BIOLOGICAL REVIEWS

Cambridge Philosophical Society

Biol. Rev. (2023), pp. 000–000.
doi: 10.1111/brv.13041

Identifying and managing disturbance-stimulated flammability in woody ecosystems

David Lindenmayer[1,*] and Phil Zylstra[2]

[1] *Fenner School of Environment and Society, Building 141, Linnaeus Way, The Australian National University, Canberra, Australian Capital Territory 2601, Australia*
[2] *School of Molecular and Life Sciences, Curtin University, Kent Street, Bentley, Western Australia 6102, Australia*

ABSTRACT

Many forest types globally have been subject to an increase in the frequency of, and area burnt by, high-severity wildfire. Here we explore the role that previous disturbance has played in increasing the extent and severity of subsequent forest fires. We summarise evidence documenting and explaining the mechanisms underpinning a pulse of flammability that may follow disturbances such as fire, logging, clearing or windthrow (a process we term disturbance-stimulated flammability). Disturbance sometimes initiates a short initial period of low flammability, but then drives an extended period of increased flammability as vegetation regrows. Our analysis initially focuses on well-documented cases in Australia, but we also discuss where these pattens may apply elsewhere, including in the Northern Hemisphere. We outline the mechanisms by which disturbance drives flammability through disrupting the ecological controls that limit it in undisturbed forests. We then develop and test a conceptual model to aid prediction of woody vegetation communities where such patterns of disturbance-stimulated flammability may occur. We discuss the interaction of ecological controls with climate change, which is driving larger and more severe fires. We also explore the current state of knowledge around the point where disturbed, fire-prone stands are sufficiently widespread in landscapes that they may promote spatial contagion of high-severity wildfire that overwhelms any reduction in fire spread offered by less-flammable stands.

We discuss how land managers might deal with the major challenges that changes in landscape cover and altered fire regimes may have created. This is especially pertinent in landscapes now dominated by extensive areas of young forest regenerating after logging, regrowing following broadscale fire including prescribed burning, or regenerating following agricultural land abandonment.

Where disturbance is found to stimulate flammability, then key management actions should consider the long-term benefits of: (*i*) limiting disturbance-based management like logging or burning that creates young forests and triggers understorey development; (*ii*) protecting young forests from disturbances and assisting them to transition to an older, less-flammable state; and (*iii*) reinforcing the fire-inhibitory properties of older, less-flammable stands through methods for rapid fire detection and suppression.

Key words: young disturbed forest, logging, prescribed burning, post-disturbance regrowth, ecological controls, spatial contagion, forest landscape management.

CONTENTS

---

[*] Author for correspondence (Tel.: +026 125 7800; E-mail: david.lindenmayer@anu.edu.au).

I. INTRODUCTION

There is an extensive literature on the extent to which forests and other natural vegetation around the world have been subject to significant human disturbance and degradation [*sensu* Watson *et al.*, 2018; Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services (IPBES), 2019]. This includes the extent to which these ecosystems have been subject to wildfires, with the burnt area of forest increasing substantially in recent years (Cattau *et al.*, 2020; Anderegg *et al.*, 2022), offset by decreases in savanna area burnt (but see Andela *et al.*, 2017). This has included an increase in the amount of high-severity wildfire in many forest ecosystems (McWethy *et al.*, 2018; Singleton *et al.*, 2019; Lindenmayer & Taylor, 2020; Collins *et al.*, 2021*a*; Lefoe *et al.*, 2021), with substantial impacts on biodiversity and ecosystem services (Ward *et al.*, 2020; Jones *et al.*, 2021).

Here we explore the role that disturbance can play in increasing the severity and spatial contagion of wildfire (here termed 'flammability' – as defined in Section I.1; *sensu* Gill & Zylstra, 2005). Our goal is not to argue for a universal pattern of disturbance-stimulated flammability, but rather to examine the potential mechanisms that may influence it, providing a framework to help identify places where it may occur. To this end, we begin by reviewing work that is consistent with the pattern of 'disturbance-stimulated flammability' in Australia, which has been described as a 'fire continent' (Pyne 2020). Australian forests are widely believed to require frequent burning to prevent uncontrollable wildfires (Gould, McCaw & Cheney, 2011; Stephens *et al.*, 2014) and are cited as exemplars of the need for (and efficacy of) disturbance-based management (e.g. Pyne, 1990; Sneeuwjagt, Kline & Stephens, 2013). The occurrence of disturbance-stimulated flammability may therefore appear unlikely in such a setting, but sound evidence suggests the likelihood that it is not uncommon. Following this initial analysis, we briefly examine evidence for disturbance-stimulated flammability in some other forest types globally. To support this assessment, we conducted a series of structured literature searches of the peer-reviewed scientific literature (see online Supporting Information, Appendix S1) and found numerous articles on flammability, fire risk, high-severity wildfire, and wildfire risk mitigation (e.g. prescribed burning), but none that directly addressed the concept of disturbance-stimulated flammability.

A core component of our approach is a discussion of the ecological controls that some vegetation communities may place on fire. Understanding such controls allows us to identify where disturbance may stimulate flammability by disrupting them. Given this, we develop a new conceptual model to predict disturbance-stimulated flammability better based on the prevalence of ecological controls in a community. Areas adjacent to places that burn at high severity also may be at risk of high-severity fire (e.g. Zald & Dunn, 2017; Lindenmayer, Taylor & Blanchard, 2021; Levine *et al.*, 2022). We therefore examine the potential for disturbance to promote spatial contagion in high-severity fire across forest landscapes. We conclude with commentary on some key consequences of disturbance-stimulated flammability for forest management. These relate to: (*i*) intensively managed or so-called 'regulated' wood-production landscapes (*sensu* Oliver & Larson, 1996; Davis *et al.*, 2001); (*ii*) intensively managed exotic tree plantations (McWethy *et al.*, 2018; Bowman *et al.*, 2021; Lindenmayer, Yebra & Cary, 2023*b*); (*iii*) abandoned 'old fields' dominated by extensive areas of young forest regenerating after previous disturbances (Egler, 1954; Chazdon *et al.*, 2020); and (*iv*) disturbance-based fire-management approaches such as prescribed burning (Safford *et al.*, 2012; McCaw, 2013; Hunter & Robles, 2020).

(1) Definition of fire severity and flammability

Fire severity is broadly defined as the loss of organic matter from fire, most often measured from above-ground foliage (Keeley, 2009). Fire severity is a continuum across a gradient of impact on above-ground (as well as below-ground) organic matter. As fire severity is a measure of the impact of the fire, it reflects aspects of both fire behaviour and the vulnerability of biota to the fire. High-severity wildfire in forests, for example, corresponds to fires that result in a crown burn and/or crown scorch. Crown scorch can occur up to seven times the height of flames (Gould, Knight & Sullivan, 1997), so a scorched canopy does not necessarily reflect extreme fire behaviour. Conversely, a crown burn is the most severe form of fire, and can result in extensive spatial contagion in fire.

We refer to aspects of fire behaviour like fire severity and fire spread collectively using the term 'flammability'. Flammability (the ability of something to burn) may be applied at multiple scales ranging from individual fuel particles to broad landscape effects (Gill & Zylstra, 2005). Here we use the term 'flammability' in a landscape sense, referring to the propensity for forest to burn in horizontal dimensions (fire spread or likelihood at a point), and/or the vertical dimension (an aspect of fire severity, *sensu* Zylstra, 2018). Flammability therefore refers to both fire likelihood or the ability of forests to burn at a point, and aspects of fire severity such as crown fire likelihood, which is the ability for a greater proportion of the forest profile to burn at that point.

(2) Stand age–flammability relationships

Disturbed stands (those in the early stages of secondary succession) are more likely to burn (and often do so) at high severity after a brief period of low flammability (e.g. Woinarski, Risler & Kean, 2004; Trauernicht *et al.*, 2012; Taylor, McCarthy & Lindenmayer, 2014; Zylstra, 2018; Wilson, Bradstock & Bedward, 2022; Zylstra, Bradshaw & Lindenmayer, 2022). Several studies in a diverse range of Australian eucalypt forests have independently found that the most flammable stage of forest development is young- to intermediate-aged stands. This period can be temporarily delayed when disturbance initially creates bare ground (e.g. after wildfire or following post-logging burns employed to consume debris left after timber harvesting). On this basis, peak flammability often occurs in forests between 10 and 70 years after disturbance by logging or burning (e.g. Taylor *et al.*, 2014; Zylstra, 2018; McColl-Gausden & Penman, 2019; Taylor, Blanchard & Lindenmayer, 2021; Barker, Price & Jenkins, 2022; Wilson *et al.*, 2022; Zylstra *et al.*, 2022). Following this pulse in flammability, older forests may enter a long-term period of greatly reduced flammability, with some studies showing the probability of high-severity fire continuing to decline over the following centuries (Lindenmayer *et al.*, 2022*c*; see Fig. 1).

Although the creation of bare ground by fire can temporarily delay the pulse in flammability (A in Fig. 1), disturbances that reduce leaf area can create a more flammable microclimate immediately. In a study of coastal forests in New South Wales, Wilson *et al.* (2022, p. 1) showed that: '…fuel was available to burn 1.4 times more often in recently logged sites (zero years since logging) compared to sites that had not been logged for 71 years'. They further concluded that: '…changes in vegetation associated with logging and to a lesser extent wildfire, increase the risk of fire'. Some disturbances (e.g. logging operations without follow-up burns, windthrow events) may create this more flammable microclimate without leaving bare ground, so that no initial delay in enhanced flammability is present (e.g. Donato *et al.*, 2006; Keenan, Weston & Volkova, 2021).

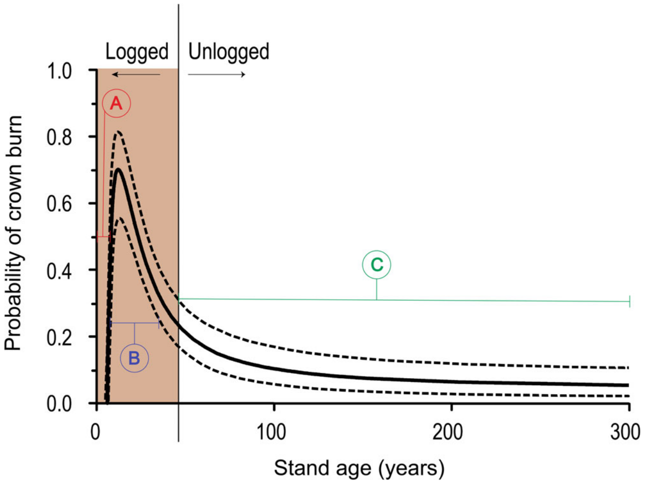

Fig. 1. Non-linear relationship between stand age, logging history, and the probability of crown burn (which peaks within ~40 years before declining as stands approach 80–100 years old) based on analyses of data from south-eastern Australia. Note values for the probability of canopy fire in 200+-year-old stands is approximately half that of 100-year-old stands. The relationship is based on a re-analysis of data in Taylor *et al.* (2014) focused on logged and unlogged sites. The mean response is shown by the central solid line with 95% credible intervals as dashed lines. A = a brief initial period of reduced flammability immediately following prior disturbance by logging. B = a period of flammable regrowth. C = a long-term period of reduced flammability in older forests. Note that regrowth stands regenerating following wildfires also can be at risk of subsequent high-severity wildfire (see Barker *et al.*, 2022; Wilson *et al.*, 2022).

Regardless of the type of post-fire seeding response, previously logged forests burned at significantly higher severity than intact forest under the same weather conditions during the 2019–2020 wildfires in eastern Australia (Lindenmayer *et al.*, 2022*e*) (Fig. 2). The response following previous burning was more complex, showing increased canopy damage for most previously burnt areas except in Victoria, where previously burnt areas experienced less canopy damage in 2019–2020 (Bowman *et al.*, 2021). More detailed analyses of these same fire effects by Lindenmayer *et al.* (2021) showed that crown burn (corresponding to extreme fire behaviour) was indeed more common in intermediate stages of regrowth in nearly all circumstances, whereas the crown-scorch relationship examined by Bowman *et al.* (2021) sometimes increased in older forests.

