The effects of topographic variation and the fire regime on coarse woody debris: Insights from a large wildfire

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Abstract

Coarse woody debris (CWD) is a common structural component of terrestrial ecosystems, and provides important habitat for biota. Fires modify the distribution of CWD, both spatially and temporally. Changes in fire regimes, such as those arising from prescribed burning and changing climatic conditions, make it critical to understand the response of this resource to fire. We created a conceptual model of the effects of fire on logs and dead trees in topographically diverse forests in which trees often survive severe fire. We then surveyed paired sites, in a damp gully and adjacent drier slope, ~3.5 years after a large wildfire in south-eastern Australia. Sites were stratified by fire severity (unburnt, understorey burnt and severely burnt), and fire history (burnt ≤3 years or ≥20 years prior to the wildfire). Both components of the fire regime influenced CWD availability in gullies. Severe wildfire and fire history ≤3 years reduced the volume of small logs (10–30 cm diameter) in gullies, while severe wildfire increased the number of large dead trees in gullies. CWD on slopes was not affected by fire severity or history at ~3.5 years post-fire. Log volumes on slopes may recover more quickly after wildfire through rapid collapse of branches and trees. Gullies generally supported more logs than slopes, but longer inter-fire intervals in gullies may allow fuel loads to accumulate and lead to comparatively larger fire impacts. Given that fire severity and fire interval are predicted to change in many fire-prone ecosystems in coming decades, this study highlights the importance of understanding the interacting effects of multiple components of the fire regime with landscape structure. In particular, variation in fire interval and fire severity in relation to topographic position will influence the pattern of accumulation of coarse woody debris across the landscape, and therefore the structure and quality of habitats for biota.

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1. Introduction

Fire shapes the composition of ecosystems through its effects on vegetation structure (Bond et al., 2005; Bowman et al., 2009), which in-turn affects the distribution of fauna (Fox, 1982; Friend, 1993). The immediate and longer-term effects of fire on faunal habitat depend on the fire regime: fire severity, fire frequency, time-since-fire, fire interval and the season of fire (Gill and McCarthy, 1998; Smucker et al., 2005; Haslem et al., 2012). Fire regimes can vary within relatively small areas, because even large, intense fires create a mosaic of severities at multiple scales (Turner et al., 1994; Román-Cuesta et al., 2009; Leonard et al., 2014).

Coarse woody debris (CWD: here defined as logs and dead trees) is a common component of many terrestrial ecosystems (Harmon et al., 1986; Jonsson and Kruys, 2001; Lohr et al., 2002). It has an important role in nutrient cycling and carbon storage, and provides habitat for plants and animals (Harmon et al., 1986; Lindenmayer and Franklin, 2002). The dynamics of CWD are driven by the interaction of long-term processes, such as senescence and decay, with shorter-term disturbance processes, such as timber harvesting and fire (Harmon et al., 1986; Haslem et al., 2011).

Fire is integral to the dynamics of CWD, as it both consumes existing debris and generates new material through its influence on tree death and collapse (Harmon et al., 1986; Tinker and Knight, 2000). Diverse responses to aspects of the fire regime have been observed. For example, the effects of time-since-fire on the abundance of logs ranges from a post-fire increase (Monsanto et al., 1994; Jonsson and Kruys, 2001; Friend et al., 2002) to pronounced declines (Haslem et al., 2012).

