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RESEARCH ARTICLE

Mechanisms by which growth and succession limit the impact of fire in a south-western Australian forested ecosystem

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Abstract

1. Forest wildfire impact is widely believed to increase with time since disturbance, presenting a dilemma for the persistence of fire-sensitive species. However, in south-western Australia, disturbance has been shown to increase wildfire likelihood for some decades before it again declines. It has been proposed that this trend occurs through 'ecological controls' on wildfire such as the self-thinning of fire-stimulated understorey growth.
2. Here, we analyse six proposed ecological controls using a surveyed chronosequence of a *Eucalyptus jacksonii* forest community. We quantify plant growth (growth and self-pruning) and succession (changing plant traits, self-thinning), along with consequent changes in surface and suspended litter. We then use a biophysical, mechanistic model to predict the dynamics of flame height and canopy scorch/consumption, along with suppression difficulty during wildfire conditions. To identify the importance of each potential ecological control, we separately manipulate them to grow hypothetical forests from 1 to 100 years; each with one of the controls removed. We then model flame height in each to compare with the original forest that had all controls present.
3. Fire initially promoted dense understorey regeneration, but ecological controls transferred this biomass from fuel (likely to ignite) to overstorey shelter (unlikely to ignite, creating a less flammable microclimate). The effect of these changes was to alter modelled fire behaviour, such that flame dimensions in mature forest were half those in regrowth, canopy damage greatly reduced, and fire suppression opportunities maximised. The primary controls were self-thinning and self-pruning.
4. Forest growth and succession explains observed trends in flammability dynamics in south-western Australian forests, and the persistence of fire-sensitive species over time. Approaches that cooperate with, rather than disrupt, these processes therefore provide a pathway to mitigate current climatic effects on fire.

KEYWORDS
fire ecology, flammability, forest ecology, plant traits, positive-feedback switches, self-pruning, self-thinning, succession

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1 | INTRODUCTION

It is widely believed that long-unburned forests are more flammable in a range of metrics when compared to recently burned forests, as a greater amount of biomass is available as fuel (Bowman et al., 2020; McCarthy et al., 2001). This understanding influences dynamic vegetation models that incorporate fire (Hantson et al., 2016; Kelley et al., 2014) and underpins much of the thinking around risk mitigation (Fernandes & Botelho, 2003; North et al., 2015). Important ecological implications arise from this view, as it describes a situation in which forest ecosystems form environments that are increasingly hazardous to their component biota unless an external intervention (lightning or human ignition) triggers the hazard and resets the sequence. It also necessitates management to minimise carbon storage, because biomass is categorised as fuel.

While this view has apparent empirical support for some areas (Jones et al., 2022), such studies predominantly examine short term trends of increasing flammability (Zylstra et al., 2022). When longer time periods have been examined, the opposite trend appears in many forests because the initial increase in flammability is followed by a decrease, so that wildfires have been least frequent in those older forests and woodlands examined (e.g. Cochrane et al., 1999; Dixon et al., 2018; Nowacki & Abrams, 2008; Taylor et al., 2014; Zylstra, 2018). In south-western Australian forests, Zylstra et al. (2022) found that disturbance by (predominantly prescribed) fire promoted a pulse in wildfire likelihood lasting some decades but which then decreased and remained low in long-unburnt forests. This closely matched the trajectory and timing of understorey dynamics, where fire is known to promote dense regrowth that later self-thins in the dominant Jarrah *Eucalyptus marginata* and Karri *E. diversicolor* forests of the region. Similar self-thinning trends in understoreys and graminoid layers are evident in semi-arid *E. wandoo* (Burrows et al., 1990), *E. salubris* (Gosper et al., 2013), mallee (Kelly et al., 2011) and *Callitris intratropica* (Trauernicht et al., 2012) woodlands, whereas succession to mesic species has been observed to exclude fire in some mixed conifer forests of the eastern U.S. (Nowacki & Abrams, 2008). Zylstra et al. (2022) proposed that processes such as self-thinning understoreys along with growth and succession represent 'ecological controls' on wildfire, limiting the impact of fire in mature forest. Thus, rather than being necessary to limit wildfire impact as widely believed, disturbance instead disrupts ecological controls in these forests, resulting in a period of heightened flammability lasting some decades.

1.1 | Mechanisms controlling flammability

Flammability (the likelihood that something will burn) may be considered in both horizontal and vertical dimensions (probability of a point in the landscape burning, and the height of vegetation consumption or severity; Gill & Zylstra, 2005). The likelihood that fire will occur at all is related to fuel moisture content (Balch et al., 2022; Nolan et al., 2016), which is a factor of climate, terrain and forest microclimate (Brown et al., 2022; Furlaud et al., 2021; Lindenmayer, Blanchard, et al., 2022). Once a fire is burning, however, its capacity to cross both horizontal and vertical barriers to consume more material in either dimension (e.g. spotting across landscape barriers or developing into crown fire) is influenced by flame dimensions (Albini et al., 2012; Wang et al., 2020; Zylstra et al., 2016). Ecological controls (Table 1) are changes in vegetation structure or composition that reduce the capacity for fire to either ignite (microclimate), or to cross horizontal or vertical barriers. The mechanistic understanding that we use here to understand this process derives from the Fire Research and Modelling Environment FRaME (Zylstra, 2021; Zylstra et al., 2016). In this model, plants may either increase or decrease flame heights, depending upon their location and flammability. If located where they can be ignited (fuel), they may increase it, but will otherwise decrease it if located beyond the reach of flames. There, they moderate the

TABLE 1 Proposed ecological controls and hypotheses.

Ecological control	Expected effect
Growth	
Plant growth	Initially increases donor flammability and flame height, but then moves plants from fuel into overstorey shelter, reducing flame heights in older forests
Self-pruning	Raises the base height of plants so that they are less likely to ignite, therefore moving them from fuel to overstorey shelter and reducing flame height in older forests
HYPOTHESIS	H1: If the tallest plant stratum grows from ground level at age zero, then removing plant growth components will reduce the strength of the positive feedback or cause negative feedback
Succession	
Self-thinning	Reduces donor flammability and therefore flame height by reducing the quantity of plant biomass close to the ground
Trait changes	Affect donor flammability (combustibility and sustainability of flames from burning plants), and receiver ignitability, thereby moderating which plants will act as fuel or overstorey shelter. Effects are expected to vary between ecosystems and trait combinations
HYPOTHESIS	H2: If self-thinning occurs in the understorey, then removing it will reduce the strength of the positive feedback or cause negative feedback
Secondary effects	
Surface litter	Acts as a 'pilot flame' to ignite the lowest plants. Accumulation increases donor flammability and therefore flame height, to a small extent
Suspended litter	Amplifies the effects of surface litter, increasing its donor flammability
HYPOTHESIS	H3: If the understorey of the forest self-thins, then preventing suspended litter from decaying will reduce the strength of the positive feedback or cause negative feedback

sub-canopy with a cooler, less windy microclimate (overstorey shelter). The heat flux from burning fuel is termed the 'donor flammability', which is the combustibility and sustainability of the flames. Whether other plants become fuel, or remain as overstorey shelter depends on their distance from the donor, the donor flammability, and the 'receiver ignitability' of the exposed plants. Receiver ignitability is affected by leaf traits and foliar moisture. As combustion removes flammable biomass and necromass on or near the ground ('fuel reduction'), forests will be less flammable for a short period afterward. Post-fire recruitment, however, promotes biomass recovery close to the ground. Vegetation dynamics beyond this point determine the nature of fire-flammability feedbacks by either separating foliage into overstorey shelter or leaving it as fuel. These processes are the ecological controls. We expect that ecological controls operate through growth and succession, which can be further divided into plant growth and self-pruning (growth) and changing plant traits and self-thinning (succession).