Mapped records suggest pronounced disturbance-stimulated flammability relationships due to prescribed burning and previous wildfire in ecosystems ranging from sub-alpine forest and woodland to low, dry woodland dominated by eucalypts and white cypress pine (*Callitris glaucophylla*) in south-eastern Australia (Zylstra, 2018). A similar trend was measured in south-western Western Australian forests disturbed primarily by prescribed fire, including those dominated by dry jarrah (*Eucalyptus marginata*), tuart (*Eucalyptus gomphocephala*), and karri (*Eucalyptus diversicolor*) (Zylstra *et al.*, 2022). Across all forests in the Greater Blue Mountains World Heritage Area in the Australian State of New South Wales, the probability of

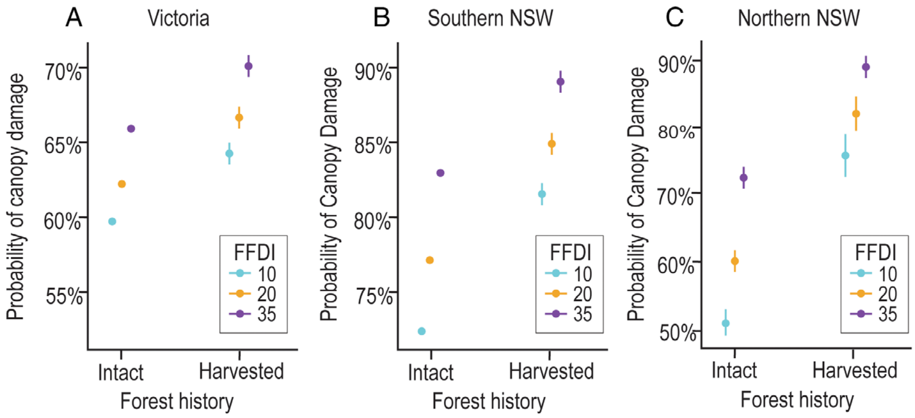

Fig. 2. Relationships between logging and the probability of canopy damage in the 2019–2020 wildfires in eastern Australia. FFDI is the Australian Forest Fire Danger Index. Figure modified from Lindenmayer *et al*. (2022*e*) which was a re-analysis of data in Bowman *et al*. (2021).

canopy scorch or crown burn remained high until ~20 years post fire, but then declined to near zero by 30 years (Barker & Price, 2018). The latter study also showed that the likelihood of canopy-damaging fires was related to the severity of the previous fire, so that one fire in disturbed forests set in motion an accelerating likelihood of future severe fires. Crown burn was most likely in dry sclerophyll forests of south-eastern Australia if they had been burned in the previous 5–15 years (Storey, Price & Tasker, 2016).

Whereas the forests and woodlands discussed above exhibited an initial brief reduction in flammability that preceded a more flammable regrowth period caused by the disturbance, this pattern was not detectable on an annual scale in an analysis of fire trends in Kakadu National Park in the Australian tropics. Flammability decreased linearly from the first year, reaching a near-zero likelihood of wildfire in all communities by 15 years (Gill *et al*., 2000). This was further demonstrated experimentally for Australian tropical savanna woodland in the Arnhem Land region where disturbed, fire-killed, stands of cypress pine (*Callitris intratropica*) became ~10 times more likely to burn (Trauernicht *et al*., 2012). Both crown fire and house loss were most likely in the 2009 Victorian fires if the area within 1 km of houses had been burnt within the previous 5 years (Price & Bradstock, 2013).

(3) Disturbance-stimulated flammability in ecosystems outside Australia

Outside of Australia, increased flammability stimulated by disturbances (including fire, logging, and land clearing) has long been recognised in a broad range of forests. Canadian forest managers spatially separate logged areas in the landscape to minimise the increased fire hazard and fire spread posed by both logging slash and increased understorey growth caused by opening of the canopy (Ministry of Forests British Columbia, 1985).

In the Klamath Mountains of north-western USA dominated by tall, slow-growing conifers such as Douglas fir (*Pseudotsuga menziesii*), Odion, Moritz & DellaSala (2010) identified a pronounced disturbance-stimulated flammability response. Forests recovering from fire in the previous 10–32 years were three times more likely to experience full canopy scorch or crown burn than forests that had not experienced fire for at least 75 years (Odion *et al*., 2010). In the same region, Thompson, Spies & Ganio (2007) showed that forests burnt 15 years previously, or which had previously been salvage logged and regenerated, subsequently burnt more severely than undisturbed areas. Protected stands of mixed conifer forest in the western USA burnt at lower severity than logged forests (Bradley, Hanson & DellaSala, 2016). The odds of high-severity fire in young even-aged and intensively managed industrial Californian forests were significantly greater than on public land where forestry practices were less intensive (Levine *et al*., 2022). Levine *et al*. (2022) hypothesised that the short rotation ages which characterised the industrial forests they studied may have contributed to the greater incidence of high-severity fire in such areas. Similar results have been recorded in industrial wood-production forests in Oregon (Zald & Dunn, 2017). Pine-hardwood forests in south-eastern USA exhibit pronounced disturbance-stimulated flammability trends, where fire-stimulated pine-dominated vegetation creates a flammable savanna that succeeds into a mesic, low-flammability forest dominated by deciduous broadleaf species (Brewer & Rogers, 2006; Nowacki & Abrams, 2008).

Studies in several parts of the world such as Brazil, Chile, and Spain have revealed that fast-growing, densely stocked, tree plantations can support large-scale, high-severity wildfires (Gómez-González, Ojeda & Fernandes, 2018; McWethy *et al*., 2018, de Castro Galizia & Rodriguez, 2019). For example, in the decade between 1996 and 2005, 3–4% of Portugal's eucalypt and pine plantations burnt annually (Rego, Louro & Constantino, 2013). Very large areas of plantations have burnt in other places such as Chile (McWethy *et al*., 2018). Plantations in Australia are also susceptible to being burnt in high-severity wildfires (Ndalila, Williamson & Bowman, 2018; Bowman *et al*., 2021; Lindenmayer *et al*., 2023*b*). Notably, the fast turnaround required for intensive wood production means that tree plantations are managed largely as regrowth stands rather than being permitted to grow through to become mature stands with reduced flammability (Lindenmayer *et al.*, 2023*b*).

Forest re-establishment on abandoned agricultural land or 'old field regeneration' is considered a major fire issue in parts of Europe (Pausas & Fernández-Muñoz, 2011) where flammable regrowth forests develop. Maritime pine (*Pinus pinaster*) and aleppo pine (*Pinus halapensis*) are primary colonisers in many areas (Santana *et al.*, 2010), eventually succeeding to broad-leaved species in the Mediterranean region, particularly evergreen oak (*Quercus* spp.) (Zavala, Espelta & Retana, 2000; Santana *et al.*, 2010). Experimental fires in these forests have found that late-successional forests burned at lower severity than early-successional pine forests, even when pine stands had been managed for fuel reduction (Fernandes, Luz & Loureiro, 2010).

(4) The need for studies spanning long periods to detect disturbance-stimulated flammability

The studies outlined above provide examples of communities where disturbance-stimulated flammability has been measured. However, they do not establish that disturbance will always stimulate flammability. Identifying communities where disturbance-stimulated flammability does not occur is an important step in understanding the phenomenon, but this requires properly designed studies. However, trends can be obscured by empirical studies that do not incorporate a sufficient time period to capture any decline in flammability. In an explicit example, data presented by Attiwill *et al.* (2014) showed that, under the worst fire weather conditions recorded so far for Australia, crown-fire incidence in mountain ash (*Eucalyptus regnans*) forest increased in forests aged up to 30 years after logging or burning. Consistent with other studies for these forests (Taylor *et al.*, 2014, 2021), the likelihood of crown fire then declined in older forests, so that stands that had been undisturbed for at least 70 years were half as likely to burn with a crown fire. However, Attiwill *et al.* (2014) reported only the increase in the first 30 years, and concluded that 'timber harvesting does not increase fire risk and severity' (p. 341). This demonstrates how a short period of analysis can obscure the influence of disturbance in stimulating flammability by failing to distinguish adequately between long-undisturbed forest and a younger, more flammable post-disturbance period. Such relatively short time periods of investigation are common in studies of fire-mitigation treatments like prescribed burning (Zylstra *et al.*, 2022), possibly arising from the perception that the influence of the treatment lasts for only a short period of time. If flammability later declines, however, then the influence of the treatment lasts for this full period and the 'untreated' flammable period can be more accurately considered the dominant effect of the treatment. Disturbance-stimulated flammability may therefore be detected only in studies that analyse a sufficient range of stand ages.

II. DETERMINANTS OF FLAMMABILITY

Determining whether disturbance-stimulated flammability applies in ecosystems beyond those for which we have presented examples requires an understanding of the mechanisms underpinning flammability. Flammability is often treated as proportional to the quantity of 'fuel' present – a term that varies in definition, but is often used interchangeably with biomass (e.g. Grzesik *et al.*, 2022). As a result, it is commonly concluded that fire risk reduction necessitates the use of some form of disturbance to reduce fuel or biomass (e.g. Byram, 1959; Agee & Skinner, 2005; Stephens *et al.*, 2021). This assertion is underpinned by the Byram (1959) equation that relates fire intensity to the product of fuel quantity, fuel energy content, and rate of fire spread. Most often, 'fuel' in this equation refers to the weight of forest litter (Alexander, 1982), but this is not specified. Although sound as a conceptual model, the application of this equation to fire behaviour and effects such as crown scorch is problematic. One of the central issues identified by Zylstra (2023) was that characterising the rate at which fuels are consumed using the rate of fire spread ignores the vertical dimension of fire spread. In the study by Zylstra (2023), 'torching' fire behaviour with little to no fire spread rate produced very large and highly damaging flames, but because of the low rate of spread, the equation by Byram (1959) described these flames as having very low intensity. By envisioning fuels as a single value, Byram's equation renders the three-dimensional structure of vegetation irrelevant, and assumes that the entire structure is simply represented by weight as the single number termed 'fuel load'. This is problematic, as – mechanistically speaking – fuel is any material that combusts and contributes heat. The foliage held in the canopy of a forest is less by weight than the weight of leaf litter on the ground. If the influence of fuel is proportional to its weight, then the transition from a surface litter fire to a crown fire should be a small change, when it is actually the largest threshold of change that occurs in forest fire behaviour (Cruz *et al.*, 2022). A fire can therefore burn with extreme severity (i.e. a crown fire), but have very low 'intensity' if it is slow moving.

In practice, much of the literature promoting the reduction of fuels does not draw on such a theoretical basis, but instead points to examples. As discussed above, such examples often focus on the short-term efficacy of treatments such as burning or thinning, excluding their long-term effects. For instance, all studies in a review of fuel-reduction effectiveness in the conifer forests of western USA (Safford *et al.*, 2012) had been treated within the previous 9 years, and all case studies reviewed by Hunter & Robles (2020) had been treated within the previous 10 years. These studies demonstrate that clearing vegetation to create bare or near-bare earth can limit fire, or temporarily reduce its severity. This is consistent with the long-term analyses we have documented, but it does not follow that the weight of fuel or biomass is what drives flammability. If this were the case, then flammability would not decline later in long-undisturbed communities as shown in the many studies we have documented (e.g. see Fig. 1). This trend of decreasing flammability at high biomass levels is evident in broad patterns such as where large fires across south-eastern Australia are less common in forests that have the greatest levels of biomass compared to those with intermediate quantities of biomass (Clarke *et al.*, 2020). In summary, all studies show that the creation of bare ground can temporarily reduce flammability, but fuel load or biomass quantity do not explain (either theoretically or empirically) the long-term stand-age-related reductions in the risk of high-severity fire.

