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Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat

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Abstract

The mean interval between tree-killing fires in mountain ash (*Eucalyptus regnans* F. Muell.) forest was inferred from information on the age structure of unlogged forest, the prevalence of mountain ash trees in the landscape, and on the abundance of live and dead hollow-bearing trees. The analyses were based on models of the local extinction and recolonization of forest patches by mountain ash trees and of the development of hollow-bearing trees in response to time since fire. The results of the analyses suggested that the mean interval between tree-killing fires was between ≈75 and 150 years in mountain ash forest. Data on mortality of mountain ash trees suggest that approximately half the trees survive fire, making the mean interval between all fires equal to 37–75 years. The model predicts that the proportion of the landscape occupied by mountain ash will decline sharply as the mean fire interval decreases, suggesting that changes in the fire regime may have abrupt and major effects on ecosystem properties.

Keywords: Fire interval; Hollow-bearing trees; Disturbance; *Eucalyptus regnans*; South-eastern Australia

1. Introduction

Disturbance by fire is a major factor in ecosystems throughout the world, influencing processes such as water and nutrient cycling, energy flow, carbon sequestration and habitat dynamics (Naveh, 1975; Gill et al., 1981; Booysen and Tainton, 1984; Goldammer, 1990; Johnson, 1992; Pyne et al., 1996). Effects of fire on a given ecosystem depend on the fire regime, which may be characterized by the type of fires, the season in which they occur, the intensity of fires and the fire intervals (Gill, 1975). Fire is a critical element in the regeneration and persistence of mountain ash (*Eucalyptus regnans* F. Muell.), a tree that dominates montane forests in parts of south-east Australia (Ashton, 1981; Attiwill, 1994). Mountain ash are the tallest flowering plants in the world, with individuals capable of growing to a height of 100 m or more (Hardy, 1935; Ashton and Attiwill, 1994). In Victoria, mountain ash forests are important sources of timber and pulpwood

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(Land Conservation Council, 1994), and their catchments supply a substantial proportion of the water consumed in Melbourne, a city of more than 3×10^6 people (O'Shaugnessy and Jayasuriya, 1991). In addition to these commercial uses, mountain ash forests cater for recreation (Land Conservation Council, 1994) and provide important habitat for a number of plant and animal species (Lindenmayer, 1996).

Many of the uses and values of mountain ash forests are influenced by the incidence of fire. High intensity fire kills mountain ash trees, with regeneration from a canopy-stored seed bank (Ashton, 1976; Ashton, 1981). Regeneration is very limited in the absence of disturbance by fire (Ashton and Willis, 1982). Thus, mountain ash forests can usually be classified by their age structure, with tree ages traced back to particular fire events (Ashton, 1976). Timber supplies (West and Mattay, 1993; Smith and Woodgate, 1985), water yields (Kuczera, 1987) and the suitability of habitat for a number of animal species (Lindenmayer, 1996) all change in response to the incidence of fire and the age of the regeneration. Hollow-bearing trees are an important habitat component for a number of species in mountain ash forest, providing nest sites and shelter (Lindenmayer et al., 1991a), and their production and maintenance is influenced by fire (Lindenmayer et al., 1997b). Because of the importance of fire in mountain ash forests, a better understanding of the fire regime is critical to ensure that these forests are managed on an ecologically sustainable basis (McCarthy and Burgman, 1995).

The season and type of fires in mountain ash forest are relatively well known. Fires usually occur in summer to early autumn after fuels have dried during the summer drought period (Rees, 1984). Fires are considered to be of the surface type in Victoria (Ashton, 1981), although they can burn in humus ('ground' fires) in Tasmania (Cremer, 1962). Surface fires refer to fires that burn fuels that are on or above the ground level (Gill, 1975). However, there is some uncertainty about certain aspects of the fire regime in mountain ash forests, such as frequency and intensity. Rugged terrain, access difficulties, and the potential for very high intensity fires up to $100\,000\ \mathrm{kW\ m^{-1}}$ (Gill and Moore, 1990) make it difficult to measure the actual intensity and variation in intensity. Inference from aerial photography suggests that fire intensity is highly variable, with canopy leaf scorch ranging from 0% to 100% (Smith and Woodgate, 1985). Estimates of fire intervals from direct observation are uncertain because fire intervals are long, especially relative to the period of record.