Plant growth initially affects the size of burning plants and therefore their donor flammability, but over time it also affects the proportion of plants acting as either fuel or overstorey shelter, altering the vertical distribution of biomass by controlling the size of gaps between strata that can limit fire spread into taller plants (Gosper et al., 2013; Tiribelli, Kitzberger, et al., 2018). Shading of branches causes self-pruning of lower branches in many situations (Hellström et al., 2018) so that the base height of plant crowns increases, reducing their likelihood of ignition and thereby increasing the likelihood that they will act as overstorey shelter. In contrast, succession affects the degree of influence of fuels by controlling donor flammability, and the transition to overstorey shelter by controlling receiver ignitability of plants. Earlier successional plant species in angiosperm-dominated forests are often characterised by fast-growing tissues with low leaf mass per unit leaf area (LMA) and wood density. The effect of this is context-dependent, as these more ignitable, but thinner leaves also produce shorter-duration flames (Grootemaat et al., 2017; Zylstra, 2011). As stands age, the mean LMA of plants typically increases (Falster et al., 2017; Lusk et al., 2010), but see also exceptions in Chelli et al. (2022). Resource limits lead to the self-thinning of vegetation (Westoby, 1984), affecting the influence of plant strata rather than the influence of individual species. This is often pronounced in lower strata where light is limiting (Hoffmann et al., 2012), reducing the donor flammability of fuels. Eucalypt forests typically follow a trend where lower strata self-thin so that foliage becomes increasingly concentrated in the upper strata (Specht, 1983). This trend describes a transition of plant biomass from fuel (increasing fire risk) to overstorey shelter (reducing fire risk). These processes produce secondary dynamics in necromass. The weight of leaf litter arises from a balance between rates of deposition and decomposition (Olson, 1963). Decomposition increases in moister environments, and deposition decreases with higher LMA of species. Self-thinning initially increases suspended fine necromass or litter by adding the necromass from collapsed shrubs, but once lower shrubs have largely thinned and the rates of necromass addition fall, decomposition exceeds deposition and suspended litter quantities decrease.

1.2 | The historical conundrum

The persistence of fire-sensitive species over geological time is difficult to explain if the build-up of fuels in unburnt forest serves to increase the likelihood of widespread, high-severity fire. Although both charcoal stratigraphy and dendrochronology indicate a significantly smaller impact of fire in eucalypt forests prior to the invasion by European colonists (Banks, 1982; Burrows, 1987; Mooney et al., 2011), this has been interpreted by some to indicate *more* rather than less frequent fire in that time, and that the reduction in fire frequency after invasion allowed for greater fuel accumulation (e.g. Bowman, 2003; Burrows et al., 1995; Mariani et al., 2022). Although this offers an apparent solution by proposing a mechanism for less severe fires, the vast majority of fire-threatened species in Australia are impacted by fire *frequency* rather than severity (DAWE, 2022). This proposed solution therefore increases rather than decreases the ambiguity. In contrast, the existence of ecological controls provides a potential explanation. The persistence of sensitive species without extensive anthropogenic burning can be readily explained if forest flammability is self-regulated through internal ecological controls, if these regulate both fire frequency and severity. If this is the case, then the much lower quantity of charcoal and fire scars prior to invasion can be interpreted as it appears: an indication that fire was less frequent in this period.

1.3 | Ecological cooperation

The capacity for forests to regulate their flammability introduces new possibilities for living with fire, collectively called *ecological cooperation* (Zylstra et al., 2022). It has been established that bushfires are significantly less frequent in long-unburnt forests of south-western Australia than in the regrowth that follows fire. However, the mechanisms for this have not yet been quantified. If, for example, fires are prevented due to a moister microclimate, then those areas may be used as fire breaks if there is knowledge of the conditions that prevent or allow fire spread. If, on the other hand, burn patches are smaller because the less flammable forest produces smaller flames that are less able to cross barriers such as rivers or roads, then other opportunities are possible. Knowledge of the size and variability of flames under certain conditions will in these cases facilitate more aggressive and effective fire-fighting techniques such as direct or parallel attack, reducing the need for less effective tactics such as backburning. Such knowledge will also facilitate the adoption of new technologies in rapid fire detection and suppression (Lindenmayer, Zylstra, et al., 2022) by better justifying their adoption, and by quantifying effectiveness thresholds for different forest ages. Ecological cooperation therefore describes an approach whereby human actions reinforce ecological controls, rather than disrupting them. Maturing forests provide more opportunities for fire containment, and more effective containment increases the area of mature forest.

1.4 | Overview of the study

Our aim is to provide a framework to quantify the ways in which ecological controls influence mean flame height and fire impacts in a study forest, thereby facilitating ecological cooperation. Given the multiple covariates involved in such complex systems, we have adopted a mechanistic modelling approach that separately quantifies each effect, enabling us to artificially control individual components so that their effects are clearly visible. We examine fire impacts using scorch height, and extend our analysis to look at implications for ecological cooperation by examining crown fire incidence and the capacity for aggressive fire control as the forest ages.

The expected effect of each proposed ecological control is listed in Table 1. Based on mechanistic analysis in south-eastern Australian forests (Zylstra et al., 2016), we expect that the dominant controls will be those affecting donor flammability, and that of these, litter weight will have minimal effect. We expect that, as the suspended litter layer is composed primarily of collapsed shrubs (McCaw et al., 2002), trends in suspended litter will follow those of the understorey. That is, suspended litter will increase as the understorey increases in density and begins to self-thin, and later decrease as understorey cover declines, inputs to the suspended litter layer are reduced, and the remaining suspended litter decays. We also expect from mechanistic analysis of a fire sensitive community (Zylstra, 2013a, 2013b) that growth factors will have a pronounced effect in forests where the canopy stratum is regrowing from seed or basal sprouts, and a smaller effect in other circumstances. We refer to the trend where fire promotes a period of increased flammability before this eventually declines as 'positive feedback', and a trend in which flammability does not decline in mature forests as 'negative feedback'.

Based on the fact that the largest mass of fine biomass and necromass in the south-western forests is held in the surface litter layer (Burrows, 1994; McCaw et al., 2002), we also test the null hypothesis:

> H0: If flammability is controlled by the mass of fine biomass and necromass (fuel load) rather than by ecological controls, and if surface fuels are prevented from declining in mass, then the flammability feedback will be negative.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study is based in Red Tingle *Eucalyptus jacksonii* forest, in part of the Pibulmun traditional country of south-western Australia (Figure 1). Red Tingle is a very tall (to 70 m), large-girthed tree (Figure 2a) locally endemic to high-rainfall, hilly coastal terrain over an area of about 6000 ha (Wardell-Johnson & Coates, 1996). Where it occurs, it is the dominant overstorey species, with a tall resprouting midstorey and an understorey of fire-stimulated shrubs over a ground-storey of sword-sedge *Lepidosperma effusum* (Appendix S1). Tingle forests are a subset of the south-western forests and share dominant understorey species with the adjacent karri *E. diversicolor* forests already studied (McCaw et al., 2002).

