old-growth forest (Oliver and Larson 1996).

## Variation among species in susceptibility to fire

Our study provides the first empirical estimates of interspecific variation in susceptibility to fire-induced mortality (both top-kill and full-kill) as a function of tree size and fire intensity. We found distinct differences among the species of the dry sclerophyll forest (DSF) and the three other forest types (cool temperate rainforest (CTR), cool temperate mixed forest (MF), and tall open forest(TOF)). Most notably, the eucalypt species that dominated the DSF showed strong size-dependent patterns of top-kill survival even at the highest fire intensities with larger trees having higher probabilities of top-kill survival than smaller trees. In contrast, the tree species from the other forest types exhibited size-independent top-kill under high-intensity fire conditions—that is, all trees were killed aboveground regardless of stem size. Under low- to moderate-intensity fires, top-kill patterns among the non-DSF tree species were more likely to be size-dependent. However, for these species the probability of mortality declined substantially only for the largest trees and for relatively low-intensity fires. Size-dependent patterns of tree survival to fire have long been recognised in the literature (Gill and Ashton 1968, Ryan *et al.* 1988, Baker and Bunyavejchewin 2006). As trees increase in stem diameter, bark thickness typically increases, providing greater insulating capacity and protection of the cambium.

Among the eucalypt species there was a clear gradient of resistance and resilience to fire-induced mortality. *Eucalyptus obliqua* and *E. dives* were the most resistant to fire—that is, the existing stems were not top-killed at relatively modest sizes even in the hottest fires. This is presumably due to their relatively thick bark and ability to produce epicormic shoots soon after fires (Burrows 2013). However, they were also the most resilient to fire, with small individuals vigorously resprouting from the stem base after high-intensity fires. *Eucalyptus radiata* and *E. viminalis* were intermediate in their resistance to fire—that is, for a given relative fire intensity, they required larger trees to have the same probability of top-kill survival as *E. obliqua* or *E. dives*. *Eucalyptus regnans* was the least resistant to fire of the modelled species with complete top-kill regardless of tree size in the highest intensity fires, although it did show evidence of size-dependent top-kill survival in low- to moderate-intensity fires. While we were not able to include *E. delegatensis* into our mortality model due to the lack of surviving individuals, all 134 individuals were full-killed (*i.e.*, complete aboveground mortality and no evidence of resprouting), which is consistent with their known sensitivity to fire (Bowman *et al.* 2014).

Future fires may act as a filter that shapes the structure and composition of forests across these landscapes in the coming decades (Stevens-Rumann *et al.* 2017, Trouvé *et al.* 2020). For example, if fires become more intense in the DSF, the species-specific differences in susceptibility to fire-induced full-kill would lead us to predict a compositional shift towards greater dominance of *E. obliqua* and *E. dives* and gradual loss of *E. radiata* and *E. viminalis*. In addition, size-specific differences in susceptibility within each species would be expected to lead to stands with fewer small trees. However, where young DSF stands dominated by small trees exist, high-intensity fires may lead to widespread top-kill followed by abundant basal resprouting. Anecdotal observations of post-fire recovery after the recent 2019/20 fires suggest that this pattern is common across eastern Victoria. It remains unclear whether DSF species would be able to persist through multiple cycles of top-kill and basal resprouting without eventually depleting their stored carbohydrate reserves and ceding the site to a different vegetation type (Fairman *et al.* 2016, 2017).

For the TOF dominated by *E. regnans*, high-intensity fires are typically stand replacing. If the burnt trees are of reproductive age (older than $\sim$ 21 years, Fagg *et al.* 2013, von Takach Dukai *et al.* 2018), a new, single cohort of *E. regnans* will establish. If not, the species will become locally extinct and be replaced by communities dominated by non-eucalypts (Fairman *et al.* 2016). This shift in composition and functional type will persist until a subsequent disturbance provides opportunities for new eucalypt seed dispersing into the site from adjacent stands to germinate and grow. In contrast, low- to moderate-intensity fires in TOF may kill a relatively small proportion of the large trees (Figure 4). This can lead to structurally complex stands with two distinct cohorts made up of surviving trees and new recruits (Ashton 2000). The subsequent dynamics of the stand will depend on the relative abundance of the young and old cohorts. If there are relatively few trees in the older cohort, the new recruits will have access to sufficient resources to grow and survive, allowing the two-cohort structure to persist. However, if the trees from the older cohort are abundant, the younger cohort will be suppressed and experience high mortality rates from competition, leading to the stand reverting to a single-cohort structure (see *e.g.*, Figure 19 in Ashton 2000).

Basal resprouting was an important component of resilience, particularly for the CTR species, *Nothofagus cunninghamii* and *Atherosperma moschatum*. CTR has long been considered highly sensitive to fire and there is concern that an increase in fire activity under future climatic conditions will lead to contraction and loss of these ecosystems. However, a multi-scale review of CTR dynamics based on evidence from fossil pollen, sub-fossil charcoal, tree rings, and direct observations after the 2009 bushfires showed that cool temperate rainforest had persisted in Victoria's Central Highlands despite tens of thousands of years of fire activity (Baker *et al.* 2012). Similarly, Worth *et al.* (2009) used chloroplast DNA to show that *Nothofagus cunninghamii* had persisted *in situ* in Tasmania through periods of global aridity during the Pleistocene. The results from our study demonstrate that the resprouting ability of the dominant canopy species of the cool temperate rainforest, *N. cunninghamii* and *A. moschatum*, is an important component of this resilience. Several previous studies have demonstrated the ability of *Nothofagus cunninghamii* to resprout after fires in Victoria and Tasmania (Baker *et al.* 2012, Prior *et al.* 2018). When basal resprouting is accounted for, full-kill rates in the highest intensity fire are $<50\%$, even for relatively small individuals (Figure 4). Simkin and Baker (2008) showed that many of the *Nothofagus cunninghamii* and *Atherosperma moschatum* in a cool temperate rainforest near Marysville, Victoria, survived in the extensive 1939 bushfires, even though all of the *Eucalyptus regnans* (mountain ash) and *E. delegatensis* (alpine ash) on the adjacent slopes were killed. It is unclear, however, how many cycles of top-kill and basal resprouting CTR species can endure before ceding ground to more resilient species (Fairman *et al.* 2016).

Despite the resilience of CTR conferred by basal resprouting, regeneration patterns were linked to fire intensity. Under low to moderate fire intensities ($I$ <0.5), seedling composition was dominated by CTR species. However, when $I$ >0.5, seedling composition was dominated by species from the TOF, particularly *E. regnans*. This interaction between fire intensity and the species composition of the post-fire regeneration has been documented in other forests around the world (*e.g.*, Hollingsworth *et al.* 2013) and raises important questions about the long-term viability of CTR in a warming world.

