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The relationship between fire severity and eucalypt health: implications for forest structure and carbon balance

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Abstract

The capacity of resprouting eucalypts to regenerate foliage determines the extent of fire induced structural change and carbon dynamics within Australian dry sclerophyll forests. Resprouting eucalypts are traditionally considered resilient to severe fire, yet records of post-fire mortality are highly varied, reflecting the limited sample size of previous studies and the complexity of factors that govern stem death. Fire regimes are predicted to become increasingly severe throughout Mediterranean ecosystems under anthropogenic climate change, increasing the risk of carbon loss within forest communities. This study sought to further the ecological understanding of the effects of fire severity on eucalypt mortality and coarse woody debris (CWD) dynamics within dry sclerophyll communities across southeast Australia. The extent of tissue death and the occurrence of resprouting were used to quantify the health response of eucalypts to fire disturbance. CWD was assessed using van Wagner's line-intercept method. Relevant additional data was obtained from the NSW Bushfire Risk Management Research Hub. Fire severity and fire frequency values were derived from digital fire extent and severity maps based on satellite imagery. As predicted, eucalypt stem mortality was significantly influenced by stem diameter and fire severity, such that rates of stem death were greatest for small stems under extreme severity fire. Furthermore, stem mortality was significantly influenced by bark type, with smooth bark stems generally the most resilient to fire disturbance. CWD biomass was not significantly influenced by fire severity or frequency yet was significantly affected by fire type. CWD was reduced in plots burnt by prescribed fire and heightened in plots burnt by wildfire, relative to long unburnt forest. This suggests that lower intensity prescribed burns consume more CWD than they produce, whilst CWD production exceeds consumption under higher intensity wildfires. This study provides the largest and most reliable field-based estimates of stem death in dry sclerophyll forests to date. Under more severe fire regimes, disproportionate age class and bark type mortality will likely decrease forest diversity and structural complexity. Both CWD production and consumption will likely increased under future fire regimes, leading to a possible reduction in forest carbon if the consumption of dead wood exceeds the production of live biomass. Whilst gradual carbon loss and demographic shifts are 4 expected under more severe fire regimes, complete ecosystem transformation of resprouting eucalypt forests seems unlikely in the near future, given the persistence of the majority of large trees and the rapid development of lignotubers in small stems which often prevents whole tree mortality.

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I would like to acknowledge the Traditional Owners of the Tharawal, Dharug, Darkingjung, Yuin, and Gundungurra nations. I pay my respects to Elders past, present and future.

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Abbreviations

cm	= centimetres
CO_2	= carbon dioxide
CWD	= coarse woody debris
DBH	= diameter at breast height
DSF	= dry sclerophyll forest
FESM	= fire extent and severity mapping
FFDI	= Forest Fire Danger Index
GLM	= generalised linear model
GLMM	= generalised linear mixed-effects model
ha	= hectares
M	= million
m	= metres
mm	= millimetres
spp.	= species

Contents

List of Figures

List of Tables

Chapter 1: Introduction and aims

1.1 General introduction

Evidence of widespread wildfire first appears in the geological record during the early Carboniferous period, following the development of forest vegetation and a rise in atmospheric oxygen levels (Bodí *et al.* 2014; Scott & Glasspool 2006). In the Anthropocene, wildfire has a fundamental influence on global ecological and social systems, affecting vegetation distribution and structure, the carbon cycle, human health and the economy (Bowman *et al.* 2013). For millennia, humanity has actively altered the seasonality, frequency and intensity of fire activity for a range of social, ecological and cultural objectives (Cavanagh 2020; Trauernicht *et al.* 2015). Accordingly, the severity and environmental impacts of contemporary prescribed fire are assumed to differ to the characteristics and consequences of wildfire.

Fire has shaped the evolutionary development of Australian ecosystems and remains a driving force affecting the Australian people and their environment (Sharples *et al.* 2016). In fire-prone landscapes, many plant species have evolved traits that provide resilience to extreme heat and enable regeneration after burning (Nicholson *et al.* 2017). The temperate dry eucalypt forests of south eastern Australia are dominated by fire adapted species capable of resprouting new foliage following leaf scorch or consumption (Burrows 2013). The capacity to resprout new leaves after fire is a fundamental determinant of the structural dynamics and carbon flow within fire-prone forests (Burton *et al.* 2021). This is evident when comparing resprouting and non-resprouting tree species in southeast Australia. Resprouting eucalypts typically have low levels of fire induced mortality compared with non-resprouting eucalypts, which rely on post-fire seed germination for reestablishment (Bradstock 2008). Patterns of carbon loss and sequestration therefore often differ between resprouting and non-resprouting eucalypt forests due to the vulnerability and gradual decomposition of large, obligate seeding trees following wildfire (Gordon *et al.* 2018).

Fires are prevalent and heterogenous landscape disturbances which are often described by *fire severity* – a measure of consumed organic matter (Keeley 2009). The severity of a fire can correlate with the scale of impact on a range of other systems. Driven by conducive fuel characteristics and ambient weather conditions, high severity fires consume more biomass, lead to a greater loss of infrastructure and human life, and cause greater tree mortality compared to low severity burns (Bennett *et al.* 2016; Blanchi *et al.* 2010; Harris *et al.* 2012; Hollis, Anderson, *et al.* 2011). As fire severity is quantified by the consumption of organic matter, it is an inherent factor affecting the ability of resprouting vegetation to recover (Fairman *et al.* 2016; Prior *et al.* 2016).

In south eastern Australia, rates of fire induced eucalypt mortality are thought to be influenced by the characteristics of the burn, the attributes of the constituent tree species, the ecological legacy of previous fire, and the compounding impact of other concurrent disturbance events (Burton *et al.* 2021; Furniss *et al.* 2020; Paine *et al.* 1998; Watson *et al.* 2020). This complexity of interacting factors ultimately determines forest structure and the dynamics of coarse woody debris (CWD) in these fire-prone ecosystems (Bassett *et al.* 2015; Bassett *et al.* 2017). Stand structure and coarse woody debris are critical components of forests systems that influence productivity, nutrient cycling, carbon stock and biodiversity through the provision of habitat and refugia for fauna, flora and microbial communities (Burton *et al.* 2021; Millar & Stephenson 2015). Dead wood, which includes both standing dead trees and fallen CWD, also impacts dry fuel loads and smoke production during future fire activity (Reisen *et al.* 2018; Volkova & Weston 2019). A comprehensive understanding of tree mortality and coarse woody debris dynamics is therefore essential for assessing the holistic impacts of prescribed fire regimes and for predicting the influence of climate change on resprouting eucalypt forests, which dominate southeast Australia.

The body of evidence involving resprouting eucalypt mortality in response to fire disturbance is somewhat inconsistent. The literature suggests that stem mortality is influenced by a range of interacting factors including stem diameter, bark attributes, fire severity, fire history and the compounding impact of other disturbances such as drought (Collins 2020; Nolan, Rahmani, *et al.* 2020; Prior *et al.* 2016). Records of fire induced topkill in resprouting eucalypt forests are varied, ranging from 2 – 52% (Prior *et al.* 2016; Vivian *et al.* 2008). This variation is likely influenced by sample size and nonuniform methods between studies, including disparate measures of fire behaviour (e.g. Bennett *et al.* 2016; Prior *et al.* 2016; Vivian *et al.* 2008). The inherent heterogeneity of both disturbance events and the landscape enhances the variability apparent in tree mortality research. At the individual plant scale, the effects of fire are spatially diverse due to the irregular transfer of heat from combusting fuels to vegetation which creates patchiness in cambial heating, crown scorch and associated tissue death (Furniss *et al.* 2020). Ambient fire weather and topography also contribute to the variation seen in the literature (Bradstock 2008).

The quantity and characteristics of coarse woody debris in forest systems are the result of inputs, primarily tree mortality and timber harvesting, and outputs, through decomposition and consumption (Burton *et al.* 2021; Harman & Hua 1991). Many of these processes are governed by climate, topography and disturbance events (Buettel *et al.* 2017; Woodall & Liknes 2008). It is well established that fire has a central role in both the creation and destruction of fallen dead wood (Stares *et al.* 2018). However, the exact influence of fire regimes on CWD within resprouting eucalypt communities remains uncertain, with disparity in the literature about the effect of fire frequency (e.g. Aponte *et al.* 2014; Bassett *et al.* 2015; Whitford & McCaw 2019) and fire severity (e.g. Burton *et al.* 2021; Hollis, Anderson, *et al.* 2011).

1.2 Aims

This research aims to assess the impact of a range of contemporary prescribed burns and wildfires on the quantity of coarse woody debris (CWD) and the survival of resprouting eucalypts within southeast Australian dry sclerophyll forests (DSF). A sound understanding of tree survival and CWD dynamics is essential for modelling carbon stock and smoke emissions in fire-prone landscapes. Considering the variability of the evidence and the compounding threat posed by anthropogenic climate change (Moritz *et al.* 2012), a greater understanding of the complex relationship between fire disturbance, eucalypt mortality and fallen dead wood is required. It was hypothesised that:

1) Eucalypt stem death will increase with fire severity.
2) Smaller stems will exhibit lower resilience (i.e. increased stem death) to fire disturbance.
3) Stems with low density bark will be the most resilient to fire.
4) Coarse woody debris will increase with fire severity but decrease with fire frequency.

Chapter 2: A review of eucalypt mortality and coarse woody debris dynamics under current and potential fire regimes

2.1 Fire regimes

The *fire regime* is a broad description of fire disturbance within ecosystems that is used to quantify patterns of burning across spatial and temporal scales (Krebs *et al.* 2010). The concept of a fire regime is widely attributed to Gill (1975), who described the core components of fire activity in terms of fire intensity, frequency, seasonality and type of fire. Contemporary definitions have expanded to include the severity and spatial scale of burning (Krebs *et al.* 2010). The individual components of a fire regime collectively determine the ecological impact on fire affected communities, which in turn influences community structure and ultimately the evolutionary pressures exerted on species within fire-prone landscapes (Keeley *et al.* 2011; Pausas & Keeley 2009).

Landscape scale variations in fire regimes across Australia are predominantly driven by moisture availability and net primary productivity (Bradstock 2010). In arid communities the incidence and intensity of fire is low due to limited and discontinuous fuel loads (Bradstock 2010; Miller & Urban 2000). Fire activity is thought to increase monotonically with moisture and productivity until a point where the fuel load is too wet to burn regularly (Murphy *et al.* 2013). In the savannah woodlands of northern Australia, monsoonal patterns of summer rainfall promote high fuel loads that reliably burn over the dry winter period. These short fire intervals limit the accumulation of fuel, preventing high intensity wildfire. Comparatively, the eucalypt forests of southeast Australia are typically subject to regimes of infrequent, high intensity wildfire due to high accumulated fuel loads and moisture levels that limit frequent fire. Accordingly, forest fire risk is highly associated with drought conditions across south eastern Australia (Verdon *et al.* 2004). These contrasting patterns of burning reveal inherent trade-offs between intensity and frequency that occur due to environmental limitations. Bradstock (2010) incorporates these limitations within his conceptual model of the four processes that govern Australian fire regimes. This model proposes that temporal and spatial variations in burning are predominantly influenced by the quantity of biomass, the availability of the fuel (e.g. fuel moisture), ambient fire weather, and ignitions. Each of these four processes are influenced by a range of interacting biogeographic factors including vegetation and soil type, topography, anthropogenic land management and climate.

The terms fire intensity and severity are used somewhat interchangeably within the public sphere; however, they describe distinct yet related components of the fire regime. Keeley (2009) describes fire intensity as “the physical combustion process of energy release from organic matter” – the total energy released over the various stages of vegetation combustion. There are several difficulties in accounting for total heat output, including the necessity of measuring the energy released through smouldering combustion in the days following the fire front. Fireline intensity refers to the rate of heat generation per unit length of fire front (Byram 1959), a more common measure of intensity used by fire managers to assess fire behaviour and suppression potential (Hirsch & Martell 1996; Salazar & Bradshaw 1986). Fireline intensity can also be challenging to evaluate due to the need to measure the weight of the biomass consumed by the active fire front, difficulties in assessing the rate of fire spread, and the uncertainty of fuel combustion efficiency (Santoni *et al.* 2011). Several surrogate measures of fireline intensity have been used in the literature to address these limitations. For example, flame length and scorch height have been commonly used as proxies for the intensity of fire in temperate forests (Alexander & Cruz 2012; Miquelajauregui *et al.* 2016). Measures of fireline intensity may struggle to explain the ecological impact of fire disturbance within Australian temperate communities as eucalypt mortality can be highly affected by the heat residency period (Burrows 2013).

The term fire severity derives from the need to describe the effects of fire intensity on vegetation communities, especially following wildfire where empirical measures of intensity are absent (Keeley 2009). Most contemporary practitioners define fire severity by the volume of organic matter consumed above or below ground, with aboveground indicators such as retained canopy volume typically used in forest systems (e.g. Barker & Price 2018; Bradstock *et al.* 2010; Schimmel & Granstrom 1996). The intensity of a fire is one of several factors that effects fire severity, others being vegetation composition, stand age, heat residence duration, topography, fuel load characteristics and fire weather (Bradstock *et al.* 2010; Keeley 2009; Taylor *et al.* 2014). Many studies concerning fire severity within temperate forests utilise a similar classification of vegetation impact that reflects the degree of organic matter consumption, ranging from understorey fire to full canopy consumption (e.g. Nolan, Rahmani, *et al.* 2020; Prior *et al.* 2016; Ryan & Noste

1985; Vivian *et al.* 2008). An outline of a typical fire severity classification is shown in **Table 1**, adapted from Gibson *et al.* (2020).

Table 1. A description of typical fire severity classes based on changes in aboveground vegetation; adapted from Gibson *et al.* (2020).