We chose Red Tingle Forest as a subset of the south-western forests because their limited extent and consequent high conservation values suggest some urgency to understand drivers and controls of fire in the community. Tingle trees are also sensitive to frequent fire of any intensity due to a weakness at the stem-root interface which leads to the formation of hollow butts and eventual mechanical failure of the tree (Figure 2b; Wardell-Johnson, 2000). This, combined with the high concentration of fire-sensitive isolated endemics and Gondwanan remnants (Wardell-Johnson & Coates, 1996) renders them as an important case study in the context of flammability dynamics and fire effects.

2.2 | Field survey of ecological controls

To quantify trends in ecological controls with time-since-fire, we conducted a space-for-time analysis of 43 sites spanning an 82-year range of years since fire, between January 2019 and January 2021 (licence no. FB62000176). Sites were randomly located between 50 and 100 m from access roads, primarily in the Walpole–Nornalup National Park, in vegetation mapped as including *E. jacksonii* (Mattiske & Havel, 1998) (34°58′S, 116°46′E, elevations 30–210 m a.s.l.). To obtain a distribution of age-classes that was focused where the most change was expected, we distributed sites across three classes of time-since-fire based on phases of understorey density that were expected from earlier work with similar species (McCaw et al., 2002) (Figure 2c–e). To ensure representation of full variability, sites were further evenly divided between two classes of sun exposure (see Appendix S2 for further methodology), although this was not used as an experimental factor. The time-since-fire classes follow the nomenclature of (Zylstra, 2018) referring to divisions defined by flammability. 'Young' forest (Figure 2c) is the low-flammability period that immediately follows fire. 'Regrowth' (Figure 2d) is a possible stage defined by elevated flammability and hypothesised to result from the dense regrowth of plants in the lower strata (Zylstra, 2018). Young and regrowth classes are further classified as 'post-disturbance' forest, as both are triggered by disturbance. The 'mature' stage (Figure 2e) does not refer to biological maturity, but to the final stage where flammability reaches a quasi-equilibrium.

We surveyed each site using 10 vertical transects at 5 m intervals along a horizontal transect randomly located perpendicular to access roads. At each point, we identified every species intercepted vertically, measuring five crown dimensions for each (crown base and top height, width, and the height of lower and upper edges of the crown describing a hexagonal shape). We also measured the traits in Table 2 representative for each species (see Appendix S2, Figure S1). We did not measure weights of litter, as previous validation of FRaME has shown surface litter to be a low sensitivity parameter (Zylstra et al., 2016), and further collection, drying and weighing required resource commitments beyond our capacity. Instead we utilised

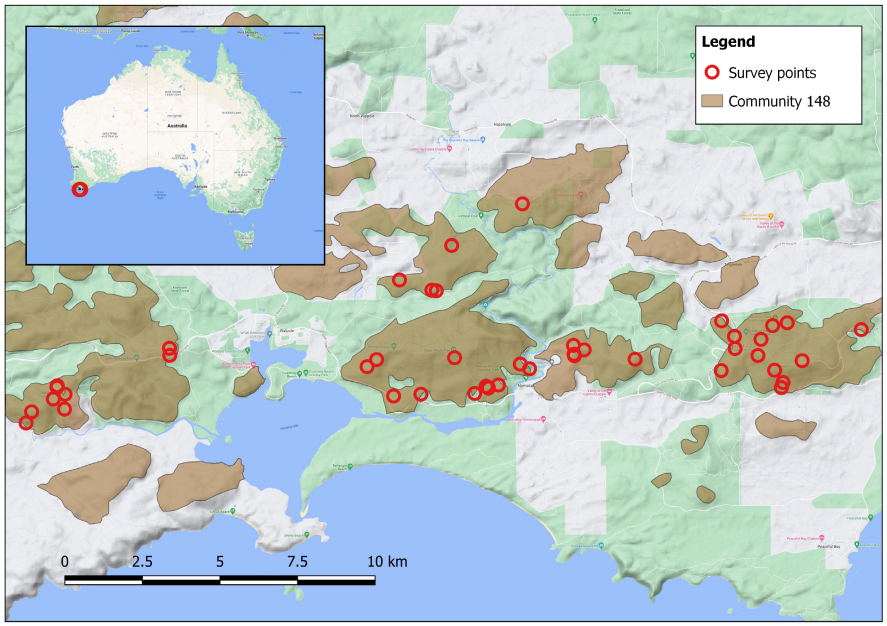


FIGURE 1 Study site locations in forest mapped for Red Tingle (Mattiske & Havel, 1998), located in National Parks near Nornalup in south-western Australia (inset). Background: Google road map.

published weights and dynamics of surface and suspended litter in similar forests (McCaw et al., 2002; Neumann et al., 2021) to provide model inputs. Combined, this allowed us to quantify the six ecological controls in Table 1.

Further methodological detail is provided in Appendix S2, and sources under Acknowledgements and data.

2.3 | Changes IN vegetation with age

To quantify temporal changes in vegetation that may act as ecological controls, we used non-linear least-squares in the R statistical environment (R Core Team, 2016) to fit statistical models to changes in cover and crown dimensions for component species. To capture the best empirical relationship, we tested the various model structures detailed in Script 1 (available online). We then compared models that had a significant fit ($p < 0.01$), as well as linear trends in allometric relationships for other crown dimensions, selecting the model with the highest R^2 value. Where no models could be fitted, we used the mean value of the relevant parameter.

2.4 | Fire behaviour and effects modelling

We modelled the effect of growth and succession on fire behaviour using the Fire Research and Modelling Environment FRaME 0.5.2 (Zylstra, 2011, 2021; Zylstra et al., 2016). FRaME provides a mechanistic framework that links models of leaf flammability and heat transfer, so that trends in fire behaviour are determined by trends in plant species and dimensions along with the fine necromass produced by them. Although some models account for forest structural parameters such as plant spacing and individual crown dimensions (e.g. Linn et al., 2002; Mell et al., 2007, 2009), FRaME is to our knowledge the most complete framework to mechanistically incorporate such structural traits and scale from species-level variation in multiple leaf traits to fire behaviour in stands. Full details of the model are in the cited references, but a short overview follows.

FRaME models fire spread through plants in one-second increments along horizontal and vertical axes. An initial pilot flame is modelled for surface litter using an empirical model developed for litter of adjacent forests (Burrows, 1999). Given the wind strength at that point in the forest profile and the effects of air entrainment resulting from slope, the angle of the convective plume is calculated and projected as a vector with temperature decaying along its length. Ignition of plant foliage occurs when the plume intersects foliage and heats it to a point at which ignition occurs, based on traits of the leaves (Table 2). At each time-step, flames from any newly ignited leaves are added and extinguished leaves removed, then the flame length is calculated from the combustibility traits of burning foliage, the quantity of foliage, and its spatial arrangement. This vector is altered each second to represent these changes as fire progresses. Litter suspended in the ground-storey is modelled using the same process. By calculating fire behaviour in this way, FRaME is able to incorporate all effects of plant growth and succession, and predictions of flammability dynamics are not predetermined by assumed trends.

In modelling plant flammability, FRaME currently considers crown dimensions, leaf dimensions and thickness, moisture, and some influences of aromatic compounds and silica-free ash along with aspects of crown architecture such as foliage clumping and density within the clump. Ongoing research continues to highlight other drivers of flammability, some of which are yet to be incorporated into the model (e.g. Archibald et al., 2019; Cui et al., 2020; Grootemaat et al., 2015; Murray et al., 2013; Pausas et al., 2016; Romero et al., 2019; Scarff et al., 2012; Schwilk, 2003; Wyse et al., 2018; Zhao et al., 2016).