At the landscape scale, spatial variability in fire intensity is a key source of heterogeneity in post-fire forest development (Turner *et al.* 2004, Schoennagel *et al.* 2008). Differences in fire intensity within and among stands and forest types contribute to variation in the density of surviving and dead trees, the predominant mode of regeneration (*e.g.*, seeding, sprouting), and spatial patterns of regeneration. Differences in initial post-fire conditions, both biotic and abiotic, can lead to differences in post-fire stand development trajectories (Ewel 1980, Christensen *et al.* 1989, Palik and Pregitzer 1993, Ashton 2000, Tepley *et al.* 2013). These, in turn, can drive the future provision of ecosystem services such as carbon sequestration, habitat development, and water uptake.

## Implications for managing forests to be more fire resistant

The relationships between top-kill survival and relative fire intensity, tree size, and species also suggest management strategies that may help adapt forested landscapes to fire and reduce the risk of widespread mortality as fire regimes change (*e.g.*, Koontz *et al.* 2020). All but one of the species in this study showed some evidence of size-dependent aboveground mortality (*i.e.*, top-kill) under specific fire intensity conditions. Where size-dependent top-kill occurred, the probability of aboveground mortality was negatively associated with stem size—bigger trees were more likely to survive a fire than smaller trees. This suggests that silvicultural prescriptions that accelerate the growth of individual trees have the potential to reduce the period of time that a tree is exposed to the risk of fire-induced top-kill.

Forest management practices, such as thinning, that accelerate the growth of individuals (West and Osier 1995) have the potential to make these stands more resistant to future fires, particularly high-intensity fires, by reducing their exposure to risk of being top-killed. To illustrate this point, we provide an example using *E. regnans* for which thinning trial data are abundant. Reducing the initial density through reduced sowing rates or early thinning can lead to substantial increases in growth rates of *E. regnans*. Historical spacing trials established in the 1960s give an indication of the scale of the potential gains (Figure 6). For stands starting at high stem densities, which are typical of current forest management practices ($>$2500 seedlings ha$^{-1}$ at four years old), it takes $\sim$35 years to reach 35 cm DBH, the size at which *E. regnans* has a 50% probability of top-kill survival under moderate relative fire intensity ($I = 0.4$). In contrast, at the lowest density in the spacing trials (120 stems ha$^{-1}$ at four years old), it took only 12 years for individual trees to reach 35 cm DBH. By growing *E. regnans* at such a low density, the length of time individuals are exposed to a high probability of top-kill under a low- to moderate-intensity fire was reduced by more than two decades. Low stem densities, whether achieved through reduced sowing densities or early thinning, may increase the diameter growth of individual trees, but they may also have a variety of drawbacks. For example, at extreme low densities the base of the live crown of individual trees may be closer to the ground and therefore prolong the period that the crown is susceptible to damaging crown scorch. Also, density effects on height growth may be positive, neutral, or negative; although among broad-leaved tree species there is often a positive effect of reduced density on height growth (Trouvé *et al.* 2019). Depending on the fire intensity, individual trees may need to reach a certain height (regardless of stem diameter) to escape being top-killed by fires. Maintaining low density stands may have other negative consequences for fire behaviour such as stimulating shrub growth, increasing fuel loads from thinning debris, and increased insolation and wind movement at the forest floor, which may accelerate fuel drying (see Zylstra *et al.* 2016, although under very dry conditions, surface fuels in open stands have been shown to be not much drier than fuels in denser stands (Bigelow and North 2012)). However, lower density stands also have reduced crown packing within the stand, which lowers the connectivity of crown fuels and reduces fire spread through the forest canopy (Van Wagner 1977, Wilson and Baker 1998).

This reduction in the period of time that individual trees are exposed to high risk of fire-induced mortality is of particular importance for landscape-scale forest management planning. While the 2009 Black Saturday fires were amongst the most devastating of the past century, only about one-third of the forest experienced catastrophic (>80% canopy loss), stand-replacing fires (Cruz *et al.* 2012). The remaining two-thirds of the burnt area was evenly divided between forest that experienced partial (20-80%) canopy loss and forest that had little (<20%) canopy loss or only experienced surface fire (Jiang *et al.* in prep.). If such a significant proportion of the landscape experienced low-to-moderate fires—even under some of the most catastrophic fire conditions ever recorded—then managing *E. regnans* to maximise individual growth rates instead of stand-level volume may increase the probability that at least some individuals survive future fires. Because the timing, location, and intensity of future fires is unknown, increasing the proportion of stands with lower densities and higher mean tree sizes for a given age should reduce the total area of stands that suffer high mortality rates across the landscape. While areas with high-intensity fires may have few surviving trees, other areas that only experienced low-to moderate-intensity fires could have significantly lower mortality rates. It is these areas of individual trees or clumps of trees that survive after fires that are critically important sources of shelter and foraging for wildlife in the months and years after the fire has passed (Meddens *et al.* 2018, Coop *et al.* 2019), as well as a critical source of seeds for regeneration after the fire.

For the other eucalypt species, which are able to survive moderate- to high-intensity fires, reducing stand density would also limit their exposure to fire-induced mortality. This is particularly important given the context of the 2019-20 bushfire season in southeastern Australian, which has seen nearly 6 million hectares of forest burn in Victoria and New South Wales. A large proportion of these forests are mixed eucalypt forests composed of resprouting eucalypt species similar to those from the DSF in this study. The predicted changes to regional climate are expected to lead to more frequent, more extensive, and potentially more severe fires. This will likely lead to significant changes in species composition and forest structure at the stand, landscape, and regional scale (*e.g.*, Fairman *et al.* 2016). Forest management practices that accelerate the growth of individual trees into more fire-safe size classes can reduce the probability of stand- and landscape-wide mortality and increase the chance that at least some forest cover is maintained within a site as fire regimes change. Understanding how different species vary in their susceptibility to fire, conditional on size and fire intensity, may help inform management practices that can mitigate some of this risk and create more resilient landscapes (Schoennagel *et al.* 2017, McWethy *et al.* 2019).

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## Open Research statement

Data (Trouvé *et al.* 2021) are available on Github at: `https://doi.org/10.5281/zenodo.4727469`.

