Relationships between mature trees and fire fuel hazard in Australian forest

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Abstract Increasing density of mid-storey vegetation since European settlement has been observed in forests and woodlands in several parts of the world and may result in greater fire fuel hazard. This phenomenon is often attributed to a longer interval between fires since European settlement, but may also be influenced by tree removal during the same period.. We hypothesised that the number of mature trees in a stand reduces mid-storey vegetation cover and the associated fire fuel hazard through competition. To test this hypothesis, we examined associations between mid-storey cover and fire fuel hazard and the mean diameter of trees within stands of open forest and woodland in south-eastern Australia, a region prone to wildfires. We found that vegetation cover between 2 and 4 m and 4 and 6 m above the ground and two measures of fire fuel hazard were negatively associated with the quadratic mean tree diameter. Our results suggested that the removal of mature trees since European settlement may have triggered tree and shrub regeneration, resulting in higher mid-storey cover and fire fuel hazard. Thus, managing stands for the persistence and replacement of mature trees may contribute to long-term fuel reduction in Australian forests and woodlands.

Summary We found that the mean tree size of stands was negatively associated with mid-storey vegetation cover and fire fuel hazard. Thus, the widespread removal of mature trees since European settlement may have contributed to a higher fuel hazard in forests. Our findings suggest that retaining mature trees could contribute to managing fire fuel hazard.

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N Wilson *et al.*

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Introduction

Increasing density, or ‘thickening’, of vegetation is a phenomenon observed in woodland and forest communities in many parts of the world (Vale 1987; Asner *et al*. 2003; Cabral *et al*. 2003; Price and Morgan 2009; Lunt *et al*. 2010; Gartzia *et al*. 2014). Greater density of vegetation in forests, particularly in the mid-storey (i.e. shrubs, subcanopy trees and regenerating overstorey trees), leads to greater vertical and horizontal connectivity of fire fuels, potentially increasing the flame height and rate of spread of a wildfire (Cheney *et al*. 2012; McCaw *et al*. 2012). Thus, the causes of vegetation thickening have drawn attention in regions prone to wildfires (Fule *et al*. 2009; Naficy *et al*. 2010), including south-eastern Australia (Lunt *et al*. 2010; Gammage 2011).

The density of mid-storey vegetation in forests is associated with many factors, including environmental variation and disturbance (Gifford and Howden 2001; Specht and Specht 2002). Changed fire regimes in the 19th and 20th centuries have been identified as the key reason for increasing tree and mid-storey density in dry conifer forests in North America (Sloan 1998; Fule *et al*. 2009; Johnston 2017). Fire is considered important in killing establishing trees and shrubs that may otherwise form dense mid-storey vegetation (Sloan 1998). A similar explanation has been suggested for forests and woodlands of south-eastern Australia (Rolls 1982; Flannery 1994; Ryan *et al*. 1995; Gammage 2011). However, in some forest types, the removal of competition from large, mature trees has contributed to denser mid-storey vegetation (Smith and Arno 1999; Dwyer *et al*. 2010; Naficy *et al*. 2010; McGregor *et al*. 2016). Demand for timber, combined with the introduction of technologies such as axes, saws and then heavy machinery, resulted widespread tree removal after European settlement in North America and Australia (Walker *et al*. 1993; Benson *et al*. 1997; Smith and Arno 1999; Cooper 2011). In south-eastern Australian forests and woodlands, stands with evidence of previous timber harvesting support fewer mature trees than unlogged stands (Lindenmayer *et al*. 2000; Gibbons *et al*. 2008).

Large, mature trees compete with other vegetation for light, space, nutrients and water. Eucalypts are mesophytes that maintain access to water by developing extensive root systems as they mature (Ashton 1975; Crombie *et al*. 1988). This results in an exponential increase in water usage as they grow larger (Eamus *et al*. 2000). Consequently, larger eucalypts have a disproportionate capacity to access water compared with young trees (Crombie 1992) and may induce water stress on adjacent smaller trees and shrubs when water is limiting (Lamont 1985; Bowman and Kirkpatrick 1986). Thus, other deep-rooted vegetation (e.g. overstorey regeneration and shrubs) may be sparse in the presence of mature trees (Rotheram 1983; Lamont 1985; Bowman and Kirkpatrick 1986; Dignan *et al*. 1998; Sloan 1998; Bauhus *et al*. 2000) or more prevalent in gaps that are unoccupied by mature trees (Harrington *et al*. 1981; Dignan *et al*. 1998; Van Der Meer *et al*. 1999). Unlike productive wet forests (Ashton 1976; Vivian *et al*. 2008), eucalypts of woodlands and open forests, where available water is typically more limiting, are inhibited from rapid self-thinning owing to a greater tolerance of competition within the same cohort and can persist as a mid-storey for many years (Florence 1996). Therefore, it is possible that the removal of large, mature trees since European settlement may have contributed to a greater amount of dense mid-storey in remnant woodlands and open forests where available water can be limiting.