Given these uncertainties, we attempted to determine intervals between tree-killing fire events in mountain ash forests. For the purpose of this paper, tree-killing fires are defined as being of an intensity that is sufficient to kill mountain ash trees (high intensity). Within a single fire event, only a proportion of the area is likely to be burnt by fire that is sufficient to kill the mountain ash tress. In this case, only a proportion of the area burnt is exposed to a tree-killing fire. The fire intervals refer to the time between fires at an arbitrary point in the landscape. Dendrochronological studies of fire regimes in mountain ash forest are only of limited value because of difficulty in obtaining suitable material due to decay and the high incidence of mortality of trees following fires (Ambrose, 1982). Gill and McCarthy (1998) argued that evidence other than from dendrochronology could be used to infer fire regimes. For example, if a species is fire sensitive and seed occurs only on mature plants (as for mountain ash), then limits imposed by the fire regime on the persistence of the species can be determined. Here, we use information on the age structure of mountain ash forests, the persistence of mountain ash trees in the presence of fires, and the frequency of occurrence of hollow-bearing trees to infer the distribution of fire intervals in mountain ash forests, assuming that other environmental factors that influence the distribution are correctly accounted for. The aim is to quantify aspects of the fire regime that has prevailed in mountain ash forests in the recent past.

2. Methods

2.1. Forest age structure

The age structure of a forest subject to random tree-killing fires is a function of the mean time between fires (van Wagner, 1978). Reed (1994) provides a method for estimating the incidence of stand-replacing fires from forest age structure, thereby providing information about the mean fire interval. This method is an analytical extension of that proposed by van

Wagner (1978). Conceptually, the method uses the fact that forest age structure is a function of the rate at which regeneration occurs.

Assuming the annual risk of high intensity fire at a point is constant with time since the last fire (a), the expected age structure of the forest is described by an exponential probability density function

$$f(t) = a\mathrm{e}^{-at}, \tag{1}$$

where t is the time since the last fire. The cumulative probability function is

$$F(t) = 1 - \mathrm{e}^{-at},$$

which gives the proportion of the forest that is expected to be younger than age t. Therefore, the proportion expected to be younger than 50 years is $1 - \mathrm{e}^{-50a}$, the proportion expected to be between 50 and 100 years old is $\mathrm{e}^{-50a} - \mathrm{e}^{-100a}$, the proportion expected to be between 100 and 200 years old is $\mathrm{e}^{-100a} - \mathrm{e}^{-200a}$, and the proportion expected to be older than 200 years is e^{-200a}. The method of Reed (1994) uses such expected proportions and fits observed data to provide an estimate of a, the annual risk of fire. The mean interval between high intensity fires is simply the inverse of a, $(1/a)$.

The expected age structure will only be observed when there is large number of areas in the forest that are burnt independently. This is rarely the case in mountain ash forest, with large fires commonly burning a significant proportion of the forest. Reed (1994) accounts for such deviations from the expected age structure by using a 'contagion' parameter that describes how the incidence of fire increases the likelihood of fire in other parts of the forest in the same year (Reed, 1994).

Kuczera (1987) summarised data on forest age structure for seven water catchments in Victoria that contain mountain ash forest. The age structure of these forests was mainly due to the incidence of high intensity fire, because natural regeneration from other disturbances was rare, and very little timber harvesting had occurred in the catchments. We aggregated the Kuczera (1987) data for the seven catchments into four age classes (0–50, 51–100, 101–200, 200+ years), with only data for mountain ash forest being included (Table 1). These data were then used to estimate the mean interval between high intensity fires (Reed, 1994).

Table 1
Age structure of mountain ash forest in seven water catchments (after Kuczera, 1987)

Age class	Proportion of forest
0–50 years	0.67
51–100 years	0.05
101–200 years	0.13
>200 years	0.15

2.2. Persistence of mountain ash

In this section, a model of the persistence of mountain ash in response to high intensity fire is developed and used to predict the proportion of the landscape that contains mountain ash forest. The prediction was compared to observations to indicate the fire interval distribution in natural mountain ash forest.

In its natural state, regeneration of mountain ash trees is rarely successful in the absence of fire (Ashton and Willis, 1982). Successful regeneration also requires a canopy seed bank, which is available after a juvenile period in mountain ash trees of $\approx$20 years (Ashton and Attiwill, 1994). There is some uncertainty about the longevity of mountain ash trees. Ashton (Ashton, 1975, p. 868) notes the 'overmature' stage as being '300–400+ years'. Ashton (1981) shows a change from mountain ash forest to rainforest occurring at ca. 300 years of age. Seed production declines as trees senesce, mature mountain ash trees die and the surviving trees may not hold sufficient seed for regeneration (Attiwill, 1994). Therefore, fires that kill trees prior to production of seed (<20 years) or after seed is no longer produced (>350–500 years) will cause the local extinction of mountain ash, unless seed from adjacent forest can colonize the burnt area. Areas that are burnt at a short interval will tend to be dominated by shrub species such as silver wattle *Acacia dealbata* Link, and hazel pomaderris *Pomaderris aspera* Sieb. ex DC. Recolonization of these areas by mountain ash would require fire as well as seed from an adjacent area.

