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LETTER

Self-thinning forest understoreys reduce wildfire risk, even in a warming climate

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Abstract

As climatic changes continue to drive increases in the frequency and severity of forest fires, it is critical to understand all of the factors influencing the risk of forest fire. Using a spatial dataset of areas burnt over a 65 year period in a 528 343 ha study area, we examined three possible drivers of flammability dynamics. These were: that forests became more flammable as fine biomass (fuel) returned following disturbance (H1), that disturbance increased flammability by initiating dense understorey growth that later self-thinned (H2), and that climatic effects were more important than either of these internal dynamics (H3). We found that forests were unlikely to burn for a short 'young' period (5–7 years) following fire, very likely to burn as the regrowing understorey became taller and denser (regrowth period), then after a total post-disturbance period of 43–56 years (young + regrowth periods), fire became unlikely and continued to decrease in likelihood (mature period). This trend did not change as the climate warmed, although increases in synoptic variability (mean changes in synoptic systems per season) had a pronounced effect on wildfire likelihood overall. Young forest and regrowth forest became increasingly likely to burn in years of greater synoptic variability and the time taken for forests to mature increased, but in years with the most severe synoptic variability, mature forests were the least likely to burn. Our findings offer an explanation for fire behaviour in numerous long-term studies in diverse forest types globally and indicate that, even in the face of a warming climate, 'ecologically-cooperative' approaches may be employed that reinforce rather than disrupt natural ecological controls on forest fire. These range from traditional indigenous fire knowledge, to modern targeting of suppression resources to capitalise on the benefits of self-thinning, and minimise the extent of dense regrowth in the landscape.

1. Introduction

The area burned by fire, particularly high-severity fire, is increasing in many forests as the climate warms (Flannigan *et al* 2013, Seidl *et al* 2017, Ellis *et al* 2021). Changing fire regimes in-turn have feedbacks on ecological processes of plant growth and vegetation succession that may act as internal controls on the flammability of forests (Olson 1963, Blackhall *et al* 2012, Kitzberger *et al* 2016). However, to date there is limited empirical evidence to determine which of these ecological processes has the greatest influence on flammability. This is critical as the dynamics of the more influential ecological processes will determine the direction of fire-vegetation-flammability feedbacks. If these vegetation-flammability feedbacks are negative, then increased fire frequency due to climate change or human action will lead to decreased flammability, and forest ecosystems will stabilise. If feedbacks are positive, then increased fire frequency will lead to increased flammability and potentially form a landscape fire trap that may accelerate ecosystem collapse (Lindenmayer *et al* 2011, Kitzberger *et al* 2012, Bergstrom *et al* 2021).

1.1. The drivers of forest flammability

Broadly, the term 'flammability' refers to the likelihood that something will burn (Gill and Zylstra 2005). The primary requirement for this is an ignition source, so that landscape flammability increases as ignitions increase (Gill and Zylstra 2005). Much landscape flammability is determined by climate (Canadell *et al* 2021, Ellis *et al* 2021). In dry and/or very hot seasons, for example, normally moist parts of a landscape may be sufficiently dry to burn and very large fires become possible (Nolan and Boer *et al* 2016, Ellis *et al* 2021), particularly where plants are moisture-stressed (Rao *et al* 2022). Despite this, fires may still remain small unless other aspects of weather such as wind or atmospheric instability lead to rapid fire spread or to behaviour that overwhelms suppression efforts or remaining barriers to fire spread (Di Virgilio *et al* 2019, Storey *et al* 2021). This is not an effect of weather alone. Rather, weather interacts with the flammability of the forest to create fire behaviour that may or may not be controllable. Views on the mechanisms underpinning forest flammability fall into two broad categories.

In one view, flammability is related to 'fuel load', although this term refers to a range of concepts and is difficult to describe adequately. Most simply, fuel is another term for vegetation biomass (Bradstock 2010, Williams 2013, Duff *et al* 2018), and is represented this way at times in fire-enabled Dynamic Global Vegetation Models (e.g. (Foley *et al* 1996, Medvigy *et al* 2009)). Most frequently though, the term refers to the weight of fine biomass in lower plant strata only, and in particular to the weight of necromass (Fernandes and Botelho 2003, McCaw 2013, Stephens *et al* 2020). Risk management efforts therefore frequently centre on the reduction of surface and near-surface litter as a proxy for fine biomass and fuel overall (Howard *et al* 2020). Given that litter mass is understood to increase in the absence of fire to an eventual equilibrium (Olson 1963, McCarthy *et al* 2001) flammability is also expected to increase with time since fire as biomass recovers. This has been referred to as the 'fuel-age paradigm' (Zedler and Seiger 2000, Fernandes and Botelho 2003).

