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Time since fire and prior fire interval shape woody debris dynamics in obligate-seeder woodlands

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Abstract. Woody debris plays an important role in many ecosystem functions, including nutrient and carbon cycling, providing substrates for plant recruitment and habitat for fauna. Fires can affect woody debris stocks, through generating new pieces by killing or severing plant parts and consuming pre-existing woody debris. We develop a model of woody debris dynamics with variation in time since fire and prior fire interval applicable to obligate-seeder forests and woodlands, considering down woody debris and standing dead trees as discrete components. We then test predictions of change in woody debris derived from this model in *Eucalyptus salubris* woodlands in South-Western Australia, using a multi-century chronosequence with recent fires varying between having short (<50 yr since the previous fire) or long (>50 yr, but often much longer) prior intervals. As per our woody debris dynamics model, most attributes measured were affected by time since fire, prior fire interval, or their interaction. Woody debris biomass was greatest shortly after fire, reflecting high quantities of standing dead trees resulting from stand-replacement disturbance. Standing dead tree density and biomass then declined with increasing time since fire, but individual dead tree size was high beyond 200 yr since fire. Down woody debris biomass remained relatively stable with time since fire, but piece size increased. Dimensions of woody debris were strongly influenced by prior fire interval, with long prior intervals resulting in pieces at least twice the size than those occurring after short prior intervals. Fire management to maximize the availability of large woody debris pieces for fauna should aim to minimize short fire intervals, while from a carbon management perspective, all fires in obligate-seeder forests and woodlands set in train large and prolonged emissions of carbon.

Key words: chronosequence; coarse woody debris; ecological fire management; eucalypt; Great Western Woodlands; logs; snag; stag; stand-replacement; succession.

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INTRODUCTION

Woody debris, comprising both standing dead trees and pieces of trunks, branches, and roots lying on the ground surface (down woody debris; DWD), has a role in many important ecosystem functions (Harmon et al. 1986). Woody debris harbors carbon and nutrients, and influences surrounding soil properties and plant recruitment (Goldin and Hutchinson 2013, Goldin and Brookhouse 2015). Woody debris also provide shelter, basking, and foraging habitat for a range of animals, and energy and nutrients for decomposer organisms (Harmon et al. 1986, Lindenmayer et al. 2002, Luck 2002). For many animals, the habitat value of woody debris is determined by the size

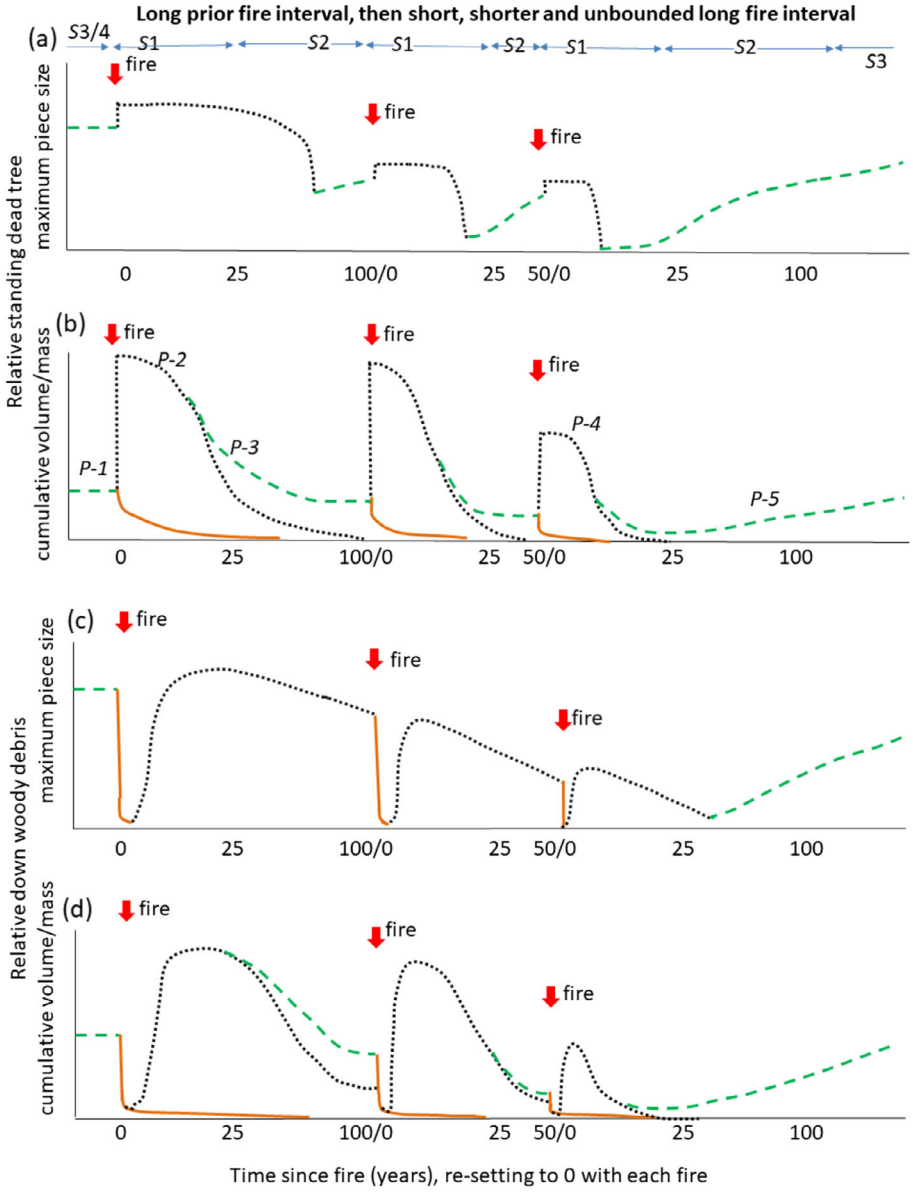


Fig. 1. Model of standing dead tree (a, b) and down woody debris (c, d) dynamics with fire in obligate-seeder forests and woodlands. A multi-fire event scenario encompassing variation in time since fire and prior fire interval is presented, starting with a long prior fire interval reflecting the current predominance of long-unburnt obligate-seeder eucalypt woodlands in the Great Western Woodlands (Gosper et al. 2013a, 2019). A 100-yr interval follows an initial fire, followed by a short 50-yr interval and then an unbroken long interval exceeding 150 yr. The time periods for what constitutes short and long intervals for the parameterization of this model and the timeframes for changes with time since fire are based on obligate-seeder *Eucalyptus salubris* woodlands of South-Western Australia. In all figure parts, the contributions of different cohorts of woody debris are indicated. In (a), the distribution with respect to time since fire of the woodland states (S) of the vegetation dynamics model of Gosper et al. (2018) are shown: S1, recruiting woodland (after stand-replacement disturbance); S2, dense sapling stand; S3, mature stand lacking inter-fire eucalypt recruits; and S4, mature stand with inter-fire eucalypt recruits.

(Fig. 1. *Continued*)