Fires expose mountain ash to chances of local extinction and recolonization. This conceptual model may be formalized by a mathematical description analogous to a metapopulation model (e.g. Hanski, 1994). In such a model, patches are defined as areas of land that may be occupied by mountain ash. In this case, a patch is an area of forest that is homogeneously affected by fire. The purpose of the model was to predict, as a function of mean fire interval, the proportion of the landscape that contains mountain ash forest. This prediction could then be compared to observations to determine the mean interval between tree-killing fires. For the model, it is assumed that the landscape is composed of many small areas (see below) that can be occupied by mountain ash. To maintain consistency with metapopulation models, these areas were referred to as patches. The proportion of patches occupied by mountain ash at the time of the most recent fire is given by the variable p. Extinctions and recolonizations occur with the incidence of fire. Given a high intensity fire in a patch, the probability of extinction of occupied patches is E, and the probability of colonisation of empty patches is C. Therefore, the change in the proportion of occupied patches after a fire is

$$\Delta p = C(1-p) - Ep.$$

The equilibrium occupancy (the occupancy at which the number of extinctions equals the number of colonizations, assuming many patches) is obtained from $\Delta p = 0$, leading to

$$p = C/(C+E). \tag{2}$$

The risk of local extinction (i.e. the loss of mountain ash from a patch) given a fire (E) is equal to the probability of the fire occurring outside the reproductive period multiplied by the probability of there not being seed within the dispersal distance.

The chance of a fire occurring outside the reproductive period depends on the probability distribution of fire intervals. Fire interval distributions may be described by a hazard function, which is an equation describing how the instantaneous risk of fire changes over time (Johnson and Gutsell, 1994). McCarthy et al. (in review) suggested a number of different fire interval distributions that may occur in nature. The simplest of these is the exponential distribution, where the annual risk of fire is independent of the time since the last fire (a in Eq. (1), see also Johnson and Gutsell, 1994). However, we additionally considered other fire interval distributions (see below).

The fire interval distributions may be solved to give the chance of a fire occurring in a particular period (time since the last fire) by using the cumulative probability function. For example, with the exponential model, the chance of a high intensity fire occurring before time J is equal to $1 - e^{-J/i}$, where i is the mean interval between high intensity fires. The chance of fire occurring after time M is equal to $e^{-M/i}$. Therefore the probability of fires occurring outside the reproductive period is equal to $1 - e^{-J/i} + e^{-M/i}$, where J is the juvenile period and M is the maximum longevity.

The chance of recolonisation is equal to the probability of there being trees with seed within the dispersal distance of the empty patch. Initially, it is assumed that the ages of patches are independent of each other and that occupied patches are distributed randomly in space. In this case, the density of patches with seed equals $p(e^{-J/i} - e^{-M/i})$. The probability of their being no trees with seed within the dispersal distance of the seed (d) equals $\exp[-\pi d^2 p(e^{-J/i} - e^{-M/i})]$, based on Poisson probability. Therefore, the chance of recolonization is

$$C = 1 - \exp[-\pi d^2 p(e^{-J/i} - e^{-M/i})], \tag{3}$$

and the chance of extinction of occupied patches is

$$E = (1 - e^{-J/i} + e^{-M/i})\exp[-\pi d^2 p(e^{-J/i} - e^{-M/i})]. \tag{4}$$

The variable p, as defined above, is the proportion of patches that were occupied with mountain ash at the time of the most recent fire. Because of senescence of old mountain ash trees, very old areas will not contain mountain ash, even if they contained mountain ash at the time of the most recent fire. Therefore, the proportion of patches containing mountain ash at a randomly chosen time (P) equals p multiplied by the proportion of patches that are less than M years

$$P = p(1 - e^{-M/i}). \tag{5}$$

Seeds of mountain ash disperse up to a distance of approximately one tree height, which is equivalent to $\approx$75 m in mature mountain ash forest (Ashton, 1975). Shorter trees will disperse seeds at shorter distances. Patches of forest in which mountain ash is absent range in area from a mean of 0.5 ha (*Acacia dealbata* patches) to 1.5 ha (seral rainforest patches) in unlogged mountain ash forest (Victorian Department of Natural Resources and Environment, unpublished data). These areas correspond to radii of 40 and 70 m. Therefore, the dispersal distance of seed (d) was estimated to be between ≈1.0 and 2.0 when scaled against patch size.