An alternative view is that it is not the weight of fine biomass that drives flammability, but its composition and arrangement. In this view, flammability is affected by the interaction of multiple factors including the proximity of foliar biomass to the ground, its continuity to the canopy (ladder fuels), the flammability of component plant species, and the microclimate of the forest (Cochrane 2003, Odion *et al* 2010, Gosper *et al* 2013, Kitzberger *et al* 2016, Zylstra *et al* 2016, Furlaud *et al* 2021, Wilson *et al* 2021). Foliage may act as fuel if it is within the reach of flames and therefore available for ignition, but if it is beyond the reach of flames, it may directly reduce fire severity by slowing the strength of the wind acting on a fire front (Zylstra *et al* 2016). In this case, foliage is no longer fuel but has become 'overstorey shelter' (Zylstra *et al* 2016). The most obvious indicator of these dynamics is the development of a more open forest understorey with time since fire (Specht and Morgan 1981), as growth, self-thinning (Yoda *et al* 1963, Westoby 1984, Hoffmann *et al* 2012) and self-pruning (Hellström *et al* 2018) cause shrub and sapling regeneration to develop into taller midstorey and canopy plants. Where this occurs, fire may be expected to initiate a temporal sequence of changes in flammability that follow a characteristic hump-shaped trend, with three periods of stand development (Zylstra 2018):

(a) A low-flammability *young* period of cleared understorey;
(b) A high-flammability *regrowth* period of dense understorey cover; and,
(c) A low-flammability *mature* forest, in which the understorey has self-thinned

1.2. Determining the key drivers of flammability

Here, we test these two views on the mechanisms underpinning forest flammability as formal hypotheses:

H1. *Biomass-driven risk*. If forest flammability (risk) is most affected by the weight of fine biomass and necromass, then flammability will be greatest in the longest-unburnt forests where fine biomass and necromass are expected to be highest (negative vegetation-fire feedback), and biomass is most often represented by the weight of fine necromass on or near the surface.

H2. *Disturbance-driven risk*. If forest flammability (risk) is most affected by the amount of fine biomass that is close to the ground (fuel), then flammability will increase during a regrowth period, but decline as the forest matures, the understorey vegetation self-thins, and increasing amounts of biomass act as overstorey shelter (positive vegetation-fire feedback). In this hypothesis, flammability is not related to the weight of biomass, but to the proportion of it likely to act as fuel compared to the proportion likely to act as overstorey shelter.

We contrast these two hypotheses with the null hypothesis H0 that fire risk is unaffected by changes occurring over time in forest regrowth.

In addition, we consider a fourth possibility, which is that climatic changes overwhelm internal effects on flammability, so that historical dynamics can be disregarded in a changing climate. To test this, we introduced a third hypothesis:

H3. *Climate-controlled risk*. If forest flammability (risk) is overwhelmingly controlled by climatic changes, then the vegetation-fire feedback will be different under changed climatic conditions compared with more historically representative years.

2. Methods

Full code and details of methodology can be found in the supplementary materials (SI Appendix).

2.1. Study area

To test our three hypotheses and the null model, we examined a 55 year spatial dataset of fire occurrence in 528 343 ha of forest in conservation areas of Western Australia (the Southern Forests), for forests burned up to 65 years earlier. These forests were well suited to our analysis as the weight of fine biomass is understood to be greatest in long-unburnt forests, but the understorey is largely germinated by fire (Wardell-Johnson 2000, Wardell-Johnson *et al* 2017) and self-thinning of shrubs is pronounced and well-documented across the area (Burrows 1994, McCaw *et al* 2002) (figures 1(a)–(f)).

The Southern Forests fall within the Swan Coastal Plain, Jarrah Forest and Warren bioregions (Thackway and Cresswell 1995). They are dominated by dry sclerophyll eucalypt forest of principally jarrah *Eucalyptus marginata*, with tall wet forests of karri *E. diversicolor*, marri *Corymbia calophylla*, and red and yellow tingle *E. jacksonii, E. guilfoylei* in the high rainfall, rich soils of the Warren bioregion (Wheeler *et al* 2002).

2.2. Measuring flammability dynamics

We measured flammability dynamics from the mapped fire history of the study area, using ArcGIS software to measure the likelihood of fire at a point. Likelihood is equal to the proportion of each available age class burnt in a given year. This has been termed Probability of Ignition at a Point (Gill *et al* 2000), but we have used 'likelihood' because the term 'ignition' may suggest a point of fire origin. We examined the likelihood of fire at a point in all years to 2018. Consistent records began in 1954, but we commenced measurement in 1964 once much of the area had been burned more recently and therefore had a more reliable baseline from which to conduct measurements.