It is critical to understand the response of this resource to fire. We created a conceptual model of the effects of fire on logs and dead trees in topographically diverse forests in which trees often survive severe fire. We then surveyed paired sites, in a damp gully and adjacent drier slope, ~3.5 years after a large wildfire in south-eastern Australia. Sites were stratified by fire severity (unburnt, understorey burnt and severely burnt), and fire history (burnt ≤3 years or ≥20 years prior to the wildfire). Both components of the fire regime influenced CWD availability in gullies. Severe wildfire and fire history ≤3 years reduced the volume of small logs (10–30 cm diameter) in gullies, while severe wildfire increased the number of large dead trees in gullies. CWD on slopes was not affected by fire severity or history at ~3.5 years post-fire. Log volumes on slopes may recover more quickly after wildfire through rapid collapse of branches and trees. Gullies generally supported more logs than slopes, but longer inter-fire intervals in gullies may allow fuel loads to accumulate and lead to comparatively larger fire impacts. Given that fire severity and fire interval are predicted to change in many fire-prone ecosystems in coming decades, this study highlights the importance of understanding the interacting effects of multiple components of the fire regime with landscape structure. In particular, variation in fire interval and fire severity in relation to topographic position will influence the pattern of accumulation of coarse woody debris across the landscape, and therefore the structure and quality of habitats for biota.
We had four primary objectives: (1) to develop a conceptual model of the effects of wildfire on CWD over time; (2) to determine the effects of fire severity and fire history on the relative abundance of CWD (logs and dead standing trees); (3) to examine the effects of the fire regime are modified by topographic position (i.e. damp gullies vs. drier slopes); and (4) to determine whether the size of logs and dead trees influences how they are affected by the fire regime.

1.1. Conceptual model and predictions

We developed a conceptual model of the post-fire dynamics of logs in forest ecosystems in which trees often survive severe fire (Fig. 1). There are four main sources of logs following fire. First, at least part of the existing log resource is likely to remain post-fire. Second, trees not killed by fire may drop branches, resulting in a pulse of smaller logs. Third, some trees are damaged at the stem base and are killed by fire, and either fall shortly after the fire or remain as standing dead trees for many years before collapsing. Finally, trees that regenerate in gaps created by fire will contribute to the log resource in the longer term.

The magnitude and rate of log consumption, tree death, tree collapse and tree regeneration will depend on several aspects of the fire regime, including fire severity and fire history. More severe fires will result in the consumption of more logs and kill more trees, but may obscure the effects of previous fire on CWD. Characteristics of logs, including their size, moisture content and level of decay, will affect their flammability; while the death and collapse of trees will be influenced by the composition of tree species, tree health and the (non-fire) disturbance history of the forest. Moisture differentials associated with topographic variation will influence the abundance of logs and dead trees, as well as their decay rate. Gullies, with their moister and more sheltered microclimate, experience longer fire intervals than drier slopes, allowing more time for logs to accumulate. These conditions allow growth

Fig. 1. Conceptual model of log volume over time following a wildfire in a forest in which trees often survive severe fire. The side panels show the trajectories of logs from four sources: (1) existing logs at the time of the fire (some of which are consumed by fire and those not consumed continue to decay); (2) input from live trees following fire (branches are lost immediately following the fire, and after time these trees continue to drop branches, die and collapse); (3) trees killed by fire (a number of trees die and collapse immediately following the fire, while some trees are killed but remain standing, and collapse as a cohort many years later); and (4) input from the next generation of trees (seedlings that grow following the fire, reach maturity and begin to drop branches). The main plot shows the cumulative volume of logs from these sources. The specific pattern of each log source will depend on the severity of the fire and topographic location (i.e. damp gullies or drier slopes). Trajectories may be affected by fire interval, with a likely overall decline in log volume over time if short fire intervals do not allow regenerating trees to mature.
of larger trees and, therefore, the potential production of larger logs, but also promote more rapid decay. The moist conditions and higher topographic relief may also mitigate the effects of fire on CWD.