Shrubs, subcanopy trees and regenerating overstorey trees (i.e. mid-storey vegetation) represent a fuel layer (Gould *et al*. 2011) in the fuel hazard rating systems used by land-management agencies in Australia (Gould *et al*. 2007; Hines *et al*. 2010). Fire fuel in the mid-storey connects fuel close to the ground to the canopy. As fuel becomes more continuous, the heat transfer between burning fuel and adjacent fuel becomes more efficient (Rothermel 1972). Flame height (and flame length), the intensity (energy output per unit of fire front) and the spread of a fire are therefore likely to be higher where mid-storey vegetation connects fuel at ground level with the tree canopy (Agee and Skinner 2005, Cheney *et al*. 2012). Thus, a greater density of mid-storey vegetation in a forest contributes to a higher risk of extreme fire behaviour and greater suppression difficulty (Gould *et al*. 2011; Cheney *et al*. 2012).

In the present study, we tested whether mean tree diameter in stands is negatively associated with: (i) mid-storey vegetation cover; and (ii) mid-storey fire fuel, while controlling for other variables that may also affect the cover of mid-storey vegetation. We hypothesised that, other things being equal, stands with more large trees will exert greater competitive pressure on adjacent, deep-rooted, mid-storey vegetation and therefore be associated with lower fire fuel hazard.

Methods

Study area

Our study area spans the western slopes and tablelands of south-eastern Australia (29.5–36.0°S, 144.7–150.0°E) (Fig. 1). The climate is characterised by consistent rainfall throughout the year, although soil moisture is limiting during hot summers (Hutchinson *et al*. 2005). Mean annual rainfall ranges from 378 to 1151 mm and mean annual temperature from 11 to 19°C. Indigenous Australians occupied the region exclusively until settlement by Europeans from the early 1800s (Benson *et al*. 1997). The dominant land uses are now improved pasture for livestock grazing and cultivation. Remnant native vegetation (predominantly open forest and woodland) (Fig. 2) occupies ~16% of the study area (Pressey *et al*. 2000). There is widespread evidence of post-European modification within remnant woodlands and forest within the study area. Gibbons *et al*. (2008) recorded evidence of logging, firewood removal, grazing by livestock, exotic plants and evidence of the European rabbit (*Oryctolagus cuniculus*) in 85% of plots they sampled within remnant vegetation across the study area. Although wildfire is actively suppressed within the study area, damaging wildfires continue to occur. The most recent examples of wildfires involving losses of buildings within the study area are Canberra (2003), Junee (2006), Wagga Wagga (2006) and Coonabarabran (2013). Prescribed burning is the most widespread fuel treatment employed in an attempt to manage forest fuel hazard across the study area (Environment, Planning and Sustainable Development Directorate 2016; NSW Rural Fire Service 2016).

Site selection

We selected 516 plots within intact stands of remnant native woodlands and open forest communities across our study area. Site selection was limited to the seven most commonly occurring vegetation alliances in the study area: grey box (*Eucalyptus microcarpa* Maiden), red ironbark (*E. sideroxylon* Woolls), river red gum (*E. camaldulensis* Dehnh.), red stringybark (*E. macrorhyncha* F. Muell. ex Benth.), white box (*E. albens* Benth.), white cypress-pine (*Callitris glaucophylla* Joy Thomps. & L. A. S. Johnson) and yellow box (*E. melliodora* A. Cunn. ex Schauer). The distribution of vegetation alliances in the study area is associated with changes in geology, soils, slope and some climatic variables (Cawsey *et al*. 2002). Because available water plays a considerable role in mid-storey development within eucalypt stands (Specht and Specht 2002), sites were further stratified by five classes of mean annual rainfall (<400, 401–500, 501–600, 601–700, >701 mm) to capture potential variation in vegetation structure within widespread vegetation alliances. To capture finer-scale variation in the availability of water to plants, we typically established three 20 × 50-m (0.1-ha) plots that spanned the topographic gradient at each location.

