Competition drives the decline of a dominant midstorey tree species. Habitat implications for an endangered marsupial

Raphaël Trouvé\textsuperscript{a,⁎}, Craig R. Nitschke\textsuperscript{a}, Loïc Andrieux\textsuperscript{a,b}, Tim Willersdorf\textsuperscript{a}, Andrew P. Robinson\textsuperscript{c}, Patrick J. Baker\textsuperscript{a}

\textsuperscript{a} School of Ecosystem and Forest Sciences, University of Melbourne, 500 Yarra Blvd, Richmond, Victoria 3121, Australia
\textsuperscript{b} Bordeaux Sciences Agro, Gradignan 33175, France
\textsuperscript{c} CEBRA & School of Mathematics and Statistics, University of Melbourne, Victoria 3010, Australia

A R T I C L E   I N F O

Keywords: Silver wattle Mountain ash Acacia dealbata Leadbeater’s possum Gymnobelideus leadbeateri Habitat suitability Stand dynamics Multi-species Mixed-species

A B S T R A C T

Context: Multi-species native forests are an important source of habitat for many plant and animal species. The dynamics of these forests are shaped by species-specific differences in growth, shade tolerance, life span, and other life-history traits, which lead to complex development patterns. Whether a particular forest stand is suitable habitat for a specific animal species may depend on various stand structural elements, which may vary in abundance due to stand dynamics, thereby generating temporal variability in habitat suitability. In the Central Highlands of Victoria, Australia, the critically endangered Leadbeater’s possum (LBP) requires both a dense lower storey of Acacia spp. for foraging and suitable hollow-bearing trees (HBTs; primarily large eucalypts) for nesting. While most LBP habitat research has focused on the dynamics of HBTs, there are uncertainties about the extent to which the occurrence and abundance of Acacia spp. are affected by competition with eucalypts.

Material and methods: We used 230 forest inventory plots to quantify how the abundance of Acacia dealbata, the most abundant of the Acacia species in these forests, varies with stand age and the abundance of overstorey eucalypts. We also took tree cores from 92 A. dealbata growing in either pure stands or stands mixed with eucalypts to test for the effects of tree age and eucalypt suppression on Acacia growth and decay patterns.

Results: The frequency and abundance of A. dealbata decreased as stand age increased, but was strongly influenced by eucalypt basal area. When eucalypt basal area was >50 m\textsuperscript{2}/ha, Acacia was almost never present. In multi-species stands, Acacia grew more slowly (by a factor of 0.66, 95% credible interval 0.51–0.86) and was more likely to have internal decay (probability increased by 0.25; 0.07–0.48) than when grown in pure stands.

Discussion: Acacia dealbata is a native pioneer species regenerating following fires. Eucalyptus overtop the Acacia after 8–10 years. The ensuing stand stratification leads to the decline and loss of the Acacia. We propose silvicultural approaches to slow Acacia decline and prolong the suitability of regrowth Eucalyptus stands as potential LBP habitat.

1. Introduction

Multi-species forests are an important source of habitat for plants and animals around the world. While many animal species associated with forests are habitat generalists, some require specific structural elements for suitable habitat. These specialist species are especially vulnerable to changes in forest structure that impact their specific habitat requirements. Developing conservation strategies that ensure the availability of suitable specialist habitat across space and through time requires understanding the dynamics of the forests (Boutin and Hebert, 2002), which in turn requires understanding how their individual elements (i.e., the various tree species) establish, grow, and interact with each other.

The tall wet forests of Victoria’s Central Highlands provide an illustrative case study of multi-species forest dynamics and their relevance to habitat suitability of a species of high conservation value, the Leadbeater’s possum (Gymnobelideus leadbeateri). Leadbeater’s possum (LBP) requires two structural elements for suitable habitat in these forests:

1. A dense lower storey dominated by Acacia spp. for foraging (Acacia gum is an important component of LBP’s diet, Smith, 1984), connectivity, and protection from predators (e.g., owls, Lindenmayer et al., 1991).
2. A pool of hollow-bearing trees (HBT, primarily *Eucalyptus regnans*, but also *E. delegatensis* and *E. nitens*) for nesting (Smith and Lindenmayer, 1988).

These two habitat features must either occur in the same stand or in relatively close proximity within the forested landscape.

Catastrophic, stand-replacing fires are the dominant disturbance type within these landscapes and have an estimated return interval of ~75–150 years (McCarthy et al., 1999). Both *Acacia dealbata* and *E. regnans* are the main mid-storey and overstorey species in these forests, establish rapidly in the high-light environment that occurs after stand-replacing fires (Ashton, 1976). *Acacia dealbata*, which lives for 1959; Simkin and Baker, 2008) with a maximum observed age of 30 to 50 years (Maslin and McDonald, 2004; Simkin and Baker, 2007). Later in stand development, although the ontogeny of hollow development is poorly understood (Fox et al., 2008; Lindenmayer et al., 1991).