We used our conceptual model as a base to predict how topography, fire severity, and fire history will interact to affect the availability of CWD ~3.5 years after wildfire. We predict that:

1. Gullies will support a greater volume of large logs and greater abundance of large dead trees than slopes.
2. Sites burnt in the 2009 wildfire will experience a reduction in the volume of logs, especially small logs, and an increase in the abundance of dead standing trees compared to sites not burnt in the wildfire. The magnitude of change will be greater at severely burnt than understorey burnt sites, and on slopes compared to gullies.
3. Unburnt sites with a short fire history (time-since fire ≤3 years) will have fewer logs, and more dead trees, compared to unburnt sites with a long fire history (time-since-fire ≥20 years).
4. Sites in which only the understorey was burnt by wildfire will have fewer logs, and more dead trees, when the fire history was short (interval ≤3 years) compared to long (interval ≥20 years), however differences will be small.
5. Severe wildfire will obscure the effects of previous fires, and there will be no detectable effect of fire history.

2. Methods

2.1. Study area

On ‘Black Saturday’, 7 February 2009, two wildfires in central Victoria, Australia, joined to form the Kilmore–Murrindindi fire complex. The study area includes private land, townships, and several State Forest and National Park reserves. Approximately half of the 228,000 ha area burnt was foothill forest, a topographically diverse forest system consisting of damp gullies and drier slopes. Our study was undertaken in these foothill forests, which range in elevation from 153 to 937 m and have a temperate climate with mean annual rainfall of ~1300 mm (Australian Government Bureau of Meteorology). The drier slopes support eucalypt forests dominated by messmate Eucalyptus obliqua and broad- or narrow-leaf peppermint E. dives or E. radiata. The understorey is characterised by a high cover and diversity of grasses and herbs, with a variable shrub layer (Oates and Taranto, 2001). Damp gullies are dominated by a mixture of Eucalyptus species, including messmate, broad and narrow-leaf peppermint and blue gum E. globulus. Gullies have a dense shrub layer, and a ground layer of herbs, grasses, and moisture-dependent ferns (Oates and Taranto, 2001).

2.2. Study design and selection of study sites

Study sites were located within or adjacent to the perimeter of the Kilmore–Murrindindi fire complex (Fig. 2). They were stratified by (1) 2009 wildfire severity; and (2) fire history (time-since-fire prior to 2009). Fire severity was categorised as either (1) unburnt, (2) understorey burnt (canopy intact), or (3) severely burnt (understorey burnt and canopy fully scorched or burnt). Fire history was defined as ‘short’ when a site had been burnt ≤3 years before 2009, or ‘long’ when a site had not burnt for ≥20 years prior to 2009. These time-since-fire/fire interval periods were selected to represent a strong contrast in fire history. Prescribed burning in foothill forests can reduce fuels for 4–5 years, with negligible effects after 10 years (Price and Bradstock, 2012; Leonard et al., 2014). By 20 years after wildfire, these forests have reached vigorous maturity (Cheal, 2010).
We selected 24 sites that represented replicated combinations of each level of fire severity and history (Fig. A.1 in Supplementary material). Each site included a damp gully and drier slope which had similar fire severities. We interrogated post-fire aerial images and spatial layers using a geographic information system (GIS; ArcMap v 9.0) and spatial data layers of previous fire boundaries, timber harvesting history, and vegetation type (provided by the Victorian Government). On-ground assessments were undertaken to verify the accuracy of spatial layers. In severely burnt areas, where evidence of previous burns was not visible, we relied on the maps to determine fire history. While it is likely that all sites had been selectively harvested within the previous 100 years, sites were selected within areas that had no record of timber harvesting within the last 50 years, and no evidence of previous clearcut harvesting.

2.3. Sampling protocol

Surveys were undertaken ~3.5 years after the 2009 wildfire. At each site we surveyed logs and dead standing trees along two 200 m transects: one in a gully and one on a parallel slope, ~100–150 m from the gully edge.