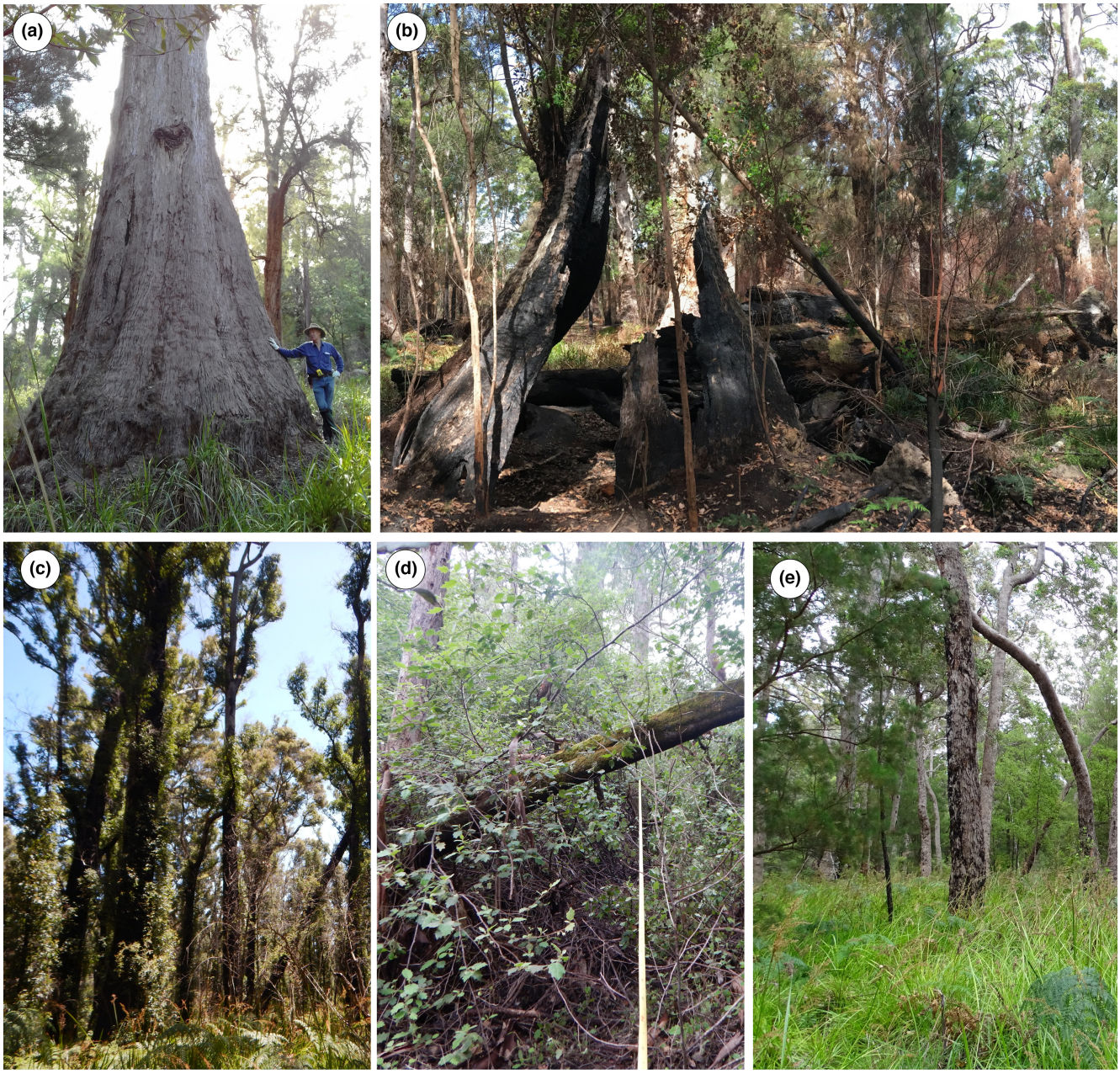


FIGURE 2 A mature *Eucalyptus jacksonii* tree with N. McQuoid for scale (a). Hollow butting and eventual structural failure of a tingle due to frequent fire (b). Recently burnt, or young forest (c) showing epicormic regrowth from the prescribed burn at Site 1. Regrowth forest (d) with typical cover of fire-germinated species such as *Chorilaena quercifolia* in this 39-year-time-since-fire stand. Young and regrowth forest collectively constitute post-disturbance forest. Mature forest (e) after self-thinning and self-pruning has produced a more open understorey and taller midstorey. Photos M. Howe, P. Zylstra, G. Wardell-Johnson.

We assessed first-order fire effects on vegetation by modelling crown scorch using methods detailed in Zylstra (2021), where scorch occurs between the maximum height of foliage consumption and an isotherm found using the flame dimensions and angle. To assess the implications for current fire suppression efforts in the context of ecological cooperation, we modelled the likelihood of crown fire using FRaME, and assessed the likelihood that flames would be too large for aggressive suppression measures (i.e. directly extinguishing flames) using an industry threshold of 3 m flame heights for delineation (Australasian Fire Authorities Council, 1996).

2.5 | Model accuracy

We assessed the accuracy of FRaME for modelling fire behaviour in Red Tingle Forest by validating predictions against a wildfire recorded in the study area, comparing the accuracy of predictions against those made with the peer-reviewed model that currently underpins management of these forests ('Project Vesta'; Cheney et al., 2012; Howard et al., 2020). Our validation wildfire burned forest that had last been burned 64-years earlier, causing crown scorch across much of the area, and flame heights in the range of 10 m (McCaw & Middleton, 2015).

TABLE 2 Variability and changes in model inputs for each control. 'Control' defines the range of values of plant traits, and describes trends for the other ecological controls. Further details in Appendix S1.

Ecological control	Variables	Control	Treatment
Plant traits		*Uses empirically measured values*	*Replaces recorded values with mean values for all species*
	Proportion dead[a]	0–0.5	0.038
	Leaf form[a]	Flat/round	Flat
	Leaf thickness[a]	0.12–0.54 mm	0.26 mm
	Leaf width[b]	0.48–45.00 mm	17 mm
	Leaf length[b]	3.00–150.00 mm	29 mm
	Leaf separation	0.20–116.70 mm	22.35 mm
	Stem order	1–5	3.54
	Endotherm[c]	220–347°C	246°C
	Proportion moisture[c]	1–2.44	1.12
	Gap: clump ratio[a]	0–10	2.42
	Clump: canopy ratio[a]	0.02–1	0.34
Self—thinning	Species % cover[a] Litter Suspended litter	Allows for increases and decreases if apparent in vegetation trends	Overrides decreases in cover and litter models
Growth	Plant height[a]	Allows for changes in height if apparent in vegetation trends	Maintains plant heights at their mean value
Self—pruning	Plant base height[a]	Allows for changes in base height if apparent in vegetation trends	Maintains plant base heights at their lowest values
Litter	Surface leaf litter up to 6 mm diameter[e]	Allows for increases and decreases if apparent in vegetation trends	Overrides decreases regardless of models
Suspended litter	Suspended leaf/twig litter, up to 25 mm diameter[d]	Allows for increases and decreases if apparent in vegetation trends	Overrides decreases regardless of models

[a]Measured from field samples.
[b]Taken from (Wheeler et al., 2002).
[c]Estimated using techniques in Zylstra (2011) and Zylstra et al. (2016).
[d]Modelled using data from McCaw et al. (2002) as detailed in Appendix S4.
[e]Modelled using data from (Neumann et al., 2021), as detailed in Appendix S4.