Severity class	Description
Unburnt	Unburnt understorey with green canopy
Low	Burnt understorey with unburnt canopy
Moderate	Partial canopy scorch
High	Full canopy scorch with partial canopy consumption
Extreme	Full canopy consumption

Prescribed burning is the practice of purposefully lighting fires under certain weather and fuel conditions to reduce the risk and severity of future wildfires through the reduction of fuel loads (Bradstock *et al.* 1998; Morrison *et al.* 1996). In Australia, the predominant aim of prescribed fire regimes is asset protection, however, land managers may prescribe burns for the conservation of biodiversity (Penman *et al.* 2011). Prescribed burns are often intended to be low intensity fires that reduce the dry fuel load without scorching or consuming the forest canopy (McArthur 1966; Penman *et al.* 2007), yet the inherent risks involved with using fire as a land management tool can result in adverse social or ecological outcomes (Keelty 2012). More recently, the effectiveness of fuel reduction burning in southeast Australia has been questioned (Altangerel & Kull 2013), as there is limited evidence to show that prescribed burning reduces the extent of wildfire in this region (Price & Bradstock 2011; Price *et al.* 2015). Notably, recent fire activity has been shown to reduce wildfire intensity in eucalypt forests; however, the duration of this effect is limited (~5 years) and is negligible under severe weather conditions (Price & Bradstock 2012; Storey *et al.* 2016).

Indigenous people have used fire as a landscape management tool for thousands of years (Bowman 1998; Laris 2002; Turner *et al.* 2000), although the extent of such practices has been substantially reduced (Bardsley *et al.* 2019; Penman *et al.* 2011; Pyne 1998). In Australia, Aboriginal people traditionally applied fire to promote medicinal and edible plants, to control understorey vegetation for ease of travel and hunting, and within the cultural practice of caring for country (Bird *et al.* 2005; Garde *et al.* 2009; Perry *et al.* 2018; Smith *et al.* 2021). Cultural burns are characterised as patchy, low severity understorey fires with minimal impact on mature trees (Cavanagh 2020; Kimber & Friedel 2015). There are typically distinct differences in the ecological impacts of indigenous cultural burns compared to patterns of wildfire due to differences in the seasonality, spatial scale, homogeneity and intensity of burning.

2.2 Tree mortality

Tree mortality is determined by dynamic interactions between plant traits, the environment and biological, physical and ecological stressors that operate at a range of spatial and temporal scales (Furniss *et al.* 2020). Drivers of background mortality, including competition, pathogens and drought, are more evident over the long-term. The impacts of acute disturbance events, such as cyclones, insect epidemics and wildfire, are typically more immediate and elicit greater levels of mortality (Das *et al.* 2016). Under recurrent disturbance regimes, species adapt traits to enhance survival and reproductive success.

The continuum of plant responses to fire disturbance varies broadly between taxa and vegetation type, from fire sensitive rainforests (Cochrane 2003) to fire tolerant savannah woodlands (Lawes *et al.* 2011). Within Mediterranean ecosystems that are exposed to canopy consuming wildfire, trees can be classified as resprouters or non-resprouters, coupled with a seeding response (Pausas *et al.* 2004; Pausas *et al.* 2016). Resprouting refers to the ability to regenerate new leaves following the destruction of living tissues. Resprouting is a key functional trait that allows the majority of eucalypts (*Angophora*, *Corymbia* & *Eucalyptus* spp.) to survive fire disturbance and re-establish vegetative dominance in Australian forest systems (Burrows 2013). Depending on the species and extent of tissue death, new foliage may resprout from protected epicormic buds or elevated apical buds on the branches or trunk, or from lignotubers protected by the soil layer. Other persistent adaptations to fire disturbance include thick, insulative bark and the production of a heat resistant seedbank that germinates profusely after fire. Species may employ one or more of these mechanisms in fire-prone ecosystems (Pausas & Keeley 2014). For example, heat resistant bark can enable obligate seeding eucalypts to survive low severity fire; however, recruitment for these species is usually restricted to a single fire-cued germination event from the in-situ seedbank following canopy consuming fire (Bradstock 2008; Pausas *et al.* 2016). The dominant characteristics of a vegetation community therefore influence demographic patterns following fire (Vesk & Westoby 2004).

Patterns of tree mortality in southeast Australian forests vary with both fire regime and dominant vegetation traits. High severity fires can cause near complete adult mortality in wet sclerophyll forests dominated by obligate seeders such as *Eucalyptus delegatensis* (Benyon & Lane 2013; Bowman *et al.* 2014; Gill *et al.* 1981). Resprouting forests are traditionally considered highly resilient to fire disturbance (Bell *et al.* 1989; Gill 1975; Gill *et al.* 1981), yet recent evidence indicates that rates of topkill for resprouting eucalypts can range between 2 – 52% following wildfire (Prior *et al.* 2016; Vivian *et al.* 2008). This variability reflects the complexity of factors that influence the survival of resprouters in fire-prone communities. For example, previous fires can cause a partial necrosis of the cambium at the stem base (i.e. basal scarring), which increases the probability of topkill during future disturbance events as the protective bark layer is compromised (Collins 2020; Gill 1974). As the likelihood of basal scarring may increase with fuel load and fire intensity (Collins & Stephens 2007; Lentile *et al.* 2005), the impact of repeated high severity wildfires may be cumulative (Fairman *et al.* 2019). By definition, higher intensity fires have greater heat output (Keeley 2009). During high intensity fire activity there is greater potential for ambient temperatures to exceed levels sufficient to cause cambial tissue death, generally resulting in greater rates of tree mortality across a range of vegetation types (e.g. Denham *et al.* 2016; Miquelajauregui *et al.* 2016; Williams *et al.* 1999). The resilience of eucalypts to fire induced heat stress is also dependent on tree diameter (Bennett *et al.* 2016; Burrows *et al.* 2010; Lawes *et al.* 2011). As stem size is proportionate to bark thickness and canopy height, the vascular and meristematic tissues of larger trees are more protected from convective and radiative heat (Burrows 2013; Wesolowski *et al.* 2014). These relationships are evident across most eucalypt forests, where “for most species, mortality is both diameter and fire dependent” (Guinto *et al.* 1999). While much of the evidence suggests that large trees in dry sclerophyll forests are likely to survive high severity fire through epicormic resprouting (e.g. Collins 2020; Fairman *et al.* 2019; Peet & Williamson 1968), some authors have found that the highest rates of mortality occurred in both the smallest and largest eucalypts following fire disturbance (Bennett *et al.* 2016; Williams *et al.* 1999). Instances of heightened mortality in large trees are likely due to the cumulative impact of previous fires on basal scar formation, a factor which varies with fire history. Tree species that experience frequent fire activity typically exhibit thick bark (Pausas 2015), however, other bark attributes, such as morphology, density and moisture content, can have a significant influence on heat penetration and stem death (Nolan, Rahmani, *et al.* 2020; Vines 1968; Wesolowski *et al.* 2014). In dry sclerophyll forests, species with thick, low-density bark are thought to be most resilient to topkill (McCaw *et al.* 1994; Nolan, Rahmani, *et al.* 2020). Rates of fire-induced tree mortality therefore vary with burn severity, fire history and stand demography.

The effects of fire in forest systems can be compounded by additional stressors such as prolonged drought, pathogens or timber harvesting, which further challenge the resilience of the system (Bradstock 2010; Paine *et al.* 1998; Watson *et al.* 2020). The compounding impact of these *megadisturbances* can substantially increase rates of tree mortality. This phenomenon is clearly evident in the conifer forests of North America, where the aggregating impacts of drought stress, insect outbreak and wildfire have driven extensive canopy dieback and tree mortality (Millar & Stephenson 2015). Wildfires usually induce stand replacement in conifer forests as these species are non-resprouting, yet the collective stressors acting on this community have increased forest mortality well beyond the typical extent. The impact of compounding disturbance events on resprouting forests is less certain due to the relative hardiness of these communities. While eucalypts have evolved several traits that confer resilience to drought and fire activity (Burrows 2013), there is growing evidence that concurrent disturbances can reduce growth rates and eucalypt survival (Bendall 2021; Nicholson *et al.* 2017; Rahmani & Price 2021). Drought is highly associated with wildfire risk in ecosystems where fire activity is moisture limited (Bradstock 2010; Verdon *et al.* 2004), which suggests that these stressors often compound in the dry sclerophyll forests of southeast Australia. In one instance, wildfire was estimated to elicit a 25% increase in eucalypt mortality within a severely drought affected community (Prior *et al.* 2016). However, these unusually high rates of resprouter mortality must be considered in the context of extensive background mortality, which may have been caused by a range of additional stressors including insect attack, soil compaction and decreased water penetration. In 2019, southeast Australia experienced its hottest and driest year, leading to extensive canopy die-back and the largest wildfires in temperate eucalypt forests on record (Abram *et al.* 2021; Nolan *et al.* 2021). The magnitude of drought stress and wildfires across southeast Australia in this period provided a sombre yet crucial opportunity to examine the effects of compounding disturbance events on eucalypt forests.

Fire is a key determinant of tree health in dry sclerophyll forests. The impact of fire at the individual level ultimately scales up to affect population health, forest structure and carbon storage (Bowman, Williamson, Price, *et al.* 2021). Tree mortality and subsequent tree fall impacts species dynamics through coarse woody debris formation, canopy gap creation and other biotic interactions such as the loss of arboreal habitat. Both standing and fallen dead wood contribute to dry fuel loads and smoke production during future burning events (Burton *et al.* 2021; Reisen *et al.* 2018; Volkova *et al.* 2018). There are a complexity of factors that determine tree mortality in communities capable of resprouting, nevertheless a comprehensive understanding of these processes is necessary as the stressors affecting these communities change.

2.3 Coarse woody debris dynamics

Coarse woody debris (CWD) is a fundamental component of forest ecosystems that refers to a range of dead material, including standing dead trees (also called stags), stumps, whole fallen trees and downed branches (Harmon *et al.* 1986; Woldendorp & Keenan 2005). In more recent literature, CWD is often defined as fallen dead woody material, excluding standing dead trees and stumps (e.g. Hollis, Anderson, *et al.* 2011; Hyde *et al.* 2011; Stares *et al.* 2018). Most studies of forest floor biomass differentiate between litter (fine surface fuel) and CWD, although the diameter threshold separating these categories varies considerably across the literature (Woldendorp & Keenan 2005). Size distinctions may shift according to the ecosystem being examined and survey effort requirements, given that the count of woody debris increases as piece diameter decreases (Harmon & Sexton 1996). McGee *et al.* (1999) defined CWD as fallen wood with a minimum diameter of 1 cm and dead standing wood as stags greater than 1 m tall. A distinction of 2.5 cm is often used in studies that quantify both litter and fallen CWD (Moore *et al.* 1967; Volkova *et al.* 2019). In a review of woody fuel combustion, Hyde *et al.* (2011) defines CWD as fallen woody material with a diameter ≥7.62 cm, while many others measure CWD as pieces ≥ 10 cm (Bassett *et al.* 2015; Burton *et al.* 2021; Harman & Hua 1991; Stares *et al.* 2018; Whitford & McCaw 2019), which aligns with the recommendations of Harmon and Sexton (1996). Consistent definitions of CWD and litter are required for more accurate comparisons between studies and across ecosystems (Woldendorp & Keenan 2005).

Coarse woody debris is an important component of stand structural complexity and has a critical role in multiple ecosystem processes (Harmon *et al.* 1986). Fallen logs support forest biodiversity by providing habitat and refugia for a variety of fauna and by creating microclimate niches that facilitate the growth of saplings and fungi (Lindenmayer *et al.* 2002; Mac Nally *et al.* 2001; Scott & Murphy 1987). Dead woody biomass is integral to the nutrient cycle, carbon storage and carbon flux, representing 19 to 30% of total above-ground biomass in Australian forests (Jia-Bing *et al.* 2005; Woldendorp & Keenan 2005). Dead wood can form an enduring carbon stock, with CWD lifetimes in eucalypt forests ranging from 7 to 375 years depending on initial wood density, piece diameter and climate (Mackensen *et al.* 2003). The attributes of CWD, namely piece size, decay stage and hollow presence, impact the carbon stock and habitat utility of this resource (Lindenmayer *et al.* 2002; Stares *et al.* 2018). Coarse woody debris is ecologically significant in stream and river systems as it enhances the complexity of aquatic habitat and functions as a sediment trap, improving water quality and the availability of nutrients (Bilby 1981; Harmon *et al.* 1986; Macnally *et al.* 2002; O'Connor 1991). The consumption of woody fuels in forest fires can impact fire behaviour (Byram 1959; Sullivan *et al.* 2018), suppression potential and firefighter safety (Page *et al.* 2013; Rothermel 1994), as well as smoke and greenhouse gas emissions (Hollis, Matthews, *et al.* 2011; Reisen *et al.* 2018; Weise & Wright 2014). The ecological significance of CWD as a structural component of forest communities is well established, which underscores the importance of management strategies that consider dead woody biomass, particularly in the context of pervasive threats like climate change.

A network of interacting factors govern the quantity and attributes of CWD in forest ecosystems. Climate drives landscape scale patterns of CWD production through effects on forest productivity and aboveground carbon stock (Burton *et al.* 2021; Gordon *et al.* 2018; Woldendorp & Keenan 2005), canopy dieback (Brouwers *et al.* 2013; Nolan *et al.* 2021) and rates of treefall (Buettel *et al.* 2017; Oberle *et al.* 2018; Peltola 2006). Climate also drives the decay of CWD, as the decomposition of organic matter increases with temperature and moisture (Harmon *et al.* 1986). The impact of climate on decomposition is particularly evident at higher latitudes, where slow-growing, cool montane forests often contain exceptionally large quantities of accumulated CWD due to low rates of decay (Richardson *et al.* 2009; Woldendorp & Keenan 2005). Coarse woody biomass within forest systems is inherently influenced by the characteristics of the constituent tree species (Burton *et al.* 2021). Live biomass is shaped by vegetation type, so it is understandable that measures of dead organic matter shift accordingly between plant communities (Threlfall *et al.* 2019; Woodall *et al.* 2013). In Australian forests, the capability to resprout foliage following disturbance events determines the scale of dead biomass creation and carbon flux (Gordon *et al.* 2018; Keith *et al.* 2014). Interrelated factors including stand age, basal area, stem density and dominant tree size can also affect dead wood inputs (Garbarino *et al.* 2015; Grove 2001; McGee *et al.* 1999). Wood density, chemical composition and bark characteristics regulate CWD decomposition and fragmentation (Burton *et al.* 2021; Dossa *et al.* 2018; Weedon *et al.* 2009). For example, phenolic compounds in eucalypts constrain fungal activity (Hart 1981), which in conjunction with high wood density, reduces rates of decay (Pietsch *et al.* 2014).