A partial explanation for the reduction in flammability with a long period since previous disturbance is that biomass influences evapotranspiration by creating shaded, cooler and more moist microclimates. Warmer, drier and more variable microclimatic conditions characterise young, disturbed forests relative to older stands (Norris, Hobson & Ibisch, 2012; Kovács, Tinya & Ódor, 2017; Jucker *et al.*, 2018; Lindenmayer *et al.*, 2022*b*; Smith-Tripp *et al.*, 2022; Wilson *et al.*, 2022). This affects the incidence of fires starting, but it does not explain trends within the burn footprints of fires that did start. The examples we have listed show that, despite greater quantities of biomass (and therefore, in theory, greater amounts of fuel), fires in older, high-biomass forests are less severe than those burning regrowth forests with apparently less fuel. Ecological control theory (Zylstra *et al.*, 2022, 2023) resolves this dilemma, positing that biomass can act as fuel (feeding the fire) if it is located where it is likely to be ignited, but it can also act as 'overstorey shelter' (calming the fire) if it is located beyond the reach of flames where it slows wind speeds acting on the fire (Zylstra *et al.*, 2016). Plant communities exert ecological controls on fire when, through the processes of growth and succession over time, they transfer biomass from acting as fuel to acting as overstorey shelter. In a mature forest where heavy biomass held in taller growth has excluded shorter plants, the only fuel available to a fire may be the layer of leaf litter on the forest floor. The living biomass in this instance acts as overstorey shelter that slows the fire (Zylstra *et al.*, 2022, 2023).

(1) Disturbance-stimulated flammability and ecological controls

Disturbance-stimulated flammability may arise when disturbance disrupts ecological controls, so that the process of converting biomass from fuel to overstorey shelter is re-instigated. This produces a short period of low flammability when biomass is initially cleared or reduced, but the following regrowth period involves the return of biomass at the ground level (e.g. seeds and basal sprouts) where it acts as fuel until the processes of growth and succession return it to its role as overstorey shelter.

Ecological controls transfer biomass from fuel to overstorey shelter by creating gaps in the vertical structure of the vegetation profile that flames cannot cross. This can occur purely through the structural change of increasing gap sizes, or by altering the flammability of the vegetation itself so that either flames below are smaller or vegetation above is harder to ignite (Zylstra *et al.*, 2016).

Four primary ecological controls have been identified to date (Zylstra *et al.*, 2023) (Fig. 3). These are shown as a conceptual model in Fig. 4, and we describe them below.

(1) Reduced flames from lower fuels through *understorey thinning*. Cruz *et al.* (2022) found that, for their empirical data set, severe fire behaviour was driven primarily by the height and density of the forest understorey. This finding was consistent with the results of mechanistic modelling (Zylstra *et al.*, 2016). Understoreys may self-thin for a variety of reasons ranging from intra-specific competition (Westoby, 1984) to the death of shorter-lived, post-disturbance ephemeral species, and forms of inter-specific competition such as root competition by larger plants (e.g. Lamont, 1985). Collapsed shrubs contribute to a lower 'near-surface' layer, which has minimal influence on fire behaviour (Schwilk, 2003; Cruz *et al.*, 2022).

(2) Reduced flames in lower fuels and/or reduced ignitibility of upper fuels through plant *trait changes*. This occurs if later successional plant species have less-flammable traits than post-disturbance colonisers, such as may occur when more shade-tolerant, higher leaf mass per area (LMA) species replace earlier successional species with lower LMA (Lusk *et al.*, 2010; Falster *et al.*, 2017). A classic case of this is the mesophication of forests, whereby lower plant strata dominated by shade-tolerant plants create cooler, wetter conditions (Nowacki & Abrams, 2008). In other instances, early successional species may contain more fine dead material in the canopy than later successional species (e.g. Baeza *et al.*, 2011). Such patterns of succession may be limited by site attributes, such as the inability of low-phosphorus soils in Australia to support mesic species (Beadle, 1966), or when historical changes have removed more mesic species from an area (e.g. the loss of deciduous oaks from parts of Spain through land clearing ~6000 years BP; Pons & Reille, 1988). Plant-trait changes with succession also may affect the flammability of the litter layer, as this is based on the traits of leaves that compose leaf-litter beds (de Magalhães & Schwilk, 2012; Grootemaat *et al.*, 2017; Burton *et al.*, 2020).

(3) Increased gap sizes through *self-pruning* of taller plants. Schwilk (2003) showed through manipulative experiments that the removal of the lower dead branches of flammable chamise (*Adenostema fasciculatum*) in the Californian chaparral could prevent its ignition, converting it from fuel into overstorey shelter. Self-pruning occurs in some species when lower, shaded branches are not retained (Hellström *et al.*, 2018).

(4) Increased gap sizes through *plant growth*. Plant growth can increase flammability by creating taller layers of vegetation that are available as fuel, but it may also lead to some plants growing beyond the reach of flames and thereby becoming overstorey shelter. While highly prone to crown fire at 10–32 years post-disturbance (Odion *et al.*, 2010), Douglas fir forests, for example, have a canopy base height averaging 1.4–7.4 m above ground. This increases to over 17 m if

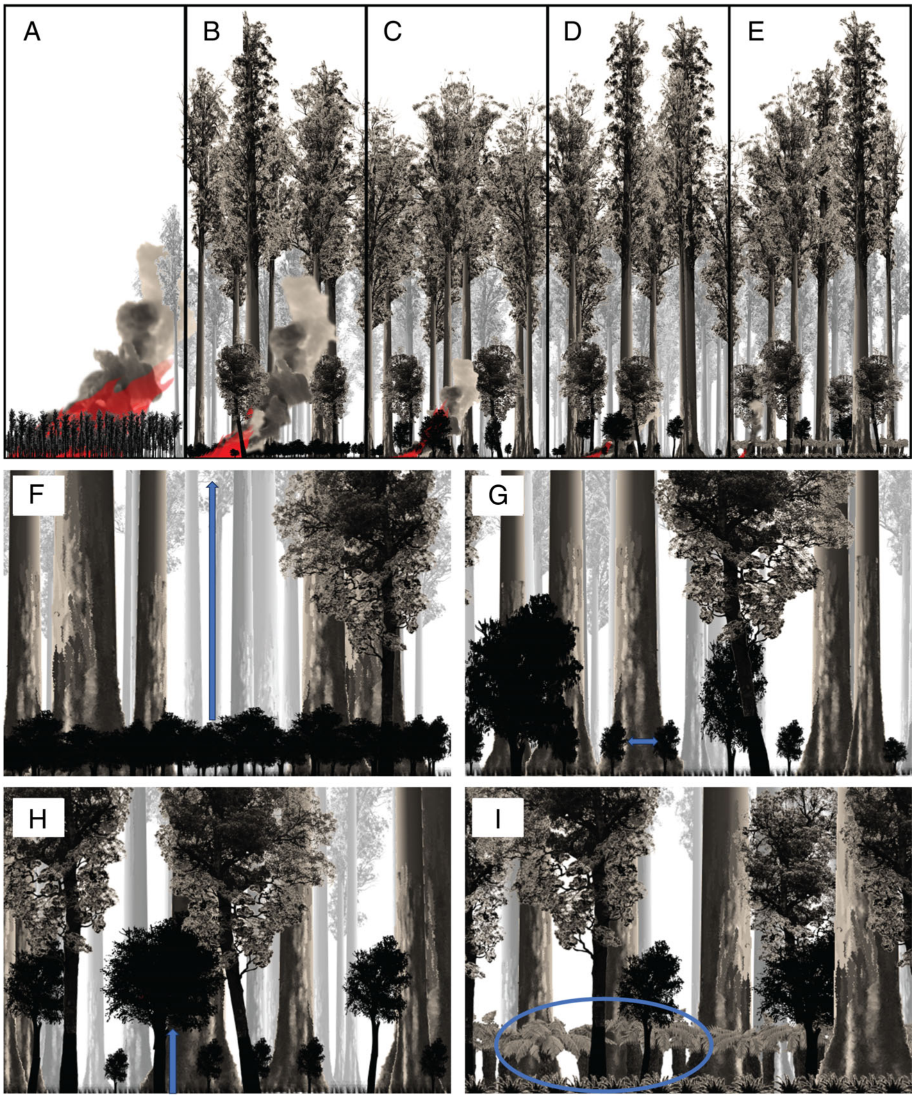

Fig. 3. Ecological controls demonstrated in an Australian mountain ash (*Eucalyptus regnans*) forest. (A) At the peak of disturbance-stimulated flammability such as regrowth from a clearcut logging operation when no ecological controls are in operation, all finely structured biomass is available as fuel and none acts as overstorey shelter. The successive influence as each ecological control is added is shown in B–E, with detail of each control shown in panels F–I. (B, F) If the eucalypt canopy was not disturbed (e.g. low-severity fire) or has regrown, *plant growth* causes tree canopies to act as overstorey shelter rather than fuel, although large flames are still possible if the understorey is dense. (C, G) *Understorey thinning* reduces flame sizes from the main strata acting as fuel, although torching of taller plants is still possible. (D, H) *Self-pruning* of midstorey plants reduces the likelihood of torching. (E, I) Mesophication (*trait changes*) of lower plant strata dominated by shade-tolerant plants that reduce flame sizes from burning vegetation, and the ignitibility of taller plants, minimising fuel and maximising overstorey shelter.

undisturbed for over 71 years (Feller & Pollock, 2006), corresponding to a threefold reduction in crown fire likelihood (Odion *et al.*, 2010).

(2) The need for an adequate chronosequence of stand age classes to document ecological controls

As with empirical detection of disturbance-stimulated flammability, studies of ecological controls must span an adequate chronosequence of stand-age classes to capture variation in a given control. To illustrate, understorey density in jarrah forest was shown to increase for 22 years, then self-thin to its original open state by 50 years (Burrows, 1994). An experimental burning program was established in this community to test the possibility that prescribed burning stimulated flammability by triggering regrowth (Gould *et al.*, 2007) but it confined experimental fires to the 22-year period of increasing understorey density. As a result, it was concluded that disturbance did not stimulate flammability, but was instead needed to reduce it (McCaw *et al.*, 2012). By testing only the increasing trend, the study obscured the

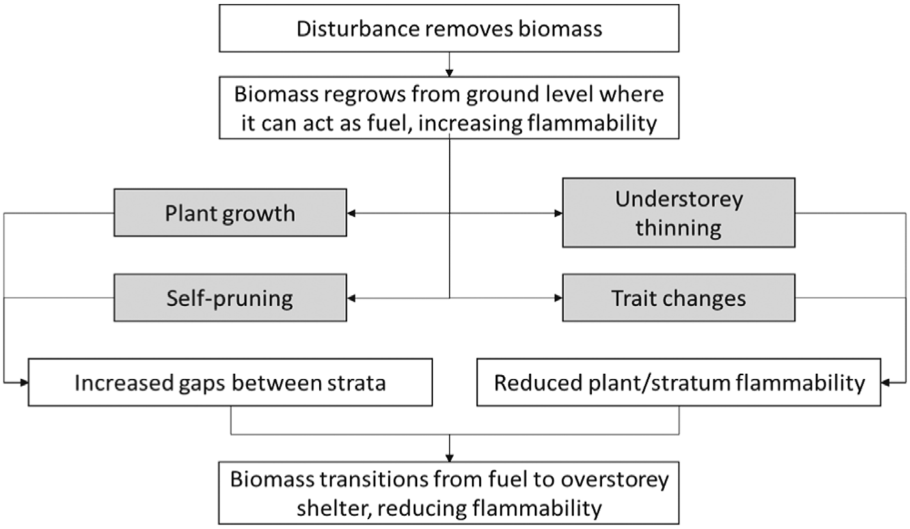

Fig. 4. Conceptual model of ecological controls and disturbance-stimulated flammability. Shaded boxes indicate ecological controls. We propose that: (*i*) disturbance-stimulated flammability is likely if disturbance disrupts one or more ecological controls; and, (*ii*) the stimulated flammability will be more intense when more ecological controls are disrupted.

fact that the increasing trend had been caused by the disturbance (Zylstra *et al.*, 2022).

