The tortoise and the hare? Post-fire regeneration in mixed Eucalyptus–Callitris forest

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Abstract. Seedling regeneration after a high intensity wildfire was assessed in a mixed forest dominated by Eucalyptus species and Callitris endlicheri (Parl.) F.M. Bailey. Patterns were compared against the ‘slow seedling’ or ‘tortoise-and-hare’ theory of competitive interactions between gymnosperms and angiosperms. Browsing effects were documented using fenced plots, and seedling density, mortality and height were assessed over 6 years, from 2004–10. Consistent with expectations, Eucalyptus seedlings grew faster than Callitris seedlings in most situations. Callitris seedlings grew faster and produced seed cones sooner in plots with fewer Eucalyptus seedlings compared with plots with dense Eucalyptus seedlings. The local growth rates of Callitris seedlings were not associated with long-term site suitability for Callitris, as many plots with diminutive Callitris seedlings and dense Eucalyptus seedlings were dominated by Callitris trees before the 2003 fire. Contrary to expectations, few Callitris seedlings died during the 6-year period, so competition during the regeneration phase did not regulate co-existence. Strong drought tolerance and the ability to persist in dense, unthinned stands may enable Callitris to persist beneath dense Eucalyptus regeneration. Nevertheless, Callitris seedlings growing with dense Eucalyptus seedlings have a longer primary juvenile period than seedlings in sites with fewer seedling or adult eucalypts, which places these stands at greater risk of mortality in future fires and greater risk of browsing in the meantime.

Introduction

A principal goal of vegetation ecology is to understand the factors that influence vegetation patterns and dynamics. In 1989, William Bond developed a general model to interpret competitive interactions among two groups of seed plants: the gymnosperms and angiosperms. Bond’s (1989) ‘slow seedling’ or ‘tortoise-and-hare’ hypothesis stated that, because gymnosperm seedlings had lower growth rates than angiosperm seedlings due to architectural constraints, gymnosperms were largely restricted to low productivity ecosystems where they escaped competition from vigorous, fast-growing angiosperms. By contrast, in productive ecosystems, competition from angiosperms would suppress gymnosperm growth rates, leaving gymnosperm seedlings vulnerable to processes that cause size-dependent mortality, such as drought, herbivory and fire. In some instances, gymnosperm decline would be hastened if angiosperms promoted adverse disturbances, for example, where grasses fuelled fires that killed gymnosperm seedlings (Bond and Scott 2010). Cast in the language of Grime’s (2001) plant strategy scheme, gymnosperms were viewed by Bond (1989) as ‘stress tolerators’, poorly equipped to regenerate and persist in productive environments dominated by more ‘competitive’ angiosperms.

Our understanding of the physiological mechanisms underlying low growth rates of gymnosperm seedlings has since been refined (Becker et al. 1999; Becker 2000; Lusk et al. 2003; Brodribb et al. 2005), and Bond’s ‘slow seedling’ model may be viewed within a broader plant leaf economics spectrum, in which relative growth rate is related to leaf longevity and specific leaf area (Cornelissen et al. 1996; Reich et al. 1999; Wright et al. 2004). Gymnosperms characteristically have long-lived leaves of low specific leaf area, which lead to lower relative growth rate than many, but not all, angiosperms (Reich et al. 1999; Lusk et al. 2003).

The most widespread and abundant genus of gymnosperms in Australia is Callitris (Family Cupressaceae), which occurs in tropical, subtropical, arid, semiarid, Mediterranean and temperate regions (Bowman and Harris 1995). Callitris dynamics have received considerable attention from fire ecologists as Callitris are often killed by fire and usually do not resprout after being subjected to 100% leaf scorch (Lacey 1973; Bradstock and Cohn 2002; Russell-Smith 2006). Consequently, population dynamics are highly sensitive to changes in fire regimes (Bowman and Panton 1993; Bradstock et al. 2006; Prior et al. 2010). Surprisingly, Bond’s (1989) model has never been referred to in studies on Callitris ecology. This may be because few studies have documented interactions between Callitris and other woody species (e.g. Clayton-Greene 1981; Bowman et al. 1988; Clayton-Greene and Ashton 1990), even though Callitris occur in heathlands, woodlands and forests dominated by Eucalyptus and
other woody plants (Bowman and Harris 1995). In savannah and arid woodlands, fire regimes and *Callitris* dynamics are regulated by dominant grasses rather than woody plants (Bowman et al. 1988; Bradstock and Cohn 2002). Indeed, we know of only one study (an unpublished seedling pot trial) that has documented competitive interactions between *Callitris* seedlings and other woody taxa (Clayton-Greene 1981).