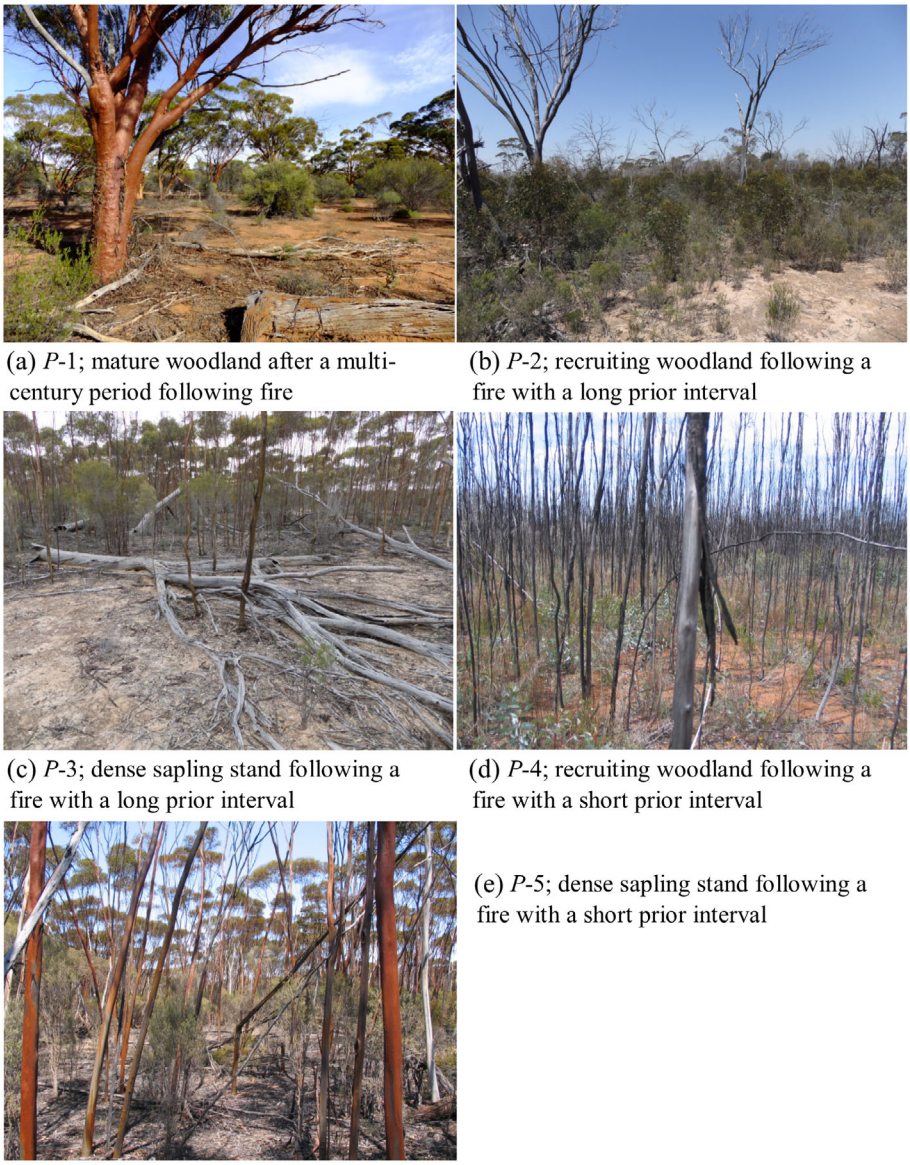
In (b), the approximate placement with respect to time since fire and prior fire interval of accompanying photographs (*P*-; Fig. 2) are shown. Note that the *x*-axis (time since fire) is square-root transformed, as per the statistical analyses in this paper. Woody debris cohort: — that persisted through a fire event; ····· derived from fire-killed vegetation; – – generated by non-fire processes.

and condition of pieces (Lindenmayer et al. 2002). For example, many vertebrates prefer large pieces with hollows to support denning, nesting, or sheltering individuals (Dickman 1991). Because of these values, it is important for ecosystem managers to understand how vegetation attributes and disturbances affect the dynamics of woody debris.

In seasonally dry woodlands and forests, fires play a critical role in the generation and persistence of woody debris (Acker et al. 2013, Aponte et al. 2014, Donato et al. 2016). Fire creates woody debris through killing or severing parts of plants, or weakening plants facilitating subsequent mortality or breakage by wind or other factors (Harmon et al. 1986). Fire can also remove woody debris by burning pieces that were present at the time of fire (Aponte et al. 2014, Donato et al. 2016). Various attributes of the fire regime, such as intensity, season, interval, frequency, and time since fire, influence the processes of generation and persistence of woody debris (Williams and Faunt 1997, Acker et al. 2013, Aponte et al. 2014, Bassett et al. 2015).

The effects of attributes of the fire regime on woody debris can be influenced by the post-fire recovery traits (sensu Clarke et al. 2015) of constituent plant species. Fires are likely to have particularly pronounced effects on woody debris in forest and woodland communities dominated by obligate-seeder species. Obligate seeders are, by definition, killed by fires of intensities typical of the habitat in which they occur, and persist after fire through fire-stimulated seedling recruitment (Clarke et al. 2015). As an example of the effects time since fire may have on woody debris dynamics in obligate-seeder forests and woodlands (see following section for more detail and specific predictions), fire events immediately produce large numbers of standing dead trees, which are subsequently incorporated into the DWD pool over time as these trees fall. Prior fire interval is also likely to have a large bearing on woody debris stocks and characteristics in obligate-seeder forests and woodlands. Pre-fire plant size, and hence potential woody debris inputs, is strongly positively linked to the length of the prior fire interval (i.e., older plants are larger; Figs. 1, 2; Spies et al. 1988, Gosper et al. 2013a, Donato et al. 2016). Intervals between stand-replacing fires in some communities dominated by obligate-seeder trees can range from decades to multiple centuries (Taylor et al. 2014, Gosper et al. 2018, Tiribelli et al. 2018), illustrating the potential for differences in tree size arising from variation in prior interval to strongly shape post-fire woody debris dynamics. In contrast, woody debris dynamics are likely to be much less strongly influenced by time since fire and prior fire interval in communities dominated by epicormically resprouting trees. In these plants, protected buds under bark typically mediate trunk survival through fire, with the consequence that these components of biomass potentially remain as live vegetation (c.f. woody debris) through multiple fire events (Pausas and Keeley 2017, Collins 2019). Many biomes contain a mix of obligate-seeder and epicormic-resprouter dominated forests and woodlands (Clarke et al. 2015), complicating efforts at generalizing the effects of fire events and regimes on woody debris dynamics if plant fire response traits are not considered.

Obligate-seeder eucalypts are found in wet forests of South-Eastern Australia, and in dry to semi-arid woodlands and scrubs in South-Western Australia where they are particularly widespread and species-rich (Nicolle 2006, Gosper et al. 2018). Obligate-seeder eucalypt woodlands occur across approximately half of the Great Western Woodlands (GWW) of South-Western Australia, a 16 million ha area comprising the world's largest extant temperate woodland (Watson et al. 2008). These woodlands support trees of unusually large stature relative to productivity in comparison to similar ecosystems globally (Milewski 1981, Gosper et al. 2018), providing the basis for significant woody debris stocks (Fig. 2). Large trees exist despite fires and other more localized disturbances leading to stand replacement (Yates et al. 1994, Gosper et al. 2018). Fires in these woodlands are rare, with discontinuities in fuel rendering



(a) *P*-1; mature woodland after a multi-century period following fire

(b) *P*-2; recruiting woodland following a fire with a long prior interval

(c) *P*-3; dense sapling stand following a fire with a long prior interval

(d) *P*-4; recruiting woodland following a fire with a short prior interval

(e) *P*-5; dense sapling stand following a fire with a short prior interval

Fig. 2. Representative photographs of obligate-seeder *Eucalyptus salubris* woodlands with various combinations of time since fire and prior fire interval. The approximate placement of the stands in the photographs (*P*-) on the model of standing dead tree and down woody debris dynamics is shown in Fig. 1b.

mature woodlands relatively resistant to burning despite regular severe fire weather (O'Donnell et al. 2011, Gosper et al. 2014). Consequently, multi-century intervals between fires are common (O'Donnell et al. 2011, Gosper et al. 2013a). Since ~1970, however, 25–30% of woodland area in the GWW has been burnt in a number of often large (>100,000 ha) fires, including large areas of formerly long-unburnt woodland (Gosper et al. 2018, 2019). As recovery of woodland vegetation composition and structure, and faunal communities, occurs over multi-century timescales (Gosper et al. 2013b, c, 2019), and woodlands regenerating after fire appear to be more flammable (O'Donnell et al. 2011, Gosper et al. 2013c, 2014), short fire intervals and the further loss of old-growth woodlands through ongoing fire is regarded as a substantial threat to the ecological values of the

region (Prober et al. 2012, Gosper et al. 2018), as it is for some other obligate-seeder eucalypt communities (Bowman et al. 2014, Fairman et al. 2016).

In this study, we quantify woody debris stocks in a widespread and representative obligate-seeder dominated eucalypt woodland with variation in time since fire over a multi-century chronosequence (Gosper et al. 2013b, c), and previous fire interval. We had two main objectives:

1. Construct a model of woody debris dynamics, based on existing literature, applicable in wooded ecosystems in which fire operates as a stand-replacement disturbance, as a framework for developing predictions for changes in woody debris with time since fire and prior fire interval; and
2. Test how attributes of woody debris change with time since fire and prior fire interval in our obligate-seeder eucalypt woodland study system, and determine whether these changes are consistent with our woody debris dynamics model.