In addition to climatic and environmental determinants, disturbance regimes can have a substantial impact on CWD stock and attributes. Timber harvesting has a dynamic influence on dead wood biomass, increasing CWD in the short term, but potentially reducing biomass over longer periods (Stares *et al.* 2018). Logging practices often create an immediate pulse of CWD when unmerchantable felled timber is retained *in situ* (Grove 2001; Threlfall *et al.* 2019; Whitford & McCaw 2019). However, the sustained removal of large trees and the employment of post-harvest prescribed fire represents a threat to the long-term supply of CWD biomass (Burton *et al.* 2021; Collins *et al.* 2012; Stares *et al.* 2018). Like silvicultural practices, fire regimes can also affect dead wood in a multitude of ways. Fire disturbance both consumes fallen woody debris and generates it through branch death and treefall (Burton *et al.* 2021). Fire is also a strong determinant of the structural attributes of CWD, driving hollow formation and exacerbating decay (Stares *et al.* 2018). The components of a fire regime, predominantly fire frequency and severity, dictate the equilibrium between fallen dead wood consumption and formation. Diverse responses to these components have been observed. For example, fireline intensity has been found to correlate with the consumption of woody fuels in eucalypt forests (Hollis, Anderson, *et al.* 2011), yet the influence of fire severity on CWD biomass may be minimal and dependent on topography (Bassett *et al.* 2015; Burton *et al.* 2021). Current research suggests that higher severity fires elicit greater levels of CWD consumption and production (Price *et* *al.*, unpublished data), so to some extent pre- and post-fire CWD fuel loads are balanced. Fire regimes characterised by frequent prescribed burns can reduce moderately to highly decayed CWD (Aponte *et al.* 2014; Stares *et al.* 2018); however, Whitford and McCaw (2019) found that CWD volume increased with the number of prescribed fires in dry sclerophyll forests since 1937. As a structural component of forest communities subject to the process of succession, detrital biomass is influenced by time since fire (Tiribelli *et al.* 2018; Volkova *et al.* 2019). While the evidence regarding the effect of time since fire on CWD is somewhat inconclusive (e.g. Monsanto & Agee 2008; Pedlar *et al.* 2002; Roccaforte *et al.* 2012), Bassett *et al.* (2015) and Burton *et al.* (2021) suggest that within Australian forests, fire elicits an immediate reduction in CWD due to consumption, which is followed by a gradual increase in fallen woody biomass through fire induced branch and tree fall. The somewhat inconclusive nature of the body of evidence stresses the need for a greater understanding of coarse woody debris dynamics within fire-prone forests, especially considering the ecological significance of CWD and the escalating threat of climate change (Moritz *et al.* 2012).

2.4 Potential for structural change and carbon loss

Shifts in fire regimes have critical implications for forest biodiversity, carbon storage and global emissions (Bowman *et al.* 2009; Bowman *et al.* 2013; Fairman *et al.* 2016). Emissions from wildfires equate to 20-40% of the total annual greenhouse gases produced by global fossil fuel combustion and cement production (Conard & Solomon 2008). Forest fires throughout the east coast of Australia emitted ~0.67 petagrams of carbon over the 2019/2020 austral fire season alone (Bowman, Williamson, Price, *et al.* 2021). Nevertheless, forests are a crucial sink in the global carbon cycle, sequestering around 1.1 petagrams of carbon per year (Pan *et al.* 2011). Tropical forests account for the largest carbon store; however, emissions from intensive deforestation and burning of this biome means that the global net uptake of atmospheric carbon is primarily driven by temperate and boreal communities (Pan *et al.* 2011; Sarmiento *et al.* 2010). Severe fire disturbance within tropical rainforests can rapidly alter stand structure and species composition through comparatively high rates of tree mortality and seedbank destruction, substantially reducing stored carbon (Bowman, Williamson, Gibson, *et al.* 2021; Cochrane 2003). The adaptation of heat tolerant seedbanks, which enable stand replacement following fire, has led to the idea that boreal forests are carbon neutral or negative over the long term

(Kashian *et al.* 2006). However, population continuity in fire affected boreal communities is reliant on fire intervals which allow for the reestablishment of the seedbank by mature trees. Altered disturbance regimes under anthropogenic climate change may impact the fecundity and reestablishment of obligate seeding boreal species, facilitating substantial carbon loss (Greene *et al.* 1999; Schimmel & Granstrom 1996; Veraverbeke *et al.* 2017). Many of the eucalypt species that dominate the temperate forests of southern Australia are capable of surviving high severity fire through epicormic resprouting (Bradstock 2008; Burrows 2013), thus fire induced carbon fluctuation in resprouting communities is often driven by the consumption and formation of fine fuel, CWD and small trees (Wilson *et al.* 2021). Nevertheless, there is increasing concern that the resilience of resprouting eucalypt forests could be challenged by the compounding disturbances of prolonged drought and extreme fire activity, which may elicit ecosystem transitions to new states of productivity and carbon sequestration (Bowman *et al.* 2013; Bowman, Williamson, Gibson, *et al.* 2021; Paine *et al.* 1998).

The prevailing scientific consensus predicts that anthropogenic climate change will increase global forest fire activity and extreme fire events (Abram *et al.* 2021; Bradstock *et al.* 2012; Jones *et al.* 2020; Moritz *et al.* 2012; Sharples *et al.* 2016), raising the possibility that forest systems shift from carbon sinks to carbon sources (Bowman, Williamson, Price, *et al.* 2021; Walker *et al.* 2019). Based on projected trends of warming and drying, it is estimated that fire risk will substantially increase across central Asia, North and South America, and parts of southern Europe, Africa and Australia (Hoegh-Guldberg *et al.* 2018; Liu *et al.* 2010). The frequency of fire at mid to high latitudes is estimated to increase by ~38% under 1.2°C of global warming, compared to ~62% increase under 3.5°C of warming (Moritz *et al.* 2012). Australia’s climate has warmed by ~1.44°C since records began in 1910, facilitating an increase in the frequency of extreme heat events (CSIRO 2020). Cool season rainfall has declined and dry lightning events have increased across southeast Australia in more recent decades (CSIRO 2020; Dowdy 2020), heightening the severity of drought conditions and increasing the likelihood of natural ignitions. At the broader scale, the Australian climate is driven by the combined effects of anthropogenic climate change and natural climatic processes, which include the El Niño Southern Oscillation (ENSO), the Indian Ocean Dipole, and the Southern Annular Mode (Bates *et al.* 2010). ENSO is the primary driver of interannual fire weather in southeast Australia, with El Niño events bringing warmer and drier conditions to the east coast. There is evidence to suggest that anthropogenic climate change is already forcing an intensification of ENSO extremes (Grothe *et al.* 2020), which may drive changes in regional patterns of disturbance (Abram *et al.* 2021; Ward *et al.* 2014). While extreme fire weather and fire season length have significantly increased across southern Australia since the 1950s (CSIRO 2020), the effects of these trends are yet to be entirely realised. Despite severe droughts and a warming climate, Bradstock *et al.* (2014) found no generalised increase in burnt area throughout southeast Australia between 1975 and 2009. Of the 32 bioregions examined, annual fire extent did increase in one woodland and seven forest systems, however, this trend was not consistently related to regional warming or drying. Research by Collins *et al.* (2021) reveals that the 2019/2020 Australian Black Summer wildfires were greater in extent yet not proportionally more severe than previous fire seasons, while Tran *et al.* (2020) found that wildfires across the state of Victoria have become more severe over the past three decades. These findings highlight the ambiguity of the current body of evidence for the effects of anthropogenic climate change on existing fire regimes in southeast Australia. Yet, the extremity of the Black Summer wildfires, which produced an unprecedented level of radiant energy and an exceptional number of extreme pyroconvective events (Abram *et al.* 2021), may suggest that the impacts of a warming climate have started to eventuate.

It is predicted that under anthropogenic climate change the severity of fire weather will continue to increase throughout temperate regions in Australia, particularly during Spring (Clarke & Evans 2019; Clarke *et al.* 2016; Liu *et al.* 2010). Shifts in fire weather will eventually facilitate widespread changes in fire activity (Bradstock *et al.* 2012; Sharples *et al.* 2016), which may manifest as a greater number of fires, shorter fire intervals, increased fire severity, or a larger area burnt earlier in the fire season (King *et al.* 2011). Changes in fire weather will be particularly consequential for forested areas where fire activity is moisture limited, compared with grassland communities where fire is typically fuel limited (Bradstock 2010; Clarke *et al.* 2020). The vegetative response of resprouting eucalypt communities to future shifts in climate and fire regimes remains somewhat uncertain. A continued rise in atmospheric carbon dioxide may enhance the photosynthetic rate within forests and consequently change fuel loads. However, CO_2 enrichment experiments suggest that the growth of mature eucalypts in southeast Australia is limited by nitrogen, and therefore elevated CO_2 is unlikely to drive a substantial increase in fuel load (Ellsworth *et al.* 2017; Jiang *et al.* 2020). As the vast majority of carbon within dry sclerophyll forests is stored within live biomass, specifically within large trees (Fedrigo *et al.* 2014; Gordon *et al.* 2018), the predominant drivers of carbon storage are the climatic factors and disturbance regimes that influence tree growth and mortality. An increase in mean annual temperature and vapour pressure deficit will likely reduce vegetation growth and biomass moisture, reducing aboveground biomass and affecting the availability of fuel to burn (Anderson-Teixeira *et al.* 2011; Bradstock 2010). Notably, Gordon *et al.* (2018) predicted that increasing mean annual temperature will drive a ~25% decrease in aboveground carbon within dry sclerophyll forests over the next 50 years, yet indicated that fire frequency and severity are poor determinants of total carbon stock. These findings contrast with several studies which show that both extreme individual fire events (Bowman, Williamson, Gibson, *et al.* 2021; Keith *et al.* 2014) and long term regime shifts (Bowman *et al.* 2013; Fairman *et al.* 2019; Fedrigo *et al.* 2014) may elicit carbon loss. Multi-decadal fire regime modelling predicts that warmer and drier climates will enhance fire activity within many eucalypt communities, which in turn will increase carbon emissions and carbon stock loss (Keane *et al.* 2013; King *et al.* 2011). Shifts in climate or disturbance regimes which reduce standing tree biomass will ultimately reduce CWD, as dead woody biomass outputs exceed inputs. For example, high severity fires are thought to both consume and produce more CWD than cool burns due to greater rates of combustion and treefall (Hollis, Anderson, *et al.* 2011; Whitford & McCaw 2019). If an increasingly severe fire regime substantially reduced standing stem density, CWD would also decline over the long term as consumption exceeds production (Burton *et al.* 2021).

Projections of future fire regimes in southeast Australia are inherently ambiguous and must attempt to account for the influence of climate change and a range of ecological factors and human impacts on vegetation and fuel loads. The potential for carbon loss or structural change in forest systems is determined by complex scale-dependent interactions between disturbance regimes, climate and vegetation specific attributes (Gordon *et al.* 2018). An accurate understanding of the health response of resprouting eucalypt communities to severe fire disturbance is intrinsic to modelling the influence of current or predicted fire regimes across southeast Australia.

Chapter 3: Materials and Methods

3.1 Study area

This study examined the effect of both contemporary prescribed burns and wildfires on eucalypt mortality and CWD dynamics in dry sclerophyll forests across a range of national parks in southeast New South Wales, Australia. Despite occurring on low nutrient soils, dry sclerophyll vegetation contains a diverse range of flora species, spanning one quarter of the mapped vegetation in New South Wales (Keith 2004). Dry sclerophyll forests in this region occur between 0 to ~1200 m elevation, with mean annual precipitation varying between ~650 to 2000 mm depending on altitude and distance from the coast (Tozer *et al.* 2010). Resprouting eucalypts reliably dominate this vegetation type, which is subject to a mosaic of high intensity wildfires and prescribed hazard reduction burns (Keith 2004; Murphy *et al.* 2013).

Under the Enhanced Bushfire Management Program, the National Parks and Wildlife Service (NPWS) conducts ~130,000 ha of hazard reduction activities annually, which primarily consists of prescribed burning (DPIE 2021). Despite prolonged drought conditions which adversely affected the ability of agencies to conduct prescribed burns, the NPWS conducted hazard reduction activities across more than 139,000 ha of National Parks in NSW throughout the 2018/2019 fire season (Readfearn 2020). Between September 2019 and March 2020, wildfires burnt ~7 M ha across southeast Australia (Collins *et al.* 2021), well exceeding the historical record for wildfire extent in Australian temperate communities (Nolan, Boer, *et al.* 2020). Many of the fires that burnt throughout southeast Queensland, New South Wales, the Australian Capital Territory and Victoria remained active for months until rainfall in February 2020 dampened fuels (Abram *et al.* 2021). The extreme fire weather and fuel conditions that facilitated the 2019/2020 wildfires were intensified by several converging climatic processes – namely a warming climate, a positive Indian Ocean Dipole and an extreme negative Southern Annular Mode (Abram *et al.* 2021; CSIRO 2020). The scale of fire activity between 2018 and 2020 provided an opportunity for further research into the relationships between fire disturbance, eucalypt survival and CWD dynamics across southeast Australia.

This study was conducted in seven National Parks across the Sydney Basin Bioregion, focusing on dry sclerophyll forest. Survey locations were based on whether the area had been burnt by prescribed fire in the 2018/2019 fire season or by the 2019/2020 wildfires, except for one location which was not subject to recent burning (**Figure 1**). Sites were restricted to National Parks to eliminate the potential effects of logging on CWD (Collins *et al.* 2012; Stares *et al.* 2018; Wilson *et al.* 2021). Field surveys were undertaken between May and July 2021. These surveys occurred more than 12 months after the 2019/2020 wildfires and between two to three years after the 2018/2019 hazard reduction burns. Delaying post-fire surveys of tree mortality is essential in resprouting eucalypt forests to accommodate for a potential resprouting response (Bennett *et al.* 2016; Collins 2020). Epicormic resprouting within eucalypts typically occurs within six months of fire disturbance (e.g. Burrows & McCaw 2013; Gill 1978), with assessments of eucalypt mortality typically occurring between one and five years after fire (e.g. Bennett *et al.* 2016; Collins 2020; Vivian *et al.* 2008). Our survey locations varied in aspect, slope, elevation and fire history, reflecting the diverse biogeography of dry sclerophyll forests the Sydney Basin Bioregion.