This paucity of information raises the question, to what extent do interactions with woody angiosperms influence *Callitris* dynamics in productive forest ecosystems? Under Bond’s (1989) model, inter-specific interactions could influence the ability of non-resprouting *Callitris* to persist in ecosystems dominated by flammable, resprouting angiosperms. In this study, we attempt to address this issue by asking: to what extent are post-fire recruitment patterns in a mixed *Callitris*–*Eucalyptus* forest in a relatively high rainfall region (~850-mm mean annual rainfall) consistent with Bond’s slow seedling hypothesis? We discuss the implications of these patterns for species co-existence and fire management. Our study is observational rather than manipulative, which means that while we can assess whether patterns are consistent with Bond’s hypothesis, we cannot be definitive about the mechanisms that underlie observed patterns.

**Materials and methods**

**Study area**

The study was conducted in Chiltern-Mt Pilot National Park in north-eastern Victoria, Australia. Mean annual rainfall in the study area is ~850 mm, based on data from nearby Beechworth (960 mm) and Beechworth Woolshed rainfall gauges (770 mm; Bureau of Meteorology 2011). The underlying geology is Devonian granite and the topography is moderately to steeply undulating (Parks Victoria 2008). The area supports dry sclerophyll forests dominated by *Eucalyptus macrorycha* F.Muell. ex Bentham. *E. goniocalyx* F.Muell., *E. polyanthemos* Schauer and *E. blakelyi* Maiden, with patches dominated by *Callitris endlicheri*. Most *Callitris*-dominated stands are small (<1 ha) and in close proximity to rocky outcrops (Watson 2004).

In January 2003, 7300 ha of the reserve burnt in a high intensity wildfire (Watson 2004). In July 2003, two, 10 × 10-m fenced plots were erected in each of three burnt *Callitris* stands near Mt Pilot to assess browsing impacts on *Callitris* seedlings. Post-fire vegetation monitoring began in autumn 2004. Twelve stands of *Callitris* were selected within a 2.2-km radius of the Mt Pilot summit (36°15’06”S, 146°40’13”E). All 12 sites were burnt at high intensity, as evidenced by complete mortality of pre-fire *Callitris* and resprouting of surviving *Eucalyptus* from basal coppice rather than from epicormic buds on trunks or branches. Six stands, including the three stands containing fenced plots, were dominated by mature *C. endlicheri*, presumed to have recruited in the late 1800s, with subdominant *Eucalyptus*. The other six stands were dominated by *Eucalyptus* above smaller *Callitris*, which were presumed to have recruited after 1950.

Permanently marked 100-m² (10 × 10 m) plots were established at each site. Paired unfenced plots were established at the three fenced sites, giving four plots in total at these sites (plus an extra unfenced plot in one large stand), and two unfenced plots were established in the nine stands without fences. Pre-fire stand structure was estimated in autumn 2004 by measuring all dead and resprouting trees in each 100-m² plot. Small saplings that were totally incinerated would not have been detected.

The height, number of stems, and girth over bark at breast height (GOBBH) of the largest stem was recorded annually for all coppicing *Eucalyptus* in each 100-m² plot. For clarity, all post-fire seedling recruits are called ‘seedlings’ in this paper, even though many had grown tall (i.e. to ‘sapling’ size) by the end of the monitoring period. The species identity, height and GOBBH of all post-fire seedlings were assessed annually in 10 (in 2004) and 20 (2005–10) randomly placed 1-m² subplots within each 100-m² plot. These subplots were re-randomised each year. GOBBH was recorded as 0.1 cm if plants were <1.3 m tall. Sampling was conducted in autumn 2004–10, but only two sites were sampled in 2009, due to inclement weather. At Beechworth, annual rainfall was slightly above average from 2003 to 2005 (965–1215 mm/year), very low in 2006 (413 mm) and ~80% of average from 2007 to 2009 (755–790 mm; Bureau of Meteorology 2011).