Time periods required for analysis of temporal changes in flammability may be extensive in low-productivity environments. In the semi-arid *ngarta* (*E. salubris*–*E. salmonophloia*–*E. dundasii*) Great Western Woodlands of Western Australia, Gosper, Prober & Yates (2013) found that fine biomass moved from lower strata (fuel) into taller strata (overstorey shelter) through self-thinning, growth, and potentially self-pruning, but that the transition required an absence of fire for 35–200 years. Tangney *et al.* (2022) found that understorey fuels in some *Banksia* spp. woodlands in Western Australia peaked in density at 14 years after fire and thinned markedly after that. By contrast, *Banksia* spp. woodlands on nearby older, more nutrient-poor, sands showed only limited thinning by the maximum age studied of 56 years. While it may be the case that thinning does not occur in such low-productivity sites, a longer chronosequence may be needed to detect any trends that may occur.

Understoreys self-thin in many vegetation communities in south-eastern Australia; peaking in stand density at 35 years on average before thinning (McColl-Gausden *et al.*, 2020). Dixon *et al.* (2018*b*) showed such patterns of thinning for mountain forests in south-eastern Australia – a finding that independently reached the same conclusions as empirical evidence for the stimulation of flammability by fire in that area (Zylstra, 2018). Elevated height and cover in drier parts of this region are inversely related to tree diameter (Wilson, Cary & Gibbons, 2018) likely reflecting competition from trees. Understorey exclusion occurs *via* tree root competition in dry Western Australian woodlands such as those dominated by wandoo (*Eucalyptus wandoo*) (Lamont, 1985; Burrows *et al.*, 1990), and in seasonally dry tropical environments where grass cover thins as tree cover is restored (Gill *et al.*, 2000; Trauernicht *et al.*, 2012; February, Cook & Richards, 2013).

The well-studied (e.g. Hoffmann *et al.*, 2009; Pausas & Bond, 2020) forest–savanna interaction is mediated in part by the exclusion of grass fuels (Platt *et al.*, 2016). In South Africa, by disrupting understorey exclusion that has been attributed to canopy shading, fire can convert low-flammability evergreen closed forest to flammable fynbos (Power *et al.*, 2021). Understorey growth in Eurasian boreal larch forests is restricted by a shallow active layer (the upper layer of permafrost that thaws in summer) which is insulated by a thick organic layer of moss and leaf litter. Removal of the insulating layer by fire allows for an increase in thickness of the active layer, permitting rapid growth of the understorey until the organic layer is restored and thinning of the understorey takes place (Osawa *et al.*, 2010). Forests dominated by ponderosa pine (*Pinus ponderosa*) in Utah, USA, responded to a cessation of frequent (4–7 years) low-severity burning with dense sapling recruitment in the understorey, whereas adjacent stands of the same forest type at a second site characterised by infrequent (69 years) fire and older trees maintained an open savannah structure with little understorey (Madany & West, 1983). Livestock grazing is also credited with maintaining a disturbance regime in the first site through browsing of palatable saplings (Madany & West, 1983).

Given the broad drivers of understorey growth and subsequent self-thinning (short-lived colonising species, inter- and intraspecific competition), similar patterns may be expected in response to other kinds of disturbances such as logging and land clearing. For example, dense understorey regrowth follows logging in south-eastern Australia (Burton *et al.*, 2020) for the same reasons that it occurs after fire: that is, disturbance removes intraspecific competition. As the trees regrow, competition recovers and the understorey thins. The mechanism for this has been analysed in ponderosa pine forests, where mechanical thinning of trees from 345 to 148 trees/ha increased understorey shrub cover by up to 94%, caused by the removal of interspecific root competition. The same is true for old-field regeneration such as in stands dominated by Scots pine (*Pinus sylvestris*) that colonised abandoned agricultural lands on the French Massif Central (Prévosto *et al*., 2000). These recolonising forests are initially typified by dense understoreys while biomass is recovering, but as the trees establish and provide greater competition, the understoreys self-thin (Fernandes *et al*., 2010).

While understorey thinning reduces the quantity of biomass available to act as fuel, changes in plant traits due to succession also can alter the flammability of the fuels available, and influence forest microclimate. Mesophication accompanies the succession of some forests in south-eastern USA from conifer dominance to mesic broadleaf species that suppress fire spread by creating a cool, dark environment (Nowacki & Abrams, 2008). This process can be reversed only through intensive disturbance (Vander Yacht *et al*., 2019). The need for protracted disturbance has been measured in Greater Yellowstone, USA, where forests subjected to frequent fire have shifted in composition from mesic to xeric understorey components (Kiel, Braziunas & Turner, 2023). Mesophication can maximise the biomass and shading leaf area in a forest, as traits such as greater leaf mass per area confer greater shade tolerance (Falster, Duursma & FitzJohn, 2018) thereby allowing for more strata of plants. Mesophication is pronounced in Australian mountain ash forests, where late-successional species include tall rainforest sub-canopy trees such as myrtle beech (*Nothofagus cunninghami*) (Gilbert, 1959; Lindenmayer *et al*., 2000). Species composition in these forests may be critical to their extremely dense carbon-storage capacity (Keith, Mackey & Lindenmayer, 2009), as traits such as open crowns and smooth bark on the canopy trees maximise corticular photosynthesis and thereby promote water efficiency in mature trees (Burrows & Connor, 2020). Tree fern species such as rough tree fern (*Cyathea australis*) and smooth tree fern (*Dicksonia antarctica*) add to this by harvesting water aerially through stems (Donoghue & Turner, 2022), potentially minimising root competition from large trees. Tree ferns are killed through disturbances such as clearcutting and salvage logging (Ough & Murphy, 2004; Bowd *et al*., 2018), but their presence optimises overstorey shelter, so that not only does a moist microclimate reduce fire incidence, but also helps minimise fire spread.

Reductions in flammability as a result of trait changes are not limited to wet forests. Early successional species in old-field regeneration in eastern Spain typically contain more dead biomass in their crowns than later-stage-successional species (Baeza *et al*., 2011) making them more likely to ignite and behave as fuel. Such features can be amplified further by more intensive disturbance regimes like the increase in foliage density and leaf flammability measured for small-flowered gorse (*Ulex parviflorus*) subject to frequent fire in Valencia, Spain (Pausas *et al*., 2012). Plant trait changes due to post-fire succession in forests of the Sierra Nevada, USA, have been used to explain the observation that forests suffer canopy damage more often when dominated by fire-stimulated longer-leaved conifers than when dominated by later successional shorter-leaved species. Schwilk & Caprio (2011) proposed that this arose because longer leaves produced more aerated litter beds than shorter leaves, and such traits have been offered as explanations for the broader biogeography of fire in western USA (Stevens *et al*., 2020).

Whereas the factors described above affect the density and flammability of plants acting as fuels, plant growth and self-pruning increase gap sizes, converting vegetation strata from fuel to overstorey shelter. Mechanistic modelling demonstrated that such gaps prevented the upward spread of flame in forests of south-eastern and south-western Australia (Zylstra *et al*., 2016, 2023). This was likely a factor when crown-fire burning in ‘catastrophic’ fire danger conditions reduced in severity to a surface fire upon entering old-growth mountain ash (Cruz *et al*., 2012). Trees at this location exceeded 80 m in height (Ashton, 2000).

Forest community structure can be critical in determining plant growth, as competition for light encourages taller growth (Falster & Westoby, 2003). Disturbances such as thinning that reduce competition between trees can result in increases in diameter at breast height at the expense of height growth (Deng *et al*., 2019), and crown length may be greater so that crown base height is lower in more openly spaced stands (Pinkard & Neilsen, 2003). The severity of fire also may be important in the development of gaps between strata, with smaller gaps evident in regrowth following high-severity fire in dry forests in Victoria and New South Wales (Collins *et al*., 2021*b*; Barker *et al*., 2022). Gap sizes are also important in shorter vegetation. Schwilk (2003) found that ignition of the chapparal dominant chamise was significantly more likely because that species did not self-prune lower branches.

The influence of ecological controls must be considered in context with climate change, which is driving larger and more severe fires (Canadell *et al*., 2021; Collins *et al*., 2022). This leads to areas being burnt that might otherwise have been fire refugia (Mackey *et al*., 2021), potentially magnifying the problems of highly flammable young forest. Climate change also may alter community structure – both through direct effects of climate envelopes such as in the transition from deciduous larch to evergreen spruce and fir in Eurasian forests (Kharuk, Ranson & Dvinskaya, 2007) and through altered fire regimes, like the transition from low-flammability forest to flammable heath in Patagonia, South America (Tiribelli *et al*., 2018). This underscores the need to tackle climate change as a core driver of disturbance.

(3) Predicting disturbance-stimulated flammability using ecological controls

As ecological controls are driven by the inherent features of each forest community, they can be used to predict the likelihood of disturbance-stimulated flammability. We expect that: (*i*) disturbance may stimulate a pulse of flammability if it disrupts one or more ecological controls; and (*ii*) the pulse of flammability will be greater if more ecological controls are disrupted. Here, we demonstrate this for two contrasting forest ecosystems – boreal forests containing black spruce (*Picea mariana*), and southwest Australian eucalypt forests.

Black spruce is a shade-tolerant component in the succession of North American boreal forests, often establishing as a late-successional dominant (Purdy, MacDonald & Dale, 2002), particularly on poorly drained soils (Shafi & Yarranton, 1973). In earlier stages of succession, however, black spruce can form an understorey in stands of jack pine (*Pinus banksiana*) and shade intolerant broadleaf species such as trembling aspen (*Populus tremuloides*). Shrub species are dominated by resprouters, with very few post-fire ephemerals (Foster, 1985), so that self-thinning of the understorey is minimal or absent. In jack pine forest, black spruce understoreys may be denser than the pine overstoreys (Taylor *et al*., 2004), creating a flammable stratum with minimal separation from the canopy and a 'fuel ladder' that facilitates crown fire.

Black spruce does not self-prune (Archibald *et al*., 2018) so that as the tree grows, basal height increase can be minimal (McClain *et al*., 1994). As time since fire increases and succession leads to canopy dominance by black spruce, lower branches may maintain sufficient density that the fuel ladder is maintained. Together, these factors suggest that forests with a significant black spruce component may not exert ecological controls on fire because no controls of growth or succession permit the portioning of biomass into overstorey shelter. This prediction fits the observation that lightning-generated ignitions are more frequent in forests dominated by black spruce compared to either trembling aspen or jack pine (Krawchuk *et al*., 2006), and that over centuries to millennia, landscapes dominated by black spruce are those that have burned the most frequently, regardless of climate (Girardin *et al*., 2013). In addition, increased fire frequency reduces the dominance of black spruce by removing the soil organic layer and allowing less-flammable broadleaf forests to develop (Johnstone & Chapin, 2006). A complicating factor is the influence of stem density on black spruce, as closer-growing trees are taller with significantly greater base heights (McClain *et al*., 1994). This has the potential to allow for plant growth to act as an ecological control, so that disturbances such as mechanical thinning may stimulate flammability.

Southwest Australian eucalypt forests have been presented as exemplars of the value of prescribed burning for fuel reduction (Sneeuwjagt *et al*., 2013), yet we may predict from ecological control theory that the increase in flammability following prescribed burning is not a return to a natural state of high flammability, but a pulse in flammability that was stimulated by the disturbance of burning. This expectation arises because self-thinning understoreys are well-documented for the dominant forest communities (Burrows 1994, McCaw, Neal & Smith, 2002). Analysis of long-term fire records for Southwest Australian eucalypt forests has confirmed these expectations, demonstrating that long-unburnt forests are 7.4 times less likely to burn than forests still recovering from fire (Zylstra *et al*., 2022). Mechanistic analysis also demonstrated that self-thinning accounted for most of the trend in flammability, and that self-pruning further fortified it (Zylstra *et al*., 2023).