The results of these investigations will inform fire management from the perspective of maximizing the ecological benefits provided by woody debris in obligate-seeder forests and woodlands.

Model of woody debris dynamics with time since fire and fire interval in obligate-seeder forests and woodlands

Several authors have developed conceptual models describing the effects of some fire regime elements on aspects of woody debris dynamics. These models, developed in ecosystems ranging from obligate-seeder coniferous forests to epicormic-resprouter eucalypt forests, project changes in total woody debris mass or volume with time since fire, considering the contributions of different cohorts of woody debris based on process and period of origin, and in some cases, the effect of subsequent disturbances (Harmon et al. 1986, Spies et al. 1988, Bassett et al. 2015, Donato et al. 2016). Here, we build on these models by explicitly including variation in fire interval, considering multiple attributes of woody debris, and by developing complementary models for dynamics of standing dead trees and DWD because of putative differences in how these woody debris pools respond to fire parameters and contribute to ecosystem functions.

Our model is proposed to be relevant to all obligate-seeder dominated forests and woodlands (e.g., Eastern Australian ash eucalypt forests, many boreal, temperate, and Mediterranean forests; Lindenmayer et al. 1999, Taylor et al. 2014, Donato et al. 2016, Tiribelli et al. 2018) experiencing stand-replacement vegetation dynamics in response to fire, albeit with differences in the scale and timing of responses reflecting differences in ecosystem productivity, decomposition processes, and biotic interactions. Specific features of the model are illustrated with photographs from our South-Western Australian obligate-seeder eucalypt woodland study system, as is the parameterization of woody debris temporal dynamics (Figs. 1, 2).

We posit that time since fire and fire interval will act singularly and in combination to affect woody debris stocks. Our conceptual model (Fig. 1) depicts these fire regime-related changes for two important attributes of woody debris, cumulative volume/biomass, and maximum piece size, with changes in additional attributes described below:

1. Immediate post-fire peak in standing dead trees, delayed peak in DWD: Obligate-seeder trees are, by definition, killed in stand-replacement fires (noting that some or most individuals may survive lower intensity fires and that in such circumstances will not follow this model of woody debris dynamics; Gosper et al. 2018). Stand-replacement fire thus results in an immediate transition from a stand of mostly live trees to one of all or mostly standing dead trees (Figs. 1, 2b, d). Collapse of fire-killed trees in the years following fire (over a period of 0–20 yr, Acker et al. 2013; but likely longer in some ecosystems) will lead to a pulse in DWD occurrence shortly, but not immediately, after fire (Taylor et al. 2014). We also predict, but do not test in this study given the temporal distribution of our samples, that DWD will occur at reduced levels immediately post-fire, with DWD that existed prior to the fire being mostly consumed in the fire (Hollis et al. 2018) but with most fire-killed trees still standing. Following the post-fire peak, the volume/mass of both standing dead trees and DWD will then decline as standing dead trees fall and woody debris derived from the

fire event weathers and decomposes. New sources of woody debris are limited for an extended period post-fire, as new additions from non-fire sources are minimal (Figs. 1, 2c, e) until trees grow in size and density-dependent thinning of post-fire recruits commences. Those pieces that are generated from stand thinning are relatively small, reflecting the size of regenerating saplings (Bassett et al. 2015, Gosper et al. 2018).

2. Vegetation dynamics over the inter-fire period: Rates of woody debris input after long periods without fire may vary with idiosyncratic features of the dominant vegetation and non-fire disturbances, such as the longevity of the post-fire tree and shrub cohorts and rates of density-dependent thinning, decomposition, wind-throw, disease, and drought. Community vegetation dynamics are likely to be particularly important in shaping whether woody debris volume/mass increases in long-unburnt vegetation compared to intermediate times since fire. A U-shaped relationship between attributes of woody debris and time since fire appears typical of Northern Hemisphere obligate-seeder coniferous or boreal forests (Spies et al. 1988, Hall et al. 2006, Fournier et al. 2012, Taylor et al. 2014), in communities which typically demonstrate relay (Clements 1916) succession. In contrast, in communities where the initial floristic composition model of vegetation dynamics (Egler 1954) is applicable, such as obligate-seeder eucalypt woodlands (Gosper et al. 2013b, 2018), the volume/mass of new woody debris with long times since fire may remain low, with new inputs plausibly being offset by decay of older pieces. In both cases, woody debris derived from the previous fire will be lost through weathering and decomposition by the time obligate-seeder forests and woodlands mature, >100 yr post-fire in the case of obligate-seeder eucalypt woodlands, such that new standing dead trees and DWD inputs are due to non-fire processes (Gosper et al. 2018; Figs. 1, 2e).
3. Large woody debris pieces in long-unburnt forests and woodlands: Individual woody debris piece sizes generated in the post-fire vegetation are predicted to increase with time since fire, reflecting the increasing average size of individual trees (Lindenmayer et al. 1999, Gosper et al. 2013a, 2018). However, an increasing proportion of the volume of woody debris in long-unburnt vegetation is likely to be contributed by hollow trunks and limbs that develop in live trees prior to their death in some ecosystems (Gosper et al. 2013a), mediated by wood traits and the activity of decomposer organisms.
4. Long prior intervals will result in larger but fewer woody debris pieces after fire than short prior intervals: This prediction is a consequence of longer times since fire (i.e., longer prior intervals) supporting larger pre-fire tree size but lower tree density than shorter times since fire (i.e., short prior interval; Ashton 1976, Gosper et al. 2013a, b, c; Figs. 1, 2a, b *c.f.* d, e). We propose that the shorter the interval (within the bounds allowing stand replacement; Gosper et al. 2018), the lower the size of post-fire woody debris pieces and the higher the abundance of woody debris (Gosper et al. 2013c, 2018, Donato et al. 2016). The effect of prior interval on total woody debris volume/mass is less certain, being dependant on the nature of trade-offs between individual size and stand density that occur with post-fire succession (Gosper et al. 2013c, 2018). Short prior intervals have resulted in substantially reduced post-fire woody debris biomass relative to long prior intervals in some cases (Donato et al. 2016). It is likely that rates of attrition of fire-killed standing dead trees vary depending on tree size (hence prior fire interval; Gosper et al. 2013a), with larger standing dead trees perhaps being more resilient to collapse than smaller standing dead trees (Lindenmayer et al. 1997, Molinas-González et al. 2017). Consequently, the post-fire peak in standing dead trees may be more prolonged, and the peak in post-fire DWD may occur later, after a long, compared to a short, prior interval.
5. Multiple short intervals will lead to loss of legacy woody debris: It is plausible that large woody debris can persist through one or more fire(s) after their fire-initiated generation. However, this legacy buffering fluxes in woody debris stocks is likely eroded with

short fire intervals (Donato et al. 2016). The loss of legacy woody debris, in combination with no generation of new large pieces, may eliminate large woody debris under a regime of multiple short fire intervals.

Methods

Study sites and their time since fire and prior fire interval

Stocks of woody debris were sampled at a subset of the *Eucalyptus salubris* F.Muell. (gimlet) chronosequence plots established by Gosper et al. (2013b, c) in the western parts of the GWW, selected to span the entire range of times since fire available (Appendix S1: Table S1). Site time since fire was derived from a combination of satellite image interpretation, growth ring counts, and modeled ring-plant size relationships (Gosper et al. 2013a; using their more conservative Model 2), giving a range of 6 to ~370 yr. We recognize that *E. salubris* trunk size, as used in the Gosper et al. (2013a) growth ring-size models, is unlikely to be independent of some attributes of woody debris (such as standing dead tree and DWD diameter), so in these cases we duplicated analyses using a time since fire distribution truncated to 100 yr, noting that these more recently burnt sites were all dated with methods independent of trunk size. As the truncated analyses gave very similar results to the untruncated analyses (Appendix S2: Tables S1, S2), we present the untruncated analyses in the main paper for consistency and to maximize value in informing management.