**Data analysis**

Linear mixed models were used to examine:

1. The relationship between initial seedling density (including live and dead seedlings in 2004) and the pre-fire basal area of each genus;
2. The effects of fencing and time on the density and height of live seedlings of each genus; and
3. Associations between seedling height in 2010 and (a) the pre-fire basal area of each genus, (b) the density of competing seedlings in 2010, and (c) the basal area of resprouting *Eucalyptus* in 2010.

The influence of fencing on seedling heights and densities was assessed using data from the three sites with fenced and unfenced plots only. In each case, year, fencing treatment, basal area (at the plot scale), and seedling density in subplots were included as fixed effects, and nested sites, plots and subplots were incorporated as random effects. Where necessary, density, height and basal area data were log-transformed to meet the assumption of constant variance. *F*-tests were used to investigate the significance of individual model term. Analyses were undertaken in *Genstat* version 13 (VSN International 2010). In addition *t*-tests were used to compare: (1) the height of *Eucalyptus* and *Callitris* seedlings in 2010, (2) the proportion of seedlings in fenced and unfenced plots with evidence of browsing in 2010, and (3) the mean height of seedlings in fenced and unfenced plots in 2010. Few *Callitris* seedlings produced seed cones by 2010. Consequently, associations between the density of *Callitris* and *Eucalyptus* seedlings versus the number of *Callitris* seedlings bearing seed cones and the number of cones produced were analysed at the plot scale, using Spearman’s rank correlation coefficients.

**Results**

**Seedling density and mortality**

*Callitris* and *Eucalyptus* seedlings both regenerated at high density after the 2003 fire. On average, there were 5.8 *Callitris* seedlings/m² and 2.8 *Eucalyptus* seedlings/m² in 2004, 16 months after the fire. The initial, post-fire density of *Callitris* seedlings was significantly and positively associated
with the pre-fire basal area of *Callitris* (*P* = 0.031). After accounting for the association of *Callitris* seedling density with *Callitris* pre-fire basal area, the association with *Eucalyptus* pre-fire basal area was not significant. By contrast, the initial density of *Eucalyptus* seedlings was not significantly associated with the pre-fire basal area of either genus (*P* = 0.333 and 0.717 for *Eucalyptus* and *Callitris*, respectively).

Mortality rates after the first monitoring event were extremely low for both genera. The mean density of live *Callitris* seedlings apparently declined from 5.2 to 3.7 seedlings/m² from 2004 to 2010; however, this change was not statistically significant (at *P* < 0.05). The mean density of *Callitris* seedlings did not change significantly over time (*P* = 0.783) nor did it differ significantly across fencing treatments, when all plots (including all unfenced plots) were compared (*P* = 0.348). Similarly, when data from only the three sites with fenced plots were analysed, the density of *Callitris* seedlings was not significantly associated with year (*P* = 0.723), fencing (*P* = 0.392) nor the year*fencing interaction (*P* = 0.945; Fig. 1a).

By contrast, there was a significant decline in the density of live *Eucalyptus* seedlings over the same period. Across all sites, mean (back-transformed) density declined from 2.8 to 1.2 seedlings/m². When data from all plots were analysed, the density of *Eucalyptus* seedlings differed significantly among years (*P* < 0.001) but not among fencing treatments (*P* = 0.122) or with the year*fencing interaction (0.348). When data from only the three sites with fenced plots were analysed, the density of *Eucalyptus* seedlings was not significantly affected by year (*P* = 0.224), fencing (*P* = 0.428) nor year*fencing interaction (*P* = 0.947; Fig. 1b).