While most research on LBP habitat has focused on the recruitment (Ball et al., 1999; Fox et al., 2008) and collapse (Lindenmayer et al., 1990, 2011) of HBTs, little is known about the dynamics of *A. dealbata* and the mechanism(s) leading to its decline. Yet, this information is crucial to LBP’s conservation given that HBT density and *A. dealbata* basal area both have a similar effect size on LBP presence (Lindenmayer et al., 1991; Smith and Lindenmayer, 1992; Lindenmayer, 2000). It has long been recognized that LBP are associated with young stands, conditional on the presence of HBTs (Lindenmayer et al., 1991; Smith and Lindenmayer, 1992; Lindenmayer and Possingham, 1995a,b). Younger stands (15–50 years old) typically have higher LBP abundance and hollow occupancy (from 0.2–1 to 0.4–3.5 LBP/ha, depending on the number of HBTs, and 23% hollow occupancy) than older stands (0.1–0.4 LBP/ha and 0.6–4.5% hollow occupancy) (Smith and Lindenmayer, 1992; Banks et al., 2013; Lindenmayer et al., 2017). *Acacia dealbata* competes with *Eucalyptus* species in the earliest stages of stand development (Hunt et al., 1999). However, after 8–10 years *A. dealbata* is overtopped by co-occurring *Eucalyptus* (May, 1999; Van Der Meer and Dignan, 2007) and progressively disappears from the stand. Previous estimates of *A. dealbata* longevity cover a large range of values, from 30 to 50 years (Maslin and McDonald, 2004; McCarthy et al., 2003; Simkin and Baker, 2007) with a maximum observed age of 94 years (Fedrigo et al., 2018). However, population viability analyses have assumed that lower storey species required for LBP habitat (not only *A. dealbata*) reached optimum cover 35 years after a stand-regenerating disturbance, declined from 60 to 100 years and subsequently remained stable at low density in perpetuity (Table 1 in Lindenmayer and Possingham, 1995a,b; Todd et al., 2016). While not explicitly stated, these population viability analyses presumably assume that *Acacia* spp. constantly recruit within a stand, given that individual trees do not live forever (cf. Table S1 in supplementary material). Given the important influence *Acacia* spp. have on LBP habitat suitability, such discrepancies among studies on how long *Acacia* spp. can persist in these stands underscore the need to better understand *Acacia* dynamics across the landscape and to identify what factors drive its growth and decline.

As *Acacia dealbata* is an early-successional species typically growing in multi-species stands, two non-exclusive hypotheses may explain its observed decline. First, *A. dealbata* rapidly declines in vigor due to senescence as it reaches maturity (Loehle, 1988). Second, *A. dealbata* are overtopped and suppressed over time by the taller *Eucalyptus* species.

To test these hypotheses, we first explored and quantified how *A. dealbata* presence and basal area varied in the landscape along gradients of stand age and *Eucalyptus* basal area. For this exploratory step, we used a database containing 230 forest inventory plots sampled across the Central Highlands of Victoria (Fig. 1). We then confirmed our exploratory observations by testing how individual *Acacia* growth and decay—two widely used indices of tree vitality (e.g., Bigler and Bugmann, 2003; Dobbertin, 2005)—were affected by tree age and competition with *Eucalyptus*. To do this, we cored 92 *A. dealbata* individuals across gradients of tree age and competition (i.e., *Acacia* growing in monospecific stands vs. *Acacia* growing with *Eucalyptus*).

The goal of the study was to quantify to what extent tree age and competition with eucalypts affect occurrence, growth, abundance, and decay of *A. dealbata*. The study is relevant because, in silviculturally managed forests, competition with eucalypts can be manipulated to improve *A. dealbata* presence and abundance in the landscape and deliver better conservation outcomes for a critically endangered marsupial.

2. Material and methods

2.1. Study area

The Central Highlands of Victoria is located east of Melbourne in southeastern Australia. It is home to tall open wet forests dominated by Ash-type *Eucalyptus* species (i.e., *E. regnans* in the 400–900 m mid-elevation range and *E. delegatensis*–800 m) and characterized by well-defined strata (Ashton, 1976). Despite receiving relatively high rainfall over the year (>1000–1200 mm/year), the ecosystem is driven by large fires that can ignite during the dry summer season. After a catastrophic, stand-replacing fire (mean return time interval of 75–150 years, McCarthy et al., 1999), *Eucalyptus* and *Acacia* spp. (including *A. dealbata*) regenerate at high densities as a single-cohort, multi-species stand and grow rapidly in the high light environment (Ashton, 1975, 2000; Simkin and Baker, 2008). During the first years of stand development *Eucalyptus* and *Acacia* grow in height at roughly equivalent rates. After 8–10 years the *Eucalyptus* begin to over-top *A. dealbata* (May, 1999; Van Der Meer and Dignan, 2007). Later in stand development, these tall open wet forests are characterized by a distinct stratification of species within the vertical profile of the stand, as the *Eucalyptus* spp. may reach heights of 80 m or more, whereas the *A. dealbata* are rarely taller than 30 m (Costermans, 2009). *Acacia dealbata* progressively declines within the stand during stand development and is thought to disappear after 30–80 years in the absence of intermediate disturbance events (Gilbert, 1959; McCarthy et al., 2003; Maslin and McDonald, 2004; Simkin and Baker, 2008; Aguilera et al., 2015).

2.1.1. *Acacia dealbata* presence and basal area from forest inventory

To quantify the effect of stand age and *Eucalyptus* spp. basal area (*BA_{Euc}*), on the presence and basal area of *A. dealbata* (*BA_{ac}*), we used the Central Highlands Ash Regrowth (CHAR) database (Cumming, 2008), an extensive forest inventory database composed of 230 plots covering a large range of stand ages (18–68 years) with regards to *A. dealbata* potential longevity and a large range of *BA_{Euc}* (0–99 m²/ha) that was inventoried in 2007 and 2008 (Table 1).