2.2.1. Quantifying flammability dynamics

We tested our first two hypotheses by examining flammability dynamics (likelihood of fire at a point) for the entire 55 year dataset. The point of differentiation between H1 and H2 was the presence or absence of a mature flammability period that was less flammable than the overall mean flammability, so we required a process to objectively differentiate between flammability periods based on their mean values. While this allows differentiation between flammability periods in one sequence of age classes, our intention also was to compare sequences across different climatic conditions, and such a comparison requires mean values based on standardised time periods. To address this, we estimated standardised ages to delineate between flammability periods, and enable the comparison of sequences across climatic groupings. These were based on flammability periods prior to the most recent warming, rounded to five yearly intervals. We therefore utilised two sets of values to delineate flammability periods—significant groupings for use within one set of climatic conditions, and standardised groupings for use across climatic classes.

To delineate young, regrowth and mature flammability periods within a sequence (significant groupings), we calculated transition points between classes using two moving windows. Window one was the mean of all wildfire likelihood values from 1 year up to and including the age class in question. Window two was the mean of all wildfire likelihood values from the age class in question up to and including the oldest age class of 65 years. For each group of ages, we compared both windows to the mean of all age classes combined by using a Student's *t*-test. We identified the length of the young period Y as the oldest point for which window one was significantly ($p < 0.05$) smaller than the mean of all values. For example, if the young period is five years, then the mean likelihood of wildfire from years 1–5 (window one) is significantly lower than the mean of the full dataset, but the mean of years 1–6 is not significantly lower than the mean of the full dataset. We then compared window two to the overall mean in the same way, to find whether a point occurred at which the mean likelihood of wildfire of all older values was significantly smaller than the mean of all likelihood values. If such a transition occurred, we termed the years between Y and this point the regrowth period R, and the years beyond that point the mature period M. For example, if the regrowth period is 40 years, then the mean likelihood of wildfire from years 41–65 (window two) is significantly lower than the mean of the full dataset and marks the mature period, but the mean of years 40–65 is not significantly lower than the mean of the full dataset. We then found the Feedback Strength FS as the mean likelihood of wildfire for the disturbed period (young, or young + regrowth years) divided by the mean likelihood of wildfire of all mature (M) years (Zylstra 2018).

Where FS was significantly ($p < 0.05$) different from unity, H0 was rejected. If it was less than unity, H1 (biomass-driven risk) was supported, and conversely if it was greater than unity, H2 (disturbance-driven risk) was supported.

To determine whether mature ages arose due to sheltering effects of complex terrain, we compared slopes in forests >50 years in the final year of analysis (2018) to the full distribution of slopes to see