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Table 1: Summary statistics of the data. The resprout column corresponds to the percentage of basal resprouting trees among the trees that were top-killed (*i.e.*, $resprout = \frac{topkilled - fullkilled}{topkilled}$).

| | Number | DBH (cm) | | Top-killed | Full-killed | Resprout |
|---|---|---|---|---|---|---|
| | of trees | Mean | Range | % | % | % |
| *Acacia dealbata* | 405 | 24 | (10, 70) | 79 | 79 | 0 |
| *Acacia melanoxylon* | 166 | 18 | (10, 48) | 64 | 57 | 11 |
| *Atherosperma moschatum* | 61 | 18 | (10, 77) | 84 | 48 | 43 |
| *Nothofagus cunninghami* | 807 | 23 | (10, 164) | 79 | 44 | 45 |
| *Olearia argophylla* | 56 | 14 | (10, 31) | 100 | 4 | 96 |
| *Eucalyptus obliqua* | 295 | 35 | (10, 112) | 35 | 23 | 33 |
| *Eucalyptus dives* | 127 | 32 | (10, 80) | 47 | 24 | 48 |
| *Eucalyptus radiata* | 348 | 36 | (10, 162) | 46 | 36 | 20 |
| *Eucalyptus viminalis* | 18 | 56 | (19, 100) | 22 | 22 | 0 |
| *Eucalyptus regnans* | 318 | 68 | (12, 376) | 42 | 42 | 0 |

Table 2: Mean and 95% credible interval of parameter values per species for the top-kill and full-kill models

| | | $\alpha$ | | | $\beta$ | | | $\gamma$ | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 95% CI | | | 95% CI | | | 95% CI | |
| Model | Species | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| Top-kill | *Acacia dealbata* | -3.87 | -6.77 | -1.93 | 196.0 | 69.2 | 470.9 | -0.53 | -0.84 | -0.26 |
| | *Acacia melanoxylon* | -3.66 | -5.83 | -2.15 | 189.5 | 60.9 | 497.6 | -0.66 | -1.05 | -0.33 |
| | *Atherosperma moschatum* | -3.61 | -7.73 | -0.99 | 68.9 | 19.3 | 197.7 | -0.28 | -0.85 | -0.02 |
| | *Eucalyptus dives* | -3.00 | -4.73 | -1.68 | 65.9 | 21.4 | 171.4 | -0.74 | -1.18 | -0.43 |
| | *Eucalyptus obliqua* | -2.77 | -3.75 | -2.02 | 479.4 | 88.5 | 1919.5 | -1.42 | -2.05 | -0.94 |
| | *Eucalyptus radiata* | -2.59 | -3.50 | -1.86 | 151.4 | 57.4 | 344.7 | -0.84 | -1.15 | -0.58 |
| | *Eucalyptus regnans* | -6.50 | -9.41 | -4.51 | 182.1 | 79.2 | 381.9 | -0.53 | -0.71 | -0.36 |
| | *Eucalyptus viminalis* | -3.10 | -6.19 | -0.87 | 158.5 | 12.4 | 801.5 | -1.16 | -4.80 | -0.15 |
| | *Nothofagus cunninghami* | -4.23 | -7.15 | -2.47 | 34.5 | 21.5 | 54.5 | -0.07 | -0.25 | -0.01 |
| | *Olearia argophylla* | -3.34 | -7.26 | 0.29 | 306.6 | 40.7 | 1472.5 | -0.29 | -0.84 | -0.01 |
| Full-kill | *Atherosperma moschatum* | -10.79 | -17.36 | -5.30 | 86.1 | 4.3 | 397.4 | -2.67 | -8.50 | -0.15 |
| | *Eucalyptus dives* | -11.02 | -18.25 | -5.85 | 79.8 | 2.3 | 327.8 | -2.19 | -11.64 | -0.23 |
| | *Eucalyptus obliqua* | -11.13 | -18.72 | -5.94 | 115.7 | 2.1 | 512.4 | -2.25 | -8.03 | -0.22 |
| | *Eucalyptus radiata* | -11.12 | -17.06 | -6.45 | 93.7 | 20.7 | 343.2 | -0.39 | -0.86 | -0.07 |
| | *Nothofagus cunninghami* | -10.57 | -16.68 | -6.21 | 167.3 | 43.4 | 706.0 | -0.76 | -1.35 | -0.38 |
| | *Olearia argophylla* | -10.99 | -18.83 | -6.00 | 105.6 | 2.4 | 307.2 | -2.72 | -12.96 | -0.18 |

Table 3: Mean estimates (and range) of latent relative fire intensity ($I$) and proportion of trees killed by the fire for each study location. Forest type describes the pre-fire forest classification based on tree species composition (DSF–dry sclerophyll forest; TOF–tall open forest; CTR–cool temperate rainforest; MF–mixed forest). Seedling composition reflects the species composition of post-fire regeneration observed in each forest type. Where the species composition of the post-fire regeneration differed from pre-fire tree species composition, the forest type association of the regeneration is highlighted in bold. At the Beeches CTR sites, post-fire seedling composition was conditional on fire intensity. So, we present the post-fire species composition for sites that experienced fire intensities above and below the observed threshold intensity value. Estimates of proportion dead are calculated as the basal area (BA) of trees within each plot that were killed in the fire divided by the total BA of the plot.

| Location | Forest type | N | Relative fire intensity ($I$) | Proportion of top-kill | Seedling composition |
|---|---|---|---|---|---|
| Acheron Way | CTR | 1 | 0.05 | 0.05 | CTR |
| | DSF | 2 | 0.55 (0.48-0.63) | 0.21 (0.14-0.29) | DSF |
| | MF | 1 | 0.09 | 0.09 | MF |
| | TOF | 6 | 0.25 (0.20-0.32) | 0.18 (0.14-0.39) | TOF |
| The Beeches | CTR | 4 | 0.28 (0.13-0.29) | 0.63 (0.31-0.83) | $I < 0.5$ = CTR<br>$I >$ **0.5 = TOF** |
| | MF | 3 | 0.79 (0.73-0.83) | 1.00 | **TOF** |
| Cambarville | CTR | 3 | 0.53 (0.35-0.88) | 0.55 (0.26-1.00) | **TOF** |
| | MF | 3 | 0.51 (0.08-0.83) | 0.58 (0.04-1.00) | **TOF** |
| | TOF | 5 | 0.33 (0.18-0.83) | 0.33 (0.17-1.00) | TOF |
| Cathedral Ranges | DSF | 11 | 0.32 (0.06-0.89) | 0.28 (0.07-0.84) | DSF |
| Marysville | DSF | 5 | 0.54 (0.38-0.71) | 0.47 (0.37-0.76) | DSF |
| Mt Margaret | CTR | 1 | 0.68 | 1.00 | **MF** |
| | MF | 2 | 0.67 | 1.00 | MF |
| | TOF | 5 | 0.7 (0.60-0.90) | 1.00 | TOF |