While we focused our analyses on *A. dealbata* as the most common *Acacia* species in these forests (*A. dealbata* was present in 127 out of 230 plots), *Acacia* species were also present in the CHAR database. This includes *A. melanoxylon* (36 plots) and unidentified *Acacia* species, likely to be *A. frigescens* or *A. obliquinervia*, two other *Acacia* found in these forests (22 plots). In total, *Acacia* spp. were present in 156 out of 230 plots. Results obtained by grouping all *Acacia* spp. together are presented in Section S2 of supplementary material. They did not differ markedly from the modelling *A. dealbata* alone. This should be expected as *A. dealbata* is the main *Acacia* spp. found in these forests.

Plots in the CHAR database were regenerated following the clearfell,
and.

\( \text{BAac} - \text{BAeu} \) (1)

\( \text{BAaca} \) represents the presence or absence of \( \text{ha2} \) in the per plot as a function of stand age and \( p \).

\( \text{ha2} \) in the landscape as a function of stand age and basal area of \( \text{Eucalyptus} \). Black lines delineates the forest management area (Central, Dandenong, and Central Gippsland).

**Fig. 1.** Plot location in the Central Highlands of Victoria. Black dots show the 14 plots where we cored \( \text{A. dealbata} \) trees to analyze the patterns of growth and decay as a function of tree age and competition treatment (with or without \( \text{Eucalyptus} \)). Grey dots show the 230 forest inventory plots from the CHAR database used to analyze the presence and basal area of \( \text{A. dealbata} \) in the landscape as a function of stand age and basal area of \( \text{Eucalyptus} \).

**Table 1**

<table>
<thead>
<tr>
<th>Plots</th>
<th>Ddbh (cm)</th>
<th>Age (years)</th>
<th>( \text{BAeuc} ) (m² ha⁻¹)</th>
<th>( \text{BAac} ) (m² ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central</td>
<td>90</td>
<td>40</td>
<td>16</td>
<td>5</td>
</tr>
<tr>
<td>Central Gippsland</td>
<td>54</td>
<td>39</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>Dandenong</td>
<td>86</td>
<td>53</td>
<td>18</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>230</td>
<td>132</td>
<td>16</td>
<td>6</td>
</tr>
</tbody>
</table>

slash burn, and sow silvicultural system, which is standard practice in the Central Highlands (Flint and Fagg, 2007). The quantification of \( \text{A. dealbata} \) presence and basal area will thus be limited to stands regenerated by clearfelling, which usually have higher abundance of \( \text{A. dealbata} \) than stands regenerated by fire (Ough, 2001; Bowd et al., 2018).

The CHAR inventory was stratified by forest management area (Central, Central Gippsland, and Dandenong), forest type (dominated by \( \text{E. regnans} \) or \( \text{E. delegatensis} \)), \( \text{Eucalyptus} \) cover, site quality, and age classes. In the original CHAR survey, each existing combination of factors was sampled at least once. Extra plots per stratum were allocated on an area-weighted basis until the number of planned plots was reached. Each plot is a 20 × 20 m rectangle, where all trees above 10 cm dbh are measured and identified to species. Based on these measurements, we calculated \( \text{A. dealbata} \) presence as well as \( \text{BAeuc} \) and \( \text{BAac} \) for each plot to be used for further modeling.

### 2.1.2. Acacia dealbata growth and decay from core samples

To explore the potential effects of tree age and the presence of \( \text{Eucalyptus} \) on \( \text{Acacia} \) growth and decay, we collected tree core samples from 92 trees in 14 sites sampled along gradients of tree age (9–70 years) and competition (monospecific \( \text{Acacia} \) stands vs. \( \text{Acacia} \) growing with \( \text{Eucalyptus} \)) (Table 2). When possible, we paired the two competition treatments in nearby sites of the same age. In each site, we installed one transect. We selected the closest non-suppressed \( \text{A. dealbata} \) every 10 m along this transect for further measurements. We measured the diameter at breast height (DBH) of each sample tree and also separately measured the basal area of \( \text{Eucalyptus} \) (mostly \( \text{E. regnans} \)) and midstorey (mostly \( \text{A. dealbata} \)) species around each sample tree using a relascopic prism with basal area factor of 4 m²/ha. We cored each sample tree to the pith in two perpendicular directions at 1.3 m height. We scanned the cores using a Microtek ScanMaker 1000XL at a resolution of 1600 DPI and then measured and counted tree rings using CooRecorder software (Cybis, n.d). Crossdating was done using a combination of visual inspection and the real-time ring width plotting display in CooRecorder. For trees > 50 yrs old, visual crossdating was verified using CDevndo (Cybis, n.d). We then averaged the two cores per tree into a single chronology and used it to estimate tree age. We used the most recent five years of tree growth as our radial growth response. We recorded the decay status of each tree as a dummy variable (decay equals one if there is visible decay or rot on the tree or core; decay equals zero otherwise).

### 2.2. Modelling

#### 2.2.1. Acacia presence and basal area from forest inventory

We used a hurdle Gamma-binomial regression to model the distribution of \( \text{BAeuc} \) per plot as a function of stand age and \( \text{BAeuc} \) in the CHAR dataset. The hurdle regression models two processes: The presence/absence of \( \text{A. dealbata} \) in a plot (Eq. (1)), and for those plots with \( \text{A. dealbata} \), the amount of \( \text{A. dealbata} \) present (i.e., \( \text{BAac} \), Eq. (2)).