Prior fire interval was determined for all sites with a time since fire of 25 yr or less, based on the presence or absence of evidence of a previous fire at those sites over the period covered by the Landsat archive (post-1972, noting that any fires over the preceding decades are distinguishable in the 1972 imagery; Gosper et al. 2012). Sites were divided into two classes: (1) short prior interval, comprising those with a prior fire occurring shortly before 1972 or more recently (i.e., prior interval <~50 yr); and (2) long(er) prior interval, comprising those with the length of the prior interval unable to be determined but with no evidence of a prior fire having occurred recently (i.e., prior interval unknown but >~50 yr, and likely much greater in most cases). Prior intervals of sites burnt >25 yr ago were unable to be derived due to the absence of comprehensive fire records for the relevant areas and period (Gosper et al. 2016).

Woody debris was sampled within a site of approximately 2 ha in area, of dimensions either ~100 × 200 m or ~400 × 50 m depending on site factors (e.g., fire boundaries, vegetation types).

Sampling woody debris

Standing dead tree size, density, and basal area.— Standing dead trees were defined as eucalypts (i.e., excluding tall shrubs *Melaleuca*, *Hakea*, etc) with a >25 mm diameter at 10 cm from the base with complete canopy death. Note that for obligate-seeder eucalypts such as community-dominant *E. salubris*, this equates to complete individual death, but for infrequent co-occurring lignotuber-resprouter eucalypts, the post-fire top-killed portion was sampled as a standing dead tree even if basal resprouting had occurred. Standing dead trees were assessed at 30 sites (Appendix S1: Table S1).

A visual assessment of the number of cohorts of standing dead trees present and tree density was used to determine which of two sampling methods would most accurately measure stand characteristics. For sites where no standing dead trees appeared to be derived from any previous fire and standing dead trees were uncommon, standing dead trees were sampled in conjunction with live trees using 13 plotless point-centered quarters (Cottam and Curtis 1956) placed at 50 m intervals in a grid. The diameter (at 10 cm from the base) and status (live or dead) of the nearest eucalypt in each of the four compass quadrants around each point was measured, from which total tree density and density of standing dead trees ($SD_{Density}$) was calculated. For sites where fire-killed trees were clearly present and where standing dead tree density was high (visually estimated as >~500 individuals per ha), 13 point-centered quarters were conducted as described above sampling only standing dead trees. At sites where fire-killed trees were clearly present and where standing dead tree density was low, a fixed-area sampling approach was used. Hierarchical sampling of cumulative 0.1-ha subplots, up to a total area of 1 ha, was conducted until the diameter of >50 individual standing dead trees were sampled, from which density could be calculated. Using both plotless

and fixed-area sampling methods potentially introduces bias into the estimates of stand density (and variables derived from stand density); however, we viewed this approach as being the best way to deal with order of magnitude differences in standing dead tree density across the span of times since fire. Specifically, in high density stands (a portion of those recently burnt), inaccuracy in plot layout and counting errors would potentially contribute to erroneous density estimates using fixed-area approaches, while in low density stands (some recently burnt), independence of point-centered quarters was no longer assured, violating an assumption of this method.

In the infrequent multi-stemmed trees, the quadratic mean of the multiple individual stems was calculated to represent total trunk size (diameter; D) in a single value:

$$D_{\text{equiv}} = \sqrt{\sum D_{\text{ind}}^2}$$

For all standing dead tree samples (and DWD), decay was scored on a 5-class scale (Woldendorp et al. 2002): (1) dead leaves and bark firmly attached; (2) leaves, bark, and/or small branches lost but little apparent decay in wood; (3) leaves, bark, and most branches lost and moderately decayed wood; (4) decayed (soft, crumbly) wood but in original shape; and (5) highly decayed (soft, crumbly) wood usually with loss of original shape.

Down woody debris size, density, and volume.—For the purposes of this study, DWD was defined as pieces of dead wood (trunks, branches, or roots) ≥25 mm in diameter that rested on the ground surface for at least part of its length. Specifically, this included fallen trees that may have been elevated off the ground in parts as long as other sections rested on the ground.

Stand-level attributes of DWD were measured with a line intercept method on transects along plot edges and, if required, at 50-m intervals placed across the plot, at the 30 sites at which standing dead trees were measured. Following Van Wagner (1968), the diameter of each piece at the point of intercept with the transect was measured, along with visual estimates of the proportion of the piece's diameter that was intact (not hollow or completely decomposed) and its decay class. Once more than 50 pieces had been sampled, sampling was curtailed to the nearest 10 m and total transect length recorded.

Total DWD volume (Total DWD_{Vol}), which included any hollow centers of pieces and can be considered as reflecting the total volume of woody debris habitat available for fauna, was calculated using Van Wagner's (1968) formula. Total wood volume of DWD (Total DWD_{WVol}) was calculated with a modified version of this formula, accounting for the absence of wood in hollow centers using the estimate of the proportion of the piece that was intact. In this calculation, the hollow portion was assumed to be the inner part of a cylindrical piece.

$$\text{Total DWD}_{\text{vol}}\ (\text{m}^3/\text{ha}) = \frac{\pi^2 \sum D^2}{8L}$$

$$\begin{aligned}\text{Total DWD}_{\text{Wvol}}\ (\text{m}^3/\text{ha}) &= \sum(\text{whole} - \text{hollow volume}) \\ &= \sum\left(\frac{\pi^2 D^2}{8L} - \frac{\pi^2 D_h^2}{8L}\right)\end{aligned}$$

D = piece diameter (cm);
D_h = diameter of hollow portion (cm);
L = transect length (m)

To specifically measure the availability of large DWD pieces that may provide habitat for vertebrate animals, a plot-based approach was used at 57 sites (29 of the above sites and 28 additional; Appendix S1: Table S1). Large DWD was defined as dead wood on the ground at least 0.5 m in length and ≥100 mm diameter at the widest point. Dimensions were visual estimates rather than measurements; however, at commencement of each plot a piece was measured to calibrate the estimate, all of which were made by the same assessor. The number of pieces of large DWD, their length (estimated to nearest meter), and diameter at widest point (estimated to nearest 5 cm) in a 0.25-ha area was recorded, from which piece volume was calculated assuming a cylindrical shape.

Separate analyses were conducted on the two DWD datasets reflecting differences in sampling methods.

Woody debris biomass.—Allometric equations were used to estimate the above-ground biomass (AGB) of live trees of equivalent size to the individual standing dead trees recorded. Reflecting major differences in stem geometry between tree and (rare) lignotuber-resprouter (mallee) growth

form eucalypts (Paul et al. 2013a, 2016), we applied different equations to these two growth forms. Allometric models were all of the power-law form, which have proven to be effective over a wide range of species, sites, and conditions (Paul et al. 2013a):

$$\ln(\text{biomass component}) = a + b\ln(S)$$

$$\text{Live tree AGB (kg)}: \ln(\text{AGB}) = -2.016 + 2.375 \times \ln(D_{130})$$

$$\text{Live mallee AGB (kg)}: \ln(\text{AGB}) = -2.771 + 2.503 \times \ln(D_{10})$$

where a and b are constants, S = a measure of plant size (trunk diameter in all cases here), and D_{130} and D_{10} are diameters (cm) measured at 130 and 10 cm above the base, respectively (Paul et al. 2013b, 2016).

Where trees had suffered substantial trunk and/or crown loss due to wind-throw (visually estimated to be > 50%), the AGB was calculated based on trunk volume, wood density, and the proportion of the trunk lost to hollow formation. Newton's formula was used to calculate volume where all the remaining trunk could be accessed, while Huber's formula was used where taking all measurements was not possible.

$$\text{Newton's volume } (\text{m}^3): V = L\left(\frac{A_b + 4A_m + A_s}{6}\right)$$

$$\text{Huber's volume}: V(\text{m}^3) = A_m L$$

where L = length (m), A_b = cross-sectional area (CSA) at large end (m^2), A_m = CSA at midpoint, and A_s = CSA at small end [CSA = πr^2 where r = radius].

As wood density values were not available for all sampled species and standing dead trees were often not identifiable to species, we used a set wood density value of 940 kg/m^3 in biomass calculations, which is the wood density of the dominant tree (*E. salubris*).

$$\text{Live broken trunk AGB (kg)} = V \times \text{proportion trunk remaining} \times \text{wood density}$$

To include changes in canopy, bark and in wood content and condition with time since plant death, the equivalent live biomass of standing dead trees was scaled to account for (1) loss of biomass in volatile components (leaves, bark; mean non-volatile fraction of a sample of Western Australian trees and shrubs was 0.766; Jonson and Freudenberger 2011); and (2) loss of wood density, using the decay fraction of Woldendorp et al. (2002) based on assessed decay class.