# List of Figures

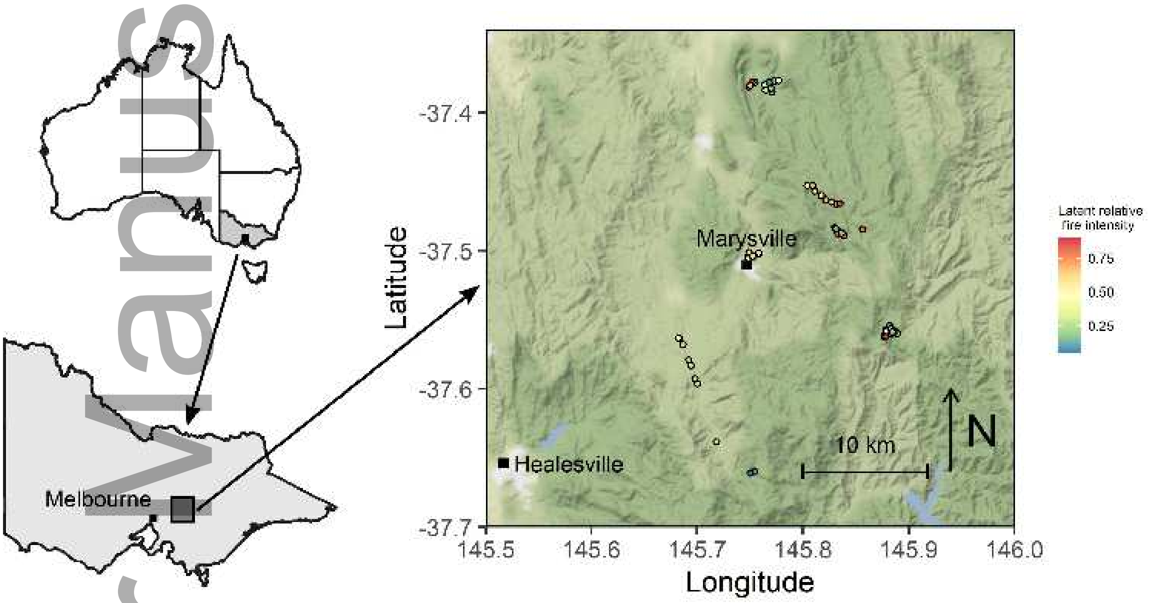


Figure 1: Plot location in the Central Highlands of Victoria. Dot colors represent the latent relative fire intensity ($I$) of each plot estimated when fitting Eq. 1. Background map tiles on the right map by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

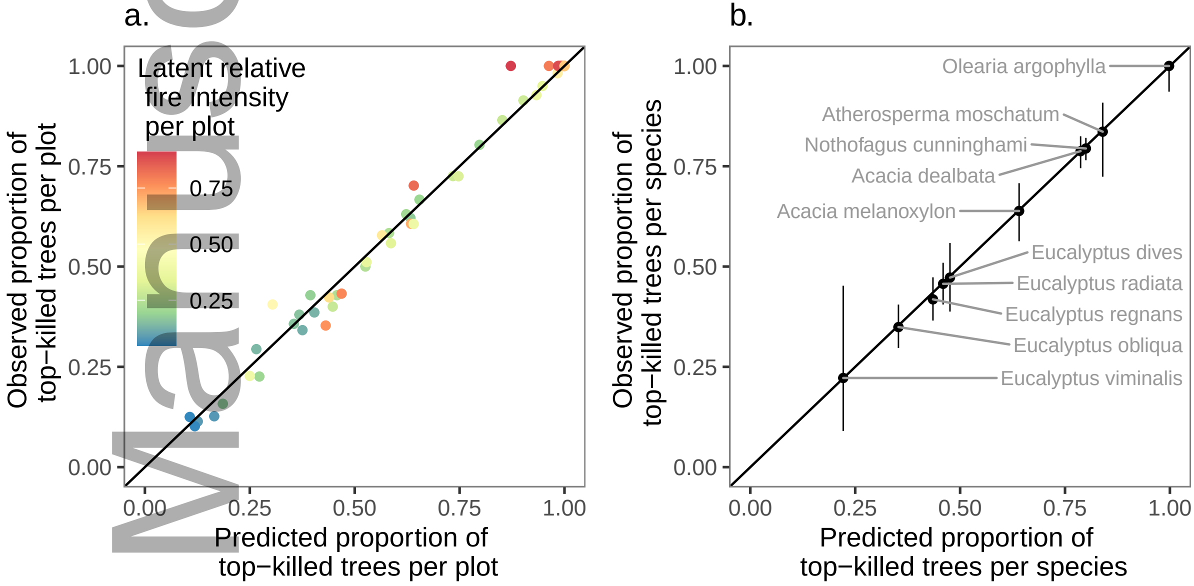


Figure 2: Goodness-of-fit of the top-kill model. a. Individual points are observed vs. predicted fire-induced proportion of top-killed trees per plot. b. Goodness-of-fit of the top-kill model per species. Dots are observed vs. predicted fire-induced proportion of top-killed trees per species. Error bars are 95% Wilson binomial CI for the observations (Brown *et al.* 2001). The black line indicates a 1:1 correspondence between observed and predicted top-kill. The model appears well calibrated at the plot and species level.

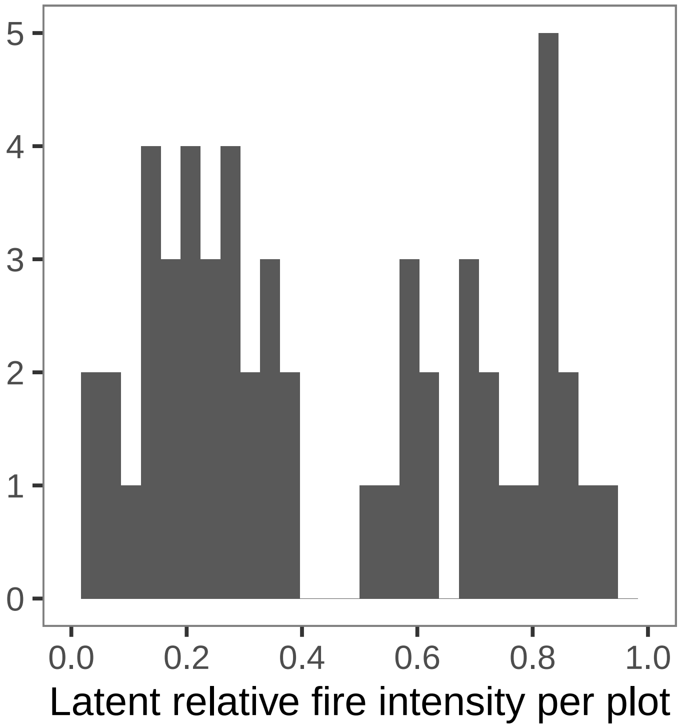


Figure 3: Distribution of latent relative fire intensity ($I$) scores for all plots (n=53) in the study.