The first step was modeled using a logistic regression as follows:

\[
\text{presence}_i \sim \text{Binom}(p_i)
\]

\[
p_i = \frac{1}{1 + \exp(-\logit_i)}
\]

\[
\logit_i = a_0 + a_1 \times \text{age}_i + a_2 \times \text{BAac}_i
\]

where \( \text{presence}_i \) represents the presence or absence of \( \text{Acacia} \) in plot \( i \),
with stand age, and $BA_{ac}$, $a_0$, $a_1$, and $a_2$ are parameters to be estimated from the data.

The second step was modelled using a Gamma generalized linear model (Gamma GLM). We used a Gamma as the stochastic function as it is positive, accounts for the overdispersion present in the data, and covered the range of values around the observed values. The model is described by:

$$BA_{ac} \sim \text{Gamma}(\text{scale} = \mu_i/\text{shape}, \text{shape})$$

where $BA_{ac}$ represent the basal area of Acacia on plot $i$, with stand age $age_i$ and $BA_{ac}$, $b_0$, $b_1$, $b_2$, and shape are parameters to be estimated (the shape parameter controls how $BA_{ac}$ is distributed around the mean $\mu$ and the overdispersion). Random effects for forest management area and forest type ($E. \text{regnans}$ or $E. \text{delegatensis}$) were introduced in a preliminary version of the hurdle model. These random effects were not required for the model to match the experimental design, and there was little evidence of an effect from either, so they were subsequently removed to simplify the model.

In Victoria, forest areas containing both >12 living or dead HBTs per 3 ha and $BA_{ac} > 5 \text{ m}^2 \text{ ha}^{-1}$ are considered suitable habitat for LBP. These areas are classified as habitat Zone 1B and are subsequently excluded from any future harvesting operations (CNR, 1995; DNRE, 1998). The hurdle model can inform us on the Acacia component of habitat Zone 1B: We first simulate $BA_{ac}$ values from the posterior predictive distribution (this takes into account the uncertainty in the mean $\mu$ and the overdispersion), given stand age and $BA_{ac}$ values. We then summarize the $BA_{ac}$ distribution by computing the proportion of plots predicted to have $BA_{ac} > 5 \text{ m}^2 \text{ ha}^{-1}$. While the current habitat definition for the identification and protection of potential LBP habitat in State Forests uses a $5 \text{ m}^2 \text{ ha}^{-1}$ threshold, any threshold $BA_{ac}$ value can be used to summarize the predicted $BA_{ac}$ distribution.

### 2.2.2. Acacia growth and decay from tree core samples

We used a hierarchical log-linear regression to relate the last five years of Acacia growth to tree age and competition treatment based on tree core data. We used a random site effect to take into account the potential for correlated growth of trees from the same site. The model is described as:

$$\text{log}(\text{growth}_{ij}) = c_0 + c_1 \times age_i + c_2 \times Treatment_i + \epsilon_i$$

$$\epsilon_i \sim \mathcal{N}(0, \sigma_{\text{error}})$$

where $\text{growth}_{ij}$ is the growth status ($0 = \text{no growth}, 1 = \text{growth}$) for tree $i$ in site $j$. Treatment $i$ is a dummy variable indicating tree competition status (treatment equals 1 if the tree is growing with Eucalyptus and 0 otherwise). $c_0$ is a site-specific random intercept, while $c_0$, $c_1$, and $c_2$ are parameters to be estimated.

We used a hierarchical logistic regression to relate Acacia decay to tree age and competition. This model also used a random site effect to account for potential within-site correlation in the probability of decay.

The model is:

$$\text{decay}_{ij} \sim \text{Binom}(p_{ij})$$

$$p_{ij} = \frac{1}{1 + \exp(-\logit p_{ij})}$$

$$\logit p_{ij} = d_0 + d_1 \times age_i + d_2 \times \text{Treatment}_i$$

$$d_0 \sim \mathcal{N}(0, \sigma_{\text{error}})$$

where $\text{decay}_{ij}$ is the decay status for tree $i$ in site $j$, and treatment $i$ represents tree competition status, $d_0$ is a site-specific intercept, and $d_0$, $d_1$, and $d_2$ are parameters to be estimated.

### 2.3. Statistical analyses

Statistical analyses were performed using R and Stan software (R Development Core Team, 2017; Stan, 2017). Hierarchical models were fit using the ‘brm’ function of the ‘brms’ package (Bürkner, 2017). We used weakly informative priors (Gelman, 2006) for all models. We used $N(0, 3)$ priors for the slopes and half-normal $N^+(0, 1)$ priors for random site effects. We used ‘brms’ default prior values for intercept and standard deviation of the residuals.

For each model, we estimated goodness-of-fit statistics by computing bayesian $R^2$ (Gelman et al., 2017) using the ‘bayes_R2’ function of the ‘brms’ package. The $R^2$ for the growth and decay models (Eqs. (4) and (1)) were computed both when excluding site-specific intercepts (marginal $R^2$, predicting at the population level) and when including site-specific intercepts (conditional $R^2$). We only computed the marginal $R^2$ for the hurdle model, as there were no random effects. Note that the $R^2m$ for the hurdle model combines both steps of the regression (Eqs. (1) and (2)).

### 3. Results

All models showed reasonable goodness-of-fit statistics with marginal $R^2$ around 0.3 (Table 3). Incorporating site-specific intercepts increased the goodness-of-fit of the growth model (marginal $R^2$ of 0.35 vs. conditional $R^2$ of 0.71). This likely comes from differences in productivity among sites but also from variability in the social status of the five sampled trees that did not necessarily averaged out on a per site basis.