Individual standing dead tree AGB (kg):

$$\text{SD}_{\text{AGB}} = \text{live AGB} \times 0.766 \times \text{decay fraction}$$

Total standing dead tree AGB (kg/ha):

$$\text{SD}_{\text{Bio}} = \bar{X}(\text{SD}_{\text{AGB}}) \times \text{SD}_{\text{Density}}$$

Total DWD biomass was calculated from individual piece DWD_{WVol} and decay fraction (kg/ha):

$$\text{DWD}_{\text{Bio}} = \sum(\text{piece DWD}_{\text{Wvol}} \times \text{wood density} \times \text{decay fraction})$$

Total woody debris biomass (kg/ha):

$$\text{WD}_{\text{Bio}} = \text{SD}_{\text{Bio}} + \text{DWD}_{\text{Bio}}$$

Statistical analyses

For those sites <25 yr since fire, for which prior fire interval in addition to time since fire was known, we used a factorial ANOVA to test the effect of prior interval (categorical; long vs. short), time since fire (continuous), and their interaction on attributes of woody debris, using Statistica V7.1 (http://www.statsoft.com/Products/STATISTICA-Features). Depending on the outcome of this analysis, we used regression models to examine the relationships between woody debris measurements and time since fire over part or all of the chronosequence, fitted using the polynomial standard curves regression module of Sigmaplot 10.0 (Systat Software, https://systatsoftware.com/). In cases where prior fire interval, or its interaction with time since fire, had a significant effect on the attribute of interest in ANOVA, time since fire regression models were fitted only using sites >25 yr post-fire (i.e., those with prior interval not known). This approach assumes that sites >25 yr post-fire have been randomly sampled to include both short and long prior fire intervals, even though prior fire interval is not known. Where prior fire interval did not have a significant effect in ANOVA,

regression models were fitted over the entire span of the chronosequence. Regression models tested represented a range of biologically plausible scenarios of temporal changes in woody debris based on our dynamics model (Fig. 1): a consistent rate of increase/decrease over time (linear), an accelerating rate of change over time (exponential), a rapid increase or decrease to an asymptote (power or inverse), or a change in the trajectory of the relationship at an intermediate time since fire (quadratic and third-order polynomial), with model selection based upon minimizing Akaike Information Criterion corrected for small sample sizes (AIC_c). To reduce the leverage of the few longest-unburnt plots, we applied square-root transformation to time since fire. Woody debris data transformations, full ANOVA results, and alternative regression model forms and summary statistics are included in Appendix S2: Table S1.

Results

Both time since fire and prior fire interval had significant roles in shaping woody debris characters, both independently and in combination, as predicted in our model of woody debris dynamics (see *Model of woody debris dynamics with time since fire and fire interval in obligate-seeder forest and woodlands*; Fig. 1). Individual woody debris piece size was strongly influenced by prior fire interval, with dimensions of pieces after long prior intervals (>50 yr, but mostly much longer) often at least twice those occurring after short prior intervals (<50 yr), as predicted in the conceptual model. Short prior intervals produced lower mean and maximum standing dead tree diameter (Fig. 3a, b), maximum DWD diameter (Fig. 3d), and shorter large (>100 mm diameter) DWD lengths (Fig. 4a). Standing dead tree intactness was strongly affected by prior fire interval, with longer prior intervals resulting in a greater extent of trunk hollowing (Fig. 5a). Down woody debris condition was not affected by prior interval (Fig. 5b), and there was no significant effect of prior interval on DWD mean diameter (Fig. 3c).

Standing dead tree density was an order of magnitude greater after a short compared to a long prior fire interval (Fig. 4c), while the converse was the case for the number of large DWD pieces (Fig. 4b). The combination of density, piece size, and piece decay responses in the calculation of biomass resulted in little evidence for an effect of prior interval on standing dead tree basal area or biomass (Fig. 6a, b), DWD biomass (Fig. 6d), or total woody debris biomass (Fig. 6e). These findings were contrary to our model of woody debris dynamics as we predicted lower biomass would occur after prior intervals of <50 yr. However, the volume of large DWD was greater following a long prior fire interval (Fig. 6c), with this outcome that appears somewhat contradictory to the biomass results presumably arising through the inclusion of non-wood hollow space in the large DWD volume measurement.

Significant interactions between prior interval and time since fire were often recorded in ANOVA (Figs. 3–6; Appendix S2: Table S1). In all cases, the effects of prior interval were greatest at the earliest times since fire. The effects of prior interval reduced as time since fire increased and are expected to become undetectable at greater times since fire than for which we were able to determine prior interval. The effect of these interactions between prior interval and time since fire across the entire span of times since fire is that long prior intervals tended to result in non-monotonic U-shaped or "humped" relationships between attributes of woody debris and time since fire (with minimum values of the U or peak of the hump at ~30–100 yr post-fire), while short intervals tended to show ± linear increases or decreases (Fig. 7).

Significant relationships between most measurements of woody debris and time since fire were detected, for the temporal period of either the entire span of times since fire (in cases where prior interval had no significant effect on woody debris attributes in ANOVA), or for those sites >25 yr since fire (in cases where prior interval had a significant effect). For sites >25 yr post-fire, dimensions of woody debris increased with greater time since fire through the entire ~400 yr chronosequence, namely mean and maximum standing dead tree diameter (Fig. 3a, b), mean and maximum DWD diameter (Fig. 3c, d), and large DWD length (Fig. 4a). The percentage of DWD that was intact was greatest shortly after fire, reached a low point at an intermediate (25–100 yr) period post-fire, before increasing again