Measured variables

In each of the 516 plots, we recorded three response variables representing percentage mid-storey cover for plants that were 0.5–2, 2–4 and 4–6 m above the ground (Table 1). Mid-storey vegetation included regenerating overstorey species. In a subset of 90 plots selected using the same stratification protocol, we recorded an additional two response variables representing the fire fuel structure contributed by elevated fuels (elevated fuel hazard score and elevated fuel height) (Table 1). Elevated fuel comprises predominantly tall shrubs and overstorey regeneration with the majority of fine fuels detached from the ground (Gould *et al*. 2011). The elevated fuel hazard score and elevated fuel height (along with weather conditions) are associated with the rate of spread (McCaw *et al*. 2012) and flame height of wildfires (Cheney *et al*. 2012). Mid-storey cover for each plot was measured using the line-intercept method along a 50-m transect running down the long axis of each 20 × 50-m plot. Percentage cover was based on the average of 10 observations from 1-m transects each spaced 5 m apart. The elevated fuel hazard score and elevated fuel height were estimated in ten 20 × 5-m subplots established within each 20 × 50-m plot, and averaged to attain a single score for each plot. The elevated fuel hazard scores range from 0 (no elevated fuel) to 4 (extreme hazard elevated fuel structure) and were based on visual estimates of the fuel cover, proportion of dead material and quantity of suspended litter (Gould *et al*. 2007). Elevated fuel height was estimated from the average of five measurements of the typical height of the elevated fuel in each 20 × 5-m subplot (Gould *et al*. 2007).

In each of the 516 plots, we also recorded a potential explanatory variable representing tree size and percentage canopy cover (Table 2) and hence potential competition with the mid-storey. We used the quadratic mean diameter at breast height (DBH) (*Dq*) to represent the size of trees at each plot. *Dq* is commonly used to describe mixed-aged stands as it accounts for the presence of larger trees by weighting a tree's contribution to the mean proportionally to its size (Curtis and Marshall 2000). This variable was calculated using the DBH measurements of all living trees ≥5 cm DBH across each 20 × 50-m plot using the equation of West (2009):

$$Dq = \sqrt{\frac{\sum_{i=1}^{n} \mathrm{DBH}_i^2}{n}}$$

where *Dq* is the quadratic mean stem diameter, DBH is the diameter at breast height (cm) and n is the number of DBH observations in the plot.

We also measured explanatory variables indicative of environmental variation and other disturbances to account for their likely influence on mid-storey vegetation and fuel structure (Table 2). Vegetation alliance, mean annual rainfall and landscape position were measured to account for variation in resources (particularly available water) that can affect the mid-storey structure of eucalypt stands (Specht and Specht 2002). Vegetation alliance was defined by the dominant overstorey species recorded in each plot. Seven vegetation alliances were recorded (Table 2). Mean annual rainfall was estimated to the nearest 100 mm (as in Gibbons *et al*. 2010) for each plot using ESOCLIM (Houlder *et al*. 2000) and a 250-m digital elevation model or, for the subset of 90 plots used to calculate fire fuel variables, we used historical data for the nearest Bureau of Meteorology weather station (Bureau of Meteorology 2015). Topographic position was recorded at each plot as one of six levels (flat, drainage line, lower slope, mid-slope, upper slope, ridge) based on observations in the field. We also recorded whether there was evidence at each plot of recent disturbance based on the presence of livestock (droppings or sightings), the presence of the European rabbit (droppings, diggings or sightings), fire (charcoal on the soil or vegetation and presence of tree scars on trees) or tree felling (presence of cut stumps). Canopy cover was also measured as a potential explanatory variable indicative of site occupancy irrespective of tree size. Percentage canopy cover was based on averaging 10 visual estimates of vegetation cover above 6 m, each spaced 5 m apart along the 50-m transect using images from Walker and Hopkins (1984) as a guide.

Statistical analysis

We used regression to examine associations between mid-storey vegetation cover (0.5–2, 2–4 and 4–6 m above ground) and fire fuel characteristics (elevated fuel hazard score and elevated fuel height) and tree size (*Dq*). We fitted the additional potential explanatory variables to account for the influence of environmental variation and disturbance history. Mid-storey vegetation cover (0.5–2, 2–4 and 4–6 m above ground) was analysed using the full dataset (516 plots), whereas fire fuel characteristics were analysed using the subset of 90 plots containing the two fire fuel response variables (Table 2). We conducted all our analyses in *R* (ver. 3.3.2, R Core Team 2016, Available from https://www.R-project.org/, Accessed 5 December 2016).