### 3.1. Acacia dealbata presence and basal area from forest inventory

The probability of $A. \text{dealbata}$ occurring on a plot decreased with both stand age ($a_1 = -0.84$) and $BA_{ac}$ ($a_2 = -0.74$), with a similar effect size for the two predictors (Fig. 2a, Table 3). Increasing the mean value of either stand age or $BA_{ac}$ by one standard deviation (+12 years and $+21 \text{ m}^2 \text{ ha}^{-1}$, respectively) reduced the probability of presence of $A. \text{dealbata}$ from 0.57 (95% CI = 0.50-0.65) to $\sim 0.37 (0.26-0.49)$.

Conditional on $A. \text{dealbata}$ being present on the plot, $BA_{ac}$ decreased slightly with stand age ($b_1 = -0.13$) but strongly with $BA_{ac}$ ($b_2 = -0.51$, Table 3). Increasing $BA_{ac}$ by one standard deviation decreased $BA_{ac}$ by a factor of 0.61 (0.50-0.73). Additionally, the range and distributions of $BA_{ac}$ values along gradients of stand age and $BA_{ac}$ were well predicted by the combined hurdle model (Fig. 2b).
Table 3
Model summary. The R²m for the hurdle Gamma-binomial regression takes into account both steps of the hurdle model (Eqs. (1) and (2)).

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Response</th>
<th>Parameter</th>
<th>Predictor</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>R²m</th>
<th>R²c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest inventory</td>
<td>Presence (Eq. (1))</td>
<td>d₀</td>
<td>Intercept</td>
<td>0.30</td>
<td>0.61</td>
<td>0.00</td>
<td>0.28</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>d₁</td>
<td>Age</td>
<td>−0.83</td>
<td>−0.45</td>
<td>−1.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>d₂</td>
<td>BA_req</td>
<td>−0.74</td>
<td>−0.39</td>
<td>−1.69</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BA_aca (Eq. (2))</td>
<td>b₀</td>
<td>Intercept</td>
<td>1.76</td>
<td>1.59</td>
<td>1.93</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₁</td>
<td>Age</td>
<td>−0.13</td>
<td>−0.33</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₂</td>
<td>BA_aca</td>
<td>−0.51</td>
<td>−0.70</td>
<td>−0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree cores</td>
<td>Growth (Eq. (3))</td>
<td>c₀</td>
<td>Intercept</td>
<td>0.87</td>
<td>0.51</td>
<td>1.21</td>
<td>0.35</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td></td>
<td>c₁</td>
<td>Age</td>
<td>−0.46</td>
<td>−0.65</td>
<td>−0.24</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>c₂</td>
<td>Treatment</td>
<td>−0.41</td>
<td>−0.68</td>
<td>−0.15</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Decay (Eq. (4))</td>
<td>d₀</td>
<td>Intercept</td>
<td>−3.21</td>
<td>−4.97</td>
<td>−1.80</td>
<td>0.21</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>d₁</td>
<td>Age</td>
<td>0.79</td>
<td>−0.12</td>
<td>1.69</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>d₂</td>
<td>Treatment</td>
<td>2.34</td>
<td>0.83</td>
<td>4.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>σ</td>
<td>Site</td>
<td>0.43</td>
<td>0.22</td>
<td>0.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>σₑₑ</td>
<td>Residuals</td>
<td>0.55</td>
<td>0.47</td>
<td>0.65</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>σₑₑ</td>
<td>Shape</td>
<td>1.32</td>
<td>1.05</td>
<td>1.62</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Because we have access to the total distribution of BA_aca, we can derive various quantities of interest to decision makers. For example, we can compute the proportion of plots that have BA_aca above any given value (Fig. 3). In Victoria, habitat Zone 1B needs to have HBT and BA_aca > 5 m² ha⁻¹. Fig. 3 shows that BA_aca > 5 m² ha⁻¹ values are unlikely to be met when BA_aca is high, even at young ages. In contrast, when BA_aca is low, even relatively old stands can have sufficient BA_aca to meet the Habitat 1B requirements.

3.2. Acacia dealbata growth and decay from core samples

Acacia dealbata radial growth decreased with both tree age (c₁ = −0.46) and competition (c₂ = −0.41) (Fig. 4a, Table 3). Increasing tree age by one standard deviation (+18 years) decreased radial growth by a factor of 0.63 (0.52–0.79). Similarly, A. dealbata radial growth decreased by a factor of 0.66 (0.51–0.86) when grown with Eucalyptus vs. when grown in pure A. dealbata stands.

Internal wood decay increased slightly with tree age (d₁ = 0.79) but strongly with Eucalyptus competition (d₂ = 2.34) (Fig. 4b, Table 3). At 32 years, Acacia growing in monospecific stands had a probability of internal wood decay of 0.05 (0.01–0.14), compared to 0.31 (0.10–0.54) for A. dealbata growing with Eucalyptus.

On a more observational level, it was challenging to find stands with 70 year old A. dealbata growing with Eucalyptus. These conditions seem to be particularly rare in the landscape. In one of the supposed 70 year old stands, the A. dealbata sampled were later found to be 30 years old instead of the expected 70 years (the time since the last stand replacing fire), highlighting the occasional presence of intermediate regeneration event in the landscape. In another plot, the 70 year old A. dealbata growing with Eucalyptus had undergone a release event in the 1990s (data not shown), which may have helped them survive until 2017.