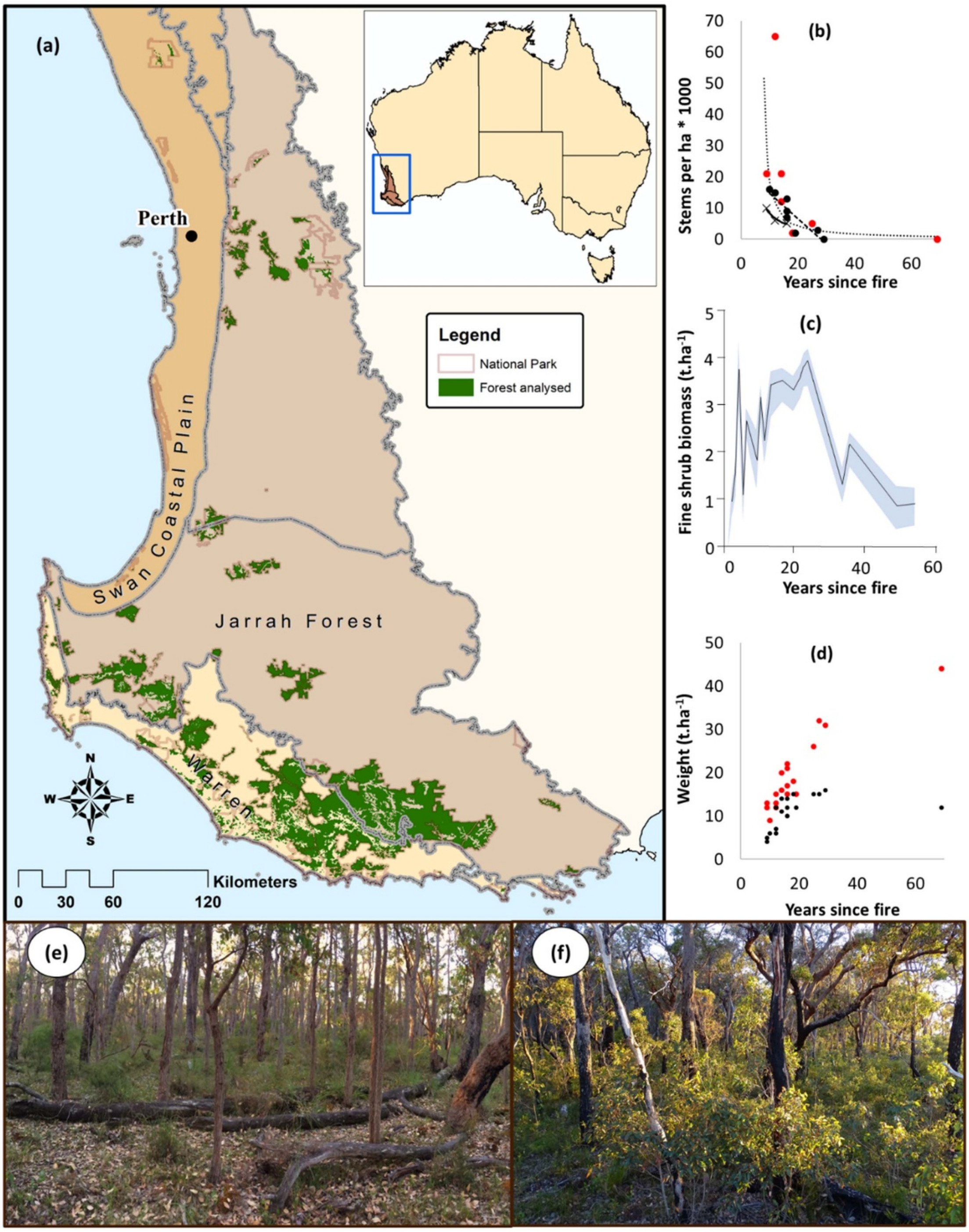

Figure 1. Understorey and litter dynamics in the study area. (a) Fire histories were analysed across forested areas (green) in National Park estate (brown polygons) in the Swan Coastal Plain, Jarrah Forest and Warren bioregions. (b) Previous analysis shows pronounced stem-thinning in the dominant understorey species of tall forests (McCaw *et al* 2002). Points mark individual sites measured for *Bossiaea laidlawiana* (red), *Acacia pentadenia* (black circles), and *Trymalium odoratissimum* (black crosses), with separate trend lines fit to each. (c) Fine shrub biomass (<4 mm diameter) in jarrah forests dominating the mid and low forest classes increases for 22 years after fire, then self-thins in a pronounced, long-term decrease (Burrows 1994). Shading shows the standard error for measurements. (d) Fine necromass $\leqslant$6 mm in the litter of tall forests (red points) increased in a negative exponential trend, and suspended litter $\leqslant$25 mm including collapsed shrubs (back points) increased initially, then decreased slowly (McCaw *et al* 2002). (e) Example of jarrah forest ∼60 years after fire with a self-thinned understorey, f) the same site showing dense understorey regrowth stimulated by a low-severity fire ∼5 years earlier.

whether there was a significant difference. As there is no standard value available that may indicate a meaningful difference, we visually compared the histograms for each distribution produced by ArcMap software (ESRI 2015).

2.2.2. Climatic interactions with flammability dynamics

We examined the relationship of annual area burned to 18 climatic variables (SI appendix table S1 available online at stacks.iop.org/ERL/17/044022/mmedia).

Sixteen of these were taken from records kept by the Australian Bureau of Meteorology (Bureau of Meteorology 2021) and covered trends in annual and seasonal temperature as well as synoptic trends. We also included the Southern Annular Mode, as trends in the SAM have been linked to increased fire impacts, particularly in the Warren Bioregion (Bates *et al* 2018, Mariani *et al* 2018). Given the influence of drought and vegetation moisture-stress on wildfire area (Nolan *et al* 2016, Ellis *et al* 2021, Rao *et al* 2022), we also included the Standardized Precipitation-Evapotranspiration Index (Beguería *et al* 2010, Vicente-Serrano *et al* 2010) in our analysis. Other factors commonly included in fire behaviour models and fire danger indices such as the Australian Forest Fire Danger Index and the Fire Weather Index (Dowdy *et al* 2009) include wind speed and vapour pressure deficit, but records of these were available only for more recent decades (NASA 2022).

First, we identified those variables having a significant ($p < 0.05$) correlation with the area of wildfire burned, and whether they exhibited a temporal trend (significant correlation with year, $p < 0.05$). After examining these variables for autocorrelation and visual trends with correlation plots, we applied transformations to any trends that were clearly non-linear, then combined predictors into multiple linear regressions. We limited these models to the strongest three predictors to avoid over-fitting. By testing all combinations of 1–3 predictors, we constructed seven models, which we ranked by AIC (Akaike 1974). Using the best predicting model, we ranked the years of our study from least likely to most likely to burn as predicted by climate alone, then divided them into tertile groups of low, moderate and high climatic risk of fire.

To test whether climatic factors overwhelmed historical flammability dynamics, we divided the data for likelihood of fire at a point into the three tertiles for climatic risk of fire. For each dataset, we delineated the flammability periods as per 2.2.1. Using the lower two tertiles to represent climatic conditions prior to the most recent warming, we rounded the cut-off ages for the moderate tertile to the nearest five years to create the standardised period, then repeated the hypothesis tests of 2.2.1. If the results of these tests differed between the three datasets (i.e. if the vegetation-fire feedback changed direction or disappeared), then H3 (climate-controlled risk) was supported. If the results were unchanged, i.e. the vegetation-fire feedbacks remained constant across climatic conditions, then H3 was rejected.