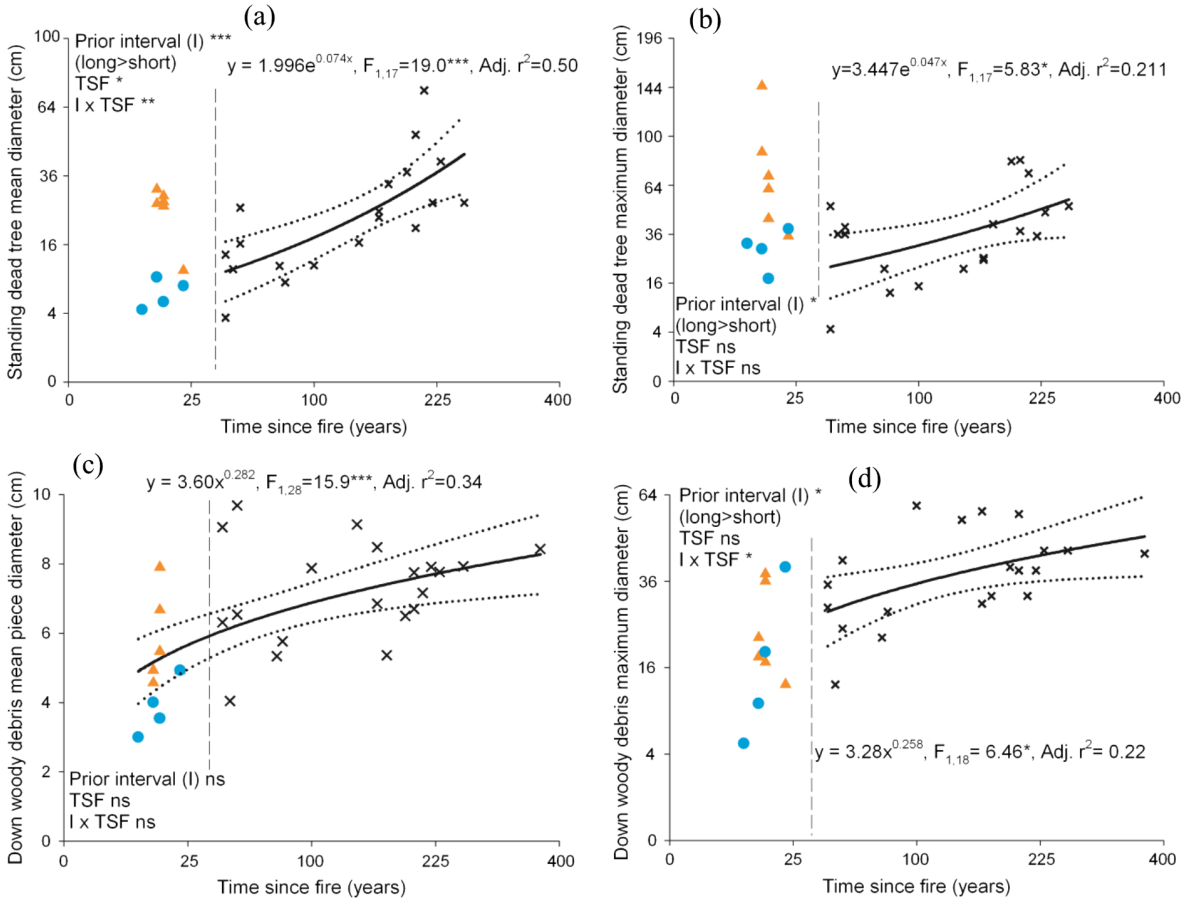


Fig. 3. Effects of time since fire (square-root transformed) and prior fire interval on woody debris piece sizes: (a) standing dead tree mean diameter (square-root transformed); (b) standing dead tree maximum diameter (square-root transformed); (c) down woody debris (DWD) mean piece diameter; and (d) DWD maximum piece diameter (square-root transformed). ANOVA tests effects of prior fire interval (I), time since fire (TSF), and their interaction on attributes of woody debris for those sites (recently burnt) for which prior fire interval is known. Regression tests the effect of time since fire on attributes of woody debris, applied including or excluding recently burnt sites depending on whether prior fire interval was a significant effect in ANOVA. ● short prior interval, ▲ long prior interval, × sites last burnt >25 yr ago for which prior fire interval is not known; --- approximate division between sites with known and unknown prior interval; ····· 95% confidence intervals; ns—not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

in longer-unburnt vegetation (Fig. 5b). Time since fire had a similar U-shaped relationship with standing dead tree intactness over the range of >25 yr to long-unburnt vegetation (Fig. 5a).

Standing dead tree density declined across the entire span of the chronosequence (Fig. 4c), as did standing dead tree basal area, with the rate of decline of the latter greatest over the first few decades after fire (Fig. 6a). The number of large DWD pieces increased with time since fire over the period >25 yr post-fire (Fig. 4b). As predicted in our dynamics model, biomass of standing dead trees declined with time since fire, from a peak often exceeding 10,000 kg/ha shortly post-fire to often <1000 kg/ha in long-unburnt woodlands (Fig. 6b). The volume of large DWD was low over the period ~25–100 yr post-fire, and then increased with greater time since fire (Fig. 6c). Note that we regard the apparent

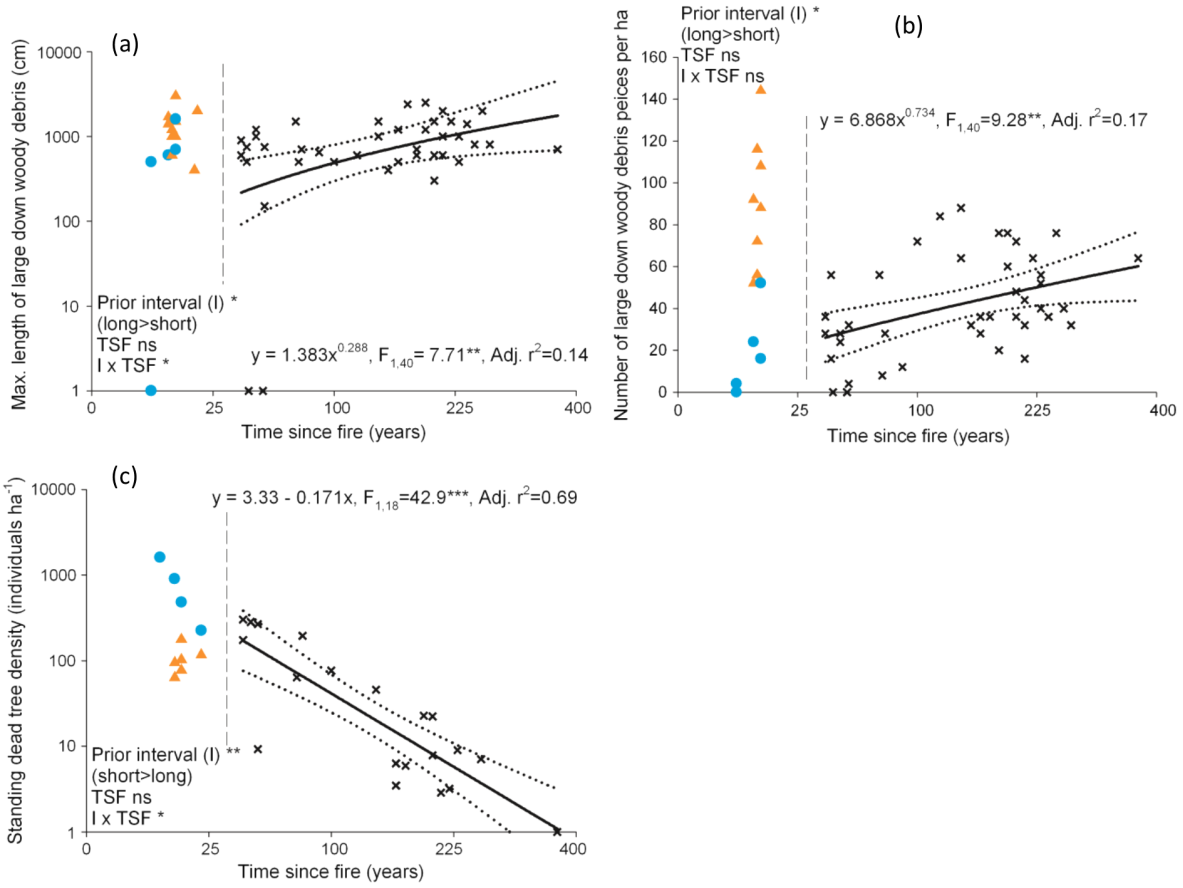


Fig. 4. Effects of time since fire (square-root transformed) and prior fire interval on woody debris piece length and density: (a) maximum piece length ($\log_{10}$ transformed) of large (≥100 mm diameter) down woody debris (DWD); (b) number of pieces of large DWD; and (c) density ($\log_{10}$ transformed) of standing dead trees. ANOVA tests effects of prior fire interval (I), time since fire (TSF), and their interaction on attributes of woody debris for those sites (recently burnt) for which prior fire interval is known. Regression tests the effect of time since fire on attributes of woody debris, applied including or excluding recently burnt sites depending on whether prior fire interval was a significant effect in ANOVA. ● short prior interval, ▲ long prior interval, × sites last burnt >25 yr ago for which prior fire interval is not known; --- approximate division between sites with known and unknown prior interval; ····· 95% confidence intervals; ns—not significant, $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

decline in large woody debris volume in the very longest-unburnt vegetation (~400 yr) as suggested from the fitted cubic function as unconfirmed, given that only one site of this time since fire range was sampled. The changes in large DWD volume were not reflected in DWD biomass, for which no relationship with time since fire was established (Fig. 6d). The summation of standing dead and DWD biomass resulted in a decline in total woody debris biomass with time since fire, with most of this decline occurring in the first few decades after fire (Fig. 6e). Shortly after fire, most of the total woody debris biomass was contributed by standing dead trees. With increasing time since fire DWD became an increasing contributor to total woody debris biomass, ultimately dominating the woody debris pool in long-unburnt woodlands.