(4) Ecological controls and ecological cooperation

The concept of 'ecological cooperation' becomes critical in the context of climate change and fire-risk mitigation (Zylstra *et al*., 2023). Ecological cooperation involves the identification of fire-fighting advantages provided by ecological controls, and the strategic use of 'reinforcement' through specialist firefighting skills and technological developments for the rapid detection and rapid suppression of fires (Yebra *et al*., 2022) (see Section IV) that target these areas. To illustrate, the low-rainfall conditions which preceded the 2019–2020 fires in eastern New South Wales led to Gondwanan rainforest remnants drying out to a degree that fire was able to enter them. The ecological controls operating in those forests, however, reduced fire severity to the extent that priority areas were successfully protected using sprinklers (de Bie, Currey & Rumpff, 2022). Reinforcement involves the identification of such opportunities where they may be used to limit fire in the broader landscape. A mechanistic analysis of red tingle (*Eucalyptus jacksonii*) forest in south-western Australia, for example, demonstrated that mature forest facilitated more successful application of fire-suppression techniques than disturbed forests under the same weather conditions (Zylstra *et al*., 2023). By understanding the underlying mechanisms, cooperation with ecological controls may enable suppression actions that gain a critical advantage in older forests, even in a warming climate.

III. THE POTENTIAL INFLUENCE OF INTACT FOREST ON SPATIAL CONTAGION IN WILDFIRE

The area of a landscape burned within a given period is affected by both the rate of fire spread and by the ability of fire to cross barriers. Very large flame heights like those produced by crown fires can lead to mass spotting and the formation of pyro-cumulonimbus events, with associated dry lightning strikes causing further ignitions (Sharples *et al*., 2016). This, in turn, could influence the prevalence and/or severity of fire in 'downstream' areas (i.e. along the direction of potential fire spread). If disturbance converts a community into a more flammable state by disrupting ecological controls or driving ecological collapse into a more flammable community, then the impacts will extend beyond the disturbed stand and into the broader landscape (Tiribelli *et al*., 2018). Spatial dependence in wildfires is well documented (Bowman *et al*., 2021; Lindenmayer *et al*., 2023*a*). For example, Levine *et al*. (2022) found strong evidence of spatial dependence in wildfires in the highly flammable, intensively managed, industrial forests of California; adjacent areas within 3 km were more likely to burn at high severity than those further away. Similar levels of spatial dependence were found in the 2019–2020 fires in Victoria (Lindenmayer *et al.*, 2021). In this way, extensive areas of fire-prone disturbed forest may contribute to the formation of a 'landscape trap' – a hypothesised condition in which the rarity of less-flammable older forest in the landscape means that the remaining more widespread and more flammable young forest is at increased risk of repeatedly re-burning at high severity (Furlaud *et al.*, 2021; Lindenmayer, Taylor & Bowd, 2022*d*). Landscape traps can preclude young forest from growing to an older, less-flammable state. Lindenmayer *et al.* (2022*d*) showed how all the necessary pre-conditions for a landscape trap had developed in the tall, wet forests of south-eastern Australia. In studies in the tall, wet forests of Tasmania, Furlaud *et al.* (2021, p. 14) noted that: '…widespread logging and wildfire can increase landscape-scale fire risk……consistent with the notion of a "landscape trap"…'. The thresholds for such dynamic changes are likely to vary depending on the forest community in question. For example, long-distance spotting from crown fires may have a greater impact on landscape-level contagion in high-severity fire than the fast spread of smaller flames. Quantifying thresholds that underpin landscape traps in different environments is therefore a complex, but critical, area for future work.

IV. CONSERVATION AND MANAGEMENT IMPLICATIONS

We have presented evidence that disturbance-stimulated flammability is evident in multiple forest communities across a wide gradient of climates, latitudes, and vegetation structures. We have also shown that ecological control theory (*sensu* Zylstra *et al.*, 2023) suggests that disturbance-stimulated flammability can be expected to occur in more environments than currently documented. This has important consequences at a landscape scale as a predominance of disturbed, fire-prone stands may promote spatial contagion in fire through fast-spreading or high-severity wildfire. These findings have implications for forest management and conservation, including for the maintenance of forest integrity, the conservation of biodiversity associated with older forests (e.g. Dixon *et al.*, 2018*a*; Jones *et al.*, 2021; Lefoe *et al.*, 2021), and the persistence of forests sensitive to the effects of high-frequency and/or high-severity wildfire (e.g. Lindenmayer *et al.*, 2013; Franklin *et al.*, 2022). We argue that disturbance-stimulated flammability needs explicit consideration in restoring forest types such as those where high-severity wildfires should naturally be rare but instead have become frequent, extensive and homogenous (e.g. see Collins *et al.*, 2021*a*; Mackey *et al.*, 2021; Levine *et al.*, 2022; Lindenmayer *et al.*, 2023*a*).

First, the stand age–fire severity relationships we have described have particular importance in intensively managed, so-called 'regulated' wood-production landscapes (*sensu* Oliver & Larson, 1996; Davis *et al.*, 2001) that are often dominated by extensive areas of young forest regenerating after previous disturbances, especially widespread logging operations. We contend that when disturbance-stimulated flammability has been identified for a community, key management actions must be to: (*i*) limit yet further disturbance-based management such as logging and prescribed burning; and (*ii*) protect disturbed forests from further disturbance so that they may transition to an older, less-flammable state.

Second, 'reinforcement' of ecological controls can be aided by the application of new technologies. Heat-sensing drones and water-carrying aerial autonomous vehicles (Yebra *et al.*, 2022) are currently being developed to detect ignitions rapidly and then quickly contain or extinguish fires whilst it is comparatively easy to do so (e.g. Lindenmayer, Zylstra & Yebra, 2022*a*). When coupled with specialist fire-fighting techniques and guidance derived from biophysical fire-behaviour modelling that accounts for ecological controls (Zylstra *et al.*, 2023), new technology can help capitalise on the advantages provided by existing mature forest to keep fire out of regenerating areas. Applicability of these management actions will depend on: (*i*) how much flammable young forest currently exists in a landscape (relative to what occurred historically); (*ii*) changes to natural fire regimes; and (*iii*) the increased potential for fires from neighbouring land uses (like plantations and peri-urban developments) to burn into adjacent areas including intact and/or older forests (e.g. see Gómez-González *et al.*, 2018; McWethy *et al.*, 2018).

Third, we argue that there is an urgent need to develop new landscape fire models to determine if there are thresholds for the number and extent of stands of young flammable forest in a landscape that elevate levels of spatial dependence in high-severity wildfire and possibly spring a landscape trap.

Fourth, careful consideration is needed in the use of some conventional methods intended to curtail the occurrence and spread of high-severity fire, but which can sometimes have unintended effects on fire behaviour. These include thinning, which may be effective in some ecosystems (Kalies & Yocom Kent, 2016) but can have limited (or even perverse) effects in others (Forestry Tasmania, 2001; Taylor, Blanchard & Lindenmayer, 2020; Taylor *et al.*, 2021; Weston *et al.*, 2022). Conversely, targeted actions like the use of watering systems might be warranted to protect very high conservation value assets from fire as occurred in the case of the range-limited stands of the Gondwana relic wollemi pine (*Wollemia nobilis*) in the 2019–2020 fires in south-eastern Australia.

Our findings underscore the need to tackle climate change as a core driver of disturbance. As an example, although long-unburnt forests are significantly less flammable than disturbed forests in south-western Western Australia, fire frequency has increased across all forest age classes as the climate has warmed (Zylstra *et al.*, 2022). During the 2019–2020 fires in south-eastern Australia, logged forests burned with the same severity under mild conditions as unlogged forests burned during more severe fire weather (Lindenmayer *et al.*, 2022*e*), but spatial contagion from areas of high severity spread fire impacts far into previously undisturbed forests (Bowman *et al.*, 2021). Where disturbance has been found to stimulate flammability, ecologically cooperative approaches may provide additional tools to mitigate fire impacts, but climate change may eventually override the advantages they provide.

Limiting the frequency and extent of high-severity wildfires will be a major challenge where disturbances such as extensive clearcutting or burning have stimulated flammability. Nevertheless, humans have direct agency in decisions about when and where to exclude these actions and allow forest to grow to an older (and potentially less flammable) age. In south-western Western Australia, for example, 80% of area burned is by prescribed fire (Boer *et al.*, 2009), and 80% of the remaining wildfire area results from human ignitions (Department of Biodiversity, Conservation and Attractions, 2021). This leaves only 4% of the burned area caused by natural ignitions, and 96% subject to human agency. At a global scale, the predominance of young forest may represent a major challenge in fire management. For instance, McDowell *et al.* (2020) reported that the percentage of young forest stands (< 140 years old) has increased from 11.3% in 1900 to 33.6% in 2015 of the total forest area at the global scale.

(1) Evolutionary and conservation conundrums

Wildfire is a natural ecological process in many forest ecosystems worldwide (Keeley & Pausas, 2019). Excluding fire in some ecosystems for prolonged periods will be undesirable and/or inappropriate, resulting in key changes to fire regimes, with major impacts on forests and biodiversity (e.g. Jones *et al.*, 2021). However, intensive forest management practices like widespread logging that create young, flammable, even-aged stands also have the potential to elevate fire severity, promote fire spread, and thereby alter fire regimes (Zald & Dunn, 2017; Koontz *et al.*, 2020), again with negative impacts on forest biodiversity and ecosystem services. Much has been written about the negative impacts of altered fire regimes (Keeley & Pausas, 2019; Halofsky, Peterson & Harvey, 2020), including the increasing prevalence of more frequent and more extensive high-severity wildfires as a result of climate change (e.g. Collins *et al.*, 2022), but also due to land management (Bradley *et al.*, 2016; Zald & Dunn, 2017; Levine *et al.*, 2022; Lindenmayer *et al.*, 2022*e*; Zylstra *et al.*, 2022).

We propose the concept of disturbance-stimulated flammability (Figs 3 and 4) to reflect stand age–fire severity relationships in which young- to intermediate-aged forests are characterised by elevated fire severity. This phenomenon presents an evolutionary paradox in some fire-sensitive forest communities. How might such a highly flammable stage of forest development have evolved if it can leave such ecosystems at risk of collapse in the event of recurrent high-severity fire? This proposition is connected to the interval squeeze problem whereby high-severity fire recurs before trees have advanced past a prolonged juvenile stage in which viable seed crops are not produced (Enright *et al.*, 2015; Le Breton *et al.*, 2022). We postulate that such a stage might have developed where trees sacrifice fire resistance, such as in the form of strategies like epicormic buds, to promote a rapid growth in height due to competition with similar-aged congeners in a stand. Tentative evidence of such a strategy can be seen in tree species like mountain ash which have epicormic buds, but weak resprouting ability. This is possibly because the species dedicates resources to rapid growth in height at the expense of increasing bark thickness that would otherwise protect epicormic structures (Waters, Burrows & Harper, 2010), with almost all young individual trees killed by high-severity fires. Such sensitivity to recurrent high-severity wildfire means that tall–wet eucalypt forests like those dominated by stands of mountain ash would likely have evolved with a fire regime in which high-severity conflagrations were rare. In fact, the natural fire regime for mountain ash forests is a wildfire every 75–150 years in the absence of human disturbance (McCarthy, Gill & Lindenmayer, 1999). Conversely, the species is maladapted to frequent high-severity wildfire. The natural fire regime would produce patterns of landscape-level forest cover dominated by relatively mature forests. However, the advent of extensive human disturbance like clearcutting has created widespread, highly flammable young forest. Obviating this problem reinforces our recommendation to limit the number of stands and the proportion of a landscape dominated by flammable young forest.

V. CONCLUSIONS

(1) The amount of young disturbed forest has increased substantially in many jurisdictions worldwide. There also have been extensive high-severity wildfires in many forest ecosystems globally.
(2) For some forest types, conservation and protection strategies to reduce the expansion of young flammable forest may help reduce the amount and spatial contagion of high-severity wildfire.
(3) In forests where disturbance stimulates flammability, ecologically cooperative approaches that reinforce the inhibitory properties of older forests may assist some stands to transition to a less-flammable state. This will, in turn, have significant benefits for many other ecological values associated with older forests, including biodiversity conservation.
(4) Core areas of research now lie in: (*i*) the identification of forest communities that are and that are not subject to disturbance-stimulated flammability; (*ii*) quantification of the effects of disturbance-stimulated flammability on spatial contagion in fire and the development of landscape traps; and (*iii*) identifying thresholds within which reinforcement to help better control of fire are possible.