2.3.1. Logs

The diameter of each log (\(\geq 10\) cm diameter, \(\geq 100\) cm length) that intersected a transect was measured at the point of intersection, and its angle to the transect recorded. The volume of logs was estimated using a modified version of the line intersect method (Warren and Olsen, 1964; Van Wagner, 1968). This method assumes that the angles of logs along a transect are random, giving a probability factor of encountering each log as \(2/\pi\). In this study, logs were consistently more likely to lie across the slope or gully than parallel to it. To correct this non-random distribution, we calculated the probability factor of encountering a log on our transects using the angles of all surveyed logs. Incorporating this factor, log volume (\(V\)) \((\text{m}^3\text{ha}^{-1})\) was estimated using the equation:

\[
V = 1.229276 \times \frac{\pi \sum d^2}{4L} \times 100
\]

where \(d\) = diameter (m) at right angles to the length of the log and \(L\) = length (m) of the transect.

2.3.2. Trees and stumps

The diameter (at breast height, DBH) of each live and dead tree stem \(\geq 1.5\) m tall was measured within a 100 \(\times\) 10 m belt transect in the gully and slope, respectively. The mean DBH of all stems was calculated for each transect. Cut tree stumps (<1.5 m tall) were surveyed and the basal area (\(\text{m}^2\) \(0.1\) ha\(^{-1}\)) was calculated to approximate the prior timber harvesting intensity at each site.

2.4. Statistical analysis

2.4.1. Response variables

Statistical modelling proceeded in two stages. First, to test initial predictions about the interacting effects of topography and fire severity, we modelled the volume of small and large logs, and the abundance of small and large dead trees, by the interaction of topography with fire severity. Second, we investigated the effects of fire regimes and timber harvesting on small logs, large logs, small dead trees and large dead trees separately for gully and slope transects. Two-stage modelling avoided the inclusion of the three-way interaction term between fire severity, fire history and topography. Higher order interaction terms are difficult to model successfully and difficult to interpret in an ecologically meaningful way, particularly when predictor variables are categorical.

Response variables were modelled using generalised linear mixed-effects models, which allow the inclusion of random grouping factors (Zuur et al., 2009). The volume of logs was modelled assuming a Gaussian distribution of errors, with values being log\(_{10}\) transformed to improve normality (with a constant of 0.01 added to all data points if zero values were present). The abundance of dead trees was modelled assuming a Poisson distribution.

2.4.2. Fire regime predictor variables and model building

Predictor variables were chosen to represent components of the fire regime (i.e. fire severity and fire history) and to account for stem size of standing trees and past timber harvesting. The variables ‘fire severity’ (unburnt, understory burnt, or severely burnt), ‘fire history’ (short or long), ‘tree DBH’ (mean DBH of live and dead stems; cm), and ‘cut stumps’ (basal area \(\text{m}^2\) \(0.1\) ha\(^{-1}\)) were considered ecologically plausible predictors for all response variables, with the exception of ‘tree DBH’ in models of dead trees.

In the first stage of modelling, we used the model ‘topography \(\times\) fire severity’ to determine whether the interaction term was important. In the second stage, the model set comprised three combinations of fire regime components: ‘fire severity’, ‘fire severity + fire history’, and ‘fire severity \(\times\) fire history’. Each model of log volume also included ‘tree DBH’ and ‘cut stumps’, while each model of dead tree abundance included ‘cut stumps’. ‘Fire history’ was only modelled in combination with ‘fire severity’, as it is ecologically implausible that fire history would affect the response variables independently of fire severity following a large wildfire.

We included random effects to account for potential spatial autocorrelation of model residuals due to sites being clustered within reserves, and gully and slope transects being paired. Thus, ‘reserve’ was included in all models; and ‘site’ was included in models that included the predictor variable ‘topography’. Where necessary, an observation-level random effect was included in Poisson family models to account for overdispersion in model residuals (Nakagawa and Schielzeth, 2010). Model fit was quantified using the marginal (fixed terms only) and conditional (full model) \(R^2\) values of the global model (Nakagawa and Schielzeth, 2013).

Scatter plots of each response variable by each continuous predictor were created to check linearity of response, and no evidence for non-linear relationships was found. There was no evidence of excessive correlation of predictor variables (Pearson pair-wise correlation coefficients <0.6).