Seedling growth rates

*Callitris* seedlings were, on average, shorter than *Eucalyptus* seedlings throughout the survey period (Fig. 2). In 2010, the mean height of *Eucalyptus* seedlings was over twice that of *Callitris* seedlings (184 cf. 84 cm; *t*-test, *P* < 0.001), and the tallest *Eucalyptus* seedling was over twice as tall as the tallest *Callitris* seedling (max. height, 800 cf. 350 cm). In 2010, 30% of *Callitris* seedlings were <0.5 m tall.

Fencing effects

In 2010, it appeared that more *Callitris* seedlings showed evidence of browsing in unfenced than fenced plots (25% cf. 2% at the plot scale) although this difference was not significant at the *P* = 0.05 level (paired *t*-test, *P* = 0.09).

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**Fig. 1.** Predicted density of live (a) *Callitris* (mean ± standard error) and (b) *Eucalyptus* seedlings in fenced and unfenced plots (back-transformed mean ± standard error) after the 2003 fire at Mt Pilot.

**Fig. 2.** Predicted mean height of (a) *Callitris* and (b) *Eucalyptus* seedlings in fenced and unfenced plots (back-transformed mean ± standard error).
taller in fenced than unfenced plots (Fig. 2a). The mean (back-transformed) height of Callitris seedlings varied significantly with year ($P < 0.001$) and fencing treatment ($P = 0.007$) with no significant year*fencing interaction ($P = 0.198$). In 2010, the mean height of Callitris seedlings in fenced plots was 145 cm compared with 116 cm in unfenced plots ($t$-test, $P < 0.001$). By contrast, only 5% of all Eucalyptus seedlings surveyed in 2010 (in all fenced and unfenced plots) displayed evidence of browsing. No Eucalyptus seedlings were browsed within the three fenced plots in 2010. Consequently, the height of Eucalyptus seedlings varied significantly with year ($P = 0.002$) but there was no significant fencing effect ($P = 0.747$) or year*fencing treatment interaction ($P = 0.558$; Fig. 2b). In 2010, the mean height of fenced and unfenced Eucalyptus seedlings was 226 and 245 cm, respectively ($t$-test, $P = 0.70$).

Factors associated with seedling height

The linear mixed model showed that the height of Callitris seedlings in 2010 was significantly and positively associated with fencing ($P = 0.025$), and negatively associated with the density of Eucalyptus seedlings ($P = 0.006$). After accounting for these terms, there was no significant association with (a) the density of Callitris seedlings, (b) the basal area of coppicing Eucalyptus, nor (c) the pre-fire basal area of Callitris or Eucalyptus (Table 1). The lack of association between Callitris seedling heights and the pre-fire basal area of either genus suggests that Callitris seedlings neither grew better nor worse in plots dominated by either genus before the fire.

In contrast, the height of Eucalyptus seedlings in 2010 was significantly negatively associated with Eucalyptus seedling density ($P < 0.001$) and positively associated with Callitris seedling density ($P = 0.002$) and the pre-fire basal area of Callitris ($P = 0.053$; Table 2), which indicates that Eucalyptus seedlings grew faster where Callitris dominated before the fire.

Table 1. Model statistics for linear mixed model describing the factors associated with Callitris seedling heights in 2010

<table>
<thead>
<tr>
<th>Fixed term</th>
<th>$F$-statistic</th>
<th>d.d.f.</th>
<th>Probability (F pr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eucalyptus density in 2010</td>
<td>7.6</td>
<td>419.5</td>
<td>0.006</td>
</tr>
<tr>
<td>Callitris density in 2010</td>
<td>3.59</td>
<td>329.3</td>
<td>0.059</td>
</tr>
<tr>
<td>Eucalyptus coppice basal area in 2010</td>
<td>2.58</td>
<td>27</td>
<td>0.120</td>
</tr>
<tr>
<td>Fencing treatment</td>
<td>5.67</td>
<td>25</td>
<td>0.025</td>
</tr>
</tbody>
</table>

Table 2. Model statistics for linear mixed model describing the factors associated with Eucalyptus seedling heights in 2010