Discussion

Woody debris dynamics

Consistent with our model of woody debris dynamics for obligate-seeder forests and

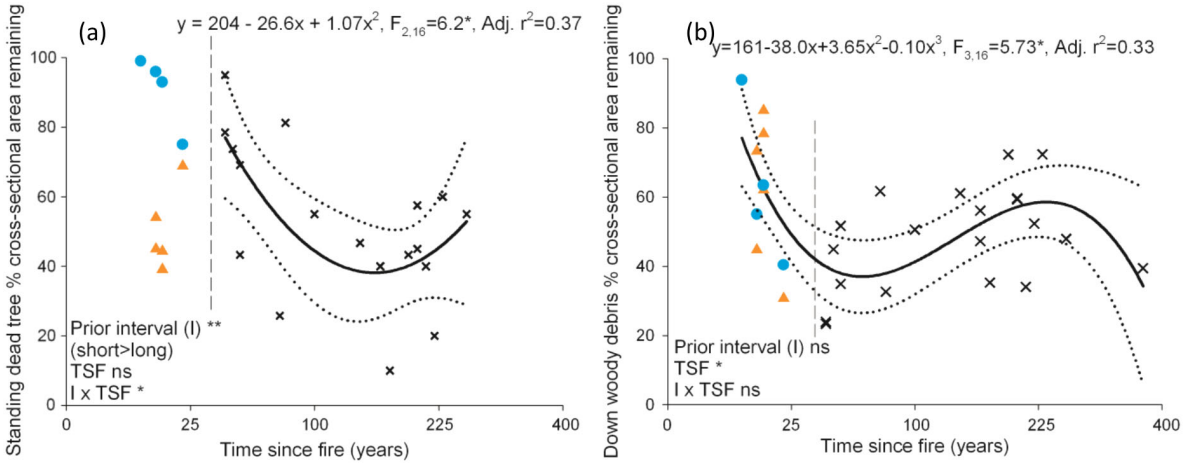


Fig. 5. Effects of time since fire (square-root transformed) and prior fire interval on woody debris form, reflected in percent of cross-sectional area remaining in: (a) standing dead trees; and (b) down woody debris. ANOVA tests effects of prior fire interval (I), time since fire (TSF), and their interaction on attributes of woody debris for those sites (recently burnt) for which prior fire interval is known. Regression tests the effect of time since fire on attributes of woody debris, applied including or excluding recently burnt sites depending on whether prior fire interval was a significant effect in ANOVA. ● short prior interval, ▲ long prior interval, × sites last burnt >25 yr ago for which prior fire interval is not known; ---approximate division between sites with known and unknown prior interval; ····· 95% confidence intervals; ns - not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

woodlands (Fig. 1), time since fire and prior fire interval had independent and interacting effects on woody debris attributes in *E. salubris* woodlands. Prior interval effects were most strongly expressed in woody debris piece sizes, with these striking lower after short (<50 yr) than longer prior intervals. Nearly all attributes of woody debris were affected by time since fire, with piece sizes increasing from a low 30–100 yr post-fire to being larger in longer-unburnt woodlands. U-shaped relationships (after a long prior interval; Fig. 7) characterized changes in many attributes of woody debris with time since fire, and such relationships appear widespread in other forest and woodland ecosystems dominated by obligate-seeder trees (Hall et al. 2006, Fournier et al. 2012, Taylor et al. 2014, Donato et al. 2016). Non-monotonic patterns of change in woody debris with time since fire mirror patterns in other aspects of community composition and function in obligate-seeder eucalypt woodlands (Gosper et al. 2013b, c). Consequently, we propose that the concepts of our model of woody debris dynamics will have relevance for a diversity of obligate-seeder forests and woodlands with stand-replacement fires, with relevant calibration of temporal patterns of change according to productivity, plant species traits, and decomposition rates of individual communities. In contrast to the strong effects of time since fire and fire interval on woody debris attributes found here, in forests and woodlands dominated by epicormically resprouting trees, woody debris changes with time since fire can be more modest or undetectable (Graham and McCarthy 2006, Loucks et al. 2008, Bassett et al. 2015), buffered by the resilience to fire of biomass stocks in epicormic-resprouter trees (Pausas and Keeley 2017, Nolan et al. 2018, Collins 2019).

Only two areas of our woody debris dynamics model for obligate-seeder forests and woodlands were not supported by the empirical data from *E. salubris* woodlands. First, there was no evidence for differences in mean DWD diameter and total biomass with prior fire interval, when the larger pre-fire tree sizes after long prior intervals were expected to result in larger DWD pieces and biomass. Plausible explanations for this finding are (1) higher resistance of larger fire-killed trees to collapse (Lindenmayer et al.

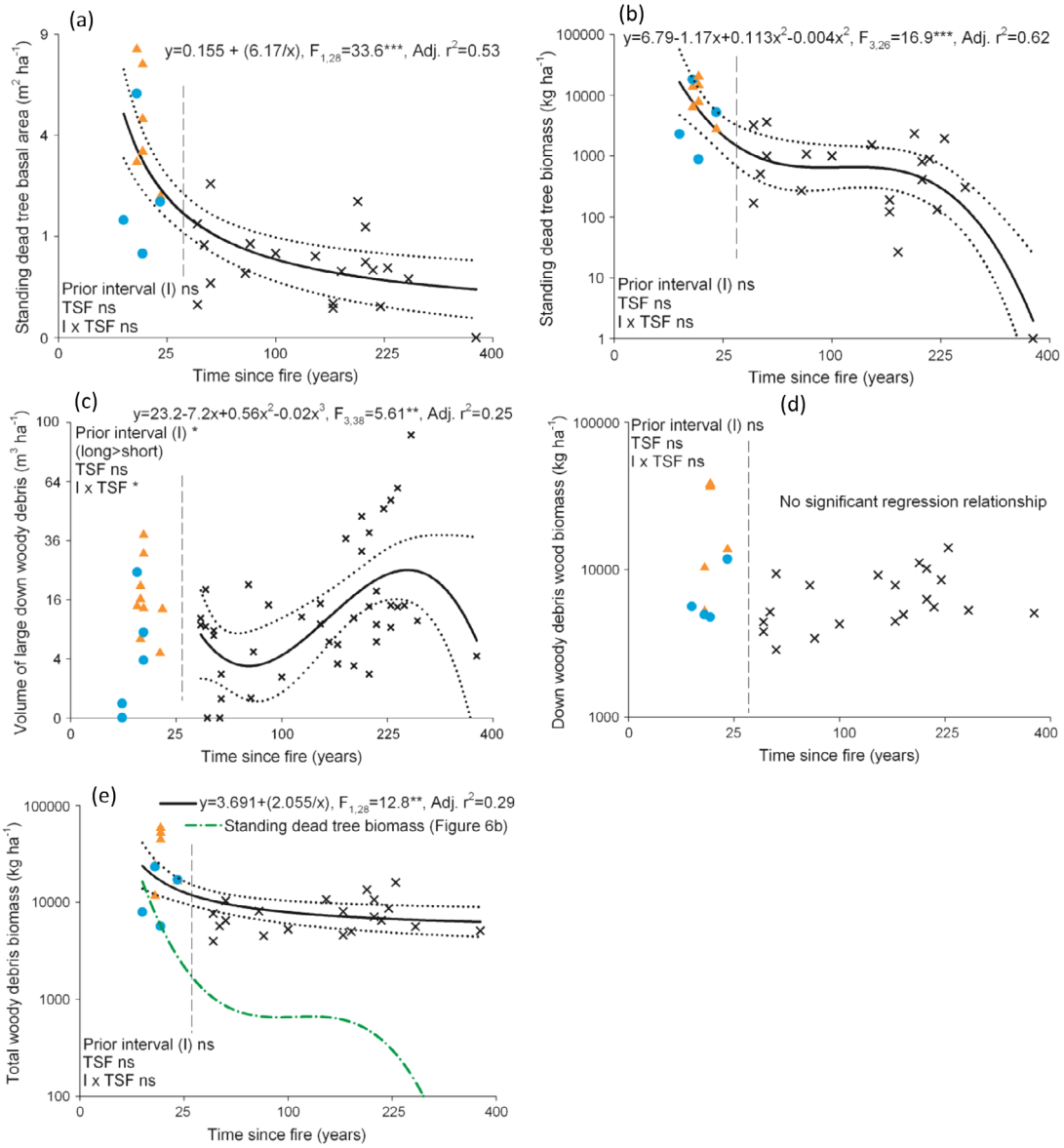


Fig. 7. Effects of time since fire (square-root transformed) and prior fire interval on woody debris volume and biomass: (a) basal area (square-root transformed) of standing dead trees; (b) above-ground biomass ($\log_{10}$ transformed) of standing dead trees; (c) total volume (square-root transformed) of large (≥100 mm diameter) down woody debris (DWD); (d) total DWD biomass ($\log_{10}$ transformed); and (e) total woody debris biomass (sum of DWD and standing dead trees; $\log_{10}$ transformed). To illustrate the relative contribution of standing dead trees and DWD to total woody debris biomass, the standing dead tree biomass function (Fig. 6b) is plotted on Fig. 6e. ANOVA tests effects of prior fire interval (I), time since fire (TSF), and their interaction on attributes of woody debris for those sites (recently burnt) for which prior fire interval is known. Regression tests the effect of time since fire on attributes of woody debris, applied including or excluding recently burnt sites depending on whether prior fire interval was a significant effect in ANOVA. ● short prior interval, ▲ long prior interval, × sites last burnt >25 yr ago for which prior fire interval is not known; --- approximate division between sites with known and unknown prior interval; ····· 95% confidence intervals; ns - not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