Temperatures were 10°C above the March 3 pm mean for the first day before falling 1–2°C below average, and wind speeds were 10–18 km h^{-1} above average for 3 of the 4 days. Along with four sets of weather conditions recorded for this fire (McCaw & Middleton, 2015), we used our modelled forest aged to 64 years to find parameters for both fire behaviour models, using 10 pseudo-transects (see Zylstra, 2021) for each set of conditions to capture variability. After modelling flame heights on flat ground, we compared the mean error from each (predicted flame height minus the 10 m reported value) using a *t*-test.

2.6 | Modelling the effect of ecological controls

To model flammability dynamics, we estimated a 100-year chrono-sequence of forest growth from our models of growth and cover. Assuming flat ground, we modelled fire behaviour for five replicates of each of the four days of fire weather used in our validation and for each year of growth, producing 2000 predictions. We then used these to compare modelled flame heights in post-disturbance forests to those in mature forest by first generalising the trend in flame height using a 3rd degree polynomial spline, then defining age classes as per (Zylstra, 2018) between the point(s) where the spline crossed its mean value. Finally, we compared the mean height of the raw modelled flames in post-disturbance forest (either young or young and regrowth if such a class existed), to the mean flame height in mature forest. The ratio of post-disturbance to mature forest flame heights constitutes the feedback strength FS (Zylstra, 2018).

Feedback strength is explained further in Zylstra (2018), but is a metric that describes the direction and intensity of fire-flammability feedbacks. If long-unburnt (mature) forests support larger flames than post-disturbance forests, then the ratio of flame height in post-disturbance forests to that in mature forest (FS) will be less than 1, indicating negative fire-flammability feedback. If mature forests support smaller flames than post-disturbance forests, however, then FS will be greater than unity, indicating positive feedback in which fire promotes greater flammability. We tested the difference in mean flame heights between periods using a *t*-test.

If the flame height in mature forests was significantly lower than in post-disturbance forest ($FS > 1$, $p < -0.01$), we further divided the mature period into early and 'mid-mature' stages to determine any

TABLE 3 Effect sizes for ecological controls of flammability in Red-Tingle forests. Compared to measured forest dynamics (all controls), each successive row shows the change in feedbacks with the removal of a single control. Significance values (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) refer to the significance of the feedback strength with that control removed, so that reduced feedback strength and significance indicates the importance of the control. Glass's Delta values give the effect size for that treatment compared to all controls for flame heights in post-disturbance and mature forests, respectively. Controls are ranked by total effect size, which is the mature effect size minus the post-disturbance effect size.

Control	Disturbed period (years)	Post-disturbance FH (m)	Mature FH (m)	Feedback strength	Glass' Δ post-disturbance	Glass' Δ mature	Total effect size
Self-thinning	99	4.7	3.9	$1.2^{N.S.}$	−0.07	1.39	1.46
Suspended litter	78	5.5	5.4	$1.0^{N.S.}$	0.05	0.8	0.75
Self-pruning	63	5.7	3.6	1.6^{***}	0.13	0.29	0.16
Leaf-trait changes	62	4.6	2.1	2.2^{***}	−0.1	−0.12	−0.02
Growth	61	5.0	2.4	2.1^{***}	−0.01	−0.02	−0.01
Litter	60	4.7	2.2	2.1^{***}	−0.08	−0.08	0
All controls	52	5.1	2.5	2.0^{***}			

trend that remained, where mid-mature refers to the *x* oldest years modelled, and *x* is equal in length to the young period.

Against this reference, we quantified the influence of six ecological controls (Tables 1 and 2) on flammability dynamics by removing each separately. With that control removed, we measured the mean flame height in post-disturbance and mature forest relative to reference behaviour, found the feedback strength and its statistical significance, and measured the effect size for flame heights in post-disturbance and mature forest relative to the control.

We individually removed each mechanism as described in Table 2. As declines in necromass production relate to reductions in plant death, the removal of self-thinning as a mechanism simultaneously removed any declines in litter models. Based on the magnitude of differences in feedback timing and strength caused by the removal of each control, we ranked the processes to determine which were most influential.

3 | RESULTS

Flammability dynamics exhibited positive feedback (feedback strength = 2.0, Table 3). The tallest stratum of plants did not grow from zero height at time zero; therefore, H1 (Table 1) could not be tested. Dynamics were instead controlled primarily by succession (self-thinning understoreys) and their secondary influence through suspended litter (Table 3), supporting both H2 and H3. Growth dynamics reinforced positive feedback to a lesser extent via self-pruning, but the lest influential drivers were plant growth and surface litter dynamics (Table 3), so that H0 was rejected.

3.1 | Changes IN vegetation with age

We surveyed a total of 43 sites covering an 82-year span of years since fire, with no suitable replicates available for the remainder due to errors in the spatial data (incorrect vegetation, fire history etc). All data are available from the Zenodo repository: https://doi.org/10.5281/zenodo.6374483 (Zylstra et al., 2023). Canopy heights for the dominant two species *E. diversicolor* and *E. jacksonii* increased only slightly, (Figure 3a, Appendix S4), although complete canopy scorch was evident at one prescribed burn site. Suppressed *E. diversicolor* trees along with *E. guilfoylei* trees increased in height with age, but these and the remaining canopy species were only minor components (Appendix S4). Most sub-canopy species showed clear self-thinning trends—initially increasing then declining as forests aged (Figure 3a, Appendix S4, Figures S4–S6). This was most pronounced in understorey species such as *Acacia pentadenia* and *E. guilfoylei* saplings. Some taller species (e.g. *Trymalium odoratissimum*) were persistent or increased in cover (e.g. *Agonis flexuosa*), so that sub-canopy foliage shifted from lower understorey plants to taller midstorey plants (Figure 3a). Older forests were increasingly dominated by Red Tingle with a ground cover of sword-sedge and increasing but still minor proportions of low shrubs such as *Crowea angustifolia*, *Boronia gracilis*, *Hovea elliptica* and *Leucopogon verticillatus* under a midstorey of tall *Agonis flexuosa* and *Allocasuarina decussata* (Appendix S4, Figures S4–S6).

Both surface and suspended litter weights declined in older forests (Appendix S4, Figure S7) consistent with declining inputs of fine material as plant strata thinned. As a result, the suspended litter data in (McCaw et al., 2002) were better explained using a quadratic function than with the negative exponential function used by those authors ($R^2 = 0.71$, c.f. $R^2 = 0.59$).

3.2 | FRaME Validation

Flame height predictions using FRaME were significantly closer to the 10 m estimate than predictions using Cheney et al. (2012; FRaME = $\bar{x}$ 8.7 m, c.f. Cheney et al. = $\bar{x}$ 67.6 m, $p < 0.001$), supporting the use of FRaME as the more suitable model for the analysis. Predictions made using Cheney et al. (2012) were highly sensitive to differences in plant dimensions, varying widely between iterations.