2.4.3. Model selection

When modelling CWD on gullies and slopes separately, we employed an information theoretic approach to identify the model(s) with most support. Akaike’s information criterion for small sample sizes (AICc) was used to rank models. If there were multiple models with substantial support (i.e. multiple models with an AICc difference \(\leq 2\) of the top ranked model), we inferred from all such models. We did not model average, as we were interested in the importance of the interaction term, for which model averaging is problematic (Docherstern and Jenkins, 2011). Predictor variables were regarded as important if the 90% confidence interval did not include zero. We chose to use the 90% confidence interval due to the relatively small sample size (24 sites) and the possible management implications of underestimating the importance of fire on CWD (Smith et al., 2013).

Statistical analyses were undertaken using the R statistical package version 2.15.2 (R Development Core Team, 2010). We used the ‘lme4’ package for regression modelling (Bates and Maechler, 2011), the ‘MuMin‘ package for model selection (Bartoń, 2009),
and the AICcmodavg package for creating model predictions (Mazerolle, 2012).

3. Results

Following initial modelling to determine whether topography and fire severity interacted to influence CWD availability (see Table A.1 for parameter coefficients and model fits), we developed separate model sets for gullies and slopes to test the relative influence of fire regime components and timber harvesting on the volume of small and large logs and the abundance of small and large dead trees in gullies and on slopes. A single ‘best model’ was evident for all CWD components except small logs in gullies, for which we based our inferences on the two models with support (Table 1).

### 3.1. Effects of topography, fire, timber harvesting and tree size on logs

Modelling gullies and slopes together revealed an important interaction between fire severity and topography for small logs. There was a higher volume of small logs in gullies than on slopes in unburnt and understorey burnt sites, but in severely burnt sites there were more small logs on slopes (Fig. 3a). The volume of large logs was greater in gullies than on slopes, regardless of fire severity (Fig. 3b).

When gully sites were modelled alone, the models ‘fire severity’ and ‘fire severity + fire history’ had support for the volume of small logs (Table 1). Model estimates and confidence intervals indicated that fire severity and fire history had important influences on the volume of small logs (Table A.2). The volume of small logs was lower in severely burnt than unburnt gullies, and fire history had an additive effect to fire severity, such that in each severity category (including unburnt), gullies with a short fire history (<3 years) had lower volumes of small logs than those with a long fire history (>20 years) (Fig. 4).

The fire severity model was the best model explaining the volume of large logs in gullies and both small and large logs on slopes (Table 1); however, no predictor variables were important in explaining these response variables (Tables A.2 and A.3).

### 3.2. Effects of topography, fire and timber harvesting on dead standing trees

Modelling gullies and slopes together showed that small dead trees were more abundant in severely burnt sites than unburnt sites (Fig. 3c). They were also generally more abundant on slopes than in gullies, with this difference most pronounced in understorey burnt sites (i.e. an important topography x fire severity interaction; Fig. 3c). Large dead trees were more abundant in severely burnt sites than unburnt (Fig. 3d).

When gullies were modelled alone, dead tree abundance was best explained by the fire severity model (Table 1). There was an increased abundance of large dead trees in severely burnt gullies compared to unburnt gullies (Fig. 5), but fire severity did not have an important influence on small dead trees (Table A.3).

On slopes, fire severity was the preferred model explaining the abundance of small and large dead trees (Table 1), but no variables were important (Table A.3).

### 4. Discussion

Despite the important role of coarse woody debris in ecosystem function (Harmon et al., 1986; Tinker and Knight, 2000), the effects of multiple fire regime components on CWD have rarely been studied concurrently. Here, we have demonstrated that the availability of CWD is influenced by two components of the fire regime – fire severity and fire history – and that the response of structural components to fire depends both on their size and topographic location.