In the above analyses, it was assumed that there was no spatial correlation in the incidence of patches. This is unlikely to be true because nearby patches are likely to be burnt in the same fire (McCarthy and Lindenmayer, 1998). The chance of a neighboring area having a different recent fire history will depend on whether the patch being considered was near the edge of the previous fire. The probability of a burnt area being near the edge of a fire will depend on the shape and size of fires. In small, elongated or patchy fires, much of the area burnt will be close to an edge. Large, round and contiguous fires will have relatively less burnt area close to the edge of the fire. For a single fire in mountain ash forest, analyses by McCarthy and Lindenmayer (1998) suggested that ≈0.25 of the fire area would be within 75 m (the approximate dispersal distance of seed) of the fire edge. If this is representative of fires in mountain ash forest, it would have the effect of reducing the area into which mountain ash seeds could disperse. To accommodate this potential reduction in effective dispersal area, dispersal distances were scaled by a half ($\sqrt{0.25}$). Therefore, d was reduced from the value of between 1.0 and 2.0, as estimated above, to between 0.5 and 1.0.

Eqs. (2)–(5) were combined and solved to predict the proportion of the landscape occupied by mountain ash as a function of the mean interval between high intensity fires, assuming a juvenile period (J) of 20 years, a longevity (M) of between 350 and 500 years, and dispersal distances (d) between 0.5 and 1.0. Predictions were made for a range of mean fire intervals between 0 and 500 years.

Fire interval distributions other than the exponential were also substituted into the above model to predict the persistence of mountain ash. In mountain ash forests, fuel loads accumulate for approximately the first 20 years after a fire (Polglase and Attiwill, 1992). As the forest matures, the forest develops a more mesic understorey and the bark of the mountain ash trees thickens (Ashton, 1981). McCarthy et al. (in review) suggested a fire interval distribution for mountain ash forest in which the hazard first increases with time since the previous fire as fuel loads increase, and then the hazard declines as fuel becomes moister and thickening bark makes the trees less likely to be killed by fire. This was referred to as the moisture model.

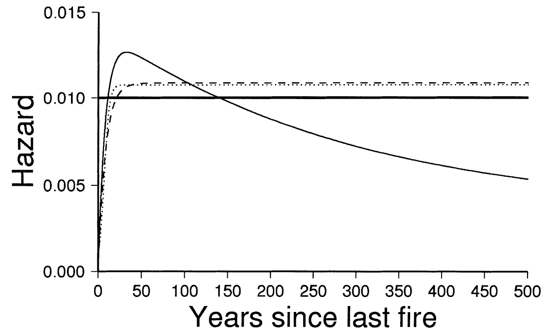

Fig. 1. Hazard functions used in this paper to model changes in the risk of fire as a function of the time since the last fire (t). The thick line represents the exponential model (h), the dashed line represents the Olson model ($h\exp[-0.12t]$), the dotted line represents the logistic model ($h/[1 + 10\exp\{-0.337^{*}t\}]$), and the thin solid line represents the moisture model ($h\exp[-0.12t]$ $[0.33 + \exp\{-0.0035t\}]$). The mean fire interval was varied by changing the value of the parameter h in each of the hazard functions.

Two other models of fire interval may be appropriate for mountain ash forest. In the Olson model (McCarthy et al., in review), the hazard increases with time in proportion to the increase in fuel load as described by Olson's (1963) fuel accumulation curve. The final model was the logistic model in which the hazard increases slowly at first and then reaches an asymptote (McCarthy et al., in review). Fig. 1 shows the four fire interval distributions, represented by their hazard functions that were considered in this paper. Each of these equations has a parameter h, which may be used to vary the mean fire interval. McCarthy et al. (in review) provide more details about the derivation and mathematical description of these models.

To compare the model predictions (Eqs. (2)–(5)) with actual data, digital maps of vegetation types within the O'Shannassy and Watts River Water Catchments (Victorian Department of Natural Resources and Environment, unpublished data) were used to estimate the proportion of the potential landscape that is occupied by mountain ash. These maps were developed from aerial photographic interpretation and confirmed with on-ground inventory. The area on the maps containing mountain ash forest was totaled, as was the area containing non-eucalypt native forest (e.g., rainforest, shrubland and *Acacia* forest). It was assumed that mountain ash could potentially occupy all this area given appropriate fire regimes.

The proportion of the area actually occupied by mountain ash was then calculated, and the mean fire interval that predicted this occupancy was determined.

2.3. Production of hollow-bearing trees

Production of hollow-bearing trees was used as a third method of inferring the mean fire interval of mountain ash forest. Hollows can occur in both living and dead hollow-bearing trees. Hollow-bearing trees provide important habitat for a number of cavity-dependent species in mountain ash forests (Lindenmayer et al., 1990), and their development and maintenance depends on the fire regime (Lindenmayer et al., 1993). Hollows develop slowly in live mountain ash trees, with hollows only being present when trees are $\approx$150–250 years old (Ambrose, 1982; Lindenmayer et al., 1993). Therefore, the proportion of the area of mountain ash forest that contains live hollow-bearing trees is

$$L = \mathrm{e}^{-O/i}, \tag{6}$$

assuming an exponential distribution of fire intervals, where O is the age at which hollows develop and i is the mean interval between high intensity fires.