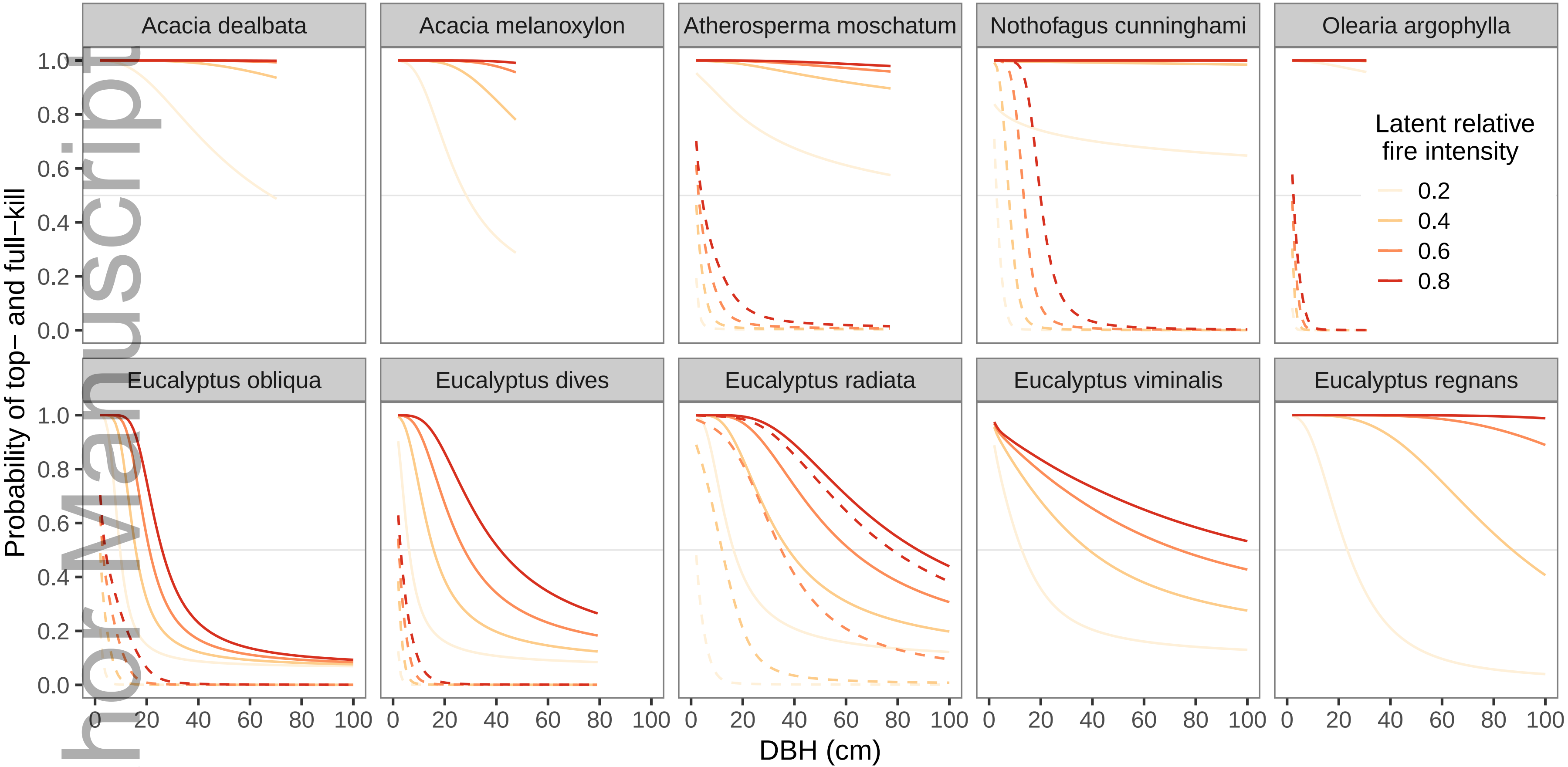


Figure 4: Susceptibility to fire-induced top- and full-kill as a function of species, tree size, and latent relative fire intensity for the 10 abundant tree species in the study. For those species that had >10 individuals resprouting, we calculated mortality with and without resprouts separately (see Methods for details). The solid lines represent results for the top-kill model; the dashed lines represent results for the full-kill model (top-killed individuals with basal resprouts are counted as surviving). The four relative fire intensities were selected to represent the range of estimated relative fire intensities.

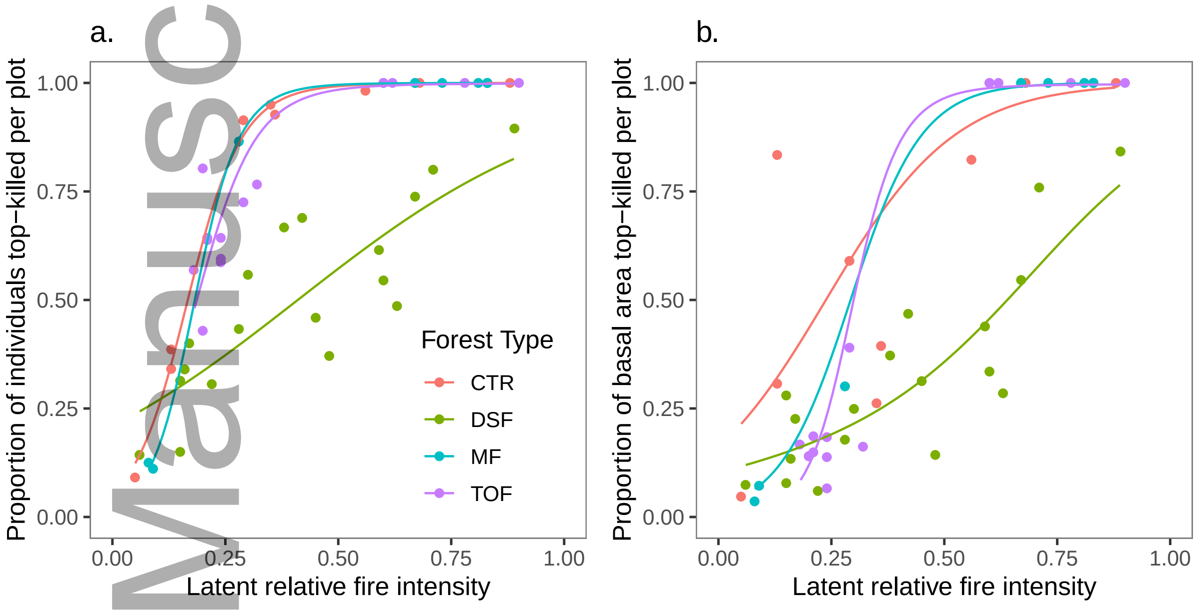


Figure 5: Proportion of top-killed trees as a function of latent relative fire intensity across the four different forest types. The left panel (a.) is the proportion of top-killed trees based on the number of individuals in each plot; the right panel (b.) is the proportion of top-killed trees based on the basal area of each plots. The forest types are cool temperate rainforest (CTR), dry sclerophyll forest (DSF), mixed forest (MF), and tall open forest (TOF). The dots show the observed proportion of top-killed trees and the estimated relative fire intensity per plot. To help visualize the relationships, we fitted a separate general additive model (GAM) with a Beta error distribution and a logit link to each forest type (solid lines).