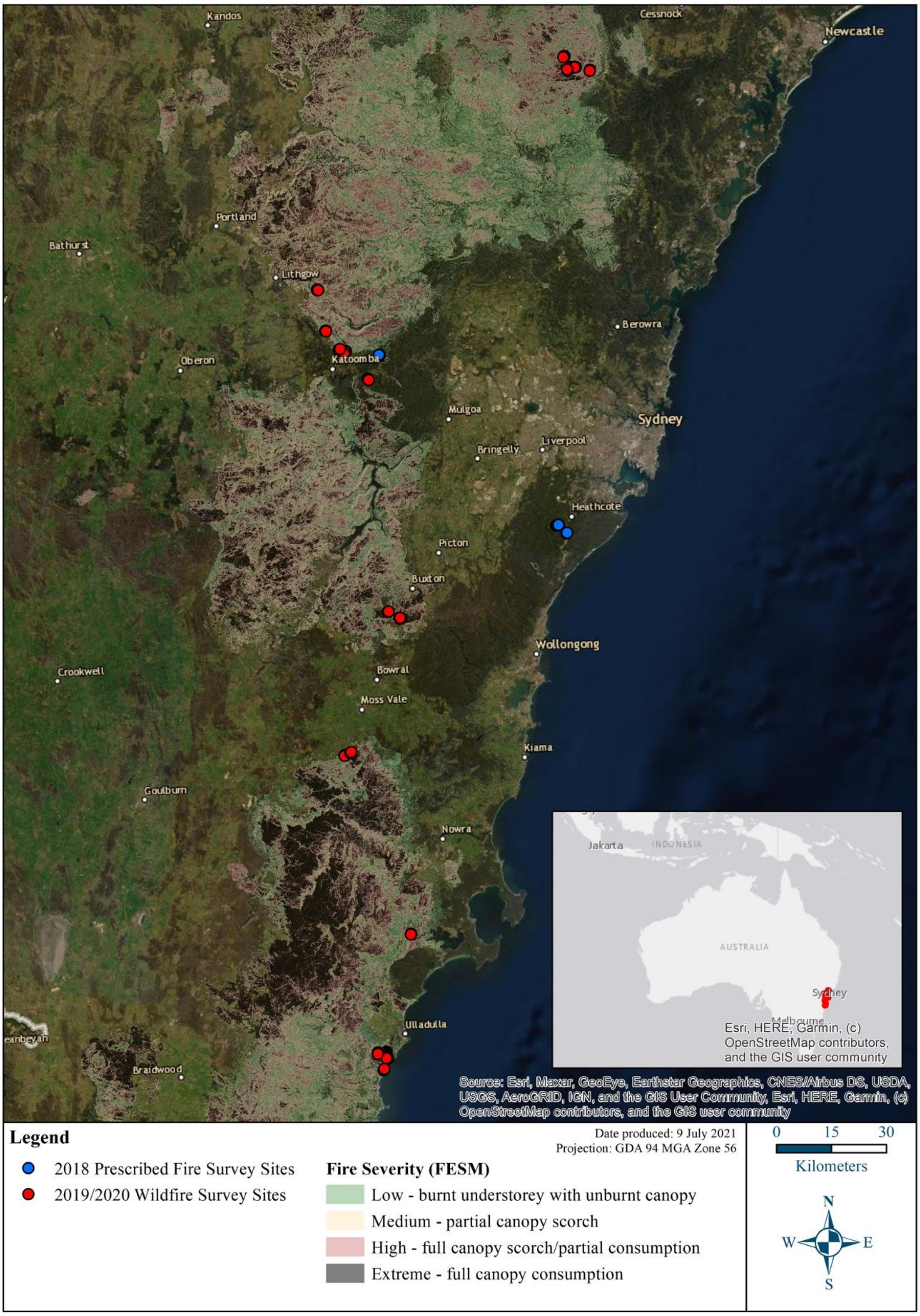

Figure 1. Map of the study area indicating the survey locations and fire severity of the 2019/2020 wildfires and the 2018/2019 prescribed fires.

3.2 Stem health

Tree species capable of epicormic resprouting may employ this trait to re-establish vegetative dominance following fire, depending on the attributes of the species, the extent of canopy scorching and the severity of woody tissue death. The vast majority of eucalypts within dry sclerophyll forests are capable of epicormic resprouting, however, the strength of this response can vary between species (e.g. *Eucalyptus oreades* vs. *Corymbia gummifera*) (Benson & McDougall 1998). Epicormic resprouting may not be induced following low intensity fires if there is insufficient canopy scorching and the original foliage remains intact. Conversely, resprouting contracts from the branch periphery to the central stem to the lignotuber as the extent of tissue death increases under severe disturbances (Burrows 2013). There is a need to quantify these responses as the location and height of resprouting dictates the extent of structural change and regulates CWD formation, as dead wood is more likely to succumb to branch cast or treefall. Dead wood is also more likely to burn than live biomass in subsequent fire activity, hence accurate measures of dead wood formation are important for modelling carbon dynamics and smoke emission.

At each survey location we established between one and four survey plots, depending on the area burnt and site accessibility. Each plot was 4 m wide and 200 m long following a compass bearing, within which we recorded tree diameter at breast height (DBH, 1.3m height), bark type and tree health impact. To sample across the often heterogenous fire severity mosaic, plots were positioned consecutively along the initial compass bearing if topographically possible, alternatively, plots were positioned in parallel at a distance of ~50m apart. Limits on survey effort required that stems ≥ 2.5 cm DBH were recorded for the first 20 m of each plot, however, only stems ≥ 10 cm DBH were recorded after the initial 20 m subsection of each 4x200 m plot. Bark type was categorised within three distinct classifications: smooth bark, stringy bark, and rough bark, which included tessellated, box and compacted bark types (**Figure 2**). An ordinal scale of tree health was used to quantify the resprouting response to fire, based on the degree of tissue death and the occurrence of epicormic or basal resprouting (**Table 2**). Data collection was restricted to eucalypts (*Angophora*, *Corymbia* and *Eucalyptus* genera) due to their resprouting capacity and dominance within almost all dry sclerophyll formations (Keith 2004). All stems were identified to species level where possible, however, extensive charring or loss of diagnostic vegetative attributes meant that species identification was sometimes not achievable.

Table 2. Eucalypt stem health classifications based on the magnitude of tissue damage and resprouting response.

Stem health impact	Description	Degree of vegetation change
Unaffected	Retention of mature green foliage	>90% original canopy foliage retained
Partially affected	Minimal branch death or resprouting	>50% original canopy foliage retained
Canopy resprouting	Majority of original foliage lost through scorch or consumption, yet resprouting present throughout canopy	Original canopy replaced with >50% branches resprouting
Trunk resprouting	Canopy branch death occurs yet resprouting is present on the main stem	>90% branch death, resprouting along trunk
Stem top kill	Absence of live foliage on original stem, basal resprouting present	Aboveground stem death, resprouting from lignotuber
Whole tree mortality	Lack of retained or resprouting live foliage	No evidence of epicormic or basal resprouting

Stringy (*E. piperita*) | Smooth (*C. maculata*) | Rough (*C. gummifera*)

Figure 2. Photographs of the bark types recorded in this study, with the species exhibiting each bark type in parentheses.

3.3 Coarse woody debris

Coarse woody debris was assessed using the line-intercept method (Van Wagner 1968) along a transect which was defined by the central line of each plot (i.e. 200 m transects). As the frequency of CWD typically increases with decreasing diameter size (Woldendorp *et al.* 2004), transect subsections were used to ensure that small CWD pieces were not over-sampled and a sufficient number of large pieces were recorded. CWD was defined as fallen dead woody matter not rooted in the soil, with a cross-sectional diameter > 10 cm (Aponte *et al.* 2014; Harmon & Sexton 1996). For consistency between stem and CWD measurements, small CWD (> 2.5 cm) was recorded in the first 20 m of each transect. For each piece of CWD that intersected a transect, we assessed: the diameter perpendicular to the central axis at the point of intersection, whether the piece had fallen before or after the most recent fire activity, and the decay class. Decay was defined using a three-class system adapted from previous assessments of eucalypt CWD (Aponte *et al.* 2014; Grove *et al.* 2011), where CWD in decay class 1 is structurally intact with bark still attached; in decay class 2 is clearly decaying with no bark, but still retains original shape; and in decay class 3 it no longer retains its original shape and is very soft or largely disintegrated. CWD dry weight was determined using van Wagner's formula (1968), with adjustments for wood density corresponding to decay class (Roxburgh *et al.* 2006):

$$M_i = \frac{\pi^2 \Sigma \rho d}{8\mathcal{L}}$$

Where *M* is the mass of wood per unit area for site *i*, ρ is piece density, *d* is piece diameter, and *L* is the transect length.

3.4 Fire severity and fire frequency

The fire severity affecting each stem or CWD record was derived from the Fire Extent and Severity Mapping (FESM) product, a digital severity map based on a random forest model of Sentinel 2 satellite imagery (Gibson *et al.* 2020). The Department of Planning, Industry and Environment produce publicly available FESM products for annual wildfire activity across NSW and datasets for prescribed burns were provided to us on request. FESM defines fire severity on an ordinal scale: Unburnt (unaffected understorey and canopy);

Low (burnt understorey with unaffected canopy); Moderate (partial canopy scorch); High (complete canopy scorch with partial canopy consumption); Extreme (complete canopy consumption). The accuracy of the FESM products ranges from 85-95% for unburnt and extreme severity scores, and between 60-85% for low, moderate and high severity scores. A visual assessment of fire severity was used to ground truth the FESM mosaic within each plot. The field assessment used a quantitative estimate of foliage loss and eucalypt leaf litter to classify fire severity (**Table 3**), as differentiating between canopy scorch and canopy consumption is challenging after leaf drop. This visual assessment was adapted from a two-strata severity classification within Hammill and Bradstock (2006), who similarly assessed burn severity 12–26 months post fire.

Fire frequency values were derived from the NPWS Fire History dataset (DPIE 1988), a feature class which contains the final burn extent for all prescribed burns and wildfires within National Parks over the past 45 years. From this dataset we determined the number of burns at each survey location since 1975, regardless of fire type.

Table 3. A delayed field assessment of fire severity within eucalypt forests adapted from Hammill and Bradstock (2006).

Fire Severity	Unburnt	Low	Moderate	High	Extreme
Field assessment	Vegetation unaffected	Understorey 10-80% burnt Canopy >90% unburnt	Understorey >80% burnt Canopy scorch 10-80%	Complete understorey consumption Canopy scorch >80% Eucalypt litter 10–40%	Complete understorey consumption & canopy scorch Eucalypt litter ≤10%

3.5 Supplementary data

Additional data was obtained from a recent study of fuel consumption by the team at the NSW Bushfire Risk Management Research Hub. Relevant stem and CWD records were extracted from this broader dataset, henceforth referred to as the supplementary data. This data was collected from National Parks within the Sydney Basin, with a similar focus on sampling in dry sclerophyll forests. Biomass sampling occurred between Autumn 2019 and Summer 2020 on sites before and after several prescribed fires, cultural burns and wildfires. Post-fire surveys occurred ~2 months after prescribed fires and cultural burns, and ~8 months after wildfires. Some evidence of resprouting may have been missed due to this relatively short delay period.

Each survey site consisted of a 45 m diameter circle with orthogonal transects oriented north-south and east-west. Stem data was measured for the first 40 trees encountered along the transects within each site. These measurements included an indication of tree mortality, DBH, bark type and genus. CWD was measured using the line-intercept method (Van Wagner 1968) along both transects. Cross sectional diameter, hollow diameter and decomposition class was recorded for each piece of CWD. As per the primary dataset, CWD dry weight was calculated using van Wagner's formula (1968), with adjustments for decayed wood density (Roxburgh *et al.* 2006). Fire severity and fire frequency values were inferred from the FESM and NPWS Fire History records.

3.6 Statistical analysis

A generalised linear mixed-effects model (GLMM) with a binomial outcome variable was used to analyse the relationship between stem mortality and the independent variables: fire severity, stem diameter and bark type. Fire frequency was excluded from this model due to overfitting. Fire severity was treated as a continuous variable to simplify interpretation and enhance the statistical power of the analyses. There is suggestion in the literature that fire disturbance has a greater impact on both small and large eucalypt stems compared to intermediate sizes (Bennett *et al.* 2016; Williams *et al.* 1999), so to test for this possibility we included the square of DBH as an independent predictor. The two interaction terms DBH*bark type and DBH*fire severity were included within the model. To reduce the number of response variables for model simplicity and to account for differences between the primary and supplementary datasets, stem impact was redefined within two juxtaposing categories which reflect the extent of structural change and potential carbon loss at the individual tree scale. Unaffected, partially affected, canopy resprouting and trunk resprouting stems were defined as 'minimally impacted', while whole plant mortality and top killed stems were collectively termed 'stem death'. This division defined the dependent binomial response variable: stem death (yes/no). Geographically proximate survey locations were grouped into six regions. This grouping was used as a random effect within the mixed model to account for climate induced variation. Model selection was based on Akaike's Information Criteria (AIC) after the interaction terms were assessed, such that any model within 2 points of the best fit (ΔAIC) was a supported alternative (Rahmani & Price 2021).

Previous measures of tree mortality may underrepresent true rates of stem death as many post-fire studies only record standing dead stems (e.g. Bennett *et al.* 2016; Benyon & Lane 2013; Nicholson *et al.* 2017), with limited consideration of live stems felled by the fire event. To find the hypothetical maximum rate of fire induced stem death, we produced a GLMM where newly fallen logs were included within the stem data as dead stems. Newly fallen logs were defined as CWD within decay class 1 or 2 with a diameter >20 cm. These definitions aimed to exclude the majority of smaller fallen branches and woody debris which may have fallen before the most recent fire event. Stem diameter and fire severity were the independent variables used in this model, with region set as the random effect. Bark type was excluded from the model as this factor was not recorded for the CWD measurements. This stem death model was compared with a GLMM using the same predictor variables on the standing stem dataset.

A generalised linear model was used to analyse the relationship between CWD mass per hectare and the independent variables: fire severity, fire frequency and their interaction term. The relationship between CWD mass per hectare and fire type was also assessed using a separate generalised linear model. Two separate Quasi-Poisson regression models were used to assess the relationships between the number of newly fallen CWD pieces (>20 cm) and fire severity, and the number of newly fallen CWD pieces (>20 cm) and fire type. For each model, the same selection method was used as in the first GLMM. All statistical analyses were conducted using R 3.6.1 (R Core Team 2021). The goodness of fit of each significant model was defined as the proportion of the null deviance captured by the model, termed pseudo r^2.