Dead hollow-bearing mountain ash trees exist where large trees are killed by fire but remain standing. Dead hollow-bearing trees also occur in mountain ash forests when large old trees die (Burgman et al., 1994). Dead hollow-bearing trees can persist for up to $\approx$75–100 years before they decay and collapse (Lindenmayer et al., 1997b). Therefore, dead hollow-bearing trees occur in areas that are younger than 75–100 years since the last fire but were older than 150–200 years when the previous fire occurred, and also in areas that are older than the longevity of mountain ash trees but <75–100 years since they died. The proportion of the area of mountain ash forest that contains dead hollow-bearing trees is

$$\begin{aligned} D &= (1-\mathrm{e}^{-Y/i})\mathrm{e}^{-O/i} + (1-\mathrm{e}^{-Y/i})\mathrm{e}^{-M/i} \\ &= (1-\mathrm{e}^{-Y/i})(\mathrm{e}^{-O/i} + \mathrm{e}^{-M/i}), \end{aligned} \tag{7}$$

where Y is the life span of dead hollow-bearing trees, and M and O are as defined previously.

Data on the prevalence of hollow-bearing trees were obtained from field surveys by Lindenmayer et al. (1991b) in the O'Shannassy water catchment, an area where virtually no logging has occurred (Land Conservation Council, 1994). A total of 69 3-ha sites was surveyed, with the number of live and dead hollow-bearing trees recorded. All living and dead trees >50 cm in diameter and containing obvious cavities were recorded on each site. The greatest observed density of live hollow-bearing trees in mountain ash forest is $\approx$30 per 3-ha site (Lindenmayer et al., 1991b). The mean number of live and dead hollow-bearing trees per 3-ha site was divided by 30 to estimate the proportion of area that is occupied by live and dead hollow-bearing trees. These values were compared to the predictions of the model to determine the mean fire interval.

3. Results

3.1. Forest age structure

The mean interval between high intensity (tree-killing) fires, estimated from the forest age structure in the seven catchments studied by Kuczera (1987), was 107 years. The 95% confidence limits were 45 years and 333 years. The contagion parameter d (Reed, 1994) was estimated as 0.169.

3.2. Persistence of mountain ash

In the Watts River and O'Shannassy water catchments, forest composed of mountain ash occupies 18 000 ha, and an additional 4000 ha is occupied by non-eucalypt forest (mostly areas with *Acacia* or rainforest overstorey). Mountain ash occupies $\approx$80% of the area of suitable habitat, assuming areas currently occupied by non-eucalypt forest could potentially be occupied by mountain ash.

The proportion of the landscape predicted to be occupied by mountain ash forest depended on the mean interval between high intensity fires. As would be expected for a fire-sensitive species with a juvenile period and with a finite longevity, occupancy was greatest when fires were of an intermediate frequency and dispersal distances were large (Fig. 2). Assuming the longest dispersal distance ($d = 1.0$), the greatest longevity ($M = 500$) and an exponential distribution of fire intervals (Eq. (1)), an occupancy of 80% suggests that the mean interval between high intensity fires is either 26 years or 290 years (Fig. 2). Within the

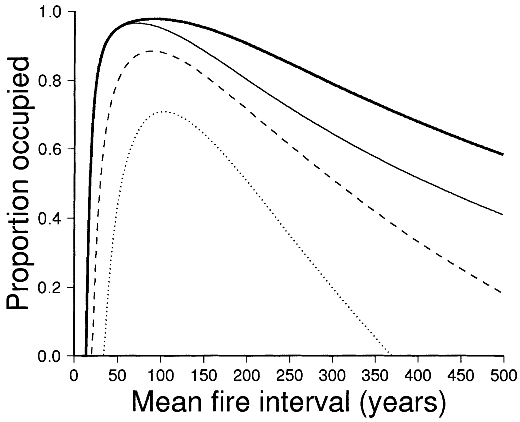

Fig. 2. The predicted occupancy of the landscape by mountain ash as a function of the mean interval between high intensity fires, assuming the exponential model for the interval between fires and a juvenile period (J) of 20 years. Results are shown for different dispersal distances of seed (dotted curve, $d = 0.5$; dashed curve, $d = \sqrt{0.5}$; solid curves, $d = 1.0$). The thick solid curve was obtained using a longevity (M) of 500 years, the thin curves were obtained using a longevity of 350 years.

range of other values of d (0.5–1.0) and M (350–500), the mean fire interval would lie between these limits of 26 and 290 years. This range of mean fire intervals would be smaller if dispersal distances were smaller or the occupancy rate was higher. Probability distributions of fire intervals other than the exponential made qualitatively similar predictions (Figs. 3–5).