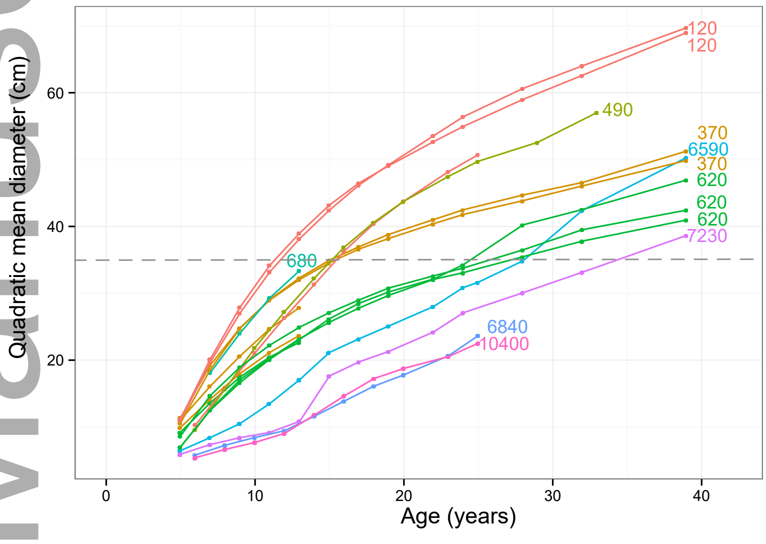
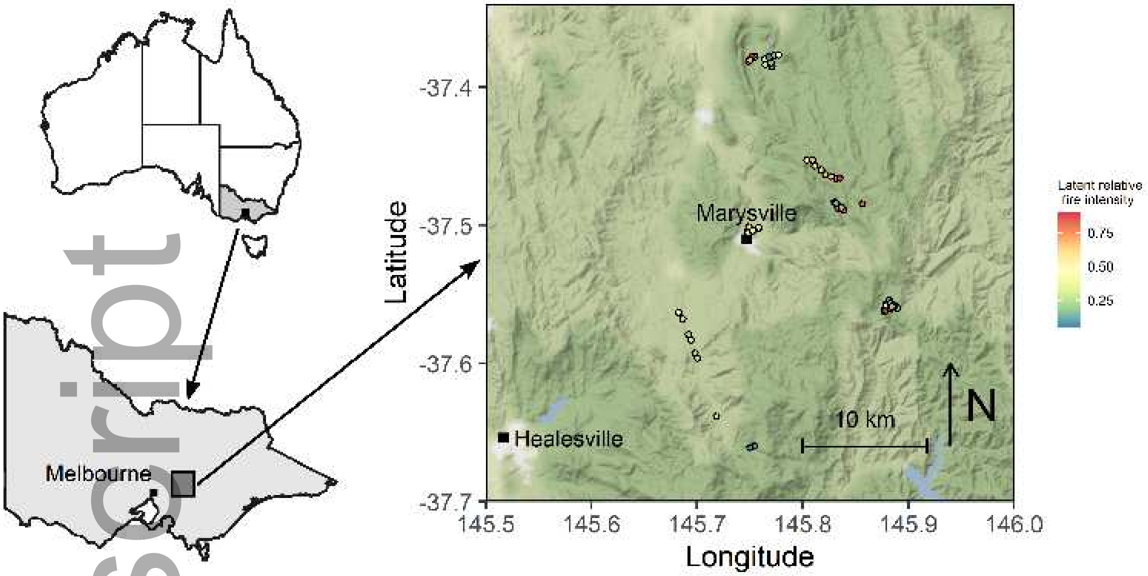


Figure 6: The effect of early stand density on diameter growth of *Eucalyptus regnans*. The stands were thinned at Year 4 to a range of residual densities (120-10400 trees ha$^{-1}$), shown to the right of each line. The y-axis values are plot-level quadratic mean diameters. The gray dashed line is the diameter (35 cm) at which mountain ash has a 50% probability of top-kill survival when $I$=0.2. The data are from long-term thinning trials originally initiated by the Victorian Forest Commission in the 1950s and 60s and subsequently maintained and managed by the Victorian Department of Environment, Land, Water, and Planning and VicForests.



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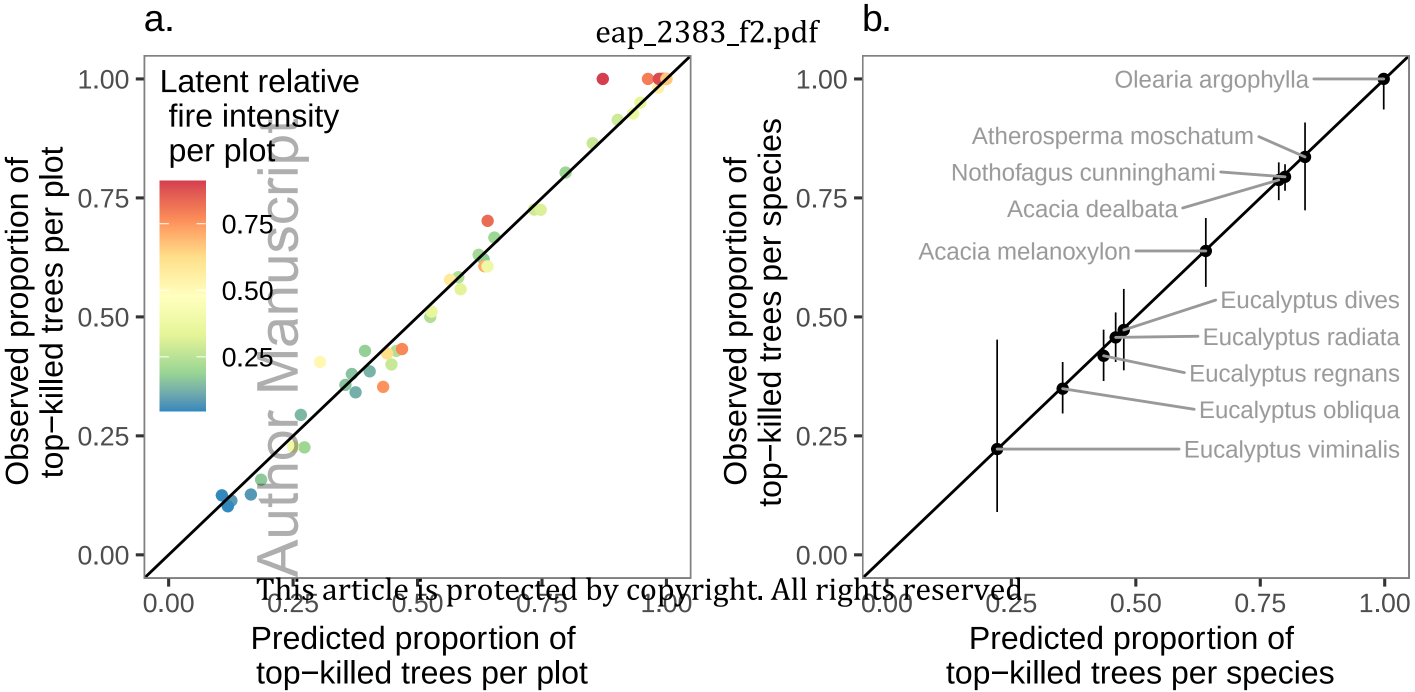
eap_2383_f2.pdf