<table>
<thead>
<tr>
<th>Fixed term</th>
<th>$F$-statistic</th>
<th>d.d.f.</th>
<th>Probability (F pr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fencing treatment</td>
<td>0.73</td>
<td>29.5</td>
<td>0.401</td>
</tr>
<tr>
<td>Log Callitris basal area in 2004</td>
<td>4.18</td>
<td>22.0</td>
<td>0.053</td>
</tr>
<tr>
<td>Log Callitris density in 2010</td>
<td>9.70</td>
<td>257.5</td>
<td>0.002</td>
</tr>
<tr>
<td>Log Eucalyptus density in 2010</td>
<td>11.25</td>
<td>251.5</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**Seed cone production**

In 2010, 7 years after the fire, 2% of Callitris seedlings possessed seed cones. Seed cones were almost entirely restricted to the tallest seedlings. Thus, 83% of cones were on seedlings taller than 150 cm (Fig. 3), and 23% of seedlings >2 m possessed seed cones ($n = 100$). The shortest seedling with seed cones was 140 cm tall. Cone production varied from <5% to almost 30% of Callitris seedlings at each plot.

In 2010, there was no significant correlation between the number of Callitris seedlings in each plot and either the number of Callitris seedlings bearing seed cones (Spearman’s rank correlation coefficient, $r = -0.030$, d.d.f. = 29, $P = 0.874$) or the number of seed cones produced ($r = -0.039$, $P = 0.833$). However, there was a significant negative correlation between the number of Eucalyptus seedlings in each plot and the number of Callitris seedlings bearing seed cones ($r = -0.454$, $P = 0.010$) and the number of seed cones produced ($r = -0.448$, $P = 0.012$). The total number of Eucalyptus and Callitris seedlings in each plot was positively correlated ($r = 0.380$, $P = 0.0352$). Thus, Callitris seedlings produced more seed cones in plots with fewer Eucalyptus seedlings.

**Discussion**

These results illustrate several patterns that are consistent with Bond’s (1989) slow seedling hypothesis: (1) Eucalyptus seedlings grew faster than Callitris seedlings; (2) Callitris seedlings grew faster, and produced seed cones sooner, in plots with fewer Eucalyptus seedlings; and (3) small Callitris seedlings growing beneath dense Eucalyptus seedlings remained vulnerable to browsing and burning for longer than tall Callitris seedlings in areas with fewer Eucalyptus seedlings. Spatial variations in the growth rate of Callitris seedlings were not related to the suitability of sites to support Callitris, as many patches with small Callitris and dense Eucalyptus seedlings were dominated by mature Callitris before the 2003 fire. However, contrary to Bond’s (1989) theory, few Callitris seedlings died, so competition during the regeneration phase did not regulate.
Seedling growth rates

The lower growth rate of Callitris compared with Eucalyptus seedlings is consistent with the global trend for lower growth rates in gymnosperms than in sympatric angiosperms (Bond 1989; Reich et al. 1999; Lusk et al. 2003), and with pot and field trials in which planted Eucalyptus seedlings grew faster than Callitris seedlings (Clayton-Greene 1981; Alcock and Hik 2004). Apart from fencing, the factor most strongly associated with the growth rate of Callitris seedlings was the density of Eucalyptus seedlings. Callitris seedlings grew slowest where Eucalyptus seedlings were most abundant, and fastest where Eucalyptus seedlings were most sparse. Removal experiments are required to disentangle the effects of abiotic site factors and competition on Callitris growth rates. Nevertheless, the negative association suggests that competition from dense, tall Eucalyptus seedlings may have slowed the growth of smaller Callitris seedlings. The lack of a significant association between the growth rate of Callitris seedlings and the pre-fire basal area of Callitris indicates that sites with dense Eucalyptus seedlings and small Callitris seedlings were not unsuitable for Callitris growth and persistence; Callitris dominated some of these sites before the fire. In contrast to savanna ecosystems, grasses had very low cover and biomass at Mt Pilot, and grass competition is unlikely to have had a substantial impact on growth rates or survival of Callitris or Eucalyptus seedlings, except perhaps in the first year or two after fire.