3. Results

3.1. Flammability dynamics

Feedback strength was significantly greater than unity, providing support for the disturbance-driven risk hypothesis (H2, positive feedback) and rejection of both the biomass-driven risk hypothesis (H1, negative feedback) and the null hypothesis H0 (table 1). Over our 55 year study period, disturbance by fire has been followed by seven years of reduced fire likelihood (Y), then by 49 years of increased fire likelihood (R). After the 56 year period of disturbance, the likelihood of fire fell below the long-term average (M) and continued to decline, so that disturbed forests have been 7.4 times more likely to burn than long-unburnt forests (table 1).

Forests older than 50 years in 2018 occurred on slopes averaging 2.0° ($s = 1.7$), which did not differ significantly from the overall mean slope for the study area ($\bar{x} = 1.9°$ ($s = 1.8°$, figure 2).

3.2. Climatic interactions

We found no support for H3 (climate-controlled risk; rather, the positive feedbacks we had measured remained positive in all three tertiles of climatic conditions (table 2 and figure 3(c)).

Of the 19 climatic variables we examined, seven exhibited a significant correlation with the area annually burned by wildfire (table S2). The strongest and most significant relationship was with synoptic variability ($r = 0.46, p < 0.001$), which is the average number of high- and low-pressure systems per season, for all four seasons. No drivers had a clearly non-linear relationship to area of wildfire (figure S1).

When model combinations were examined, the most parsimonious model was a linear relationship with synoptic variability (table S3), so that an annual average increase of one synoptic change per season equated to an additional 14 400 ha burned in the study area (figure 3(a)). Synoptic variability declined slightly in initial years to reach a minimum in the late 1960s, then increased to a much greater extent for the remainder of the study period (figure 3(b)).

This climatic effect did not remove or reverse the vegetation-flammability feedback, which was positive for all three tertiles of climatic effect for both the significant divisions and the standardised divisions of 1–5 years (Y), 6–50 years (R), and >50 years (M) (table 2). Instead, years with high synoptic variability (>12.30 changes per season) experienced increased likelihood of fire at all forest ages, compared to years with low (<11.34 changes per season) to moderate (11.34–12.30 changes per season) synoptic variability (figure 3(c)). This increase was consistent, even when standardised time periods were used to divide young, regrowth and mature periods. The period of maximum flammability (regrowth) also increased from 37 years in periods of low synoptic variability, to 49 years in periods of high synoptic variability (table 2).

The likelihood of fire in disturbed forests during years with high synoptic variability was approximately twice that in years of low to moderate variability (table 2). Mature forests that had been unburnt for at least 50 years did not reburn except in periods of

Table 1. Flammability dynamics. For each period, 'transition' is the statistically-significant ($p < 0.05$) age at which the period ends, and 'likelihood' is the likelihood of fire (ha^{-1} $year^{-1}$) averaged over that time period. Feedback strength is the mature-period likelihood/disturbed-period likelihood. For the disturbed and mature periods, the fire return interval (1/likelihood, years) is shown in brackets.

Young period		Regrowth period		Disturbed period	Mature period	Feedback strength
Transition	Likelihood	Transition	Likelihood	Likelihood	Likelihood	FS
7	0.010	56	0.0232	0.023 (1/43)	0.0031 (1/323)	7.4

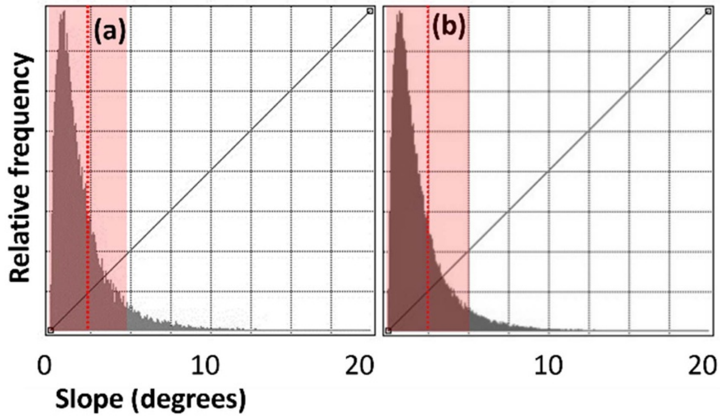

Figure 2. Slope distributions. (a) Distribution of slopes across the full study area, and (b) in mature (>50 years) forests in 2018. Red line and shaded area show the mean and standard deviation for each.

high synoptic variability, but even under these conditions, they were over three times less likely to burn than young, recently-burned forests (table 2).