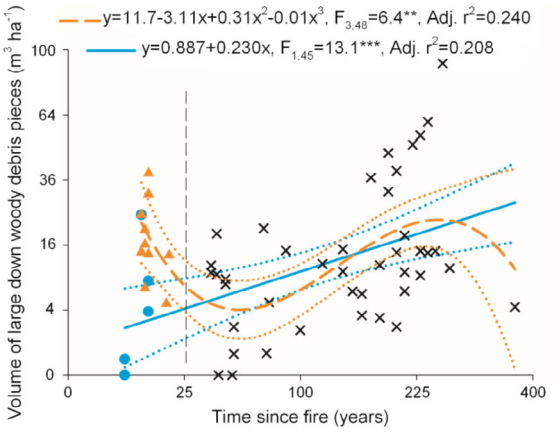


Fig. 7. Alternative approach to analysis and presentation of data illustrating the interaction of time since fire and prior fire interval on woody debris. In this example of the volume of large (≥100 mm diameter) down woody debris pieces (square-root transformed; see Fig. 6c), separate regression models were tested across the entire spans of time since fire (square-root transformed) using for recently burnt (<25 yr) sites with known prior fire interval either those sites with (1) short prior interval (<50 yr) or (2) long prior interval (>50 yr, and often much longer). ●, — short prior interval, ▲, – – long prior interval, × sites last burnt >25 yr ago for which prior fire interval is not known; --- approximate division between sites with known and unknown prior interval; ·····/····· 95% confidence intervals; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

1997), meaning most DWD shortly post-fire after long intervals is contributed by fallen branches, compared to both branches and trunks following short prior intervals; and (2) insufficient statistical power to detect differences given large variation in DWD biomass in particular, noting that the highest biomass sites did have long prior intervals. Second, the basal area and biomass of standing dead trees were similarly seemingly not affected by prior fire interval. Although the possibility of insufficient statistical power cannot be discounted, this result suggests that *E. salubris* woodlands reach biomass carrying capacity in the dense sapling stand state. Under this vegetation succession model, subsequent increases in individual tree size are offset at a stand level by declines in tree density (Gosper et al. 2013c, 2018).

Our inability to determine the prior fire interval for sites last burnt >~25 yr ago prevented us from establishing the longevity of fire interval effects, although the frequent significant prior interval × time since fire interactions indicate that prior interval effects diminish over time and paths of development following short and long prior intervals converge beyond 50 yr post-fire (Fig. 7).

Importance of woody debris for carbon and fauna

The strong effects of time since fire and prior fire interval on woody debris attributes have implications for a variety of aspects of ecosystem function and biodiversity conservation. As time since fire and prior fire interval have independent and interacting effects, knowledge of both these components of the fire regime is required to accurately predict attributes and quantities of woody debris in obligate-seeder dominated communities.

Obligate-seeder eucalypt woodlands support significant carbon stocks (Berry et al. 2010). Our results show that differences in prior fire interval and time since fire lead to substantial fluxes in biomass of woody debris. A single fire event produces substantial quantities of new woody debris, resulting from the transition of biomass in pre-fire living vegetation into post-fire woody debris. Carbon stocks in fire-generated woody debris release their stored carbon over the decades following fire (Campbell et al. 2016), being offset to an unknown extent (measurements are needed) by carbon sequestered in regenerating vegetation. Decomposition of fire-generated woody debris is only partly replaced by new woody debris inputs generated by non-fire processes. Consequently, if maximization of carbon stocks is of management value (Berry et al. 2010), long fire intervals will reduce pulses of carbon loss from the system due to fire.

Even shorter fire intervals than those examined here have the potential to have even more dramatic effects on woody debris stocks, if such intervals result in regeneration failure in the obligate-seeder eucalypts and subsequently lead to a transition to a non-treed vegetation type with lower carbon stocks (Berry et al. 2010, Gosper et al. 2018). Short fire intervals have led to collapse of tree populations in obligate-seeder eucalypt wet forests (Bowman et al. 2014), but similar

occurrences have not been documented in the GWW to date.

Woody debris, particularly large pieces, is important for a range of vertebrate fauna (Dickman 1991, Lindenmayer et al. 2002). Obligate-seeder woodland age classes that support large woody debris pieces, which were primarily recruiting woodlands after a long prior interval and mature woodlands, may thus be more important for woody debris-associated animals than recruiting woodlands after short intervals or dense sapling stands at an intermediate (30–100 yr) time since fire. The value to woody debris-associated vertebrate fauna of the post-fire peak in the volume and number of large woody debris pieces after long prior intervals is uncertain, however, as this vegetation state mostly lacks co-occurring large live trees (Gosper et al. 2018), which are often also important for these animals (Dickman 1991, Luck 2002). At least in the case of woody debris-associated woodland birds, such as Rufous Treecreepers (*Climacteris rufa*; Luck 2002), recruiting woodlands with abundant and sometimes large pieces of woody debris do not appear to provide suitable habitat (Gosper et al. 2019). Furthermore, while Australian eucalypt communities support irruptive post-fire colonization of fire-derived dead wood by invertebrates (Schmitz et al. 2015), fire-derived dead wood specialist birds that thrive in some other obligate-seeder forests after stand-replacement fires (e.g., some woodpeckers; Hutto 1995) are absent.

Management implications

The great length of our time since fire chronosequence has demonstrated that changes in woody debris stocks and attributes can occur over multi-century timescales. Larger-diameter pieces of standing dead trees and DWD, which may be of particular importance to fauna and for persistence of sequestered carbon, were found mainly in woodlands that have not been burnt for over 200 yr, and to some extent in recently burnt woodlands following long prior fire intervals. Following attrition of fire-generated woody debris by ~50 yr post-fire, it then takes another 100–150 yr for these features to re-establish, emphasizing the long-term consequences of contemporary fire events. There are few management options available to augment large woody debris availability in locations where it has been removed by fire, with the exceptions of reintroductions of large woody debris (e.g., Goldin and Hutchinson 2013) and instillation of artificial woody debris (e.g., artificial hollows to provide nesting sites for birds; Saunders and Dawson 2017). Both these management actions are only likely to be feasible across limited areas of the highest conservation value.

A landscape-scale perspective is needed to assess the implications of recent fire regimes for woody debris stocks and the ecosystem functions they support. Fires over recent decades have burnt a substantial proportion of the obligate-seeder eucalypt woodlands of the GWW, 25–30% of total area over the period ~1969–2016, but with spatial differences in fire occurrence (Gosper et al. 2018, 2019). The prior interval of these fires is, however, largely unknown, although both long and short prior intervals have occurred (Berry et al. 2010; Fig. 2). These recent fires have resulted in much regenerating woodland that will develop into dense sapling stands with low woody debris piece sizes over the coming decades. Furthermore, dense sapling stands appear more flammable than long-unburnt woodlands (O'Donnell et al. 2011, Gosper et al. 2013c, 2014, 2018), which in combination with indications of an increase in season length of lightning-ignited fires (Bates et al. 2018) poses a risk that these areas of woodland will experience a short fire interval, locking in a long-term absence of large woody debris pieces. The development of a short interval cycle trap (positive fire-vegetation feedback as per Tepley et al. 2018) is plausible.

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Data Availability

Data are available from the CSIRO Data Access Portal: https://doi.org/10.25919/5d845a861739c

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2927/full