#### 4.1. Fire severity

Log volume and abundance of dead trees in gullies were influenced by fire severity ~3.5 years after wildfire, but there was less evidence of an effect of fire severity on CWD on slopes. While initial models of topography and fire severity indicated that the abundance of small and large dead trees on both slopes and gullies increased after severe wildfire, when CWD was modelled separately for slopes and gullies, only small logs in gullies and large dead trees in gullies were affected by fire severity. The apparent stronger effects of severe wildfire in gullies than slopes may have occurred as a result of either replacement of logs on slopes but not in gullies, and/or higher loss of logs in gullies compared to slopes. Moisture stress before fire has been associated with increased tree death after fire (van Mantgem et al., 2013), and it is likely that the decade-long drought prior to 2009 negatively affected the health and resilience of trees, particularly on dry slopes (Bennett et al., 2013). Fire-related tree death may therefore have been higher on slopes than in gullies, with rapid fall of branches and collapse of trees on slopes replacing logs consumed by fire. The dip in log volume following wildfire that we expected (conceptual model; Fig. 1) may, therefore, have occurred prior to our surveys. If this is the case, the availability of logs on slopes will decrease in the coming decades, as the trees that were most likely to collapse have already done so. Additionally, although gullies more often escape fire (Leonard et al., 2014), when gullies burn following long dry periods, the accumulation of dry fuels can result
in severe fire effects (Pettit and Naiman, 2007), sometimes more severe than surrounding slopes (Segura and Snook, 1992).

There was some indication of loss of large logs in severely burnt gullies and slopes, but the confidence intervals were large relative to effect sizes. Large logs and dead trees are rare in the landscape, and the study may not have had sufficient power to detect small changes in their availability. Loss of large logs and dead trees is important, because they have disproportionate habitat value for flora and fauna (Harmon et al., 1986; Lindenmayer et al., 2000).

4.2. Fire history

A short time-since-fire or fire interval can reduce the availability of logs (Catling, 1991; Spencer and Baxter, 2006) but increase the abundance of dead trees (Harmon et al., 1986). We predicted that this would be the case in our study, but that any effects would be obscured by severe wildfire. We found no effects of fire history on logs or dead trees on slopes, regardless of wildfire severity, indicating that prior fires, which were predominantly low severity prescribed fires, did not substantially affect CWD on slopes.

In gullies, severe wildfire did not obscure the effects of fire history on small logs; a short fire history reduced volumes of small logs in all fire severity categories. While prescribed fires can consume logs (Fahnestock and Agee, 1983; Knapp et al., 2005), the effects of prescribed fire on habitat structure in moist gullies are often negligible (Bêche et al., 2005). We found that dead tree abundance in gullies was not largely affected by fire history, consistent

Fig. 3. Predicted volume (±SE) of (a) small (10–30 cm diameter) and (b) large (>30 cm diameter) logs (log$_{10}$), and predicted abundance (±SE) of (c) small and (d) large dead trees from generalised linear mixed models that included the fixed predictor variables topography, fire severity, and their interaction.
with evidence that dead trees collapse predominantly following severe wildfire (Collins et al., 2012a). Drought conditions prior to fires, however, may result in log combustion and even low severity fires should not be considered benign.

4.3. Topography and timber harvesting

Consistent with our predictions, gullies had higher volumes of logs than slopes, with the exception of small logs in severely burnt sites. Large logs, which provide the most important ecosystem functions (Harmon et al., 1986), showed a particularly strong association with gullies. Logs are more abundant in gullies in various forest types (Webster and Jenkins, 2005; Collins et al., 2012a), as moist gullies are highly productive. We expected to find more large dead trees in gullies than on slopes, but abundances did not differ. The higher volume of large logs, but not large dead trees, in gullies compared to slopes may be the result of a higher rate of collapse of dead trees in gullies during wet periods (Franklin et al., 1987), as well as past timber harvesting of large trees across the study area. Timber harvesting removes potential CWD, but can also cause an influx of logs if cut stems are left onsite. Felled rotten stems were historically left onsite (Grove, 2001) which, in our study area, may have contributed to the higher volume of large logs in gullies than on slopes. Our estimation of the basal area of cut stumps, and therefore the role of timber harvesting in shaping CWD dynamics, is most likely an underestimate, as it was difficult to determine whether burnt out stumps were the result of timber harvesting or natural tree fall.