4. Discussion

We found that wildfire has been rare (1/323 years, table 1) in the Southern Forests of southwestern Australia, except where previous disturbance has promoted the development of a shrubby understorey (1/43 years, table 1). This was particularly pronounced in years with low to moderate synoptic variability mostly occurring prior to 2000 (figure 3(b)), in which no wildfire at all was recorded in forests after 50 years of recovery since a previous disturbance (table 2).

The effect of the shrub understorey on wildfire risk has previously been demonstrated mechanistically (Zylstra *et al* 2016), and is well documented for major areas of the Southern Forests dominated by *E. marginata*. An extensive experimental burning program in these forests found that the understorey is the primary driver of both flame height and rates of spread (Cheney *et al* 2012, Cruz *et al* 2022). While such a finding provides mechanistic support for our finding in favour of H2, that research also reported that wildfire behaviour was most extreme in long-unburnt forests (McCaw *et al* 2012), apparently supporting H1. This apparent discrepancy likely arose because all forests studied in that experiment had been burned within the previous 22 years, which was the point at which earlier work in the same forests had identified the maximum fine shrub biomass (<4 mm diameter, figures 5–7 in (Burrows 1994)). As a result, the oldest 'long-unburnt' sites were actually at the peak of their disturbance-induced period of flammability (figure 1(c)). The flammable regrowth period continues for some decades after this until the cover of senescent shrubs declines. For these reasons, we suggest that the term 'long-unburnt' properly applies to forests in the mature flammability stage, and that its application to disturbed forests may produce misleading results.

This example of the mis-alignment of flammability periods to flammability risk highlights a source of confusion in the global body of literature addressing flammability dynamics. For example, a recent review of empirical analyses of flammability dynamics identified only two studies that examined forests not burnt within the previous 10 years (Hunter and Robles 2020). Earlier reviews suffered similar limitations (Fernandes and Botelho 2003, McCaw 2013), reflecting a widespread focus on the first decade as the period during which any benefits of disturbance-based management can be detected (Buma *et al* 2020). Our concern is that such an approach excludes any subsequent decline in flammability resulting from processes of growth and succession that are not anthropogenic, such as those we have recorded for the Southern Forests. Given the widespread occurrence of dynamics such as self-thinning of understoreys (Wilson *et al* 2018, McColl-Gausden *et al* 2020) and

Table 2. Climatic interactions with flammability dynamics. For each period, 'transition' is the climatic grouping, which is the statistically-significant ($p < 0.05$) age at which the period ends, and 'likelihood' is the likelihood of fire ($ha^{-1}year^{-1}$) averaged over that time period. Likelihood is also shown for standardised periods in each age range, and feedback strength is given as both the mature-period likelihood/disturbed-period likelihood, and using standardised time periods (likelihood in forest > 50 years/likelihood in forests ⩽ 50 years). For the disturbed and mature periods, the fire return interval (1/likelihood, years) is shown in brackets. Synoptic variability classes are are the tertile divisions of the full dataset.

	Young period			Regrowth period			Disturbed period		Mature period		Feedback strength	
	Significant division		Standardised division	Significant division		Standardised division	Significant division	Standardised division	Significant division	Standardised division	Significant division	Standardised division
Synoptic variability	Transition	Likelihood	0–5-year likelihood	Transition	Likelihood	6–50 year likelihood	Likelihood	0–50 year likelihood	Likelihood	>50 year likelihood	FS	Standardised FS
Low (<11.34 changes/season)	6	0.0040	0.0033	43	0.0204	0.0235	0.0245 (1/41)	0.0214 (1/47)	0.00087 (1/1149)	0 (never)	28.1	∞
Moderate (11.34–12.30 changes/season)	5	0.0029	0.0029	49	0.0131	0.0148	0.0138 (1/72)	0.0136 (1/74)	0 (never)	0 (never)	∞	∞
Low-moderate (<12.30 changes/season)	5	0.0031	0.0031	43	0.0158	0.0167	0.0162 (1/62)	0.0153 (1/65)	0.0032 (313)	0 (never)	5.1	∞
High (>12.30 changes/season)	7	0.015	0.0085	56	0.033	0.0348	0.0325 (1/31)	0.0322 (1/31)	0.0048 (1/208)	0.0187 (1/53)	6.8	1.6