Silvicultural trials have demonstrated that the growth rate of retained Callitris is enhanced when dense Callitris stands are thinned (Knott 1995; Ross et al. 2008). However, few studies have documented competitive interactions between Callitris and Eucalyptus. Clayton-Greene (1981) reported that Eucalyptus melliodora seedlings suppressed the growth of Callitris glaucophylla seedlings in a pot competition experiment. In a small thinning trial, Bowman et al. (1988) found that Callitris grew fastest in treatments with the lowest representation of co-occurring Eucalyptus and Callitris, but unfortunately their results do not clearly differentiate the competitive effects that were exerted by the two genera.

Browsing damage

Results from the fencing trial indicate that slow-growing Callitris seedlings were vulnerable to browsing, and that browsing magnified the height difference between the two genera. However, this set-back was temporary rather than persistent. As time progressed, the height difference between fenced and unfenced Callitris seedlings diminished, perhaps because taller, older plants were less accessible to browsing animals. Nevertheless, a high proportion of Callitris seedlings at Mt Pilot remain vulnerable to future damage by browsing animals and other disturbances.

The low level of mortality in grazed plots is likely to reflect low herbivore densities, as few large herbivores were observed in the first few years after the 2003 wildfire (I. Lunt, pers. obs.). In contrast, Mackenzie and Keith (2009) recorded high mortality of C. endlicheri seedlings in an area grazed by feral Cervus timorensis (Rusa Deer) in coastal New South Wales. Over 12 months, 98% of unprotected seedlings were browsed at least once, leading to a 59% decline in seedling density (Mackenzie and Keith 2009). Seedlings of the related species, C. glaucophylla, are known to be sensitive to repeated browsing by rabbits and sheep (Lacey 1972).

Seedling mortality

In contrast with Bond’s (1989) theory, Callitris populations did not decline markedly during the establishment period due to direct competition with angiosperms nor any other cause. We recorded no significant decline in the density of Callitris seedlings over 6 years, despite a high sampling intensity. By contrast, the density of Eucalyptus seedlings declined by 57% during the 6-year period, consistent with many studies that have documented self-thinning in Eucalyptus stands after fire (Florence 1996).

The stability in Callitris numbers was surprising, as small seedlings are usually highly susceptible to mortality arising from insufficient resources and disturbances, and the survey period included years with marked rainfall deficiencies. By contrast, Mackenzie and Keith (2009) found that the density of protected (ungrazed) C. endlicheri seedlings declined by 19% within a 12-month period, from 2 to 3 years after fire. Initial seedling densities may have been underestimated in our study, as sampling began in April 2004, 15 months after the fire. Nevertheless, greater mortality was expected over the following 6 years, especially given that Callitris seedlings were so much smaller than associated Eucalyptus seedlings. Post-fire rainfall at the nearby Beechworth weather station was slightly higher than the long-term average for the first 3 years after burning (2003–05), which would have assisted initial seedling establishment. However, rainfall in subsequent years was relatively low, with just 43% of mean annual rainfall in 2006 (413 mm) and ~80% of average from 2007 to 2009 (755–790 mm; Bureau of Meteorology 2011).

Callitris species are extremely drought tolerant (Attiwill and Clayton-Greene 1984; Zeppel and Eamus 2008; Brodribb et al. 2010), and saplings self-thin extremely slowly, forming dense ‘locked stands’ containing suppressed, slow-growing trees (Lacey 1973; Thompson and Eldridge 2005; Ross et al. 2008). Lacey (1973) reported that ‘in excess of... 125 000 [trees]/ha are commonly encountered over widespread areas’ in 20-year-old stands of C. glaucophylla. At the 100-m² plot scale, the maximum density of C. endlicheri seedlings at Mt Pilot in 2010 was 13 050 seedlings/ha. In unburnt areas at Mt Pilot, stands suspected to be over 100 years old contain up to 50 live Callitris/100 m² (5000 Callitris/ha) and exceed 60 m²/ha basal area (I. Lunt, unpubl. data). Thus, C. endlicheri can persist in dense stands for many decades, similar to C. glaucophylla. This ability to tolerate low resource levels, especially low levels of soil moisture (Brodribb et al. 2010), for lengthy periods, may allow C. endlicheri to persist in mixed forests containing dense Eucalyptus regrowth, provided that plants are not killed by fire or other disturbances.