4.4. Foothill forests and effects on fauna

Foothill forests in south-eastern Australia are composed of trees which predominantly survive even severe fire, resprouting from the stem and canopy. The impacts of wildfire on CWD appear to be smaller in these forests compared with systems where whole stands of trees are killed by fire (Harmon et al., 1986). Forests that experience only patchy tree death are unlikely to experience extreme shifts in forest type, which can occur when stand replacing fire intervals are insufficient for trees to reach maturity (Lindenmayer, 2009). The exception in our system may be some damp gullies, as frequent fire will encourage drying, and therefore fire, resulting in changes in species composition (Pettit and Naiman, 2007).

Many animal species use CWD for shelter, nesting and foraging (Harmon et al., 1986; Lindenmayer and Franklin, 2002), and fire-mediated changes to their habitat have long-term impacts on persistence (Smith et al., 2013). For example, decreased fecundity was observed in a population of hollow-dependent mountain brushtail possums Trichosurus cunninghamii after loss of den trees following wildfire (Banks et al., 2011); while saproxylic invertebrates are threatened by fire regimes that reduce the abundance of dead wood (Davies et al., 2008). Large logs, which provide important habitat for fauna (Harmon et al., 1986), were resistant to fire in our system, potentially providing habitat legacies (Foster et al., 1998). Small logs, which were reduced by fire in gullies, provide relatively fewer ecosystem services (Harmon et al., 1986), but do provide important habitat for some species (Nordén et al., 2004; Brin et al., 2011). Severe wildfire resulted in more large dead trees
in gullies: this may increase the availability of hollows and other resources while these standing trees decay (Inions et al., 1989), but depletes the availability of large living trees. Thus, wildfire both removes and creates CWD from ecosystems. The persistence of native fauna species in many ecosystems is threatened by habitat loss (Millennium Ecosystem Assessment, 2005), and the influence of wildfire, prescribed fire and timber harvesting should be managed to ensure that CWD is not depleted over time.

5. Implications and conclusions

Our results suggest that, while coarse woody debris in foothill forests is relatively resilient to fire, both wildfire severity and fire history are important determinants of CWD dynamics. Damp gullies, which support the greatest abundance of CWD in this system and many others (e.g. Webster and Jenkins, 2005; Collins et al., 2012a), may be particularly vulnerable to changed fire regimes (Bradstock et al., 2010). Frequent fires in gullies, particularly severe wildfires, will reduce the existing CWD resource, and will slow the accumulation of CWD that occurs when gullies remain unburnt for many years. Reduced CWD could, in turn, lead to diminishing fauna populations, particularly as animals may use gullies as both drought and fire refuges (Mackey et al., 2012; Robinson et al., 2013).

Use of low-severity prescribed fire for ecological management of forests should be carefully planned to ensure that some areas remain unburnt for many years. Long unburnt ‘fire refuges’ provide distinct habitats in many ecosystems (Robinson et al., 2013). Foothill forests reach vigorous maturity within 20 years, but large reserves of CWD, as well as habitat components such as tree hollows, may take many more years to develop (Cheal, 2010). During times of drought, prescribed fire may not be an appropriate ecological management tool, and measures will be required to exclude fuel reduction fires from damp gullies.

This study has revealed important effects of fire regime components on CWD at a ‘snap shot’ in time, but was not able to examine changes in CWD over time. Our conceptual model provides a useful framework for designing longer-term studies to investigate and test the complex interactions between fire regimes and landscape processes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.12.028.

References

Bates, D., Maechler, M., 2011. lme4: Linear Mixed Effects Models using S4 Classes. R package, version 0.999999-0.