Chapter 4: Results

4.1 Stem death

The primary data contained 2788 stems from thirty-four eucalypt species across 45 sites. Common species included *Corymbia gummifera*, *Eucalyptus piperita*, *E. sieberi* and *E. sparsifolia*. All eucalypt species within the primary dataset were capable of epicormic or basal resprouting (Benson & McDougall 1998), although a number of stems were unidentifiable to the species level in their post-fire state. The supplementary data contained 2643 eucalypt stems from 107 sites. This included pre- and post-fire surveys of the same sites which were treated as individual measurements. Trees within the supplementary dataset were only identified by genus, however, the majority of eucalypts that inhabit dry forests around the Sydney region are capable of epicormic resprouting (Benson & McDougall 1998).

Overall, the occurrence of stem death increased with fire severity, with standing dead trees accounting for 8.6% of all stems in unburnt plots, compared with 28.1% of stems in plots burnt by extreme severity fire (**Table 4**). The influence of fire severity on the occurrence of stem death varied with stem diameter. Stems were grouped into three size classes to illustrate these differences (**Table 4**; **Figure 3**). The largest increase in stem death was observed for small stems (≤20 cm), where the mean rate of standing dead stems increased from 8.8 (± 0.78) % in unburnt plots to 37.5 (± 2.31) % under extreme fire severity (**Figure 3**). The mean proportion of standing dead stems in the medium size class (20-60 cm) increased from 7.6 (± 1.12) % in unburnt plots to 17.5 (± 2.02) % in plots affected by extreme fire severity. In contrast, the proportion of large dead standing stems (≥60 cm) displayed a nonlinear relationship with fire severity, with rates of stem death reduced following low, moderate and high severity fire and heightened after extreme severity fire, relative to unburnt plots (**Table 4**; **Figure 3**). The rate of large standing stem death within unburnt plots was 14.6 (± 5.15) %, which declined to 6.5 (± 4.49) % under moderate fire severity and increased to 15.6 (± 6.52) % under extreme fire severity. Variation in rates of stem death were generally higher for the large stem size class as fewer large trees were recorded. The standard error for small stems ranged between 0.78 – 2.31% across the five fire severity classes, while the standard error for large stems varied between 4.32 – 6.56%. Within the primary dataset, which differentiated between topkill and whole plant mortality, similar relationships between fire severity, stem diameter, bark type and stem death were observed. However, rates of whole plant mortality were not substantially impacted by the independent variables.

Fire severity had a strong significant influence on stem death across the entire standing stem dataset (**Table 5**). Stem diameter (DBH) alone did not significantly influence the occurrence of stem death; however, DBH^2 was a significant predictor, which suggests the effect of stem diameter on stem death may be non-linear. Stem death was strongly affected by all three bark types, with the interaction terms between DBH and bark type having a weaker yet still significant influence on stem death for both the rough and smooth bark categories (**Table 5**). The occurrence of stem death was significantly affected by the interaction between stem diameter and fire severity, which supports the finding that fire severity had a disproportional impact across stem size class. While fire severity, bark type and DBH^2 were significant predictors of stem death, this model was a relatively poor fit to the stem data, with a pseudo r^2 value of 0.171.

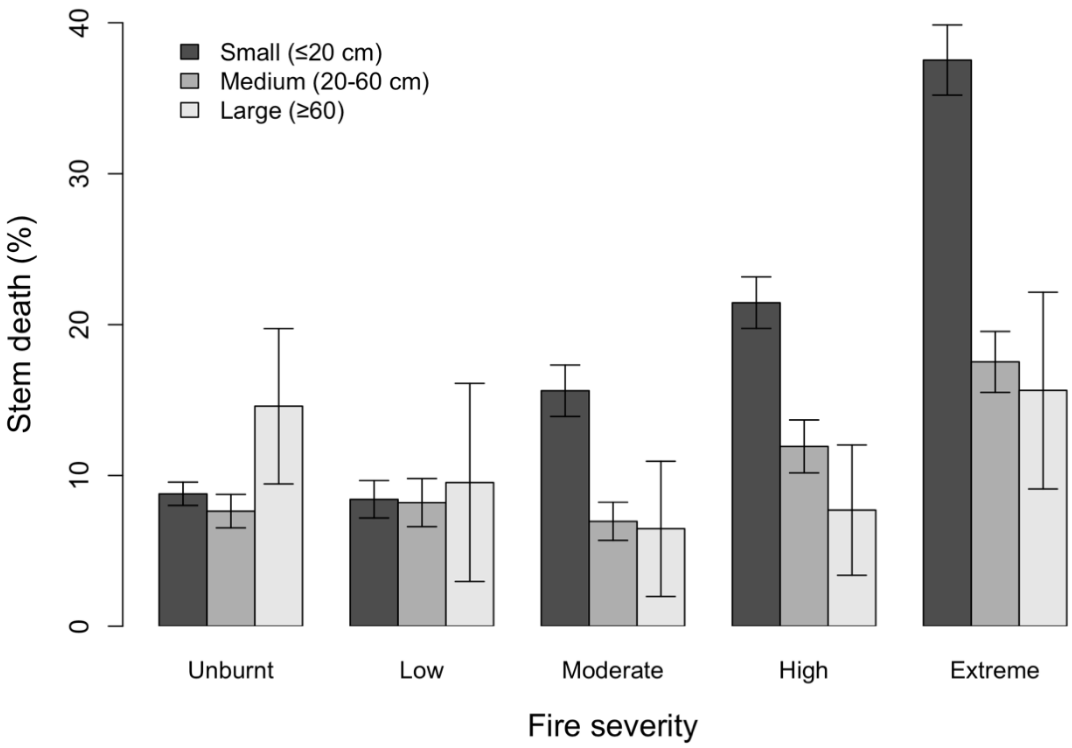

Figure 3. The effect of fire severity on standing stem death across stem size class. Values are means (± SE) by size and severity class (n = 5431).

Table 4. The number of stems recorded in each size class grouped by ambient fire severity. The proportion (%) of dead stems in each size and severity class is shown in parentheses.

Severity class	Unburnt	Low	Moderate	High	Extreme
Small (≤20 cm)	1333 (8.8%)	499 (8.4%)	455 (15.6%)	578 (21.5%)	437 (37.5%)
Medium (20-60 cm)	564 (7.6%)	293 (8.2%)	403 (6.9%)	344 (11.9%)	354 (17.5%)
Medium + newly fallen (20-60 cm)	600 (13.2%)	309 (12.9%)	423 (11.3%)	369 (17.9%)	396 (26.3%)
Large (≥60 cm)	48 (14.6%)	21 (9.5%)	31 (6.5%)	39 (7.7%)	32 (15.6%)
Large + newly fallen (≥60 cm)	49 (16.3%)	21 (9.5%)	32 (9.4%)	39 (7.7%)	34 (20.6%)
Total standing	1945 (8.6%)	813 (8.3%)	889 (11.4%)	961 (17.5%)	823 (28.1%)
Total standing + newly fallen	1982 (10.3%)	829 (10.1%)	910 (13.4%)	986 (19.6%)	867 (31.7%)

Table 5. The binomial generalised linear mixed effects model of DBH, bark type, fire severity and DBH^2 on the proportion of standing dead stems (n = 5431). An 'x' indicates an interaction.

Variable	Estimate	Standard error	*z*-value	*P*-value
Intercept	0.955	0.653	1.462	0.144
DBH	3.141	2.582	1.217	0.224
Stringy bark	-3.510	0.623	-5.634	$1.77e^{-08}$***
Smooth bark	-4.032	0.661	-6.100	$1.06e^{-09}$***
Rough bark	-3.645	0.617	-5.907	$3.48e^{-09}$***
Fire severity	0.531	0.056	9.498	$<2e^{-16}$***
DBH^2	1.111	0.483	2.301	0.021*
DBH x Stringy bark	-4.771	2.498	-1.907	0.057
DBH x Smooth bark	-7.660	2.899	-2.642	$8.23e^{-03}$**
DBH x Rough bark	-6.944	2.548	-2.726	$6.42e^{-03}$**
DBH x Fire severity	-0.770	0.275	-2.798	$5.14e^{-03}$**

*P ≤ 0.05, **P ≤ 0.01, *** P ≤ 0.001

The influence of fire severity and bark type on the occurrence of stem death was determined for each stem size class (**Figure 4**). Standing stem mortality was generally greatest for stringy bark stems across all burnt plots. Smooth bark stems were typically the most resilient to fire disturbance, with no mortality recorded for large smooth bark stems at any fire severity. Large rough bark dead stems were only recorded following extreme fire severity. For small and medium sized stems in burnt plots, smooth bark stems generally displayed the lowest rates of stem death; although, stem mortality substantially increased for this subset under extreme fire severity (**Figure 4**). Live stems were recorded for each bark type, size class and severity combination; however, the sample size of each subset was reduced relative to **Figure 3**, substantially increasing the variation.

The standing stem death model was plotted to further explore the interaction between fire severity and stem diameter for each bark type (**Table 5**; **Figure 5**). Across all bark types, the likelihood of stem death under extreme fire severity was greatest for small stems. For most combinations of severity and bark type, the probability of stem mortality gradually decreased with increasing diameter so that large trees were typically the most resilient to fire disturbance (**Figure 5**). The main exception was rough bark stems under extreme fire severity, with the likelihood of stem death negligible for stems in the medium size class (20-60 cm), yet substantial for both the smallest and largest stem sizes. This parabolic relationship, where intermediate sized stems show most resilience to extreme fire disturbance, is somewhat supported by the raw data (**Figure 4**). However, this model should be examined with caution as there is considerable variation in the rates of stem death for large stems.

The addition of 143 newly fallen logs to the stem data increased overall rates of stem death by 1.7 to 3.6% across the five fire severity classes (**Table 4**). The degree of change produced by the inclusion of newly fallen stems differed with both fire severity and stem size. The definition of newly fallen logs (>20 cm) restricted comparisons between the two datasets to the medium and large stem size classes. The largest shifts in rate of stem death occurred under extreme severity fire (**Table 4**). The rate of stem death under extreme severity fire for stems in the medium size class increased from 17.5% to 26.3% with the inclusion of newly fallen logs. The mortality rate of large standing eucalypt stems increased by 1% following extreme severity fire, however, this rate increased to ~4% with the inclusion of newly fallen large logs.

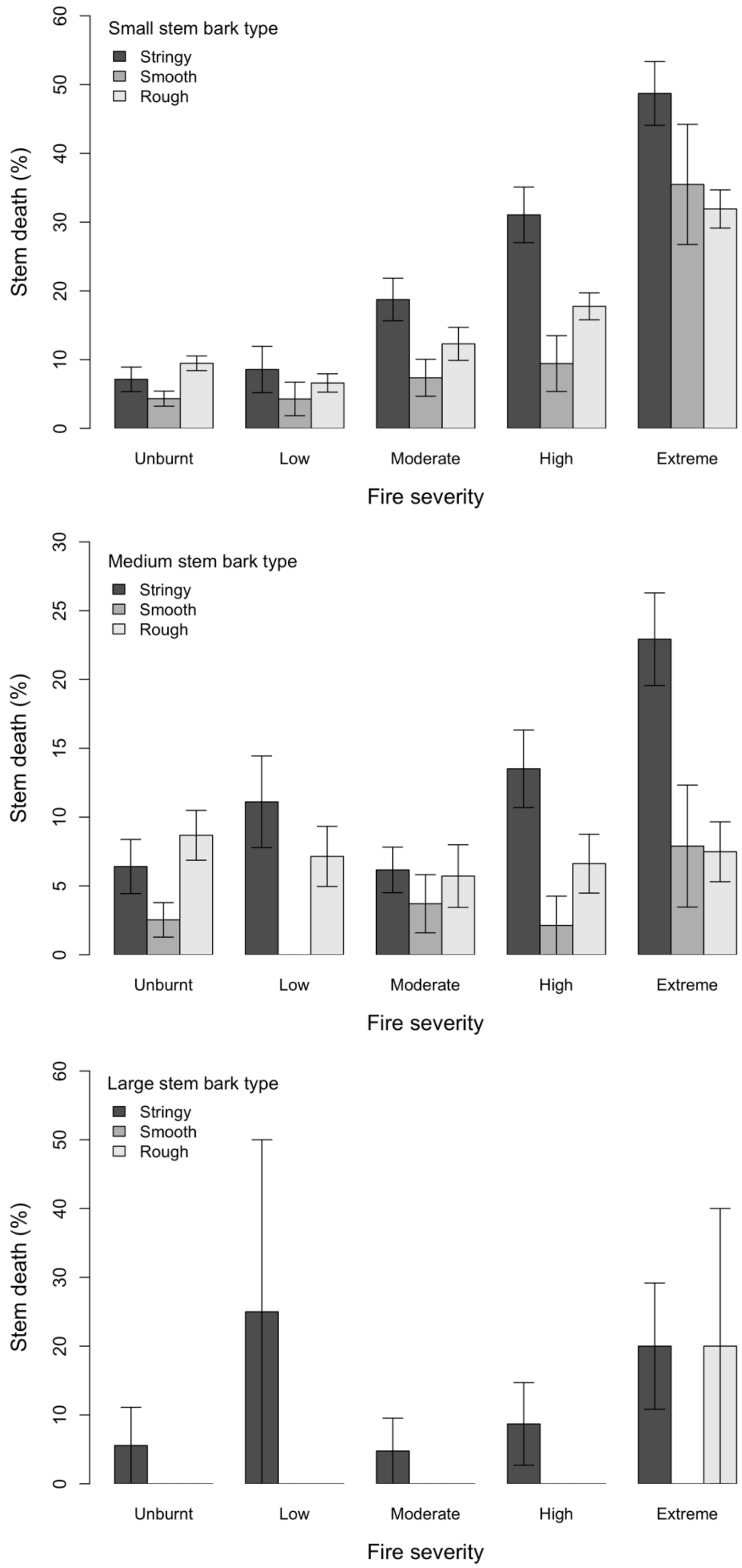

Figure 4. The effect of fire severity on standing stem death across bark type for small (≤20 cm), medium (20-60 cm) and large (≥60 cm) stems. Values are means (± SE) by bark type and severity class. Empty columns indicate no stem mortality was recorded.