VI. ACKNOWLEDGEMENTS

We thank Professor Mark Burgman, Professor Michael McCarthy, Professor Charles Krebs, and several anonymous reviewers for very insightful comments which improved earlier versions of this review. Luke Gordon and Karen Brock provided expert editorial assistance. Luke Gordon assisted in detailed searches of the literature.

VII. REFERENCES

References identified with an asterisk (*) are cited only within the online supporting information.

Agee, J. K. & Skinner, C. N. (2005). Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* **211**, 83–96.

Alexander, M. E. (1982). Calculating and interpreting forest fire intensities. *Canadian Journal of Botany* **60**, 349–357.

Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., De Fries, D. S., Hantson, S., Kloster, S., Bachelet, D., Forrest, M., Lasslop, G., Li, F., Mangeon, S., Melton, J. R., et al. (2017). A human-driven decline in global burned area. *Science* **356**, 1356–1362.

Anderegg, W. R., Chegwidden, O. S., Badgley, G., Trugman, A. T., Cullenward, D., Abatzoglou, J. T., Hicke, J. A., Freeman, J. & Hamman, J. J. (2022). Future climate risks from stress, insects and fire across US forests. *Ecology Letters* **25**, 1510–1520.

Archibald, S., Lehmann, C. E. R., Belcher, C. M., Bond, W. J., Bradstock, R. A., Daniau, A., Dexter, K., Forrestel, E. J., Greve, M., Higgins, T., He, S. I., Hoffmann, W. A., Lamont, B. B., McGlinn, D. J., Moncreiff, G. R., et al. (2018). Biological and geophysical feedbacks with fire in the earth system. *Environmental Research Letters* **13**, 033003.

Ashton, D. H. (2000). The big ash forest, Wallaby Creek, Victoria – changes during one lifetime. *Australian Journal of Botany* **48**, 1–26.

Attiwill, P. M., Ryan, M. F., Burrows, N., Cheney, N., McCaw, L., Neyland, M. & Read, S. (2014). Timber harvesting does not increase fire risk and severity in wet eucalypt forests of southern Australia. *Conservation Letters* **7**, 341–354.

Baeza, M. J., Santana, V. M., Pausas, J. G. H. & Vallejo, V. R. (2011). Successional trends in standing dead biomass in Mediterranean basin species. *Journal of Vegetation Science* **22**, 467–474.

Barker, J. W. & Price, O. F. (2018). Positive severity feedback between consecutive fires in dry eucalypt forests of southern Australia. *Ecosphere* **9**, e02110.

Barker, J. W., Price, O. F. & Jenkins, M. E. (2022). High severity fire promotes a more flammable eucalypt forest structure. *Austral Ecology* **47**, 519–529.

Beadle, N. C. W. (1966). Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. *Ecology* **47**, 992–1007.

Boer, M. M., Sadler, R. J., Wittkuhn, R. S., McCaw, L. & Grierson, P. F. (2009). Long-term impacts of prescribed burning on regional extent and incidence of wildfires—evidence from 50 years of active fire management in SW Australian forests. *Forest Ecology and Management* **259**, 132–142.

Bowd, E. J., Lindenmayer, D. B., Banks, S. C. & Blair, D. P. (2018). Logging and fire regimes alter plant communities. *Ecological Applications* **28**, 826–841.

Bowman, D., Williamson, G. J., Gibson, R., Bradstock, R. A. & Keenan, R. J. (2021). The severity and extent of the Australia 2019-2020 eucalyptus forest fires are not the legacy of forest management. *Nature Ecology Evolution* **5**, 1–8.

Bradley, C. M., Hanson, C. T. & DellaSala, D. A. (2016). Does increased forest protection correspond to higher fire severity in frequent- fire forests of the western United States? *Ecosphere* **7**, e01492.

Brewer, S. & Rogers, C. (2006). Relationships between prescribed burning and wildfire occurrence and intensity in pine-hardwood forests in North Mississippi, USA. *International Journal of Wildland Fire* **15**, 203–211.

Burrows, G. E. & Connor, C. (2020). Chloroplast distribution in the stems of 23 eucalypt species. *Plants* **9**, 1–21.

Burrows, N. D. (1994). *Experimental Development of a Fire Management Model for Jarrah (Eucalyptus marginata Donn ex Sm.) Forest*. Australian National University, Canberra, Australia.

Burrows, N. D., Gardiner, G., Ward, B. & Robinson, A. (1990). Regeneration of *Eucalyptus wandoo* following fire. *Australian Forestry* **53**, 248–258.

Burton, J. E., Cawson, J. G., Filkov, A. I. & Penman, T. D. (2020). Leaf traits predict global patterns in the structure and flammability of forest litter beds. *Journal of Ecology* **109**, 1344–1355.

Byram, G. M. (1959). Combustion of Forest fuels. In *Forest Fire: Control and Use* (ed. K. P. Davis). McGraw-Hill, New York.

Canadell, J. G., Meyer, C. P., Cook, G. D., Dowdy, A., Briggs, P. R., Knauer, J., Pepler, A. & Haverd, V. (2021). Multi-decadal increase of forest burned area in Australia is linked to climate change. *Nature Communications* **12**, 6921.

Cattau, M. E., Wessman, C., Mahood, A. & Balch, J. K. (2020). Anthropogenic and lightning-started fires are becoming larger and more frequent over a longer season length in the USA. *Global Ecology and Biogeography* **29**, 668–681.

Chazdon, R. L., Lindenmayer, D. B., Guariguata, M. R., Crouzeilles, R., Rey Benayas, J. M. & Chavero, E. L. (2020). Fostering natural forest regeneration on former agricultural land through economic and policy interventions. *Environmental Research Letters* **15**, 43002.

Clarke, H. G., Penman, T. D., Boer, M. M., Cary, G. J., Fontaine, J., Price, O. & Bradstock, R. (2020). The proximal drivers of large fires: a pyrogeographic study. *Frontiers in Earth Science* **8**, 1–11.

Collins, L., Bradstock, R., Clarke, H., Clarke, M. F., Nolan, R. H. & Penman, T. D. (2021*a*). The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters* **16**, 044029.

Collins, L., Clarke, H., Clarke, M. F., McColl- Gausden, S. C., Nolan, R. H., Penman, T. & Bradstock, R. (2022). Warmer and drier conditions have increased the potential for large and severe fire seasons across South-Eastern Australia. *Global Ecology and Biogeography* **31**, 1933–1948.

Collins, L., Hunter, A., McColl-Gausden, S. C., Penman, T. D. & Zylstra, P. J. (2021*b*). The effect of antecedent fire severity on reburn severity and fuel structure in a resprouting eucalypt forest in Victoria, Australia. *Forests* **12**, f12040450.

Cruz, M. G., Cheney, N. P., Gould, J., McCaw, W. L., Kilinc, M. & Sullivan, A. L. (2022). An empirical-based model for predicting the forward spread rate of wildfires in eucalypt forests. *International Journal of Wildland Fire* **31**, 81–95.

Cruz, M. G., Sullivan, A. L., Gould, J. S., Sims, N. C., Bannister, A. J., Hollis, J. J. & Hurley, R. J. (2012). Anatomy of a catastrophic wildfire: the Black Saturday Kilmore East fire in Victoria, Australia. *Forest Ecology and Management* **284**, 269–285.

Davis, L. S., Johnson, K. N., Bettinger, P. S. & Howard, T. E. (2001). *Forest Management to Sustain Ecological, Economic and Social Values*, Fourth Edition. McGraw-Hill, New York.

de Bie, K., Currey, K. & Rumpff, L. (2022). What did we learn about biodiversity management, policy and operations from the 2019-20 wildfires? In *Australia's Megafires. Biodiversity Impacts and Lessons from 2019–2020* (eds L. Rumpff, S. M. Legge, S. van Leeuwen, B. A. Wintle and J. Woinarski), pp. 377–388. CSIRO Publishing, Melbourne.

de Castro Galizia, L. P. & Rodriguez, M. (2019). Modeling the influence of eucalypt plantation on wildfire occurrence in the Brazilian savanna biome. *Forests* **10**, 844.

de Magalhaes, R. M. Q. & Schwilk, D. W. (2012). Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology* **100**, 1153–1163.

Deng, C., Zhang, S., Froese, Y., Lu, R. E., Ming, A. & Li, Q. (2019). Thinning effects on the tree height-diameter allometry of Masson Pine (*Pinus massoniana* Lamb.). *Forests* **10**, 1–15.

Department of Biodiversity, Conservation & Attractions (2021). *Annual Report*. Department of Biodiversity, Conservation and Attractions, Perth, Western Australia.

Dixon, K. M., Cary, G., Worboys, G. L., Seddon, J. & Gibbons, P. (2018*b*). A comparison of fuel hazard in recently burned and long-unburned forests and woodlands. *International Journal of Wildland Fire* **27**, 609–622.

Dixon, K. M., Cary, G. J., Worboys, G. L. & Gibbons, P. (2018*a*). The disproportionate importance of long-unburned forests and woodlands for reptiles. *Ecology and Evolution* **8**, 10952–10963.

Donato, D. C., Fontaine, J. B., Campbell, J. L., Robinson, W. D., Kauffman, J. B. & Law, B. E. (2006). Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**, 352.

Donoghue, S. & Turner, P. A. M. (2022). A review of Australian tree fern ecology in forest communities. *Austral Ecology* **47**, 145–165.

Egler, F. E. (1954). Vegetation science concepts. I. Initial floristic composition – a factor in old field vegetation development. *Vegetation* **4**, 412–417.

Enright, N. J., Fontaine, J. B., Bowman, D. M., Bradstock, R. A. & Williams, R. J. (2015). Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* **13**, 265–272.

Falster, D. S., Brännström, Å., Westoby, M. & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence.

Proceedings of the National Academy of Sciences of the United States of America **114**, E2719–E2728.

Falster, D. S., Duursma, R. A. & FitzJohn, R. G. (2018). How functional traits influence plant growth and shade tolerance across the life cycle. *Proceedings of the National Academy of Sciences* **115**, E6789–E6798.

Falster, D. S. & Westoby, M. (2003). Plant height and evolutionary games. *Trends in Ecology and Evolution* **18**, 337–343.

February, E. C., Cook, G. D. & Richards, A. E. (2013). Root dynamics influence tree-grass coexistence in an Australian savanna. *Austral Ecology* **38**, 66–75.

Feller, M. C. & Pollock, S. L. (2006). Variation in surface and crown fire Hazard with stand age in managed coastal Western hemlock zone forests in southwestern British Columbia. In *Fuels Management-How to Measure Success* (eds P. L. Andrews and B. W. Butler), pp. 367–380. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-41, Fort Collins, CO.

Fernandes, P. M., Luz, A. & Loureiro, C. (2010). Changes in wildfire severity from maritime pine woodland to contiguous forest types in the mountains of northwestern Portugal. *Forest Ecology and Management* **260**, 883–892.

Foster, D. R. (1985). Vegetation development following fire in *Picea mariana* (Black Spruce) – Pleurozium forests of South-Eastern Labrador, Canada. *Journal of Ecology* **73**, 517–534.

Franklin, M. J., Major, R. E., Bedward, M. & Price, O. F. (2022). Forest avifauna exhibit enduring responses to historical high-severity wildfires. *Biological Conservation* **269**, 109545.

Furlaud, J. M., Prior, L. D., Williamson, G. J. & Bowman, D. M. J. S. (2021). Fire risk and severity decline with stand development in Tasmanian giant Eucalyptus forest. *Forest Ecology and Management* **502**, 119724.

Gilbert, J. M. (1959). Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings Royal Society Tasmania* **93**, 129–151.

Gill, A. M., Ryan, P. G., Moore, P. H. R. & Gibson, M. (2000). Fire regimes of World Heritage Kakadu National Park, Australia. *Austral Ecology* **25**, 616–625.

Gill, A. M. & Zylstra, P. J. (2005). Flammability of Australian forests. *Australian Forestry* **68**, 87–93.

Girardin, M., Ali, A., Carcaillet, C., Blarquez, O., Hely, C., Terrier, A., Genries, A. & Bergeron, Y. (2013). Vegetation limits the impact of a warm climate on boreal wildfires. *New Phytologist* **199**, 1001–1011.