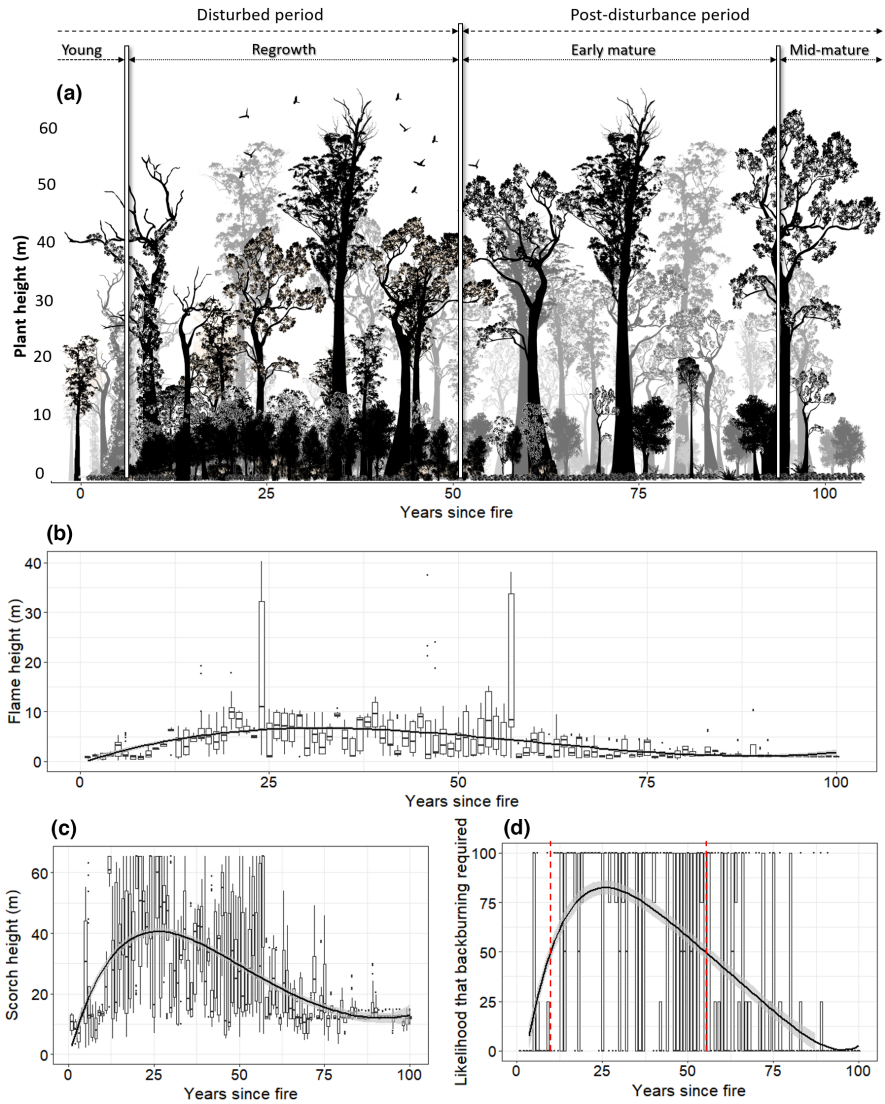


FIGURE 3 (a) Measured vegetation dynamics for Red Tingle Forests, based on species-specific trends detailed in Appendix S4, Figures S4–S6 and Tables S4–S6. Note that tree height is largely unchanged, as no surveyed sites followed recent stand-replacement events. The timeline is divided into the broad flammability periods. (b) Flame heights modelled across the age sequence, showing 20 model replicates per age. (c) Scorch height modelled for the same data, with the upper estimates trimmed to the height of the tallest trees. (d) Likelihood that flame heights will be too large for direct or parallel attack strategies (aggressive containment), and instead limit containment options to backburning. Vertical broken lines mark the 50% likelihood points. Boxplots show standard interquartile ranges, and fitted splines show indicative trends with standard error shading.

3.3 | Modelling the effect of ecological controls

All six ecological controls followed the patterns expected from fundamental principles, with the effect of reducing flame heights after an initial period of increased flammability following fire (Figure 3b, Table 3). The effects of burning the forest on flame height in subsequent fires lasted for 52 years, with flame heights averaging 5.1 m during this post-disturbance period (young $\bar{x} = 1.4$ m for 7 years, regrowth $\bar{x} = 5.7$ m) and falling to a mean of 2.5 m in mature forest ($\bar{x} = 2.8$ for early-mature, $\bar{x} = 1.0$ m for mid-mature, $p < 0.001$ for FS = 2.0).

All controls served to shorten the period of high flammability. The primary control on both feedback strength (flammability of disturbed forest/flammability of undisturbed forest) and timing was the self-thinning of the understorey (Table 3; Figure 4) supported by the decay of these collapsed shrubs. The third most influential factor was the self-pruning of shaded branches. We did not detect an effect of plant growth, leaf-trait changes or declining surface fuel loads on feedback strength, although all factors served to shorten the period of high flammability.

3.4 | Ecological effects of FIRE

Trends in scorch height closely followed flame height trends as expected from the causal relationship and the lack of change in tree height across our data (Figure 3c). Canopy scorch was common across the regrowth period but uncommon in young forest and rare in mature stands.

3.5 | Metrics for ecological cooperation

Crown fires were rare across all ages due to the height of trees above lower plant strata, with the only incidents occurring in regrowth or very early mature forest (Figure 3b). Aggressive suppression tactics (direct flame extinguishment) was briefly possible in very recently burnt forests, but flames were most often too tall for aggressive suppression in regrowth forest. Opportunities for aggressive attack began to increase again from about 25 years after fire, until they were again most likely after 55 to 60 years (Figure 3d).

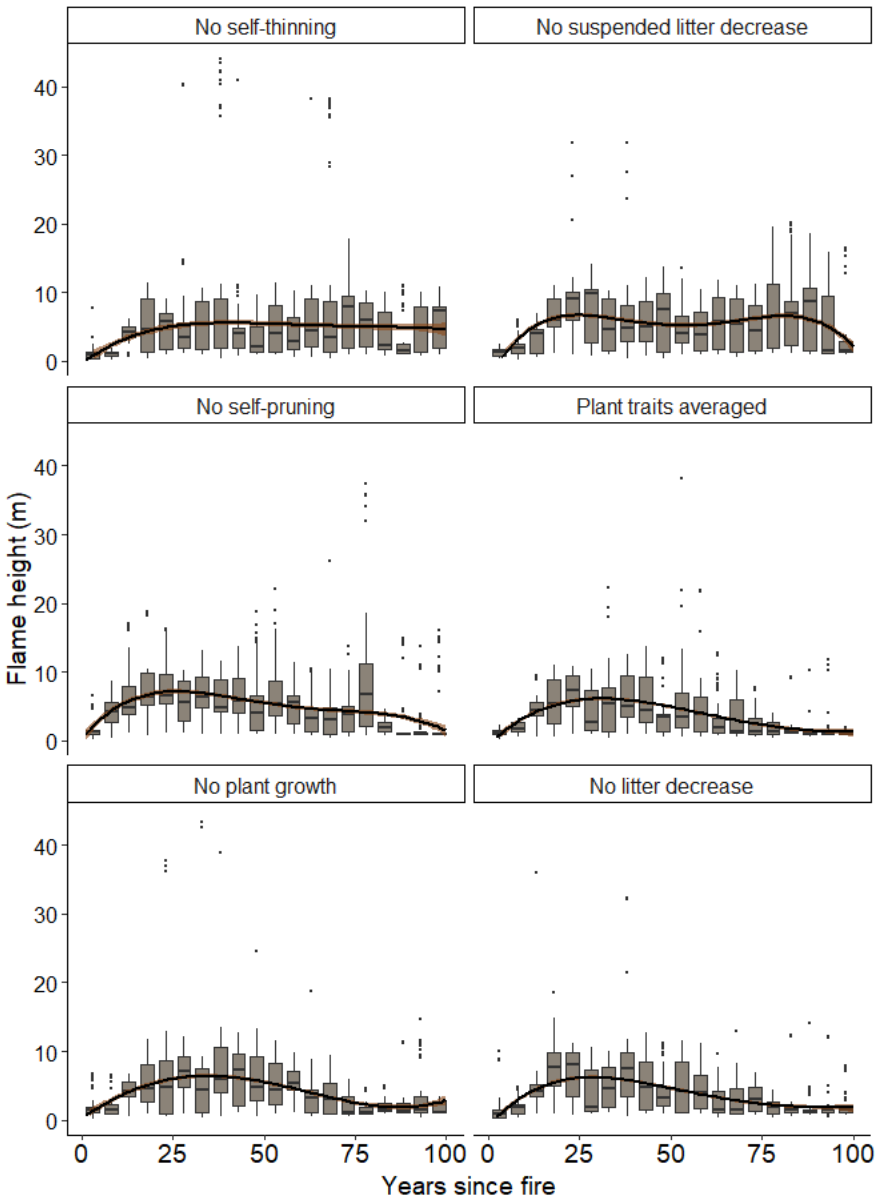


FIGURE 4 Ecological controls on fire behaviour. Each panel shows modelled flame heights across the range of ages, with one control turned off. These are ordered from the most to least influential, as per Table 3.