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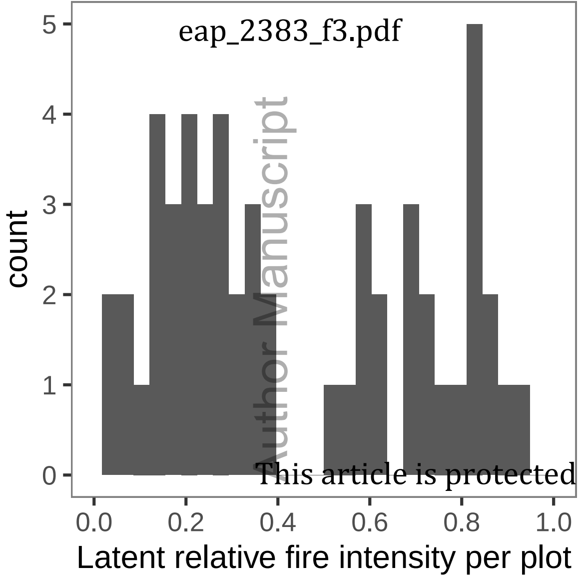
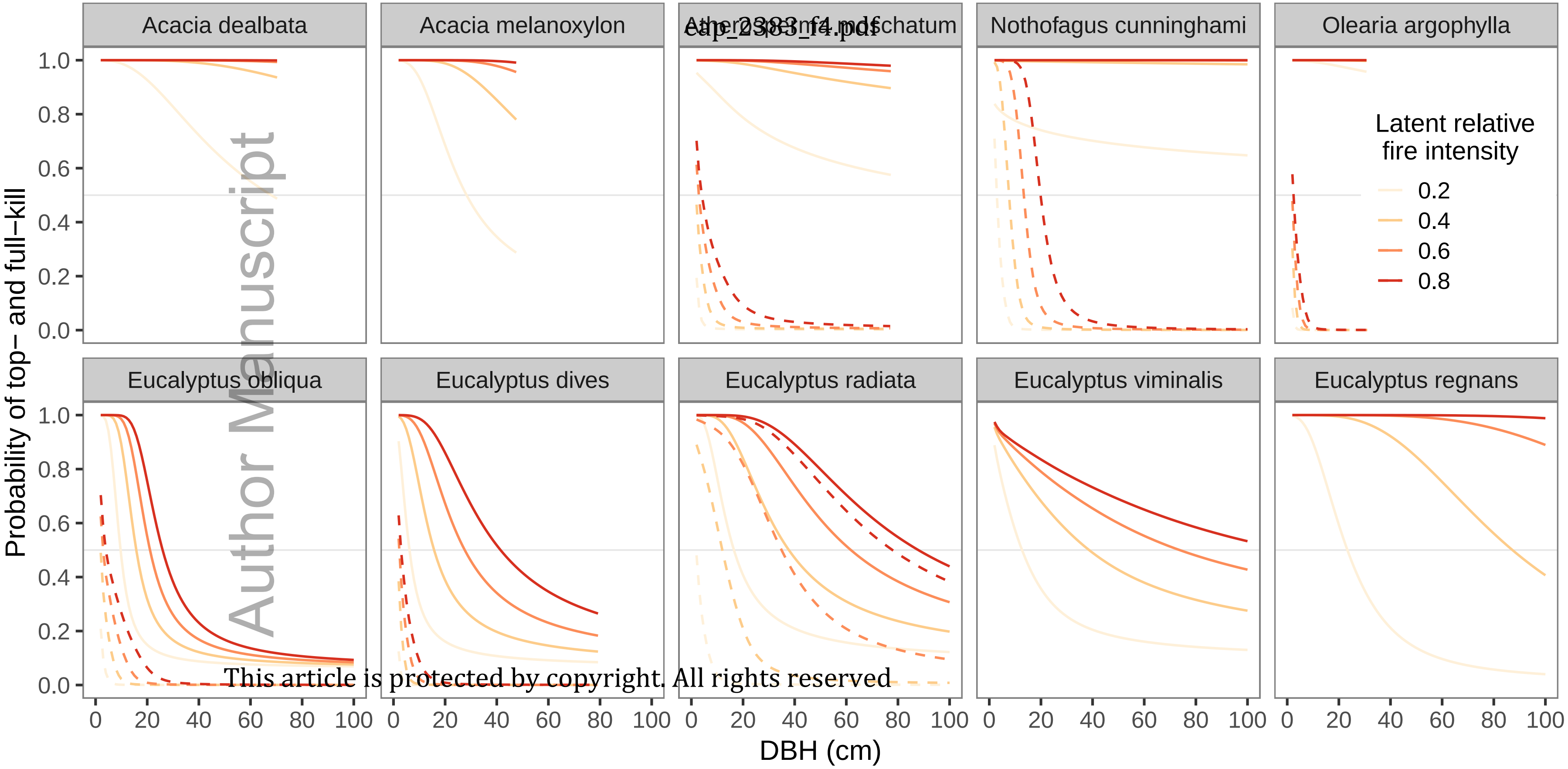
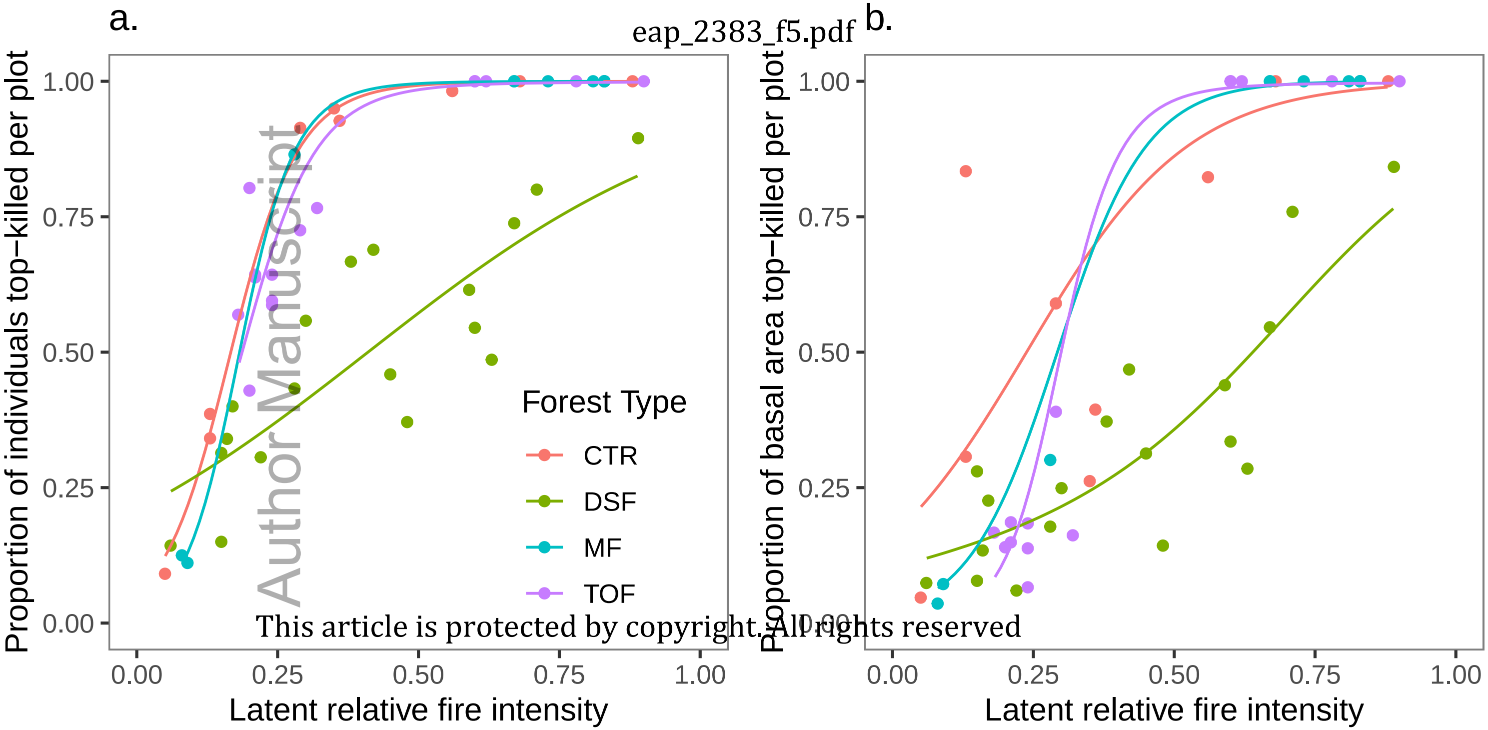
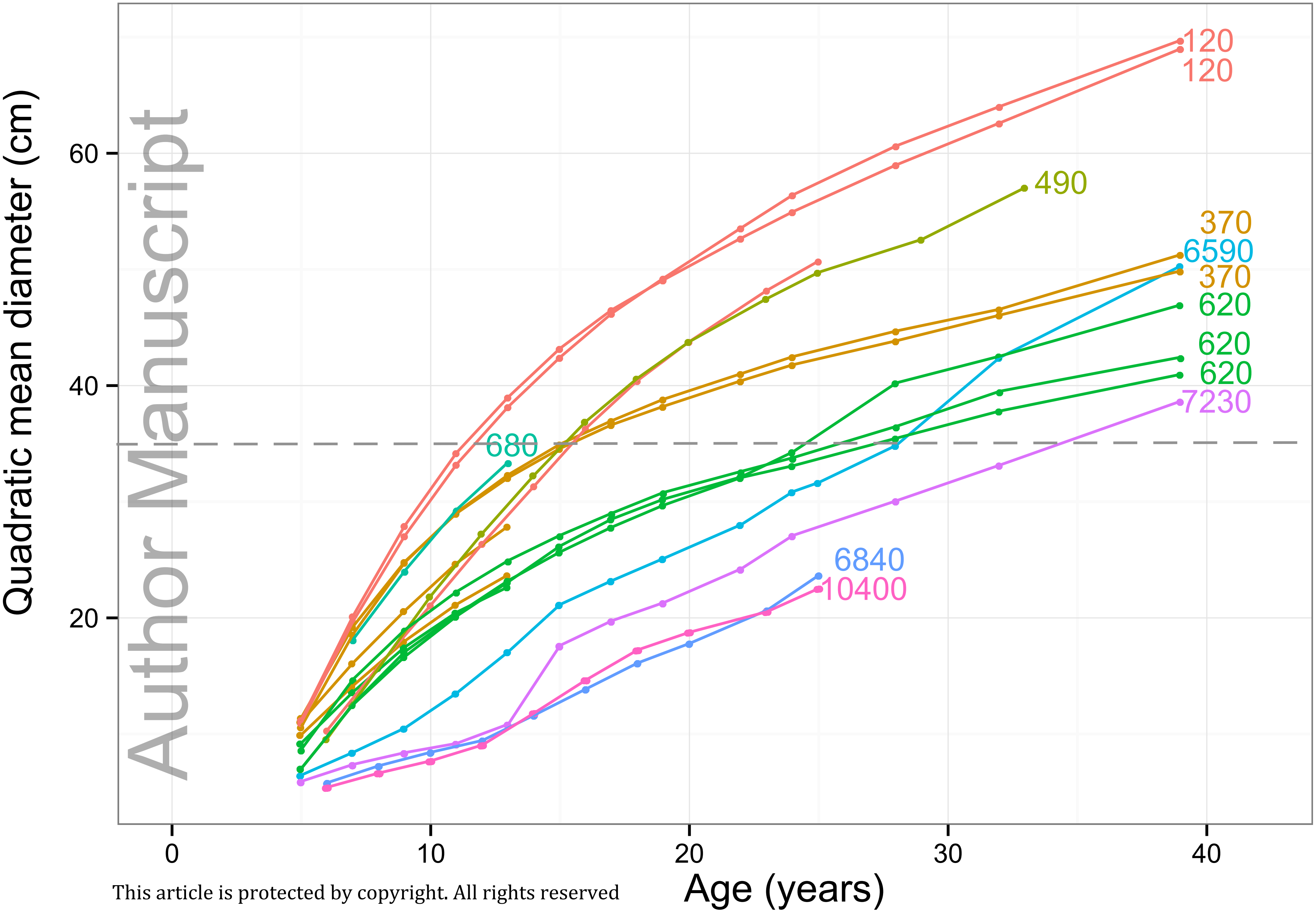



Acacia dealbata
Acacia melanoxylon
Atherosperma moschatum
Nothofagus cunninghami
Olearia argophylla
Eucalyptus obliqua
Eucalyptus dives
Eucalyptus radiata
Eucalyptus viminalis
Eucalyptus regnans
Probability of top− and full−kill
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
DBH (cm)
Latent relative fire intensity
0.2
0.4
0.6
0.8


a.
b.
Proportion of individuals top−killed per plot
Proportion of basal area top−killed per plot
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.00
Latent relative fire intensity
Forest Type
CTR
DSF
MF
TOF


Quadratic mean diameter (cm)
60
40
20
0
10
20
30
40
Age (years)
120
120
490
370
6590
370
620
620
620
7230
680
6840
10400