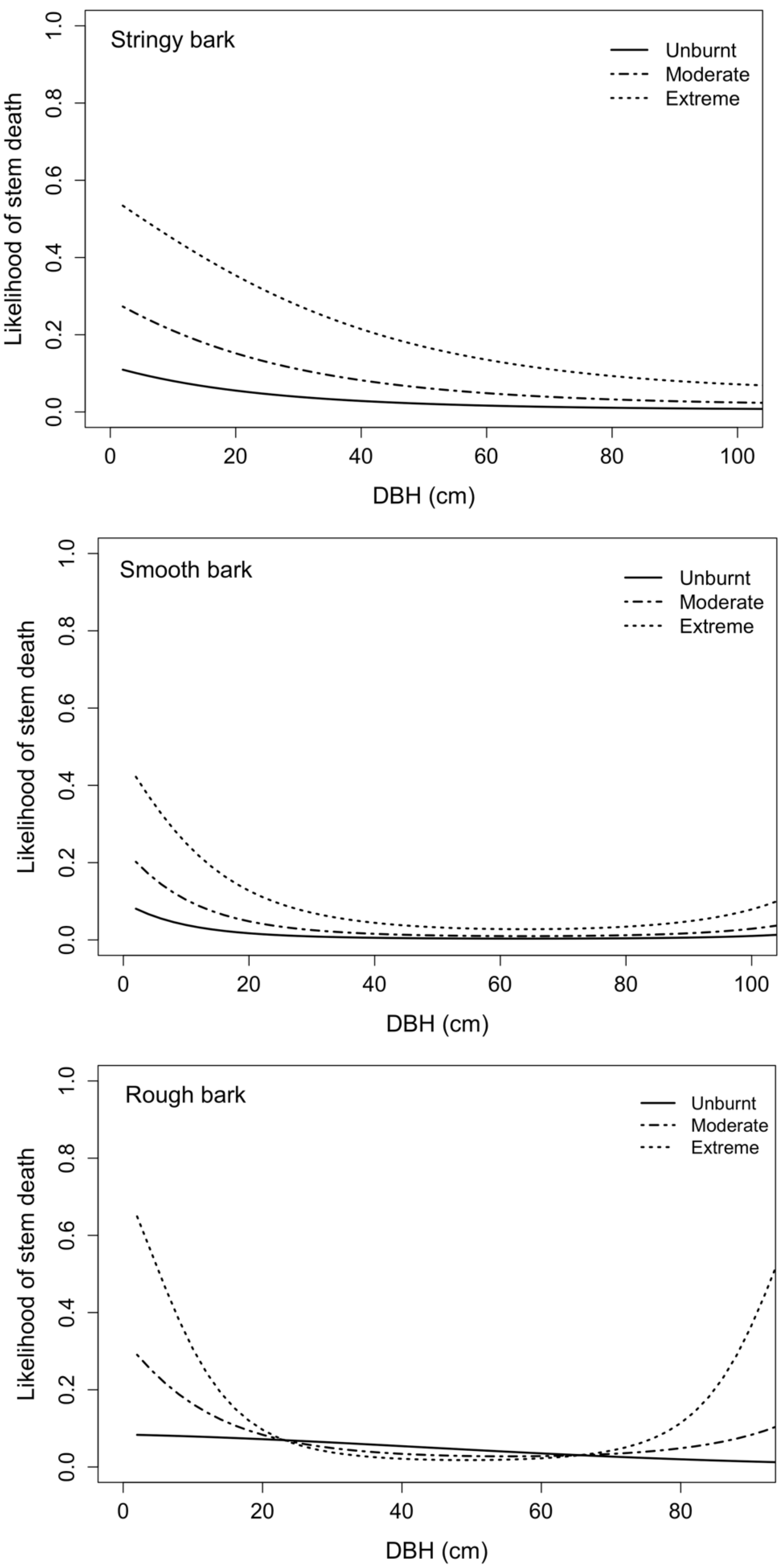

Figure 5. The likelihood of stem death for each bark type plotted against stem diameter under unburnt, moderate and extreme severity fire.

The inclusion of newly fallen logs produced a relatively similar model to a comparative standing stem model using the same predictor variables (**Table 6**). For both models, fire severity was the strongest predictor of stem death and the interaction terms between stem diameter and fire severity were also significant. For the standing stem analysis, DBH was not a significant predictor of stem death; however, this variable was a significant predictor in the combined stem and newly fallen logs model. The addition of newly fallen logs also strengthened the power of DBH^2 as a predictor of stem death, yet for both models this was not a significant variable (**Table 6**). These models were plotted to further explore their distinctions (**Figure 6**). The likelihood of eucalypt stem death under unburnt or moderately severe conditions was low for either model, especially in stems > 20 cm. For both models, the likelihood of death for small stems increased substantially under extreme fire severity. Notably, the inclusion of newly fallen logs into the model slightly increased the likelihood of stem death for large stems under extreme severity fire (**Figure 6**).

Table 6. The binomial generalised linear mixed effects model of DBH, fire severity and DBH^2 on the proportion of dead stems for a) standing stems (n = 5431); b) standing stems and newly fallen logs (n = 5574). An 'x' indicates an interaction.

a)

Variable	Estimate	Standard error	*z*-value	*P*-value
Intercept	-3.121	0.283	-11.022	$<2e^{-16}$***
DBH	1.447	1.272	1.138	0.255
Fire severity	0.670	0.064	10.542	$<2e^{-16}$***
DBH^2	-1.531	1.424	-1.075	0.282
DBH x Fire severity	-1.992	0.421	-4.732	$2.22e^{-06}$***
DBH^2 x Fire severity	1.535	0.512	2.999	$2.71e^{-03}$**

b)

Variable	Estimate	Standard error	*z*-value	*P*-value
Intercept	-3.289	0.288	-11.406	$<2e^{-16}$***
DBH	4.043	1.516	2.667	$7.66e^{-03}$**
Fire severity	0.675	0.067	10.014	$<2e^{-16}$***
DBH^2	-3.700	2.013	-1.838	0.066
DBH x Fire severity	2.089	0.473	-4.415	$1.01e^{-05}$***
DBH^2 x Fire severity	1.682	0.635	2.647	$8.12e^{-03}$**

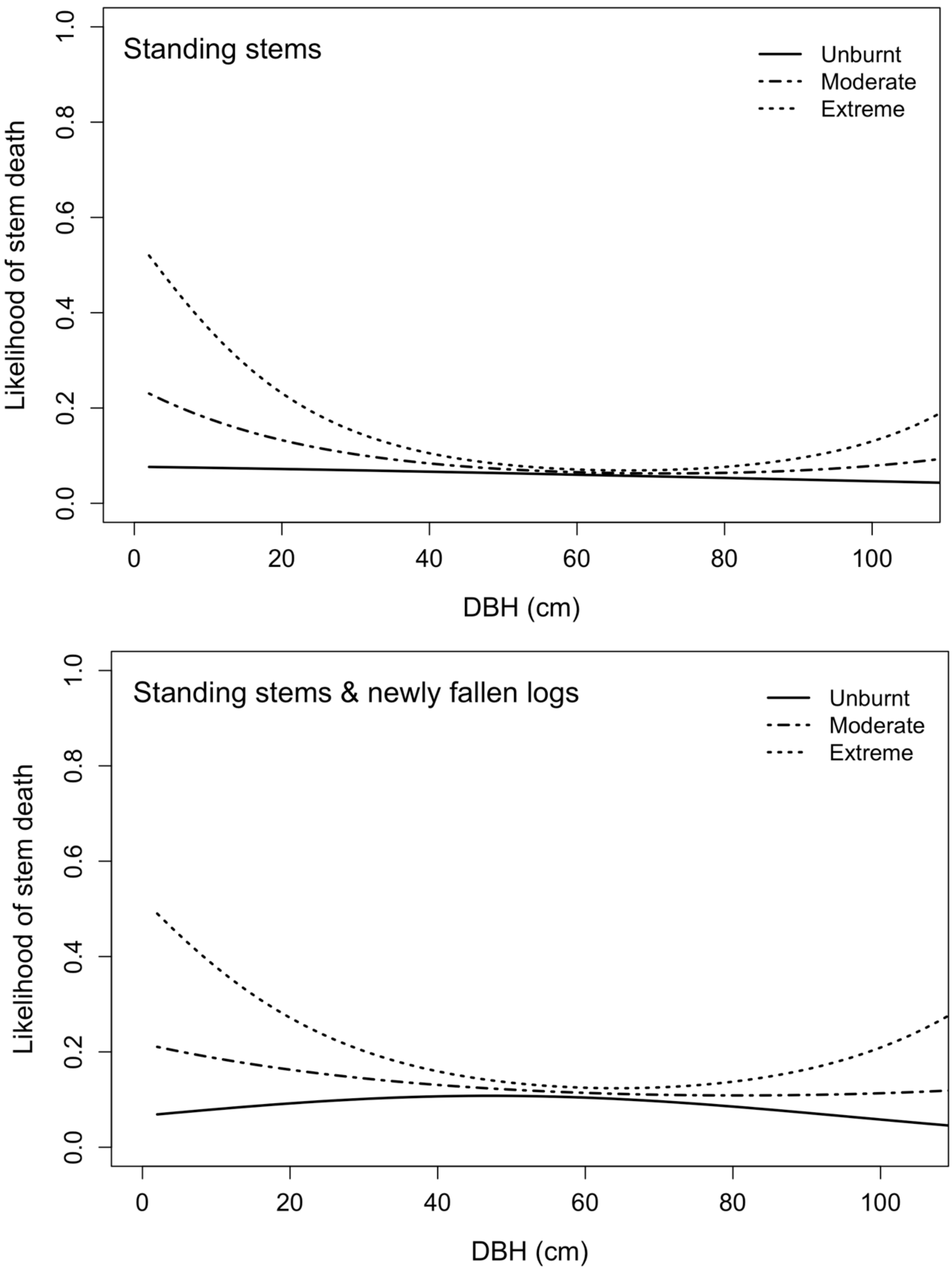

Figure 6. The likelihood of stem death plotted against stem diameter under unburnt, moderate and extreme severity fire, using the standing stem data with and without the inclusion of newly fallen logs.

4.2 Coarse woody debris

The primary data contained 590 pieces of CWD across 45 survey sites. The supplementary data contained 1658 pieces of CWD across 107 survey sites, including pre- and post-fire surveys which were treated as discrete records. The mean CWD fuel load across the 152 survey sites was 12.8 t/ha. The complete dataset was dominated by small CWD, with 73.4% of pieces having a cross-sectional diameter <10 cm. In contrast, we recorded 143 newly fallen pieces of CWD >20 cm, accounting for 6.3% of the data.

CWD mass per hectare was not significantly affected by fire severity, fire frequency or the interaction term between these variables (**Table 7**). However, CWD mass per hectare was significantly affected by fire type (**Table 8**). Fire frequency was excluded from this model based on goodness of fit (ΔAIC). The mean CWD fuel load in unburnt plots was 13.1 t/ha. The impact of fire activity on CWD differed with fire type, such that the average CWD fuel load following prescribed fire was 8.1 t/ha compared to 15.8 t/ha after wildfire (**Figure 7**).

Table 7. The generalised linear model of the effect of fire severity and fire frequency on CWD mass per hectare (*n* = 152). An 'x' indicates an interaction.

Variable	Estimate	Standard error	*t*-value	*P*-value
Intercept	0.853	0.145	5.877	$2.66e^{-08}$***
Fire severity	0.029	0.053	0.538	0.592
Fire frequency	-0.041	0.043	-0.969	0.334
Fire severity x Fire frequency	0.002	0.016	0.115	0.909

*P ≤ 0.05, **P ≤ 0.01, *** P ≤ 0.001

Table 8. The generalised linear model of the effect of fire type on CWD mass per hectare (*n* = 152).

Variable	Estimate	Standard error	*t*-value	*P*-value
Intercept	0.540	0.084	6.432	$1.61e^{-09}$***
Unburnt	0.256	0.109	2.341	0.021*
Wildfire	0.482	0.109	4.422	$1.87e^{-05}$***

*P ≤ 0.05, **P ≤ 0.01, *** P ≤ 0.001

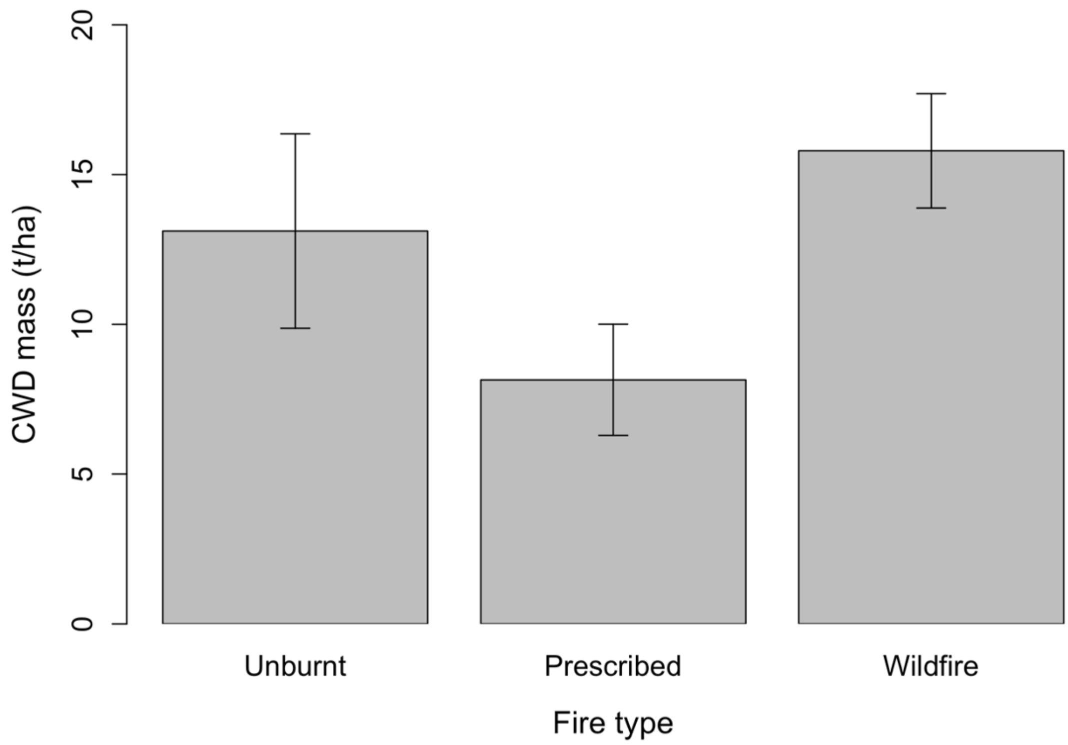

Figure 7. The mean (± SE) CWD mass (t/ha) for each fire type.