Gómez-González, S., Ojeda, F. & Fernandes, P. M. (2018). Portugal and Chile: longing for sustainable forest while rising from the ashes. *Environmental Science and Policy* **81**, 1–4.

Gosper, C. R., Prober, S. M. & Yates, C. J. (2013). Multi-century changes in vegetation structure and fuel availability in fire-sensitive eucalypt woodlands. *Forest Ecology and Management* **310**, 102–109.

Gould, J. S., Knight, I. & Sullivan, A. L. (1997). Physical modelling of leaf scorch height from prescribed fires in young *Eucalyptus sieberi* regrowth forests in south-eastern Australia. *International Journal of Wildland Fire* **7**, 7–20.

Gould, J. S., McCaw, W. L. & Cheney, N. P. (2011). Quantifying fine fuel dynamics and structure in dry eucalypt forest (*Eucalyptus marginata*) in Western Australia for fire management. *Forest Ecology and Management* **262**, 531–546.

Gould, J. S., Mccaw, W. L., Cheney, N. P., Ellis, P. F., Knight, I. & Sullivan, A. L. (2007). *Project Vesta – Fire in Dry Eucalypt Forest: Fuel Structure, Fuel Dynamics and Fire Behaviour*. CSIRO Publishing, Melbourne.

Grootemaat, S., Wright, I. J., van Bodegom, P. M. & Cornelissen, J. H. C. (2017). Scaling up flammability from individual leaves to fuel beds. *Oikos* **126**, 1428–1438.

Grzesik, E. J., Hollingsworth, T. N., Ruess, R. W. & Turetsky, M. R. (2022). Fuel loads and plant traits as community-level predictors of emergent properties of vulnerability and resilience to a changing fire regime in black spruce forests of boreal Alaska. *Journal Geophysical Research Biogeosciences* **127**, e2021JG006696.

Halofsky, J. E., Peterson, D. L. & Harvey, B. J. (2020). Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. *Fire Ecology* **16**, 1–26.

Hellström, L., Carlsson, L., Falster, D. S., Westoby, M. & Brännström, Å. (2018). Branch thinning and the large- scale, self-similar structure of trees. *The American Naturalist* **192**, E37–E47.

Hoffmann, W. A., Adasme, R., Haridasan, M., de Carvalho, M. T., Geiger, E. L., Pereira, M. A., Gotsch, S. G. & Franco, A. C. (2009). Tree topkill, not mortality, governs the dynamics of savanna – forest boundaries under frequent fire in Central Brazil. *Ecology* **90**, 1326–1337.

Hunter, M. E. & Robles, M. D. (2020). Tamm review: the effects of prescribed fire on wildfire regimes and impacts: a framework for comparison. *Forest Ecology and Management* **475**, 118435.

Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services (IPBES) (2019). *IPBES Global Assessment Summary for Policymakers*. IPBES Secretariat, Bonn.

Johnstone, J. F. & Chapin, F. S. (2006). Fire interval effects on successional trajectory in boreal forests of Northwest Canada. *Ecosystems* **9**, 268–277.

Jones, G. M., Kramer, H. A., Berigan, W. J., Whitmore, S. A., Gutiérrez, R. J. & Peery, M. Z. (2021). Megafire causes persistent loss of an old-forest species. *Animal Conservation* **24**, 925–936.

Jucker, T., Hardwick, S. R., Both, S., Elias, D. O., Ewers, R. M., Milodowski, D. T., Swinfield, T. & Coomes, D. A. (2018). Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global Change Biology* **24**, 5243–5258.

Kalies, E. L. & Yocom Kent, L. L. (2016). Tamm review: are fuel treatments effective at achieving ecological and social objectives? A systematic review. *Forest Ecology and Management* **375**, 84–95.

Keeley, J. & Pausas, J. (2019). Distinguishing disturbance from perturbations in fire-prone ecosystems. *International Journal of Wildland Fire* **28**, 282–287.

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* **18**, 116–126.

Keenan, R. J., Weston, C. J. & Volkova, L. (2021). Potential for forest thinning to reduce risk and increase resilience to wildfire in Australian temperate Eucalyptus forests. *Current Opinion in Environmental Science and Health* **23**, 100280.

Keith, H., Mackey, B. G. & Lindenmayer, D. B. (2009). Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences* **106**, 11635–11640.

Kharuk, V. I., Ranson, K. J. & Dvinskaya, M. L. (2007). Evidence of evergreen conifer invasion into larch dominated forests during recent decades in Central Siberia. *Eurasian Journal of Forest Research* **10**, 163–171.

Kiel, N. G., Braziunas, K. H. & Turner, M. G. (2023). Peeking under the canopy: anomalously short fire-return intervals alter subalpine forest understory plant communities. *New Phytolologist* **239**, 1225–1238.

Koontz, M. J., North, M. P., Werner, C. M., Fick, S. E. & Latimer, A. M. (2020). Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. *Ecology Letters* **23**, 483–494.

Kovács, B., Tinya, F. & Ódor, P. (2017). Stand structural drivers of microclimate in mature temperate mixed forests. *Agricultural and Forest Meteorology* **234**, 11–21.

Krawchuk, M. A., Cumming, S. G., Flannigan, M. D. & Wein, R. W. (2006). Biotic and abiotic regulation of lightning fire initiation in the mixedwood boreal forest. *Ecology* **87**, 458–468.

Lamont, B. B. (1985). Gradient and zonal analysis of understorey suppression by *Eucalyptus wandoo*. *Vegetation* **63**, 49–66.

Le Breton, T. D., Lyons, M. B., Nolan, R. H., Penman, T., Williamson, G. J. & Ooi, M. K. (2022). Megafire-induced interval squeeze threatens vegetation at landscape scales. *Frontiers in Ecology and Environment* **20**, 327–334.

Lefoe, M., Rendall, A. R., McKinnon, F. & Whisson, D. A. (2021). Logging and wildfire limit the distribution of a vulnerable arboreal mammal. *Forest Ecology and Management* **503**, 119773.

Levine, J. I., Collins, B. M., Steel, Z., de Valpine, P. & Stephens, S. L. (2022). Higher incidence of high-severity fire in and near industrially managed forests. *Frontiers in Ecology and Environment* **20**, 397–404.

Lindenmayer, D., Zylstra, P. & Yebra, M. (2022*a*). Adaptive wildfire mitigation approaches. *Science* **377**, 1163–1164.

Lindenmayer, D. B., Blanchard, W., McBurney, L., Blair, D., Banks, S., Driscoll, D., Smith, A. & Gill, A. M. (2013). Fire severity and landscape context effects on arboreal marsupials. *Biological Conservation* **167**, 137–148.

Lindenmayer, D. B., Blanchard, W., McBurney, L., Bowd, E., Youngentob, K., Marsh, K. & Taylor, C. (2022*b*). Stand age related differences in forest microclimate. *Forest Ecology and Management* **510**, 120101.

Lindenmayer, D. B., Bowd, E., Taylor, C. & Zylstra, P. (2022*c*). Chapter 19. Interacting and compounding impacts: fire and forestry in the 2019-2020 wildfires. In *Megafires* (eds L. Rumpff and J. Woinarski). CSIRO Publishing, Melbourne.

Lindenmayer, D. B., Mackey, B. G., Cunningham, R. B., Donnelly, C. F., Mullen, I. C., McCarthy, M. A. & Gill, A. M. (2000). Factors affecting the presence of the cool temperate rain forest tree myrtle beech (*Nothofagus cunninghamii*) in southern Australia: integrating climatic, terrain and disturbance predictors of distribution patterns. *Journal of Biogeography* **27**, 1001–1009.

Lindenmayer, D. B. & Taylor, C. (2020). New spatial analyses of Australian wildfires highlight the need for new fire, resource and conservation policies. *Proceedings of the National Academy of Sciences* **117**, 12481–12485.

Lindenmayer, D. B., Taylor, C. & Blanchard, W. (2021). Empirical analyses of the factors influencing fire severity in southeastern Australia. *Ecosphere* **12**, e03721.

Lindenmayer, D. B., Taylor, C., Blanchard, W., Zylstra, P. & Evans, M. J. (2023*a*). What environmental and climatic factors influence multi-decadal fire frequency? *Ecosphere* **14**(8), 1–16. https://doi.org/10.1002/ecs2.4610.

Lindenmayer, D. B., Taylor, C. & Bowd, E. (2022*d*). Interacting fire, logging and climate change has sprung a landscape trap in Victoria's montane ash forests. *Plant Ecology* **223**, 733–749.

Lindenmayer, D. B., Yebra, M. & Cary, G. (2023*b*). Better managing fire in flammable tree plantations. *Forest Ecology and Management* **528**, 120641.

Lindenmayer, D. B., Zylstra, P., Kooyman, R., Taylor, C., Ward, M. & Watson, J. E. M. (2022*e*). Logging effects outweighed fire weather effects to promote crown fire in the 2019–20 Australian forest fires. *Nature Ecology and Evolution* **6**, 533–535.

Lusk, C. H., Onoda, Y., Kooyman, R. M. & Gutiérrez-Girón, A. (2010). Reconciling species- level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. *The New Phytologist* **186**, 429–438.

Mackey, B., Lindenmayer, D. B., Norman, P., Taylor, C. & Gould, S. (2021). Are fire refugia less predictable due to climate change? *Environment Research Letters* **16**, 114028.

Madany, M. H. & West, N. E. (1983). Livestock grazing-fire regime interactions within montane forests of Zion. *Ecology* **64**, 661–667.

McCarthy, M. A., Gill, A. M. & Lindenmayer, D. B. (1999). Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. *Forest Ecology and Management* **124**, 193–203.

McCaw, W. L. (2013). Managing forest fuels using prescribed fire – a perspective from southern Australia. *Forest Ecology and Management* **294**, 217–244.

McCaw, W. L., Gould, J. S., Cheney, N. P., Ellis, P. F. M. & Anderson, W. R. (2012). Changes in behaviour of fire in dry eucalypt forest as fuel increases with age. *Forest Ecology and Management* **271**, 170–181.

McCaw, W. L., Neal, J. E. & Smith, R. H. (2002). Stand characteristics and fuel accumulation in a sequence of even-aged Karri (*Eucalyptus diversicolor*) stands in south-west Western Australia. *Forest Ecology and Management* **158**, 263–271.

McClain, K. M., Morris, D. M., Hills, S. C. & Buse, L. J. (1994). The effects of initial spacing on growth and crown development for planted northern conifers: 37-year results. *Forestry Chronicle* **70**, 174–182.

McColl-Gausden, S. C., Bennett, L. T., Duff, T. J., Cawson, J. G. & Penman, T. D. (2020). Climatic and edaphic gradients predict variation in wildland fuel hazard in South-Eastern Australia. *Ecography* **43**, 443–455.

McColl-Gausden, S. C. & Penman, T. D. (2019). Pathways of change: predicting the effects of fire on flammability. *Journal of Environmental Management* **232**, 243–253.

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., *et al.* (2020). Pervasive shifts in forest dynamicsin a changing world. *Science* **368**, 964.

McWethy, D. B., Pauchard, A., Garcia, R. A., Holz, A., Gonzalez, M. E., Veblen, T. T., Stahl, J. & Currey, B. (2018). Landscape drivers of recent fire activty (2001–2017) in south-Central Chile. *PLoS One* **13**, e0201195.

Ministry of Forests British Columbia (1985). *1984 Forests and Range Resource Analysis*. Ministry of Forests British Columbia, Victoria, BC.

*Moher, D., Shamseer, L., Clarke, M., Ghersi, D., Liberati, A., Petticrew, M., Shekelle, P., Stewart, L. A. & Prisma-P Group (2015). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015 statement. *Systematic Reviews* **4**, 1–9.

Ndalila, M. N., Williamson, G. J. & Bowman, D. M. (2018). Geographic patterns of fire severity following an extreme eucalyptus forest fire in southern Australia: 2013 Forcett–Dunalley fire. *Fire* **1**, 40.