Initial exploratory analyses were used to identify outliers, frequency distributions and correlation between potential explanatory variables. Explanatory variables with a Pearson's correlation coefficient greater than 0.6 were not included in the same model. One observation with a *Dq* value more the twice as large as the next largest value was removed from all analyses. Its inclusion disproportionately influenced the model predictions. Thus, the sample size was reduced to 515 and 89 for the mid-storey vegetation cover and fire fuel datasets respectively. *Dq* and elevated fuel height were transformed using the natural log (ln) to achieve an approximately normal distribution before model fitting (Zuur *et al*. 2014). There were no highly correlated explanatory variables.

Zero values accounted for 41–49 % of the observations of 0.5–2-, 2–4- and 4–6-m vegetation cover. To avoid issues with zero-inflated data, the presence or absence of mid-storey vegetation cover was modelled using a binomial generalised linear model (GLM) to determine what explanatory variables are associated with the presence of mid-storey vegetation. Plots where the mid-storey was present were separately analysed to determine relationships between the percentage cover of mid-storey vegetation and the potential explanatory variables. Percentage mid-storey vegetation cover and Fuel Hazard Scores were analysed using β regression with a logit link, using the *betareg* package in *R* (Zeileis *et al*. 2016, Available from https://cran. r-project. org/package= betareg, Accessed 5 December 2016), because these data are bound by upper and lower limits (i.e. they are not true continuous data). Beta regression models account for the unique properties of bounded data (Ferrari and Cribari-Neto 2004). Data analysed using β regression were divided by the maximum possible value (i.e. 100 for percentage data and 4 for Fuel Hazard Scores) so that values were between 0 and 1. At the time of writing, the *betareg* package did not support reliable confidence interval predictions, which are consequently absent from predictions made from these models. Elevated fuel height (ln transformed) was analysed using linear regression. Models were selected using backwards stepwise selection informed by the change in Akaike Information Criterion (AIC) (all candidate models and their respective AIC values are listed in Table S1 in the Supplementary material). We assessed the goodness-of-fit for each model using pseudo r^2 values for β and logistic regression models, and r^2 values for linear models (r^2 values for each candidate model listed in Table S1). Model fits were assessed by plotting residuals against an index of observations for β regression models (Ferrari and Cribari-Neto 2004), and residuals against predicted values for all other models

(Fig. S1 in the Supplementary material). Cook's distance was used to check for observations with high leverage.

Results

Stand characteristics

The number of tree stems ≥5 cm DBH in the plots surveyed ranged from 1 to 203, with a mean of 32. The diameter of these stems ranged from 5 to 315 cm DBH with a mean *Dq* of 36 cm. The mean DBH of the largest tree in each plot for each vegetation alliance was 82 cm (grey box alliance), 74 cm (red ironbark alliance), 112 cm (river red gum alliance), 73 cm (red stringybark alliance), 81 cm (white box alliance), 73 cm (white cypress-pine alliance) and 88 cm (yellow box alliance). There was a strong, negative log–log correlation between *Dq* and the number of stems ≥5cm DBH in a stand (Pearson's correlation coefficient = –0.78).

Canopy cover was not strongly correlated with either *Dq* (Pearson's correlation coefficient = 0.12) or the number of stems ≥5cm DBH (Pearson's correlation coefficient = 0.16). We recorded evidence of previous logging (i.e. at least one cut stump) in 72 % of all stands.

0.5–2-m vegetation cover

Zero values accounted for 42% of observations for vegetation cover 0.5–2 m above the ground. Non-zero values ranged from 1 to 51% (mean = 6.1%). The probability vegetation cover for plants 0.5–2 m above the ground was present decreased significantly with ln *Dq* and was lower when livestock and evidence of fire were present at the site (Table 3). The percentage cover of vegetation 0.5–2 m above the ground was significantly lower in the red ironbark, river red gum and white box vegetation alliances (Table 3).

2–4-m vegetation cover

Zero values accounted for 49% of observations of vegetation cover 2–4 m above the ground. Non-zero values varied from 1 to 21% (mean = 5.4%). The probability vegetation cover 2–4 m above the ground was present decreased significantly with ln *Dq* and when tree scars were present, and was significantly lower where the mean annual rainfall was 601–700 mm (Table 3). The percentage cover of vegetation 2–4 m above the ground decreased significantly with ln *Dq* (Fig. 3*a*) and increased significantly with canopy cover (Table 3).