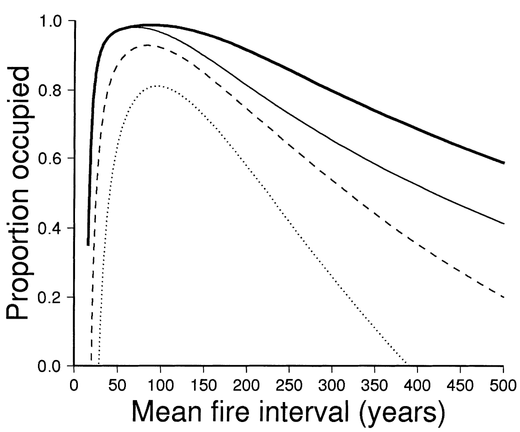

Fig. 3. The predicted occupancy of the landscape by mountain ash as a function of the mean interval between high intensity fires, assuming the Olson model for the interval between fires. Otherwise, the parameter values are identical to those in Fig. 2.

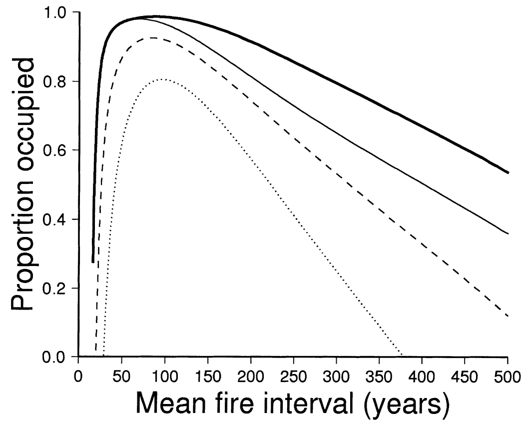

Fig. 4. The predicted occupancy of the landscape by mountain ash as a function of the mean interval between high intensity fires, assuming the logistic model for the interval between fires. Otherwise, the parameter values are identical to those in Fig. 2.

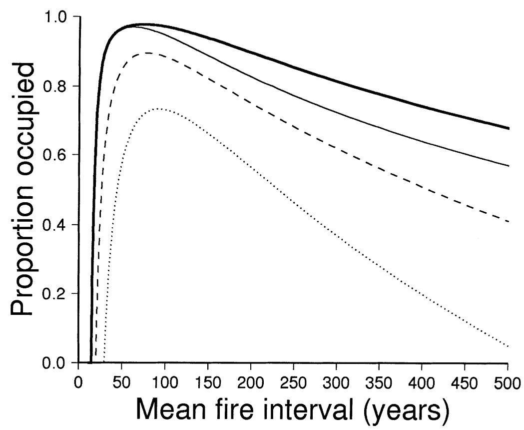

Fig. 5. The predicted occupancy of the landscape by mountain ash as a function of the mean interval between high intensity fires, assuming the moisture model for the interval between fires. Otherwise, the parameter values are identical to those in Fig. 2.

3.3. Production of hollow-bearing trees

Occupancy of patches by live hollow-bearing trees in the O'Shannassy water catchment was 16% (323 trees in 69 3-ha sites). Occupancy by dead hollow-bearing trees was 13% (274 trees in 69 3-ha sites).

The proportion of mountain ash forest predicted to be occupied by live hollow-bearing trees increased with the mean fire interval (Fig. 6). Assuming mountain ash trees develop hollows at between 150 and 250

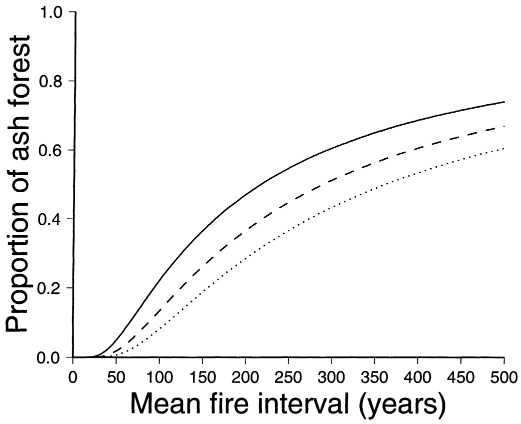

Fig. 6. The predicted proportion of mountain ash forest occupied by live hollow-bearing trees as a function of the mean interval between high intensity fires. Results are shown when hollows form at 150 years (solid curve), 200 years (dashed curve) and 250 years (dotted curve).

years of age (Ambrose, 1982; Lindenmayer et al., 1993), the mean interval between high intensity fires was predicted to be between 82 and 136 years (Fig. 6) when the occupancy of live hollow-bearing trees is 16%.