4 | DISCUSSION

The positive vegetation-flammability feedbacks which had been measured for the south-western Australian forests (Zylstra et al., 2022) were predictable from trends in plant growth and succession in our study area. This demonstrates a clear causal role for ecological controls in limiting the impact of wildfire in south-western Australian forests. Disturbance by fire briefly decreased flammability by clearing biomass and necromass, but then increased the likelihood of more severe fire by stimulating regrowth close to the ground. Flame heights later decreased when these lower plants self-thinned to produce less-flammable strata (less fuel), taller plants self-pruned their lower branches and became less likely to ignite (more overstorey shelter), and the taller, denser leafy biomass facilitated a moister and less-windy microclimate. Our findings are consistent with the experimental findings of Cruz et al. (2022), who reported that understorey height and cover were the most important predictors of wildfire risk in their experiments in south-western Australian Jarrah forests. Our study differed from that study in that we showed this effect mechanistically, whereas that study inferred the effect statistically.

As flame heights declined in mature stands rather than reaching their maximum, we rejected H0 (no effect of ecological controls). The largest effect size was measured from self-thinning understoreys and the consequent decline in suspended litter. This was consistent with our expectations given that the trees in our study forest were large throughout the full period of analysis, therefore H1 was supported.

4.1 | Biophysical drivers of variability in positive feedbacks

The understorey in our study area was dominated by species that are readily germinated by low-intensity fires (Wardell-Johnson et al., 2004). As this fire-induced stimulation of understorey growth

is evident in the understorey dynamics measured for dominant forests across the south-west (Burrows, 1994; McCaw et al., 2002), we expect from our results, that these vegetation dynamics are important controls of flammability in the area. Our study found pronounced thinning in mid-height fire-stimulated species such as *Acacia pentadenia* but a slower rate in the taller midstorey *Trymalium odoratissimum* and a potential increase in the cover of the tallest midstorey species *Agonis flexuosa*. This resulted in self-thinning of the understorey and an increase in the midstorey (Figure 3a), consistent with existing generalisations regarding eucalypt forest dynamics (Specht & Morgan, 1981). Canopy growth rates in our plots were negligible as no sites included early stand establishment.

Positive fire-flammability feedbacks can be stronger (e.g. greater increase in flame height) following high, compared to low severity fire (Barker & Price, 2018; Collins et al., 2021), if the previous severity has not prevented the restoration of vegetation (e.g. Lydersen et al., 2014). Depending on the life-history traits of the vegetation, high severity fire may result in the short or long-term removal of overstorey shelter, so that succession and growth are more pronounced and the regrowth period more flammable than it would have been following a less-severe fire. Although no systematic data were available on the severity of fires that had affected our study area, more than 80% of previous fires in the bioregion had been prescribed burns rather than wildfire (Boer et al., 2009). Where our sites occurred in blocks that had recently been prescribed burnt, one site was high severity with complete crown scorch (site 1, Figure 2c), and the other had an intact canopy. Above-ground fire severity may have little impact on below-ground heating and seed germination (Bradstock & Auld, 1995; Stoof et al., 2013), which can be predicted mechanistically from surface flame duration as well as soil texture, moisture and other properties (Zylstra, 2021). When 'stand-replacing' fire occurs, canopy restoration must occur from the ground upward as either seedling or basal sprouting. In this case, the regrowth is most dense, as both understorey and regrowing canopy plants temporarily share the same space (e.g. Gordon et al., 2017). Thus, we expect that unless it delays the restoration of vegetation, higher severity fire will likely result in more flammable regrowth periods and stronger positive feedbacks. In our conceptual framework, this occurs because growth-related ecological controls are added to the existing succession-related controls.

4.2 | Reconciling with history

Our findings for the Red Tingle Forest offer a coherent explanation for the historical conundrum. The Tingle Mosaic (Wardell-Johnson & Williams, 1996) provides habitat for highly fire-sensitive relictual fauna including the Quokka *Setonix brachyurus*, and the Gondwanan monotypic Sunset Frog *Spicospina flammocaeulea* (Wardell-Johnson et al., 2018; Wardell-Johnson & Coates, 1996). Red Tingle itself is geographically restricted to granitic hilltops in high rainfall locations. It is genetically diverse within a very limited area, and readily killed by repeated fires, even of low severity (Wardell-Johnson & Coates, 1996). The basal bark of these trees provides habitat for the Tingle Pygmy Trapdoor Spider *Bertmanius tingle*, which is vulnerable to the lowest severity fires and extremely slow to recolonise (Main, 1987, 1991). Species such as Quokkas which are sensitive to both fire frequency and severity (Bain et al., 2015, 2016) become rare in regrowth forest where the understorey is dense (Bain et al., 2015), and where the likelihood and severity of fire are highest (Zylstra et al., 2022 and this study). As mentioned earlier, the persistence of such species over geological time is difficult to explain if the build-up of fuels in unburnt forest serves to increase the likelihood of widespread, high-severity fire. However, their persistence becomes probable if forest flammability is regulated by the ecological controls that we have demonstrated. This occurs due to the positive fire-flammability feedbacks enforced by these controls.

Positive feedbacks such as the fire-flammability feedbacks in the Red Tingle and surrounding forests of the south-west skew patch-age distributions away from normality and toward either young or old forests. If ignitions are uncommon, the patch-age distribution will be skewed toward older age classes, creating a landscape of low-flammability old-growth forest interspersed with small patches of younger forest. This occurs because ignitions will burn only small areas of the low-flammability forest. As ignition frequency increases, however, a tipping point may be reached if the collective burned areas convert a sufficiently large proportion of the landscape into a flammable state (Tiribelli, Morales, et al., 2018). In this case, the patch-age distribution will shift toward the left of the peak in flammability. This occurs because the broad landscape is now in a flammable state, so each ignition burns a larger area than in the mature forest. As a result, only a very small proportion will remain in the low-flammability mature state, because the surrounding flammable forest constantly introduces new ignitions to those areas. This pattern has been referred to as a 'landscape trap' (Lindenmayer et al., 2011).