4–6-m vegetation cover

Zero values accounted for 41% of observations of vegetation cover 4–6 m above the ground. Non-zero values ranged from 1 to 25% (mean = 6.2 %). The probability of vegetation cover being present for plants 4–6 m above the ground decreased significantly with canopy cover; was significantly lower in plots where evidence of fire was present; and was significantly lower where the vegetation alliance was either red stringybark or yellow box, and significantly higher where the vegetation alliance was river red gum or white cypress pine (Table 3). The percentage cover of vegetation 4–6 m above the ground decreased significantly with ln *Dq* (Fig. 3*b*); increased significantly with canopy cover; was significantly lower at plots where tree stumps were present; and was significantly higher when the vegetation alliance was white cypress-pine or yellow box (Table 3).

Elevated fuel hazard score

Average elevated fuel hazard scores ranged from 0.1 to 2.9 (mean = 1.2). The average elevated fuel hazard score decreased significantly as ln *Dq* increased (Table 3, Fig. 3*c*). The average elevated fuel hazard score was also significantly lower in plots where tree stumps were present and significantly higher where the vegetation alliance was red ironbark (Table 3).

Elevated fuel height

Average elevated fuel height ranged from 0.4 to 4.8 m (mean = 2.1 m). Average elevated fuel height decreased significantly as ln *Dq* increased (Table 3, Fig. 3*d*).

Discussion

We examined associations between the quadratic mean diameter of trees in a stand and mid-storey vegetation cover and fire fuel characteristics in woodlands and open forests in south-eastern Australia. We hypothesised that stands with more large, mature trees (measured as *Dq*) exert greater competitive pressure on adjacent, deep-rooted, mid-storey vegetation. Using *Dq* as a measure of tree size while accounting for environmental variation and disturbance history, we found support for our hypothesis that stands dominated by larger trees have significantly lower cover of mid-storey vegetation in some mid-storey strata, significantly lower average elevated fuel hazard scores and significantly lower average elevated fuel heights (Table 3).

Mid-storey cover

The percentage cover of mid-storey vegetation 2–4 and 4–6 m above the ground declined with increasing quadratic mean tree diameter (ln *Dq*) while controlling for the effects of other variables associated with environmental variation and disturbance. Thus, our results suggested that the cover of mid-storey vegetation may increase with the removal of large, mature trees. Similar relationships between numbers of mature trees in stands and mid-storey cover have been observed in forests dominated by alpine ash (*E. delegatensis* R.T. Baker) (Bowman *et al*. 2014) and ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) (Sloan 1998; Naficy *et al*. 2010). The deeper and more extensive root systems of larger trees (Ashton 1975; Crombie *et al*. 1988; Eamus *et al*. 2000) may induce water stress in smaller deep-rooted individuals in the stand (Lamont 1985), limiting their establishment and growth (Rotheram 1983; Bowman and Kirkpatrick 1986; Dignan *et al*. 1998; Bauhus *et al*. 2000). The absence of a significant relationship between mid-storey cover 0.5–2 m above the ground and the quadratic mean diameter of trees (*Dq*) is likely due to the presence of non-woody vegetation, such as grasses, occurring in this stratum. Grasses utilise water in the upper soil profile and thus are less likely to compete directly with deep-rooted plant life-forms such as trees, particularly on sites with fine-textured soils such as clays (Sala *et al*. 1997).

However, our results also indicated that other disturbances and environmental variation influence the amount of mid-storey vegetation in stands. Disturbances such as fire are known to affect the mid-storey structure of some forests (Sloan 1998; Fule *et al*. 2009; Johnston 2017). In our study, the presence of a fire scar on at least one tree within the stand and evidence of recent fire significantly decreased the probability of the mid-storey being present. Mid-storey cover 2–4 m above the ground was also less likely to be present where at least one tree had a fire scar, which is indicative of past fire, and mid-storey cover 4–6 m above the ground was less likely to be present where there was evidence of recent fire. However, visual evidence of fire, such as the presence of charcoal or tree scars at the base of trees, provides only a coarse indication of the fire history at a given plot (hence the low r^2 values in Table S1). Other aspects of fire history (e.g. time since fire and fire frequency) may play a greater role in mid-storey structure than observed in our study (e.g. Zylstra 2013), so more detailed fire history data may indicate a greater role that fire plays in the mid-storey structure of stands. Mid-storey structure in eucalypt forests and woodlands may also be influenced by available resources (e.g. water) (Specht and Specht 2002), which can be mediated by factors such as soil properties and fine-scale topographic features (Beadle 1981). Rainfall or vegetation alliance were included in five of the six models explaining mid-storey vegetation cover, and were significant in four of them. Part of the variation in mid-storey vegetation structure in south-eastern Australian woodlands and open forests is therefore likely to be a function of environmental variation and disturbance history.