4. Discussion

Acacia dealbata is an essential source of food (Acacia gum), forest connectivity, and protection against owls for Leadbeater’s Possum (LBP). It is a fast-growing, shade-intolerant tree species that regenerates at high densities after stand-replacing disturbances and rarely lives more than 80–90 years and regenerates at high densities after stand-replacing disturbances. While both the presence and abundance (i.e., basal area) of A. dealbata later decrease with stand age, the rate of decrease is amplified when BA_aca was high. When BA_aca was >70 m²/ha, A. dealbata was almost never present. This pattern was also reflected in the growth dynamics of the A. dealbata. When Eucalyptus was abundant,
A. *dealbata* growth was significantly reduced and the probability of having internal decay was significantly increased. These results have important implications for understanding how variability in the stand dynamics in these forests will influence habitat suitability for LBP. Early conceptual models of forest stand dynamics in these forests proposed that after establishment, *A. dealbata* remains in the stand in perpetuity. Recent LBP population viability analyses (e.g., Lindenmayer and Possingham, 1995a,b; Todd et al., 2016) have been based on this assumption. Our results demonstrate that at the stand level *A. dealbata* is a transient habitat resource for LBP and that, absent further intense disturbance, it will disappear within a century of the stand-initiating disturbance. This result holds for *A. dealbata* alone, as well as when all *Acacia* spp. in the stand instead are accounted for (Fig. S2 in supplementary material). This finding has significant implications for forest management planning and the development and application of silvicultural prescriptions to deliver better conservation outcomes for a critically endangered marsupial.

### 4.1. Stand development in tall open wet forests

The tall open wet forests of the Central Highlands of Victoria are fire-driven ecosystems in which infrequent, high-intensity crown fires can kill most or all of the trees in the forest. The fires initiate a pulse of recruitment as *Eucalyptus* seeds released from the forest canopy and *A. dealbata* seeds in the soil seed bank germinate (Ashton, 1975). *Acacia dealbata* seeds are relatively ubiquitous within the tall wet forests of the Central Highlands landscape (Wang, 1997). In our forest inventory plots database, ~90% of the plots with low or no BA$_{\text{ave}}$ had *A. dealbata* 20 years after the stand-initiating fire (Fig. 2a). Since we modelled *A. dealbata* presence and abundance from stands regenerated using the clearfell, burn, and sow method (which typically have higher *A. dealbata* but lower *Eucalyptus* abundances than stands regenerated by fire, Ough, 2001; Bowd et al., 2018), the response curves observed in Fig. 2a are likely to be shifted downward for fire-regenerated stands.

In the first decade after a fire, the shade-intolerant *A. dealbata* and *Eucalyptus* spp. grow rapidly in height with rates approaching 1–2 m/year (May, 1999). In some sites, both species may occur in approximately equal abundance, but in most sites one of the species will be more abundant than the other. While our study examined the response of *A. dealbata* across a wide range of *Eucalyptus* spp. abundance, there was considerable variability in *A. dealbata* abundance at any given level of *Eucalyptus* spp. abundance (Fig. 2b). This variability in *A. dealbata* abundance may be due to several factors including seed limitation in the soil seed bank and competition with other understorey species that regenerate after fires in these ecosystems. On sites where *Eucalyptus* was absent or rare (i.e., <10 m$^2$/ha), the *A. dealbata* persisted for up to 70 years (Fig. 2b) and grew rapidly (up to 1.5 cm in diameter per year during the first two decades post-fire; Fig. 4a). In contrast, when *Eucalyptus* was abundant (i.e., >70 m$^2$/ha), *A. dealbata* individuals disappeared from the site long before reaching their maximum lifespan of 80–90 years.

The observed decrease in *A. dealbata* presence and abundance with increasing *Eucalyptus* abundance suggests that inter-specific competition is the primary driver of the decline of *A. dealbata* as these forests develop after fires. Vertical stratification of multi-species forests has been described for a wide range of forest types around the world (Kohyama, 1993; Oliver and Larson, 1996; Falster et al., 2017). Interspecific differences in long-term height growth rates lead to a species or group of species overtopping and suppressing slower-growing tree species. The tall wet forests of Victoria’s Central Highlands that are dominated by *Acacia* and *Eucalyptus* provide one of the most dramatic examples of canopy stratification in multi-species forests in the world. Mature *E. regnans* and *E. delegatensis* regularly grow >75 m tall, whereas the next tallest species, the midstorey *A. dealbata*, typically does not exceed 30 m in height (Gospermans, 2009). The differentiation in height between *A. dealbata* and the *Eucalyptus* spp. begins to manifest 8–10 years after a fire, when the height growth of *A. dealbata* begins to slow (May, 1999). In subsequent years and decades the relative
abundance (i.e., basal area) of the overtopping *Eucalyptus* continues to increase as they get larger. Typically, the basal area of *Eucalyptus* increases with time and will reach 60–80 m² ha⁻¹ at 50 years (Trouvé et al., 2017), suppressing *A. dealbata* growth and increasing the prevalence of decay. In these stands, within 50 years of the fire, most of the *A. dealbata* that established in the initial pulse of post-fire regeneration are either dead or dying. In the absence of another disturbance that removes a significant proportion of the *Eucalyptus* canopy, few stands in the landscape will have standing *A. dealbata* trees more than 50 years old, as the *A. dealbata* will have been largely eliminated through suppression from the taller *Eucalyptus* spp.