Seed cone production

Callitris species are usually killed when subjected to 100% leaf scorch and do not resprout after fire or form a soil seed bank (Hawkins 1966; Stocker 1966; Bowman et al. 1988; Cohn et al. 2010)
2011). Consequently, populations are prone to extinction if high intensity fires occur before regenerating plants set seed (Keith 1996). Callitris populations at Mt Pilot will remain susceptible to fires for many years as only 2% of plants had formed seed cones within 7 years of the 2003 fire. A fire-free period of at least 15 years is considered necessary to maintain populations of Callitris species elsewhere (Price and Bowman 1994; Russell-Smith et al. 1998; Bradstock and Cohn 2002).

Our results show that the length of the primary juvenile period (or duration of 'immaturity risk') is size dependent, as fast-growing, tall seedlings produced seed cones earlier than smaller, slow-growing seedlings. Moreover, rates of plant growth and seed production were both negatively associated with the density of Eucalyptus seedlings. Callitris seedlings grew faster and produced seed cones earlier in plots with fewer Eucalyptus seedlings, regardless of the density of Callitris seedlings.

Thinning trails have shown that competition constrains plant growth and levels of seed production in Callitris (Lacey 1972; Knott 1995; Thompson and Eldridge 2005). However, little information is available on the effects of stocking levels on the primary juvenile period, other than the general observation that, 'suppressed trees exhibit little flowering and therefore have poor seed production' (Lacey 1972), and similar observations (Prober and Thiele 2004). However, competition has been shown to extend the primary juvenile period in other conifers, including Pinus species (Cremer 1992; Verkaik and Espelta 2006). Thus, while removal experiments are required before spatial variations in primary juvenile periods can unequivocally be attributed to competition from Eucalyptus seedlings, this interpretation is consistent with prior information (Lacey 1972, 1973; Clayton-Greene 1981; FCNSW 1988), and it appears highly likely that competition contributes at least partly to the observed pattern.

These patterns have implications for future fire management. Under all but extreme conditions, fires are more likely to kill small than large Callitris (Bowman et al. 1988; Prober and Thiele 2004; Cohn et al. 2011). Consequently, if managers aim to maintain Callitris populations, then fires of moderate to high intensity should be excluded from areas containing young Callitris and moderate to dense Eucalyptus regeneration for longer than areas containing young Callitris amid sparse Eucalyptus regeneration. High basal area of Callitris reduces fire intensity in mixed Eucalyptus–Callitris stands (Bowman and Wilson 1988; Cohn et al. 2011). Consequently, over the longer term, protection of Callitris populations may reduce forest flammability and potential fire intensity.

Conclusion
These results indicate that Bond’s (1989) model provides a useful framework for interpreting Callitris dynamics in mixed forests co-dominated by Eucalyptus. Australian ecologists have commonly interpreted Callitris dynamics in fire-prone ecosystems in relation to immaturity risk, or the risk of repeated fires occurring before regenerating plants set adequate seed (Bowman et al. 1988; Russell-Smith et al. 1998; Bradstock and Cohn 2002; Thompson and Eldridge 2005). This attribute is clearly important at Mt Pilot, as elsewhere. However, Bond’s (1989) model highlights that immaturity risk may be strongly influenced by competition from co-occurring species. By inhibiting plant growth and lengthening the primary juvenile period, competitors may extend the period of immaturity risk, and potentially reduce the habitability of productive environments for Callitris and other non-resprouters. The mechanism of this extended immaturity risk may include an extended opportunity for browsing to eliminate Callitris seedlings and for fires to burn (and hence kill) plants before adequate seed is set. Regardless of the physiological or anatomical mechanisms that control growth rates, the spatial pattern of slower Callitris growth in areas with dense Eucalyptus regeneration has implications for future fire management. To maintain Callitris populations, fire-free intervals should be longer in areas stocked with Callitris, particularly areas in which Callitris is a minor component of the flora and where dense Eucalyptus regeneration dominates the regrowing vegetation.

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