The occupancy of dead hollow-bearing trees was predicted to increase as the mean fire interval

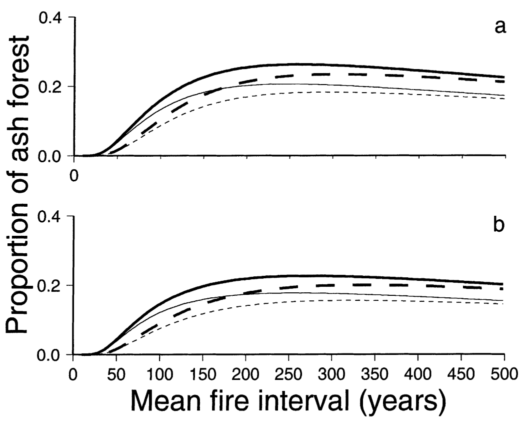

Fig. 7. The predicted proportion of mountain ash forest occupied by dead hollow-bearing trees as a function of the mean interval between high intensity fires. Results are shown for cases in which dead hollow-bearing trees persist for 75 (thin) or 100 years (thick), and for cases in which trees from the previous stand must be at least 150 (solid) or 200 years old (dashed) before they will persist as dead hollow-bearing trees after a fire. Results are also shown for cases in which trees older than 350 (a) and 500 years (b) die and become dead hollow-bearing trees.

increased to ca. 100 years, after which the occupancy was relatively constant (Fig. 7). Fig. 7 suggests that the mean interval between high intensity fires is between 86 and 172 years when the occupancy of dead hollow-bearing trees is 13%.

4. Discussion

The different methods that we used to estimate the mean interval between high intensity fires in mountain ash forests in water catchments produced consistent results, in that the bounds on their predictions overlapped. Using data on forest age structure, the statistical estimation of the mean interval between high intensity fires provided an estimate of 107 years with 95% confidence limits of 45 to 333 years. The occupancy of the landscape by mountain ash indicated that the mean interval was between 26 and 290 years. The production of live hollow-bearing trees suggested that the mean interval was between 82 and 136 years, and the production of dead hollow-bearing trees suggested that the mean interval was between 86 and 172 years. A mean interval between high intensity fires of between 86 and 136 years would simultaneously satisfy all the methods. Providing for some error in the analyses, this suggests that the mean interval is within an approximate range of 75–150 years, a range consistent with that suggested by Ashton and Attiwill (1994).

McCarthy and Lindenmayer (1998) developed a model of the development of multi-aged mountain ash forest in response to fire. The model predicted the prevalence of multi-aged mountain ash forest as a function of the mean fire interval. The predictions were consistent with observations when the mean fire interval was between 75 and 200 years, with the best fit when the mean fire interval was $\approx$100 years. The study by McCarthy and Lindenmayer (1998) is consistent with the results presented here and provides more evidence that the mean fire interval of mountain ash forest is within the approximate range of 75–150 years. Although the mean interval is predicted to be within this range, the actual intervals will be variable. For example, the model predicts that $\approx$5% of fire intervals will be longer than three times the mean fire interval (McCarthy and Burgman 1995).

Fires in mountain ash forest can be of an extremely high intensity, with estimates of up to 100 000 kW/m

(Gill and Moore, 1990). However, actual measurements of intensity are difficult to obtain in these forests. Variation in intensity can be inferred from variation in tree mortality following fire. Smith and Woodgate (1985) recognized considerable variation in mortality of mountain ash trees after an extensive fire, but they did not provide details of the level of mortality. Squire et al. (1991) commenting on the effects of the fire studied by Smith and Woodgate (1985), stated that a majority of trees survived in ca. 70% of the area of mountain ash forest that was burned. This suggests that, at the very least, 35% (50% of 70%) of mountain ash trees survived when they were burnt. The actual figure is probably closer to ca. 50%, although data from other studies may indicate different results. The mean interval of 75–150 years suggested above is the mean interval between fires that kill trees. If mountain ash trees survive in approximately half of the area burnt by fires, the actual mean interval between fires of all intensities will be approximately half that estimated, i.e., 37–75 years.