Given that the average return time for stand-replacing fires in the tall open wet forests of the Central Highlands ranges from 75 to 150 years (37 to 75 years for intermediate intensity fires) (McCarthy et al., 1999), the persistence of *A. dealbata* in the landscape relies on its early maturation, its abundant seed crops, and the longevity of seeds stored in the soil. Indeed, the hard-coated seeds of *Acacia* spp. can remain viable for over 50 years in the soil (Richardson and Kluge, 2008), which means that half or more of the life cycle of *A. dealbata* may be spent in the soil seed bank.

### 4.2. Predicting *A. dealbata* resources in the landscape

Our results underscore the ephemeral nature of the *Acacia* resource within the tall wet forests of the Central Highlands and highlight a significant conservation challenge for the critically endangered Leadbeater’s possum. The two structural features required by LBP for suitable habitat are a dense understorey/midstorey (dominated by *Acacia* spp.) and the presence of hollow-bearing trees (predominantly *Eucalyptus* that are >150–200 cm diameter) (Smith and Lindenmayer, 1992; Fox et al., 2008; Todd et al., 2016). However, because of the dynamics of stand development in these forests, these resources will be temporally segregated within a stand, spatially segregated within a landscape, or both. That is, when the *Acacia* resource is abundant, HBTs will need to either have survived the fire, be in an adjacent stand unaffected by fire, or require 100+ years to develop. In contrast, when HBTs have begun to form in a stand, the relatively short-lived *Acacia* resource will have long disappeared and will be confined primarily to the soil seed bank.

To develop robust conservation strategies focused on the long-term persistence of LBP habitat within the landscape, it is necessary to estimate the current distribution of each resource and anticipate how they will change over time. Stand-scale estimates of both resources across the entire Central Highlands landscape would allow for the identification of potential suitable habitat for targeted surveys to improve existing estimates of population sizes, prioritize areas for ecological restoration and conservation-focused silvicultural prescriptions (see below), as well as identify potential sites for translocation of particularly vulnerable sub-populations. For example, existing regulations specify that forest that has >12 HBTs and >5 m² ha⁻¹ of *Acacia* spp. basal area is high priority LBP habitat (i.e., known as Habitat 1B in the Leadbeater’s Possum Advisory Group Action Statement) and should be protected from harvesting. Our models (namely, Eqs. (1) and (2)) provide a tool to estimate *A. dealbata* presence and abundance based on the basal area of overstorey eucalypts and stand age. Stand age can be estimated from fire history and harvest history maps (DELWP, 2018); maps of eucalypt basal area could be estimated from remote sensing data such as lidar, which has recently become available for most of the Central Highlands. Together these would allow landscape-scale estimates of the *Acacia* resource. Rough estimates of the density of HBTs can be derived from fire history maps (Fox et al., 2009). Models to estimate the density of HBTs from remotely sensed data are currently being developed, but are complicated by the difficulty of identifying standing dead hollow-bearing trees in the advanced stages of decay, particularly where the understorey/midstorey is dense.

It is important to recognize, however, that these approaches provide only a static description of the landscape. Forecasting trajectories of *Acacia* stands with different initial conditions and simulating the impacts of disturbances, such as fire or harvesting, will require dynamic models. Since the abundance of eucalypts appears to drive the decline of the *Acacia*, one promising approach would be to structure dynamic models around $B_{A_{ue}}$ and $B_{A_{ue}}$ state variables; for example, using a two-species Lotka-Volterra competition model based on logistic growth (Lotka, 1934; Gause and Witt, 1935). In the Lotka-Volterra model, the carrying capacity of *Acacia* will decrease toward zero over time with increasing $B_{A_{ue}}$. It is worth noting, though, that calibrating such dynamic models will require time series data and the establishment of a network of permanent sample plots in these forests.

Another aspect of stand development in the tall wet forests that requires further research is the potential for establishment of new individuals of *Acacia* spp. after the first century of development. By that time the initial cohort of *A. dealbata* will likely have disappeared. Given its high light requirements, establishment of a new *A. dealbata* cohort requires a disturbance that can trigger germination. Whether new *Acacia* recruits can persist and grow in the understory will depend on how much light is available. Where a canopy gap is created by the death of a single tree or small group of trees, there may be sufficient resources for *Acacia* in the soil seed bank to germinate. However, unless the canopy gap is sufficiently large, the *Acacia* will be growing underneath a large overstorey basal area of *Eucalyptus*. As such, they will likely only persist for a short period before dying. This may not be sufficient *Acacia* in the understory to provide the necessary connectivity for LBP. Simulation models and field experiments to determine the minimum necessary canopy disturbance to allow *Acacia* to germinate, establish, and persist are critically necessary to understand how managed and natural disturbances may perpetuate (or not) LBP habitat in these forests.

### 4.3. Managing a transient resource for long-term habitat suitability

Maintaining a transient resource, such as the relatively short-lived *Acacia* in Victoria’s tall wet open forests, presents a challenge for forest managers, particularly when the resource is a critical component of the habitat of a critically endangered species such as Leadbeater’s Possum. While occasional treefalls may allow for the recruitment of individual trees and understory fires may allow for an ephemeral pulse of recruitment, neither creates the long-lasting, high-light environment that the shade-intolerant *A. dealbata* requires to persist. As our results demonstrate, even small amounts of competition from taller trees will significantly reduce the ability of *A. dealbata* to persist in the stand for more than 50 years. The primary limitation to the persistence and persistence of *A. dealbata* is the presence and abundance of overtopping *Eucalyptus*. From a silvicultural perspective there are several potential avenues to manage eucalypt abundance to increase the chance of existing *A. dealbata* persisting or to re-establish the *A. dealbata* within the stand.