Elevated fire fuel

The significant negative relationships we found between mid-storey vegetation cover and large trees translated to a reduction in elevated fire fuel where larger trees were present (Fig. 3). Higher densities of tree and shrub regrowth after the removal of large trees from logging or high-severity fire have been documented in *Eucalyptus* woodlands (Haslem *et al*. 2011; McGregor *et al*. 2016) and wet forests (Park 1975), as well as in North American conifer forests (Smith and Arno 1999; Naficy *et al*. 2010). Although these findings appear to be contradicted by our analysis showing that average elevated fuel hazard scores were significantly lower when tree stumps were visible, most tree stumps that we observed were of recently cut, small regrowth stems, rather than from historic removal of mature trees. Like mid-storey vegetation cover, there was variation in elevated fuel with changes in vegetation alliance, thus indicating that elevated fuel is a function of environmental variation in addition to the presence of large trees.

Management implications

The presence of mid-storey fire fuel can positively influence both the rate of spread (McCaw *et al*. 2012) and flame height (Cheney *et al*. 2012) of a wildfire. Consequently, mid-storey fire fuel may increase the difficulty of suppressing a wildfire (Cheney *et al*. 2012). Fuel reduction burning is the dominant fire fuel management tool in our study area. The influence of prescribed burning on subsequent fire behaviour diminishes within 2 to 10 years (Fernandes and Botelho 2003; McCarthy and Tolhurst 2004; Tolhurst and McCarthy 2016). Maintaining prescribed burning at such a frequency across a region as large as our study area is logistically challenging. Our findings suggest that the loss of mature trees in stands since European settlement may have contributed to increased mid-storey cover and fire fuel. Logically, this process can slowly be reversed through re-establishment of mature overstorey trees, which could improve the effectiveness of existing fuel management practices such as prescribed burning, or represent an alternative long-term fuel management strategy.

Conflict of interest

The authors declare that they have no conflicts of interest.

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Table 1. Response variables representing mid-storey vegetation cover and fire fuel characteristics recorded at each plot

Variable	Description
0.5–2-m vegetation cover	Average percentage vegetation cover between heights of 0.5 and 2 m
2–4-m vegetation cover	Average percentage vegetation cover between heights of 2 and 4 m
4–6-m vegetation cover	Average percentage vegetation cover between heights of 4 and 6 m
Elevated fuel hazard score	Visual assessment of fuel cover, proportion of dead material and quantity of suspended litter combined into a score out of 4 (Gould *et al*. 2007) and averaged for each plot
Elevated fuel height	Average elevated fuel height (Gould *et al*. 2007)

Table 2. Description of potential explanatory variables representing tree size, environmental variation and disturbance at each plot

Variable	Description
Dq	Quadratic mean DBH (diameter at breast height, cm) of all living trees 5 cm DBH
Canopy cover	Average percentage canopy cover for plants 6 m above the ground
Rainfall	Mean annual rainfall (mm) recorded as one of five levels (<400, 401–500, 501–600, 601–700, >701 mm)
Vegetation alliance	Dominant overstorey species recorded as one of seven levels (grey box, red ironbark, river red gum, red stringybark, white box, white cypress-pine, yellow box)
Topographic	Topographic position recorded as one of six levels (flat, drainage line, lower slope, mid-slope, upper slope or ridge)

position	
Livestock	Presence or absence of evidence of livestock
Rabbit	Presence or absence of the European rabbit
Evidence of fire	Presence or absence of recent fire based on the occurrence of charcoal
Tree scars	Presence or absence of past fire based on the presence of a fire scar on one or more trees
Tree stumps	Presence or absence of human-cut tree stumps

Table 3. Parameter estimates with standard errors (in parentheses) and statistical significance codes for each statistical model

Parameters in parentheses represent different levels for factors. Parameter estimates are for transformed response variables (see *Methods* for transformations). Presence/ or absence models were analysed using binomial regression, percentage cover and fuel hazard scores were modelled using β regression and elevated fuel height was modelled using linear regression. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ., $P < 0.1$. Response variables 0.5–2P/A, 2–4P/A and 4–6P/A are presence/absence response variables, and 0.5–2C, 2–4C and 4–6C are percentage cover response variables. E FHS, elevated fuel hazard score; E Height, elevated fuel height