The number of newly fallen logs >20 cm per site significantly increased with fire severity (**Table 9; Figure 8**). When fire type was used as the predictor variable, the mean number of newly fallen logs in plots burnt by wildfires was significantly greater than unburnt plots or plots burnt by prescribed fire (**Table 10**; **Figure 9**). Notably, the mean number of newly fallen logs did not significantly differ between unburnt plots and plots burnt by prescribed fire (**Figure 9**).

Table 9. The Quasi-Poisson regression model of the effect of fire severity on the number of newly fallen logs >20 cm (n = 152).

Variable	Estimate	Standard error	t-value	P-value
Intercept	-0.823	0.272	-3.023	$2.92e^{-03}$**
Fire severity	0.282	0.079	3.564	$4.83e^{-04}$***

*P ≤ 0.05, **P ≤ 0.01, *** P ≤ 0.001

Table 10. The Quasi-Poisson regression model of the effect of fire type on the number of newly fallen logs >20 cm (n = 152).

Variable	Estimate	Standard error	t-value	P-value
Intercept	-0.668	0.342	-1.950	0.053
Unburnt	0.049	0.429	0.114	0.910
Wildfire	1.189	0.376	3.159	$1.90e^{-03}$**

*P ≤ 0.05, **P ≤ 0.01, *** P ≤ 0.001

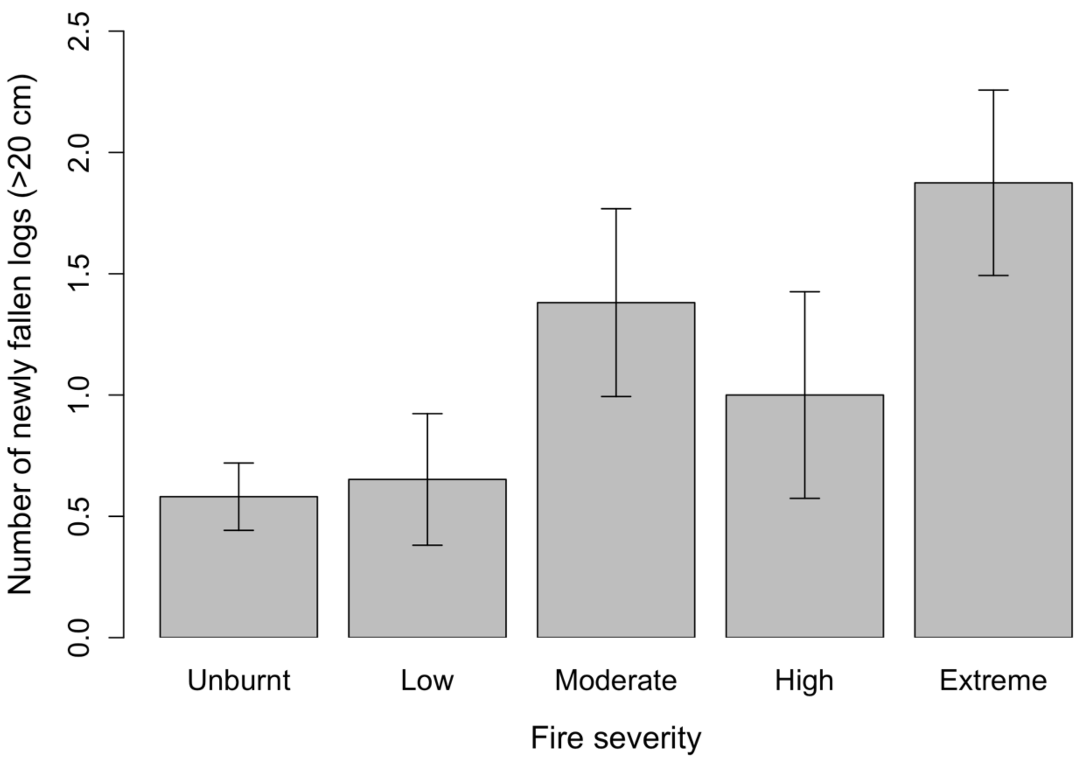

Figure 8. The mean (± SE) number of newly fallen logs (> 20 cm) across fire severity.

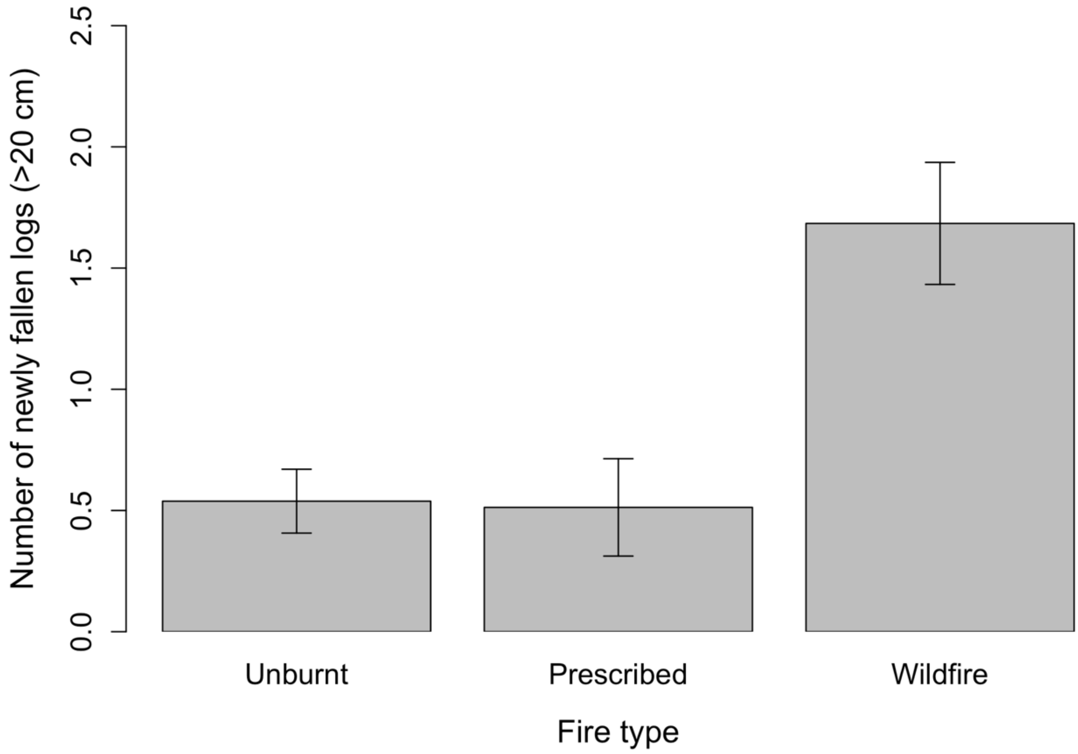

Figure 9. The mean (± SE) number of newly fallen logs (> 20 cm) for each fire type.

Chapter 5: Discussion

This thesis sought to further the ecological understanding of the effects of fire severity on eucalypt mortality and coarse woody debris dynamics in southeast Australia. More specifically, this study compared rates of eucalypt stem death and CWD quantity across satellite-based fire severity scores within dry sclerophyll forests. To date, this is one of the largest field-based assessments of fire induced mortality in eucalypt forests. Previous estimates of tree mortality in southern eucalypt forests have contained substantially higher uncertainty due to their smaller sample size (e.g. Bennett *et al.* 2016; Collins 2020; Pickup *et al.* 2013; Prior *et al.* 2016). It was predicted that both fire severity and stem diameter would influence the likelihood of stem death. This study supported these predictions, with rates of stem death greatest for small stems under extreme severity fire. It was also predicted that eucalypt bark type may influence the resilience of stems due to differences in insulation capacity. Whilst bark type did influence the likelihood of stem mortality, stems with low density bark were not the most resilient to fire disturbance. Contrary to initial predictions, CWD was not significantly affected by either fire severity or fire frequency; however, plots recently burnt by wildfires contained a significantly greater amount of CWD compared with plots recently burnt by prescribed fires.

5.1 Eucalypt stem dynamics

Rates of stem mortality are determined by a myriad of environmental, physical and ecological factors that influence the equilibrium between stem death and treefall (Furniss *et al.* 2020). Rates of eucalypt stem death increased with recent fire severity, confirming the first hypothesis. Sampling within long unburnt sites revealed that the background proportion of dead standing stems was ~9%. Within long unburnt forest, the proportion of standing dead stems is a result of previous fire activity, gradual accumulation through processes such as senescence and competition, and gradual depletion through decomposition and windthrow (Burton *et al.* 2021; Das *et al.* 2016). This study revealed that fire activity can substantially increase the proportion of standing dead stems and newly fallen logs. Nevertheless, when comparing long unburnt plots and plots recently burnt by low severity fire, rates of stem death differed by <1%. This finding is supported by the existing literature, which suggests that mature eucalypt survival is minimally impacted by low severity burns (Bassett *et al.* 2017; Bennett *et al.* 2016). Rates of stem death following moderate and high severity fire increased considerably compared to unburnt forest, yet these shifts were relatively consistent with the 5-15% increased mortality rate reported for resprouting eucalypts in several other studies of wildfire induced topkill (Collins 2020; Pickup *et al.* 2013; Vivian *et al.* 2008). When newly fallen logs were considered within mortality estimates, overall rates of stem death increased by 1.7% within unburnt plots and ~2% in areas burnt by low, moderate and high severity fire. After extreme severity fire, the rate of stem death in dry sclerophyll forests was 28.1%, which grew to 31.7% when including newly fallen logs. While extreme severity fire often only accounts for a limited proportion of the total area burnt by wildfire (Collins *et al.* 2021), the results of this study show that severely burnt areas disproportionately contribute to the total number of dead stems and newly fallen logs.

The effect of fire disturbance on stem death was governed by stem diameter, with rates of stem death considerably higher for small trees. This relationship was exacerbated by increasing fire severity, so that small stems subject to extreme severity fire showed the greatest levels of mortality. This result supports the second hypothesis and is consistent with previous research in Australian temperate forests (e.g. Bell *et al.* 1989; Benyon & Lane 2013; Collins 2020; Fairman *et al.* 2019). Stem diameter is a principal determinant of the resprouting response of eucalypts to fire as stem size is proportionate to bark thickness and canopy height, which help protect vascular and meristematic tissues from convective and radiative heat (Burrows 2013; Wesolowski *et al.* 2014). The likelihood of fire induced stem death generally decreased as stem size increased; however, modelling indicated a slight increase in the likelihood of stem death for the largest stems. This trend was exacerbated by the inclusion of newly fallen logs. These findings somewhat challenge the traditional conceptual model of fire tolerant eucalypt forests, which assumes that large trees are perpetually resistant to wildfire. As previously mentioned, these findings should be examined with caution due to the comparatively small sample size of very large trees. For example, 437 small stems (≤20 cm) were recorded in plots burnt by extreme severity fire, whilst only 32 large stems (≥60 cm) were recorded across the same area. A recent publication by Bennett *et al.* (2016) was one of the first to demonstrate a similar curvilinear relationship in southern eucalypt forests following the 2009 *Black Saturday* wildfires in Victoria. This particular phenomenon was attributed to prolonged drought conditions (Bennett *et al.* 2016), yet the cumulative impact of previous fires may also increase the vulnerability of large eucalypts. As stem diameter is relative to tree age

(Brookhouse 2006), the largest trees in a stand will have endured the greatest number of fire events, all of which have the potential to elicit basal scarring (Bradstock 2008; Collins 2020). Basal scarring damages the protective bark layer, allowing pathogen entry (Burrows 2013) and increasing the likelihood of successive fires to cause cambium necrosis, hydraulic failure and subsequent stem death (Hood *et al.* 2018).

When comparing stem mortality across fire severity for the largest stem size class, the number of large dead stems declined following low, moderate and high severity fire relative to unburnt plots, yet slightly increased under extreme fire severity. This suggests that large dead trees can remain standing for long periods with the exclusion of fire, however, subsequent fire activity increases stag fall (Burton *et al.* 2021). Only under extreme severity fire does the proportion of large trees killed exceed the number felled. This supposition could be verified through a pre-post fire tree mortality assessment with stem tagging (e.g. Guinto *et al.* 1999; Williams *et al.* 1999). However, this data may be difficult to collect for areas burnt by extreme severity fire due to the aleatory nature of wildfire activity in southern eucalypt forests. Understanding the dynamics of large tree death and treefall is critical for habitat conservation and managing carbon stock, as large trees have a greater likelihood of containing hollows and store more carbon than small stems (Collins *et al.* 2012; Gordon *et al.* 2018). The transition of large dead standing stems to fallen logs would likely improve forest floor habitat (Lindenmayer *et al.* 2002) yet may increase the rate of carbon loss due to faster decomposition of fallen wood (de Bruijn *et al.* 2014).

The effects of fire in forest systems are often compounded by other stressors such as prolonged drought, pathogens or timber harvesting (Paine *et al.* 1998; Watson *et al.* 2020). Throughout 2018 and 2019, almost 100% of New South Wales was drought affected, with isolated areas in the southeast experiencing intense drought conditions (DPI 2019). This resulted in extensive canopy die-back in temperate eucalypt forests (Nolan *et al.* 2021) and may have increased whole tree mortality generally (Matusick *et al.* 2013). As smaller trees tend to be more vulnerable to hydraulic failure and subsequent canopy die back (Nolan *et al.* 2021), the antecedent drought conditions in New South Wales likely weakened the most vulnerable stems prior to fire activity. These compounding stressors may have increased rates of fire induced stem death across all burnt areas, especially for small stems. The mean rate of standing dead stems in plots burnt by the 2019/2020 wildfires was ~19%, slightly higher than the average rate of topkill elicited by the 2013 West Gippsland wildfire (Collins 2020), yet well below the known extremity for dry sclerophyll forests in southeast Australia. Following high severity fires in the Tasmanian Midlands, Prior *et al.* (2016) recorded a eucalypt stem death rate of 52%; although this finding should be considered in the context of severe background mortality and multiple compounding disturbance events. Evidently, eucalypt stem death can increase substantially with fire severity; however, the primary dataset revealed fire severity did not have the same influence on whole plant mortality. This suggests that the majority of dead stems within burnt plots were capable of basal resprouting. A similar trend was observed within dry sclerophyll forests in northern NSW. Croft *et al.* (2007) found that whole tree survival was similar between unburnt and severely burnt areas after a multi-year drought, yet burnt trees were more likely to resprout from lignotubers, whereas unburnt trees typically resprouted from epicormic buds in the canopy or trunk. Despite the elevated rates of stem death observed following severe drought and fire in this study, and others (Bradstock 2008; Croft *et al.* 2007), the resilience of resprouting eucalypts to compounding disturbance events is illustrated by negligible shifts in whole tree mortality (i.e. survival through basal resprouting).