For our study area, charcoal and dendrochronological evidence suggests that fire was uncommon prior to European invasion. Charcoal traces were rare in south-western Australian forests (Hassell & Dodson, 2003), and almost no fire scars prior to invasion were recorded in the tall-open forests dominated by *E. diversicolor* that merge with our study area (Rayner, 1992). The earlier mentioned argument that this lack of evidence for fire indicates fire of such frequency that the lack of fuels and subsequent low intensity of fire left no record in the landscape (Bowman, 2003; Burrows et al., 1995; Gammage, 2011; Mariani et al., 2022) is problematic for four reasons. Firstly, in this argument, the absence of evidence is interpreted as evidence itself. Secondly, in our study area, Red Tingle trees, Tingle Pygmy Trapdoor spiders and Quokkas are threatened by high fire frequency, so their persistence throughout such a time period of extreme fire frequency is highly improbable—regardless of its intensity. Thirdly, as we have shown here, fire severity in regrowth forest is higher, not lower than in mature forest, so more frequent fire would result in more evidence of fire both through increased frequency and through increased severity. Finally, fire intensity as inferred from surface fuel loads (Byram, 1959) in these arguments, bears no relationship to fire severity. This is because the calculation relates to horizontal rates of spread and ignores vertical spread through the fuel ladder. Consequently, purportedly low

intensity fires can still burn with high severity, and cause mass mortality of species that are sensitive to high severity fire (Zylstra, 2023).

We have found that ecological controls drive positive fire-flammability feedback. Therefore, we argue, that all lines of evidence can be reconciled if forests were skewed toward mature age classes prior to invasion. Firstly; understoreys are more open in long-unburnt forest as frequently observed by early Europeans in the south-western Australian forests (Hallam, 2014). Secondly; the likelihood and severity of wildfire is lower so that evidence of fire in the landscape is low, and thirdly; the persistence of fire-sensitive species is made possible. This is consistent with traditional knowledge held by the current indigenous owners of these forests, who argue that they deliberately left the broad area of the tall forests unburnt (Pers. Comms Dr. Wayne Webb, Pibulmun elder, 24 September 2021; Pedro, 2017).

In this historical context, it is worth noting that aridification of the Australian landmass during the Neogene led to the loss of mesic species from the south-western forests (Byrne et al., 2011). Such high LMA, more shade-tolerant species typically begin to dominate angiosperm forests in later successional stages (Falster et al., 2017; Lusk et al., 2010), resulting in larger leaf-trait changes than those that currently occur in the south-west. These potentially add biomass into overstorey shelter and increase shade at ground level to reduce the quantity of vegetation acting as fuel. It is likely then that positive feedbacks were even stronger prior to the Neogene due to the addition of leaf trait changes as a significant ecological control. Whereas the addition of growth intensifies feedback strength by increasing post-disturbance flammability as discussed earlier, the addition of leaf-trait changes increases feedback strength by reducing the flammability of mature forest.

4.3 | Ecological cooperation

The First Nations' tradition of not burning large areas of tall forest forms part of what has been referred to as the Indigenous Renaissance discourse of land management (Wardell-Johnson et al., 2018). It typifies the approach of ecological cooperation (Zylstra et al., 2022), in which humans do not attempt to dominate or 'subdue' other species, but instead work in cooperation with the ways that other species affect the landscape. In their approach, the entire landscape was managed, but rather than utilising broadscale burning, targeted and confined locations were burned for specific reasons unrelated to the Western concept of fuel reduction (Lullfitz et al., 2020). This left the broader mosaic of vegetation to grow, self-thin and develop into accessible forests with open understoreys, with a consequent reduced likelihood and impact of fire. As stated by a contemporary proponent of indigenous fire use: 'Aboriginal fire knowledge is based on Country that needs fire, and also Country that doesn't need fire. Even Country we don't burn is an important part of fire management knowledge and must be within the expertise of a fire practitioner' (Steffensen, 2020). Such decisions not to disrupt the existing ecological controls on fire constitute the 'reconciliation' aspect of ecological cooperation (Zylstra et al., 2022).

Our study demonstrates the scientific validity of such deep time traditions, and demonstrates that they offer critical insights to the contemporary challenges of fire risk mitigation. In addition to this, FRaME modelling such as that conducted here also provides critical guidance for the 'reinforcement' aspect of ecological cooperation (Zylstra et al., 2022), in which interventions including rapid fire detection and specialist firefighting skills and technology (Independent Bushfire Group, 2020; Lindenmayer, Zylstra, et al., 2022) are deployed to reinforce the natural trends in flammability. Such actions take advantage of the reduced severity of fires and likelihood of crown fires in mature forest to enable more aggressive forms of attack and minimise backburning as a containment strategy, and aim to protect flammable regrowth from fire until it has the chance to mature. Such measures are needed to curb the increase in extraordinary landscape fires (United Nations Environment Programme, 2022).

5 | CONCLUSIONS

We found that burning Red Tingle Forest produces dense understorey regrowth, consistent with other forested communities in south-western Australia such as Jarrah (Burrows, 1994) and Karri (McCaw et al., 2002). Self-thinning of these understorey species coupled with self-pruning of lower, shaded branches in taller plants act as ecological controls on fire, so that post-disturbance forests are predicted to burn with flames twice the height of mature forests where such controls have taken effect, with expected flame heights continuing to decline as forests age further. This understanding provides a mechanistic explanation for the observed decline in frequency of forest fires burning mature forests in south-western Australia.

Our findings provide an explanation for the historical persistence of fire-sensitive species in fire-prone forests that reconciles all available lines of evidence on the subject. By imposing positive feedback between fire and flammability, ecological controls would have skewed the age-class distribution of forests toward maturity, so that fire frequency and severity were both lower than they are currently. This finding also demonstrates the scientific validity of the First Nations' tradition of not burning tall forests in the south-west. Contrary to the post-invasion view in which management necessitated domination and modification of the landscape, First Nations utilised an ecologically cooperative approach that permitted natural processes to maintain the broad area of forests in a state of minimal fire risk and maximum accessibility.

In the context of a warming climate, our work provides guidance for ecological cooperation in a modern context. By considering the influence of ecological controls on fire behaviour and its impacts, complex modelling tools such as FRaME can be used to guide the implementation of specialist firefighting skills and emerging technologies, allowing mitigation efforts to capitalise on and reinforce the natural advantages provided by the vegetation.

Although this study was focused on a specific forest community, it has demonstrated the mechanistic influence of two ecological controls so far: self-thinning understoreys and self-pruning branches. Where such dynamics occur in other forests, there is now mechanistic

reason for expecting them to also act as ecological controls. This adds significant weight to the argument that forest biomass (and by extension, carbon storage) are not hazards that must be reduced, but can in fact reduce fire hazard. Our findings advance the knowledge needed for a cooperative approach that will minimise fire risk, maintain biodiversity, and maximise carbon storage.

AUTHOR CONTRIBUTIONS

All authors contributed directly to the wording of the manuscript throughout each version; Philip Zylstra and Melissa Howe conceived the design; Philip Zylstra analysed the data and performed the modelling; Grant Wardell-Johnson provided ecological expertise and guidance for the study area; Daniel Falster provided expertise on the broad ecological trends and context; Melissa Howe and Nathan McQuoid performed the field data collection and coordinated the volunteer input; and Simon Neville performed the spatial analysis and planning.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

We sourced departmental fire records from https://catalogue.data.wa.gov.au/dataset/dbca-fire-history, and mapped tingle forest was taken from https://catalogue.data.wa.gov.au/dataset/vegetation-complexes-swf-50k. All field survey data, derived datasets and code used in analysis are available at https://doi.org/10.5281/zenodo.6374483. FRaME is regularly updated, and the latest version can be installed in RStudio using: devtools::install_github('pzylstra/frame_r').

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Species data.

Appendix S2: Survey methodology.

Appendix S3: Details and code for FRaME modelling.

Appendix S4: Additional results.

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