Explanatory variable	Response variables						
	0.5–2	0.5–2	2–4	2–4	4–6	4–6	E FHS
Intercept	4.50 (0.98)***	–1.54 (0.42)***	4.71 (1.01)***	–1.43 (0.34)***	1.08 (0.31)***	–1.79 (0.41)***	3.85 (0.65)***
ln *Dq*	–1.19 (0.23)***	–0.22 (0.12).	–0.92 (0.22)***	–0.47 (0.1)***		–0.31 (0.1)**	–1.39 (0.18)***
Canopy cover			–0.01 (0.01)	0.01 (0.01)*	–0.02 (0.01)*	0.01 (0.01)*	
Tree stumps (absent)		0			0	0	0
Tree stumps (present)		–0.18 (0.1).			0.38 (0.23).	–2.3 (0.09)*	–0.46 (0.16)**

Livestock (absent)	0	0					0
Livestock (present)	–0.63 (0.2)**	–0.18 (0.1).					0.24 (0.15)
Rabbit (absent)							
Rabbit (present)							
Evidence of fire (absent)	0				0		
Evidence of fire (present)	–0.49 (0.23)*				–0.49 (0.26)*		
Tree scars (absent)	0	0					
Tree scars (present)	0.4 (0.22).	–0.13 (0.09)	–0.50 (0.2)*				
Rainfall (<400 mm)	0		0			0	
Rainfall (401–500 mm)	0.2 (0.61)		–0.58 (0.7)			0.03 (0.21)	
Rainfall (501–600 mm)	1.12 (0.6) ns		–0.36 (0.69)			0.15 (0.22)	
Rainfall (601–700 mm)	0.25 (0.59)		–1.65 (0.69)*			–0.02 (0.24)	
Rainfall (>701 mm)	–0.09 (0.61)		–1.32 (0.71).			–0.34 (0.26)	
Vegetation alliance (grey box)		0			0	0	0
Vegetation alliance (red ironbark)		–0.37 (0.15)*			–0.05 (0.36)	0.07 (0.14)	0.68 (0.24)**
Vegetation alliance (river red gum)		–0.71 (0.24)**			1.07 (0.54)*	–0.15 (0.18)	–0.21 (0.33)
Vegetation alliance (red stringybark)		0.04 (0.13)			–1.54 (0.36)***	0.15 (0.21)	–0.06 (0.23)

Vegetation alliance (white box)	–0.42 (0.17)*			0.04 (0.34)	0.28 (0.15).	0.48 (0.25).
Vegetation alliance (white cypress-pine)	–0.27 (0.15).			1.16 (0.46)*	0.27 (0.16)*	0.01 (0.26)
Vegetation alliance (yellow box)	–0.16 (0.13)			–0.02 (0.01)*	0.45 (0.15)**	–0.08 (0.2)

Fig. 1. Location of the 515 study plots throughout New South Wales, the Australian Capital Territory and Victoria in south-eastern Australia.

Fig. 2. Examples of variation in the mid-storey of open forests and woodlands in the study area: stands dominated by large, mature trees (top left and right) and stands dominated by smaller trees (bottom left and right).

Fig. 3. Relationships between the log-transformed quadratic mean diameter at breast height (DBH) of trees (ln *Dq*) and: (*a*) vegetation cover for plants 2–4 m above the ground; (*b*) vegetation cover for plants 4–6 m above the ground; (*c*) elevated fuel hazard scores; and (*d*) elevated fuel height. Solid lines are the predicted values, dotted lines are confidence intervals and grey dots are the observed values. Fitted lines for (*a*), (*b*) and (*c*) were predicted using β regression, and (*d*) using linear regression. Values were predicted with all other covariates held at their base level (see Table 3).

Supplementary material

Table S1. Explanatory variables, AIC and pseudo-r^2 (r^2 for all E Height models) values for each candidate model considered as part of the model selection process for each response variable

P/A, presence or absence response variable; C, percentage cover response variable; E FHS, elevated fuel hazard score; E Height, elevated fuel height