Eucalypt health is occasionally classified as a dichotomous response within fire ecology literature, where stems either resprout from epicormic buds or are killed (e.g. Denham *et al.* 2016; Vivian *et al.* 2008). Yet, the height of epicormic resprouting can act as an indication of the extent of tissue death and structural change. For this study, field observations revealed that canopy resprouting was the dominant response to extreme severity fire, although resprouting was restricted to the central trunk for a substantial proportion of stems (~31%). Following extreme severity fire, it was noticeable that many canopy resprouting trees were resprouting only from the lowest branches in the canopy. This decline in live branch height is the result of a reduction in the hydraulic conductivity of xylem within the smallest branches (Burrows 2013). A reduction of live branch height increases the connectivity between the canopy and understorey over the medium term, facilitating canopy consumption during future fire events (Collins 2020). Branch death can provide points of entry to pathogens, further impacting tree health (Burrows 2013). Under a regime of more frequent severe wildfires, enhanced tissue necrosis and a persistent reduction of canopy height could create canopy fire feedbacks which have substantial impacts on stand structure and carbon stock.

Stem death was significantly influenced by bark type; however, the effect of this attribute was complicated by interactions with stem diameter and fire severity. Smooth bark stems were generally most resilient to fire disturbance, rejecting the third hypothesis, which predicted that stems with low bark density would be the most fire resilient. The relationship between bark thickness and fire induced stem death is well established (Gill & Ashton 1968; Wesolowski *et al.* 2014), however, difficulties arise when attempting to establish axioms for other bark attributes. For example, there is conflicting evidence about the effects of bark moisture on thermal conduction and stem survival (e.g. Gill & Ashton 1968; Vines 1968). Smooth bark is typically denser and has a higher moisture content than other bark types (Vines 1968). A higher moisture content helps prevent bark combustion yet can increase conduction and heat residency during a fire (Wesolowski *et al.* 2014). Following wildfires in dry sclerophyll forests, Nolan, Rahmani, *et al.* (2020) found that species with thick, low-density bark were most resistant to topkill, whilst a smooth bark eucalypt (*E. rossii*) was one of the most vulnerable. In a laboratory assessment of the thermal conductivity of three bark types, Wesolowski *et al.* (2014) found that a smooth bark eucalypt, *Eucalyptus leucoxylon*, had the greatest capacity to withstand high temperatures due the evaporative cooling effect conferred by a high bark moisture content. The results of this thesis demonstrate that the impacts of fire disturbance differ between eucalypt bark types (and presumably taxa) within dry sclerophyll forests, although further research is clearly required to determine the exact influence of this factor on the likelihood of stem mortality. The validity of these findings is slightly restricted by the broad bark type categories used when collating the primary and supplementary datasets. For example, the rough bark category included stem records from *E. crebra*, *E. sieberi* and *E. botryoides*, three species with quite distinct bark morphology. The use of more explicit bark categories (e.g. Slee *et al.* 2015) may help to clarify the relationships between eucalypt bark type and stem vulnerability to fire disturbance.

5.2 Coarse woody debris dynamics

Contrary to initial expectations, coarse woody debris was not significantly influenced by fire frequency or severity. Several previous studies have found that CWD in dry sclerophyll forests was significantly affected by the frequency of burning (Aponte *et al.* 2014; Bassett *et al.* 2015; Whitford & McCaw 2019), however, there is currently limited evidence of the effects of fire severity (Bassett *et al.* 2015; Burton *et al.* 2021; Threlfall *et al.* 2019). Studies of fire frequency in southern eucalypt forests often focus on the impact of repeated burns over a short period (e.g. Aponte *et al.* 2014; 7 fires over 27 years) compared with the effects of low fire frequency. This was not the emphasis of our study, and as such fire frequency values were random and determined post hoc, which may account for our ability to detect such effects (Burton *et al.* 2021). The current study revealed no significant relationship between fire severity and total CWD. The satellite-based severity scores used in this study, and several others (Bassett *et al.* 2015; Burton *et al.* 2021; Maestrini *et al.* 2017), are essentially measures of vegetation blackening, which may not directly correlate with CWD consumption as vegetation impact is influenced by extraneous factors such as canopy height and bark type.

Fire type was a more effective predictor of total CWD, with mean CWD biomass reduced in plots recently burnt by prescribed fire and heightened in plots recently burnt by wildfire, relative to unburnt forest. The significant relationship between CWD and fire type illustrates that lower intensity prescribed burns consume more CWD than they produce through stem death and treefall, while the opposite is true for higher intensity wildfires, where CWD production exceeds consumption. Research by Hollis, Matthews, *et al.* (2011) recommends the use of McArthur's Forest Fire Danger Index (FFDI) as an alternative post hoc indicator of CWD consumption in Australian eucalypt forests. FFDI is a continuous measure of fire behaviour potential that considers the effect of ambient temperature, wind speed, relative humidity and precipitation. As extreme fire weather and fuel conditions are more associated with severe wildfires than prescribed fires (Abram *et al.* 2021; Clarke *et al.* 2020; NPWS 2020), CWD consumption should typically be greater in areas recently burnt by wildfire than areas burnt by prescribed fire. This relationship is somewhat obscured in the current study as site scale records reflected the balance between CWD consumption and production, so that overall CWD mass was greatest in plots recently burnt by wildfire. While the consumption of CWD may not directly correlate with measures of fire severity, there is likely a strong relationship between severity scores based on vegetation impact and CWD production. As stated previously, rates of stem death increased substantially with fire severity, as did the number of newly fallen logs. On average, plots affected by wildfire had three times as many newly fallen logs as unburnt plots or plots burnt by prescribed fire. This implies that high intensity fires not only consume more CWD than lower intensity fires (Hollis, Anderson, *et al.* 2011), they cause more stem death and subsequent treefall (Price *et al.*, unpublished data). Under increasingly severe fire regimes, both the production and consumption of CWD may increase.

5.3 Ecological and management implications

Variation in eucalypt mortality and woody fuel consumption has important implications for carbon dynamics, smoke production and biodiversity within southeast Australian eucalypt forests (Bowman *et al.* 2013; Bowman *et al.* 2016; Bradstock 2008; Reid *et al.* 2005). Resprouting eucalypt forests are traditionally considered highly resilient to fire disturbance (Gill 1975; McArthur 1967), however, debate remains regarding the potential impact of compounding disturbance events and fire regime shifts on eucalypt resilience (Bowman *et al.* 2013; Croft *et al.* 2007; Fairman *et al.* 2019; Prior *et al.* 2016). As aboveground carbon within dry sclerophyll forests is predominantly stored within the largest live stems (Fedrigo *et al.* 2014; Gordon *et al.* 2018), small shifts in the mortality rate of large eucalypts would have significant consequences for carbon loss and smoke emissions. Within increasingly fire-prone temperate landscapes (Moritz *et al.* 2012), differences in fire resilience across taxa or bark morphology could have significant consequences for forest biodiversity. The results of this study suggest that whilst the total number of standing dead stems may substantially increase after severe drought and extreme severity fire in dry sclerophyll forests, this shift predominantly occurs in small and medium sized eucalypts. Extreme severity fire also accentuates the differences in stem mortality between eucalypt bark types. Overall, these findings support the view that dry sclerophyll communities may experience demographic shifts under more frequent, high severity fire regimes (Collins 2020; Fairman *et al.* 2016). Disproportionate age class or bark type mortality may decrease forest diversity and structural complexity, leading to demographic legacies that influence long term stand development, such as bottlenecks in the transitional development stages of trees (Bennett *et al.* 2016; Bond *et al.* 2012). However, given the persistence of the majority of large trees, the short secondary juvenile period in resprouting eucalypts and the rapid development of lignotubers in seedlings, ecosystem conversion and catastrophic carbon loss seem unlikely in the near future (Collins 2020).

Despite the regenerative capacity of resprouting eucalypts that confers a degree of resilience to ecosystem transition (Bowman *et al.* 2013), carbon stock within dry sclerophyll communities may gradually decline under anthropogenic climate change. Forest carbon will likely decline with increasing mean annual temperature, despite elevated levels of atmospheric CO_2 (Anderson-Teixeira *et al.* 2011; Gordon *et al.* 2018). Larger, more frequent and more severe wildfires are predicted across southeast Australia as fire weather becomes more extreme (Bates *et al.* 2010; Clarke & Evans 2019; Clarke *et al.* 2020; King *et al.* 2011). This shifting disturbance regime will likely increase eucalypt stem death and subsequent CWD production. Concurrently, heightened fire weather and intensity will enhance the consumption of CWD (Hollis, Anderson, *et al.* 2011; Hollis, Matthews, *et al.* 2011), reducing the longevity of forest floor habitat. The balance of woody fuel production and consumption is influenced by a multitude of variables (Burton *et al.* 2021; Byram 1959; Hollis, Matthews, *et al.* 2011; Hyde *et al.* 2011), yet under these escalating conditions, the consumption of dead wood may come to exceed the production of live biomass, leading to gradual carbon loss. This carbon loss may be compounded by a change in canopy structure, driven by canopy fire feedbacks which persistently reduce live branch height (Collins 2020).

Management strategies that alter fuel structure and quantity may reduce the risks posed by severe wildfire to forest biodiversity and ecosystem services (Price *et al.* 2015). Prescribed burning has been used extensively in fire-prone landscapes to alter fuel loads with the aim of reducing the likelihood of ignition, rate of spread and intensity of wildfires (Fernandes & Botelho 2003; Price & Bradstock 2012; Stephens *et al.* 2009). As prescribed burns are typically patchy and less severe than wildfires (Penman *et al.* 2007), the application of prescribed fire may increase eucalypt sapling survival and enhance the structural and taxonomic diversity of dry sclerophyll forests (Holland *et al.* 2017). However, the ecological impacts of prescribed fire regimes remain under researched (Penman *et al.* 2011), with some studies indicating that the frequency of hazard reduction burns may be asynchronous with the minimum fire intervals required for the conservation of structurally important plants (Bradshaw *et al.* 2018; Kelly *et al.* 2015; Pastro *et al.* 2011). The practice of introducing more frequent, less severe patterns of burning within dry sclerophyll forests to retain stored carbon or increase rates of sapling survival relies on the assumption that prescribed burns reduce the severity of subsequent wildfires. Whilst recent burning has been shown to reduce wildfire intensity in southern eucalypt forests, this effect is limited to around a five-year period and is negligible during catastrophic fire weather (Fernandes & Botelho 2003; Price & Bradstock 2012; Stephens *et al.* 2009). Land managers face a complex challenge of prescribing fire for multiple objectives, and must adapt to the shifting expectations of government, current ecological theory, and increasingly severe fire weather under a changing climate (Bowman *et al.* 2013; Burrows & McCaw 2013).

5.5 Conclusion

As the most widespread and fire-prone forest type in southeast Australia (Keith 2004; Tozer *et al.* 2010), the response of dry sclerophyll forests to fire disturbance has critical implications for carbon stock, smoke production and biodiversity. Compounding disturbance events amplified by climate change are increasing the stressors acting on this vegetation community. A more comprehensive understanding of the impacts of fire severity on eucalypt survival and coarse woody debris dynamics is required to accurately predict potential ecological shifts and make informed management decisions. This study has provided the most reliable estimates of eucalypt stem death in dry sclerophyll forests to date. Rates of stem death are compared against satellite-based fire severity scores, a widely used measure of fire behaviour.

The results revealed that eucalypt stem mortality was significantly influenced by stem diameter, bark type and fire severity. Overall, this study strongly suggests that increasingly severe fire activity across southeast Australia will elicit greater rates of stem death and subsequent demographic shifts in dry sclerophyll forests. More severe wildfires will reset the recruitment process by substantially increasing the rate of stem death in saplings and small stems. As disparities in fire resilience between bark types are more apparent under extreme severity fire, future fire regimes will likely reduce the abundance of the most vulnerable taxa, reducing forest diversity. More frequent and more severe fire regimes may reduce canopy height and modify crown structure within dry sclerophyll forests, creating positive canopy fire feedbacks that have the potential to reduce carbon stock.

Contrary to initial predictions, CWD was not significantly influenced by fire severity. By definition, fire severity is a measure of fire induced vegetation change, which is influenced by several factors unrelated to the consumption or production of CWD. Nonetheless, CWD was significantly reduced in plots burnt by prescribed fire and significantly heightened in plots burnt by wildfire, relative to long unburnt forest. This relationship suggests that lower intensity prescribed burns consume more CWD than they produce, while the opposite is true for higher intensity wildfires, where CWD production exceeds consumption. Both CWD production and consumption will likely increase under more severe fire regimes, potentially increasing CWD biomass in the short term, but reducing the longevity of forest floor habitat due to greater CWD turnover. Over the long term, the consumption of dead wood may exceed the production of live biomass, leading to carbon loss.

Whilst gradual carbon loss and demographic shifts are expected under more severe fire regimes, complete ecosystem transformation is less likely for vegetation communities dominated by eucalypts capable of epicormic resprouting compared to communities dominated obligate seeders, given the persistence of the majority of large trees and the short secondary juvenile period of resprouting eucalypts following severe fire. Future research should assess the potential cumulative effect of basal scarring on large trees and the durability of large stags due to the disproportionate impact of large trees on carbon stock and habitat provision. Further research is also required to clarify the role of bark type on eucalypt survival under more severe fire regimes. This study reflects how the complex relationship between resprouting eucalypts and disturbance regimes ultimately determines forest structure and carbon stock within southeast Australian dry sclerophyll forests.

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