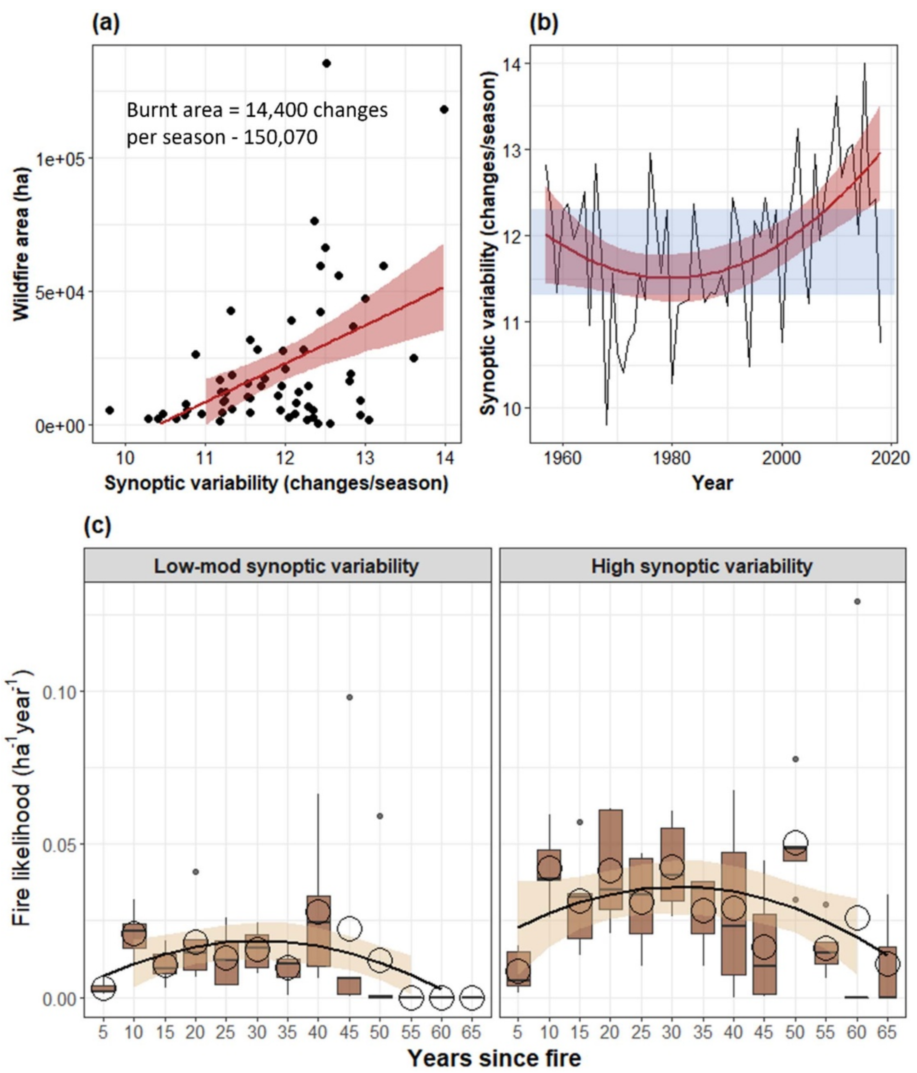

Figure 3. Climatic drivers and flammability feedbacks. (a) Annual area of wildfire correlates closely with the mean annual number of synoptic changes per season (synoptic variability, red shaded area shows standard error). (b) Synoptic variability has a strong, nonlinear temporal trend with a pronounced increase since 1980 (red shaded area shows standard error, blue shading marks moderate synoptic variability). (c) The likelihood of forest fire at a one-hectare point had an initial increase after fire, followed by a long-term decrease in likelihood as forests matured in both years of low (left) and high (right) synoptic variability. Circles mark mean values for each age class, and the lines mark the long-term trends, with the brown shaded area marking the standard error.

the fact that so many studies exclude evidence that may indicate a positive feedback, positive feedbacks may be more common than currently realised. Indeed, where longer time periods have been examined, positive feedbacks between stand age and reduced flammability have been measured in forest ecosystems including conifer forests (Nowacki and Abrams 2008, Odion *et al* 2010, Malone *et al* 2011); semi-arid to montane and subalpine eucalypt forests (Haslem *et al* 2011, Gosper *et al* 2012, Zylstra 2018, Lindenmayer *et al* 2021); temperate forest and tropical rainforest (Cochrane *et al* 1999, Kitzberger *et al* 2016); montane *Nothofagus* forest (Tepley *et al* 2016, Tiribelli *et al* 2018); and savanna-forest systems (Scott *et al* 2012, Oliveras and Malhi 2016).

High-severity fire has been found in some cases to promote denser regrowth in understoreys and consequent positive feedbacks to flammability (e.g. (Collins *et al* 2021b)). Severity data were unavailable for much of the period of our study, but the increased flammability that we measured may be broadly characterised as a response to prescribed burning, as that accounts for more than 80% of fire in the majority of our forested study area (Boer *et al* 2009). A recent study found that the median severity of prescribed burns in Eastern Australian eucalypt forests was 'high' (complete crown scorch, (Price *et al* 2022)), compared to a median severity of 'moderate' in wildfires for the same region (Collins *et al* 2021a). Given that positive severity feedbacks in that region have been most pronounced following high severity fire (Barker *et al* 2021), it is possible that a regime dominated by wildfires may have a less pronounced peak in flammability. Cultural burning practices have been shown to both consume less surface litter and burn at a significantly lower severity than prescribed burns (Price *et al* 2022), potentially reflecting their very small scale and location-specificity (Lullfitz *et al* 2020). Consumption of surface litter can promote regeneration following even low severity fire (e.g. figures 1(e) and (f)) by heating soil seed banks (Zylstra 2021). Therefore, cultural burning may promote less regeneration than either prescribed or wildfire.