Norris, C., Hobson, P. & Ibisch, P. L. (2012). Microclimate and vegetation function as indicators of forest thermodynamic efficiency. *Journal of Applied Ecology* **49**, 562–570.

Nowacki, G. J. & Abrams, M. D. (2008). The demise of fire and "Mesophication" of forests in the eastern United States. *Bioscience* **58**, 123–138.

Odion, D. C., Moritz, M. A. & DellaSala, D. A. (2010). Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology* **98**, 96–105.

Oliver, C. D. & Larson, B. C. (1996). *Forest Stand Dynamics*. John Wiley and Sons, New York.

Osawa, A., Zyryanova, O. A., Matsuura, Y., Kajimoto, T. & Wein, R. W. (2010). Permafrost ecosystems: Siberian Larch forests. *Ecological studies: Analysis and synthesis* **209**, 1–330.

Ough, K. & Murphy, A. (2004). Decline in tree-fern abundance after clearfell harvesting. *Forest Ecology and Management* **199**, 153–163.

Pausas, J. G. H., Alessio, G. A., Moreira, B. & Corcobado, G. (2012). Fires enhance flammability in Ulex parviflorus. *New Phytologist* **193**, 18–23.

Pausas, J. G. H. & Bond, W. J. (2020). Alternative biome states in terrestrial ecosystems. *Trends in Plant Science* **25**, 250–263.

Pausas, J. G. H. & Fernández-Muñoz, S. (2011). Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. *Climate Change* **110**, 215–226.

Pinkard, E. A. & Neilsen, W. A. (2003). Crown and stand characteristics of *Eucalyptus nitens* in response to initial spacing: implications for thinning. *Forest Ecology and Management* **172**, 215–217.

Platt, W. J., Ellair, D. P., Huffman, J. M., Potts, S. E. & Beckage, B. (2016). Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecological Monographs* **86**, 352–372.

Pons, A. & Reille, M. (1988). The holocene- and upper pleistocene pollen record from Padul (Granada, Spain): a new study. *Palaeogeography Palaeoclimatology Palaeoecology* **66**, 243–263.

Power, S. C., Verboom, G. A., Bond, W. J., Packer, K. F. & Cramer, M. D. (2021). The role of shade in maintaining alternative stable states between open- and closed-canopy vegetation. *Journal of Ecology* **109**, 1–14.

Prévosto, B., Curt, T., Gueugnot, J. & Coquillard, P. (2000). Modeling mid-elevation Scots pine growth on a volcanic substrate. *Forest Ecology and Management* **131**, 223–237.

Price, O. F. & Bradstock, R. (2013). Landscape scale influences of forest area and housing density on house loss in the 2009 Victorian bushfires. *PLoS One* **8**, e73421.

Purdy, B. G., MacDonald, S. E. & Dale, M. R. (2002). The regeneration niche of white spruce following fire in the mixedwood boreal forest. *Silva Fennica* **36**, 289–306.

Pyne, S. J. (1990). Firestick history. *The Journal of American History* **76**, 1132.

Pyne, S. J. (2020). The Pyrocene comes to Australia: a commentary. *Journal and Proceedings of the Royal Society of New South Wales* **153**, 30–35.

Rego, F., Louro, G. & Constantino, L. (2013). The impact of changing wildfire regimes on wood availability from Portuguese forests. *Forest Policy and Economics* **29**, 56–61.

Safford, H. D., Stevens, J. T., Merriam, K., Meyer, M. D. & Latimer, A. M. (2012). Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *Forest Ecology and Management* **274**, 17–28.

Santana, V. M., Baeza, M. J., Marrs, R. H. & Vallejo, V. R. (2010). Old-field secondary succession in SE Spain: can fire divert it? *Plant Ecology* **211**, 337–349.

Schwilk, D. W. (2003). Flammability is a niche construction trait: canopy architecture affects fire intensity. *American Naturalist* **162**, 725–733.

Schwilk, D. W. & Caprio, A. C. (2011). Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology* **99**, 970–980.

Shafi, M. I. & Yarranton, G. A. (1973). Vegetational heterogeneity during a secondary (postfire) succession. *Canadian Journal of Botany* **51**, 73–90.

Sharples, J. J., Cary, G., Fox-Hughes, P., Mooney, S., Evans, J. P., Flectcher, M.-S., Fromm, M., Grierson, P. F., McRae, R. & Baker, P. (2016). Natural hazards in Australia: extreme bushfire. *Climatic Change* **139**, 85–99.

Singleton, M. P., Thode, A. E., Sánchez-Meador, A. J. & Iniguez, J. M. (2019). Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *Forest Ecology and Management* **433**, 709–719.

Smith-Tripp, S. M., Eskelson, B. N. I., Coops, N. C. & Schwartz, N. B. (2022). Canopy height impacts on the growing season and monthly microclimate in a burned forest of British Columbia, Canada. *Agriculture and Forest Meteorology* **323**, 109067.

Sneeuwjagt, R. J., Kline, T. S. & Stephens, S. L. (2013). Opportunities for improved fire use and management in California: lessons from Western Australia. *Fire Ecology* **9**, 14–25.

Stephens, S. L., Battaglia, M. A., Churchill, D. J., Collins, B. M., Coppoletta, M., Hoffman, M. A., Lydersen, J. M., North, M. P., Parsons, R. A., Ritter, S. M. & Stevens, J. T. (2021). Forest restoration and fuels reduction: convergent or divergent? *Bioscience* **71**, 85–101.

Stephens, S. L., Burrows, N., Buyantuyev, A., Gray, R. W., Keane, R. E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K. G. & van Wagtendonk, J. W. (2014). Temperate and boreal forest mega-fires: characteristics and challenges. *Frontiers in Ecology and the Environment* **12**, 115–122.

Stevens, J. T., Kling, M. M., Schwilk, D. W., Varner, J. M. & Kane, J. M. (2020). Biogeography of fire regimes in western US conifer forests: a trait-based approach. *Global Ecology and Biogeography* **29**, 944–955.

Storey, M. G., Price, O. F. & Tasker, E. M. (2016). The role of weather, past fire and topography in crown fire occurrence in eastern Australia. *International Journal of Wildland Fire* **25**, 1048–1060.

Tangney, R., Miller, R. G., Fontaine, J. B., Veber, W. P., Ruthrof, K. X. & Miller, B. P. (2022). Vegetation structure and fuel dynamics in fire-prone, Mediterranean-type Banksia woodlands. *Forest Ecology and Management* **505**, 119891.

Forestry Tasmania (2001). *Native Forest Silviculture Technical Bulletin 13: Thinning Regrowth Eucalypts*. Forestry Tasmania, Hobart.

Taylor, C., Blanchard, W. & Lindenmayer, D. B. (2020). Does forest thinning reduce fire severity in Australian eucalypt forests? *Conservation Letters* **14**, e12766.

Taylor, C., Blanchard, W. & Lindenmayer, D. B. (2021). What are the relationships between thinning and fire severity? *Austral Ecology* **46**, 1425–1439.

Taylor, C., McCarthy, M. A. & Lindenmayer, D. B. (2014). Non-linear effects of stand age on fire severity. *Conservation Letters* **7**, 355–370.

Taylor, S. W., Wotton, B. M., Alexander, M. E. & Dalrymple, G. N. (2004). Variation in wind and crown fire behaviour in a northern Jack pine – black spruce forest. *Canadian Journal of Botany* **34**, 1561–1576.

Thompson, J. R., Spies, T. A. & Ganio, L. M. (2007). Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Sciences* **104**, 10743–10748.

Tiribelli, F., Morales, J. M., Gowda, J. H., Mermoz, M. & Kitzberger, T. (2018). Non-additive effects of alternative stable states on landscape flammability in NW Patagonia: fire history and simulation modelling evidence. *International Journal of Wildland Fire* **28**, 149–159.

Trauernicht, C., Murphy, B. P., Portner, T. E. & Bowman, D. M. J. S. (2012). Tree cover-fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna. *Journal of Ecology* **100**, 958–968.

Vander Yacht, A. L., Keyser, P. D., Barrioz, S. A., Kwit, C., Stambaugh, M. C., Clatterbuck, W. K. & Simon, D. M. (2019). Reversing mesophication effects on understory woody vegetation in mid-southern oak forests. *Forest Science* **65**, 289–303.

Ward, M., Tulloch, A. I. T., Radford, J. Q., Williams, B. A., Reside, A. E., Macdonald, S. L., Mayfield, H. J., Maron, M., Possingham, H. P., Vine, S. J., O'Connor, J. L., Massingham, E. J., Greenville, A. C., Woinarski, J. C. Z., Garnett, S. T., *et al.* (2020). Impact of 2019-2020 mega-fires on Australian fauna habitat. *Nature Ecology and Evolution* **4**, 1321–1326.

Waters, D. A., Burrows, G. E. & Harper, J. D. (2010). *Eucalyptus regnans* (Myrtaceae): a fire-sensitive eucalypt with a resprouter epicormic structure. *American Journal of Botany* **97**, 545–556.

Watson, J. E., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J. C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J. G., Painter, M., *et al.* (2018). The exceptional value of intact forest ecosystems. *Nature Ecology and Evolution* **2**, 599–610.

Westoby, M. (1984). The self-thinning rule. *Advances in Ecological Research* **14**, 167–225.

Weston, C. J., Di Stefano, J., Hislop, S. & Volkova, L. (2022). Effect of recent fuel reduction treatments on wildfire severity in southeast Australian *Eucalyptus sieberi* forests. *Forest Ecology and Management* **505**, 119924.

Wilson, N., Bradstock, R. & Bedward, M. (2022). Disturbance causes variation in sub-canopy fire weather conditions. *Agricultural and Forest Meteorology* **323**, 109077.

Wilson, N., Cary, G. J. & Gibbons, P. (2018). Relationships between mature trees and fire fuel hazard in Australian forest. *International Journal of Wildland Fire* **27**, 353–362.

Woinarski, J. C. Z., Risler, J. & Kean, L. (2004). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* **29**, 156–176.

Yebra, M., Barnes, N., Colleen Bryant, C., Cary, G. J., Durrani, S., Mahony, R., Palethorpe, E., Stocks, M., Stocks, R., Tridgell, A., Zhou, X. & Wilson, N. (2022). Towards an integrated hi-tech solution to detect small fires. *Australian Journal of Emergency Management* **37**, 44–47.

Zald, S. J. & Dunn, C. (2017). Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape. *Ecosphere* **28**, 1068–1080.

Zavala, M. A., Espelta, J. M. & Retana, J. (2000). Constraints and trade-offs in Mediterranean plant communities: the case of holm oak-Aleppo pine forests. *Botanical Reviews* **66**, 119–149.

Zylstra, P. (2018). Flammability dynamics in the Australian Alps. *Austral Ecology* **43**, 578–591.

Zylstra, P. (2023). Quantifying the direct fire threat to a critically endangered arboreal marsupial using biophysical, mechanistic modelling. *Austral Ecology* **48**, 266–288.

Zylstra, P., Bradshaw, D. & Lindenmayer, D. B. (2022). Self-thinning forest understoreys reduce wildfire risk, even in a warming climate. *Environment Research Letters* **17**, 1350–1365. https://iopscience.iop.org/article/10.1088/1748-9326/ac5c10.

Zylstra, P. J., Bradstock, R. A., Bedward, M., Penman, T. D., Doherty, M. D., Weber, R. O., Gill, A. M. & Cary, G. J. (2016). Biophysical mechanistic modelling quantifies the effects of plant traits on fire severity: species, not surface fuel loads determine flame dimensions in eucalypt forests. *PLoS One* **11**, e0160715.

Zylstra, P. J., Wardell-Johnson, G. W., Falster, D. S., Howe, M., McQuoid, N. & Neville, S. (2023). Mechanisms by which growth and succession limit the impact of fire in a south-western Australian forested ecosystem. *Functional Ecology* **37**, 1350–1365.

VIII. SUPPORTING INFORMATION

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

Appendix S1. Literature search details for publications associated with disturbance-stimulated flammability.

(*Received 29 June 2023; revised 7 December 2023; accepted 11 December 2023*)