Response	Explanatory	AIC	r^2
4-6P/A	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	614.05	0.19
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	611.02	0.18
	Canopy cover + Tree stumps + Tree scars + Livestock + Topographic position + Evidence of fire + Vegetation	609.04	0.18

	alliance + Rabbit		
	Canopy cover + Tree stumps + Tree scars + Livestock + Evidence of fire + Vegetation alliance + Rabbit	607.37	0.17
	Canopy cover + Tree stumps + Livestock + Evidence of fire + Vegetation alliance + Rabbit	606.16	0.17
	Canopy cover + Tree stumps + Evidence of fire + Vegetation alliance + Rabbit	605.32	0.16
4-6C	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	–1126.71	0.13
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–1133.10	0.12
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Evidence of fire + Vegetation alliance	–1135.10	0.12
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Vegetation alliance	–1136.45	0.12
	ln Dq + Canopy cover + Tree stumps + Rainfall + Livestock + Vegetation alliance	–1138.05	0.12
	ln Dq + Canopy cover + Tree stumps + Rainfall + Vegetation alliance	–1138.66	0.11
2-4P/A	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	656.61	0.14
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Rabbit	650.71	0.14
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Topographic position + Evidence of fire + Rabbit	648.85	0.14
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Topographic position + Evidence of fire	647.00	0.14
	ln Dq + Canopy cover + Tree scars + Rainfall + Topographic position + Evidence of fire	645.46	0.13

	ln Dq + Canopy cover + Tree scars + Rainfall + Topographic position	645.24	0.13
	ln Dq + Canopy cover + Tree scars + Rainfall	644.58	0.12
2-4-C	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	–1050.96	0.15
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–1056.04	0.13
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–1059.97	0.11
	ln Dq + Canopy cover + Tree scars + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–1061.86	0.11
	ln Dq + Canopy cover + Tree scars + Livestock + Vegetation alliance + Rabbit	–1063.58	0.12
	ln Dq + Canopy cover + Livestock + Vegetation alliance + Rabbit	–1065.14	0.11
	ln Dq + Canopy cover + Livestock + Rabbit	–1066.38	0.08
	ln Dq + Canopy cover + Livestock	–1067.21	0.07
	ln Dq + Canopy cover	–1067.30	0.06
0.5-2P/A	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	658.32	0.13
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Rabbit	651.19	0.12
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Evidence of fire + Rabbit	647.94	0.11
	ln Dq + Canopy cover + Tree scars + Rainfall + Livestock + Evidence of fire + Rabbit	646.35	0.11

	ln Dq + Canopy cover + Tree scars + Rainfall + Livestock + Evidence of fire	646.23	0.11
	ln Dq + Tree scars + Rainfall + Livestock + Evidence of fire	646.14	0.10
05-2C	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	–1073.69	0.16
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–1078.45	0.14
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–1082.17	0.13
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Vegetation alliance + Rabbit	–1084.15	0.13
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Vegetation alliance	–1085.74	0.13
	ln Dq + Tree stumps + Tree scars + Livestock + Vegetation alliance	–1086.87	0.12
E Height	LDq + Canopy + Fstump + Fscar + Rain + Stock + TopoID + Fire2 + Veg + Rabbit	181.46	0.39
	LDq + Canopy + Fstump + Fscar + Rain + Stock + Fire2 + Veg + Rabbit	173.86	0.36
	LDq + Canopy + Fstump + Fscar + Stock + Fire2 + Veg + Rabbit	169.28	0.33
	LDq + Canopy + Fstump + Fscar + Stock + Fire2 + Veg	167.28	0.33
	LDq + Fstump + Fscar + Stock + Fire2 + Veg	165.30	0.33
	LDq + Fstump + Stock + Fire2 + Veg	163.84	0.33
	LDq + Fstump + Stock + Veg	162.56	0.32
	LDq + Fstump + Stock	161.41	0.23

	LDq + Fstump	159.90	0.23
	LDq	159.17	0.22
E FHS	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Topographic position + Evidence of fire + Vegetation alliance + Rabbit	–104.46	0.62
	ln Dq + Canopy cover + Tree stumps + Tree scars + Rainfall + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–109.05	0.59
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Evidence of fire + Vegetation alliance + Rabbit	–111.26	0.56
	ln Dq + Canopy cover + Tree stumps + Tree scars + Livestock + Vegetation alliance + Rabbit	–113.18	0.56
	ln Dq + Tree stumps + Tree scars + Livestock + Vegetation alliance + Rabbit	–114.82	0.55
	ln Dq + Tree stumps + Livestock + Vegetation alliance + Rabbit	–116.26	0.55
	ln Dq + Tree stumps + Vegetation alliance + Rabbit	–117.60	0.55

Fig. S1. Diagnostic plots for the models predicting the presence of vegetation cover between 4 and 6 m (*a*), 2 and 4 m (*b*), 0.5 and 2 m (*c*), percentage vegetation cover between 4 and 6 m (*d*), 2 and 4 m (*e*), 0.5 and 2 m (*f*), elevated fuel height (*g*) and elevated fuel hazard score (*h*).