The model of the persistence of mountain ash forest (Eqs. (2)–(5)) predicts a relatively abrupt change in occupancy as the mean fire interval decreases. This prediction is consistent with the sharp boundaries that are commonly observed between stands of mountain ash and stands of more fire-tolerant eucalypt species such as messmate *E. obliqua*. The fire regime that we determined for mountain ash forests is based principally on that which has prevailed during the last two centuries since occupation by Europeans and Asians, and the displacement of indigenous Australians. Ignitions by humans, effectiveness of fire detection and suppression, and climate change are likely to have changed over time. Such changes would influence the mean fire interval with concomitant influences on forest composition (Figs. 2–5) and the abundance of hollow-bearing trees within mountain ash forest (Figs. 6 and 7). While this qualitative result is intuitively obvious, the potentially abrupt changes predicted by the model are less so (Figs. 2–5).

Hollow-bearing trees provide important habitat for numerous species in these forest (Gibbons and Lindenmayer, 1996; Lindenmayer, 1996). The predicted abundance of hollow-bearing trees is equal to the proportion of hollow-bearing trees within extant mountain ash forest. The abundance of mountain ash forest in the landscape that also contains live or dead hollow-bearing trees is the product of the two curves (Figs. 1, 5, 6). Therefore, the total abundance of mountain ash trees with hollows would be maximized when the mean interval between high intensity fires is relatively long (≈250 years).

The ability of at least some mountain ash trees to survive fire (Squire et al., 1991) allows the development of multi-aged stands of mountain ash (McCarthy and Lindenmayer, 1998). Multi-aged stands of mountain ash provide important habitat for arboreal marsupials. It is especially important for Leadbeater's possum (*Gymnobelideus leadbeateri*), an endangered species that requires a combination of hollow-bearing trees for nesting and shelter, and *Acacia* shrubs, which act as foraging substrates (Lindenmayer et al., 1991c). In mountain ash forest, *Acacia* shrubs regenerate after fire from a long-lived soil seed bank, and persist for up to 100 years (Adams and Attiwill, 1984). Therefore, multi-aged mountain ash forest provides the relatively rare combination of abundant hollow-bearing trees and abundant *Acacia* shrubs that characterizes optimum habitat for Leadbeater's possum.

Timber harvesting in mountain ash forest involves a uniform silvicultural treatment of clearfelling followed by a high intensity slash burn (Squire et al., 1991). If the natural mean fire interval is ≈100 years, clearfelling to produce timber and pulpwood on a 100-year rotation will not be similar to the natural disturbance regime. Fires and clearfelling have different effects on the forest age structure (McCarthy and Burgman, 1995), soil properties (Rab, 1994), understorey plant composition (Ough and Ross, 1992) and stand structure (Lindenmayer et al., 1991d; Lindenmayer, 1996; McCarthy and Lindenmayer, 1998). The variability in natural disturbance regimes is difficult to replicate with prescribed disturbance, unless it is done so explicitly (McCarthy and Burgman, 1995; McCarthy and Lindenmayer, 1998). This raises the question of what is an appropriate disturbance (fire and timber harvesting) regime in mountain ash forests? The answer requires that the management goals be defined explicitly, which is well beyond the scope of this paper. Nevertheless, to have similar effects on forest structure to random fires, it is clear that managed disturbance would need to operate over a wide range of intensities and rotations. However, this paper is not intended as a blueprint for management.

This paper further develops a methodology suggested previously by Gill and McCarthy (1998), and demonstrates the use of life history attributes (and surrogates such as hollow-bearing trees) to help determine fire regimes. The predicted mean fire interval depended on the parameter values used, with, for example, the predicted occupancy by mountain ash forest depending on the dispersal ability of seeds between patches (and, therefore, size of patches). Errors in the parameters (e.g., longevity and dispersal distance) will contribute to errors in the predicted mean fire interval, making it important to make predictions over a range of reasonable parameter values. Analyses for a combination of attributes provided consistent results, which helped reinforce the individual predictions and narrow the range of likely mean fire intervals. Using different models for the distribution of the fire intervals had little influence on the predictions, provided the mean interval was the same. This suggests that life history attributes may not be useful for distinguishing between competing models of fire regimes, unless the mean intervals are closer to the limits imposed by the juvenile period and longevity of the species. Biological information about changes in factors such as vegetation and fuel may be more useful (McCarthy et al., in review).

The above analyses depended on the assumption that the mean fire interval does not vary in the landscape. This is almost certainly *not* true. Mountain ash forests in gullies and southern-facing slopes are likely to burn less frequently than on exposed slopes and ridges. Fires on plateaux may be less intense than those on slopes, with the potential for lower tree mortality (Chesterfield et al., 1991). Nevertheless, we believe that the above analyses provide reasonable estimates of the mean fire interval across mountain ash forests. The actual mean fire interval at any given point in the landscape is likely to vary around the average. Determining this variation is an avenue of further study.

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