The onset of anthropogenic climate change has increased the frequency of years in our study area that have high synoptic variability, with a coincident increase in wildfire area. One part of the mechanism driving this may be the weather associated with the onset of low-pressure systems, potentially including strong winds, atmospheric instability, lightning, and other factors that drive extreme fire behaviour (Di Virgilio *et al* 2019). The relationship between wildfire likelihood and synoptic variability was stronger than with the frequency of low pressure systems alone, however, and this may indicate the influence of other factors. In particular, fire suppression operations such as backburning rely on suitable 'windows' of still, stable atmospheric conditions that are less conducive to severe fire behaviour and typical of high-pressure systems (Di Virgilio *et al* 2019, Simpson *et al* 2019). Greater synoptic variability implies a faster rate of change and therefore shorter windows of opportunity, so such seasons may limit the chances for such strategies, or expose backburns to the stronger winds and greater instability of low-pressure fronts, leading to their escape and contribution to the total burnt area (Simpson *et al* 2021).

It is possible that the findings presented in this study relating synoptic variability to wildfire likelihood are particular to our study site and not transferrable to other locations where management differs or other factors have greater influences. It is also possible that other factors such as wind speed and vapour pressure deficit may have exhibited stronger correlations with annual area burned, but as long-term data were unavailable, this could not be tested. Despite this, our analysis considered 16 possible climatic influences in addition to the two climatic drivers of drought and SAM-induced lightning trends previously examined (Boer *et al* 2009, Bates *et al* 2018, Mariani *et al* 2018). As a result, we have identified a previously unconsidered climatic relationship that is stronger than those examined earlier (Boer *et al* 2009, Bates *et al* 2018). Critical to our study, we also showed that the internal ecological controls on flammability afforded by understorey thinning continues to operate as the climate changes. Even in years with a severe climatic influence on wildfire, mature forests were the least likely to burn.

4.1. Conclusions: ecological cooperation

Our findings indicate that self-thinning forest understoreys result in long-term reductions in fire risk that are robust even in the face of global warming. Where shrubs are known to self-thin with time since disturbance, management that minimises disturbance and capitalises on the value of mature forests for risk reduction will likely lead to long-term reductions in fire likelihood, countering the climate-driven trend of increased fire impact.

Much research has focused on the short period of reduced flammability that may be achieved through disturbance (young period) and excluded the longer-term dynamics initiated by this disturbance. Ignoring these long-term dynamics can introduce a misleading anthropocentric conceptualization of fire in forests, in which human intervention is needed to minimise the risks of fire. Our findings demonstrate that forests have natural, ecological controls on wildfire that have likely enabled the persistence of fire-sensitive species over geological time (Wardell-Johnson and Coates 1996, Kooyman *et al* 2020) and continue to operate effectively even in the face of a warming climate.

Here, we introduce the concept of 'ecological cooperation' to describe a response to fire that accomodates this reality. This may be understood in two levels—reconciliation and reinforcement. Reconciliation is the process by which managers no longer treat mature forest as a hazard that must be mitigated, and instead minimise anthropogenic disturbance of it. Reinforcement accounts for the fact that wildfire likelihood has increased due to climate change and other anthrogenic activity, and that landscape flammability has also increased if previous intervention has promoted widespread, dense understorey growth. Ecologically cooperative approaches therefore aim to balance these factors with interventions that assist forest to mature, and suppress fires in areas where self-thinning has reduced their severity. Actions may include the use of rapid suppression to encourage the development of contiguous mature forest in strategic areas by protecting regrowth forests from disturbance.

Ecological cooperation allows for Indigenous ways of coexistence with fire without the pressure to appropriate them into colonial paradigms. For example, studies in eastern Australia indicate that, compared to prescribed burning, cultural burns remove only ~2/3 of what is considered 'fuel' in the biomass-driven risk hypothesis (Price *et al* 2022). Cultural burning traditions in southwestern Australia are also highly site-specific and localised (Lullfitz *et al* 2020) rather than broadscale. Prior to colonisation, for example, the tall forests with the heaviest fuel loads were deliberately left unburned (Pers. Comms Dr Wayne Webb, Pibulmun elder, 24 September 2021, (Pedro 2017)), so that fire scars on karri were extremely rare prior to 1850, despite their ready scarring by modern prescribed burns (Rayner 1992). These traditions fit poorly with a paradigm in which management implies intervention and measures success by the quantity of fuel removed, but are consistent with an approach of ecological cooperation.

If human societies are to sustain long-term interactions with forests in the context of a changing climate, it is essential that we develop ecologically-cooperative approaches that reinforce rather than disrupt such natural controls.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://github.com/pzylstra/SW_PIP.

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