The first is to manage the regeneration immediately after a disturbance—whether it is fire or timber harvesting—to create pockets or strips of *Acacia* within the stand where the degree of overtopping and suppression by eucalypts as the stand develops is minimized. The standard operating practice for regenerating clearfelled and burned stands is broadcast sowing of seeds from a GPS-guided helicopter (Flint and Fagg, 2007). The flight patterns are programmed to ensure that the seeds on each flight path overlap with the neighboring parallel flight paths. However, the helicopter flight patterns could be modified to leave gaps of sufficient width between the flight paths to allow establishment of strips of *Acacia* without direct competition from eucalypts. This would have the advantage of creating long strips that spanned the whole coupe, allowing LBP to move and forage across relatively large areas within the stand. In addition, creating within-stand heterogeneity in the distribution and relative abundance of *Acacia* and *Eucalyptus* would better mimic the patchy natural regeneration that occurs after
bushfires (Sherriff et al., unpublished). An alternative strategy would be to reduce Eucalyptus sowing densities with the expectation that this would allow a greater proportion of the stand to regenerate to Acacia. However, these approaches come with an obvious trade-off—in stands managed for timber there will be a reduction in the stand area that is dominated by the commercial eucalypt species.

A second silvicultural approach to prolonging the presence of A. dealbata within tall wet open forest stands would be to thin existing stands to reduce overstorey density. This could be done to (1) release Acacia that had been overtopped by Eucalyptus spp. or (2) create a sufficiently intense canopy disturbance to allow a new cohort of Acacia to establish. High levels of eucalypt basal area suppress the growth and accelerate the loss of Acacia in multi-species stands. Thinning the overstorey to reduce the eucalypt basal area would increase resource availability (particularly light) for the Acacia in the lower strata of the forest. This should lead to increased growth and reduced fungal infections, both of which should extend the life-span of individual Acacia. As with any thinning prescription, the key questions are: How many trees should be removed and when? Fig. 3 highlights that the earlier the density is reduced, the better—young stands will support more Acacia than older stands. It also suggests that to have a >50% probability of 5 m²/ha of Acacia basal area (the minimum threshold for classification as Habitat 1B), the overstorey basal area would need to be reduced to ~10–30 m²/ha within the first 30 years of post-disturbance stand development. The thinning should also be carried out carefully to avoid damaging the midstorey. From the perspective of traditional timber-oriented stand management practices in these forests, this would be an extremely heavy thinning (50–80% reduction in eucalypt basal area). However, in addition to creating better conditions for A. dealbata growth, it would cause a rapid increase in the growth of the residual eucalyptics, which may have benefits in terms of faster development of large trees and high-quality sawlogs (La Sala, 2007).

If the post-disturbance A. dealbata cohort is 50 years old or older, thinning the overstorey is unlikely to provide any significant extension to the lifespan of the trees (even in the absence of competition, A. dealbata trees will die when they reach their maximum lifespan of 80–90 years, cf. Table S1 in supplementary material). Instead, it is likely more important for silvicultural prescriptions at that point in stand development to focus on the establishment of a new cohort of Acacia. Successful establishment of new Acacia requires (1) scarring the forest floor to promote germination of seeds and (2) creating a persistent high-light environment for rapid growth. This would require a significant disturbance to the overstorey, whether a heavy thinning, a group selection harvest, or a patch clearcut, accompanied by either mechanical scarification or fire.

Both of these silvicultural approaches focus on stand-scale dynamics in an attempt to ensure that Acacia and HBTs co-occur on the same site. An alternative solution is to create a mosaic of stand ages within the landscape, with young stands that support dense Acacia regeneration interdigitated amongst older stands with HBTs. This might be done through conventional harvesting practices, if the harvested area is not too large and is located near stands with sufficiently large or old trees. Alternatively, conventional harvesting practices could be modified to favor a greater degree of retention and the establishment of strips of Acacia regeneration around older stands. This approach—to promote a mosaic of old and young stands in the landscape through targeted retention—was initiated in the forests of the Central Highlands in 2014 through regrowth retention harvesting methods on ~50% of the coupes located within the Leadbeater’s possum range (DELWP, 2016).

5. Conclusion

Peak densities of Leadbeater’s Possum occur in regrowth forests (15–50 years post-initiating disturbance), with abundant hollow-bearing trees and dense A. dealbata (Smith and Lindenmayer, 1992; Lindenmayer et al., 2017). Acacia dealbata declines in stands as individuals are overtopped and suppressed by Eucalyptus. Maintaining suitable habitat for Leadbeater’s Possum requires maintaining both A. dealbata and HBTs in the landscape. This presents a challenge because the Acacia resource is relatively short-lived and transient, whereas the hollow-bearing trees require more than a century to develop, creating a temporal disconnect in the two structural features that Leadbeater’s Possum requires for suitable habitat. Our results suggest that at the stand scale (1) locally reducing Eucalyptus sowing densities at the time of regeneration and/or (2) early or mid-rotation thinning to either maintain or re-establish A. dealbata will prolong the presence of A. dealbata within stands. At the landscape scale, juxtaposing young and old stands within the landscape should ensure that both of the critical elements of LBP habitat are maintained in close proximity within the landscape. However, this requires careful planning of the spatial and temporal arrangement of forest management activity over the long-term. Understanding the stand dynamics of multi-species forests is critically important for developing effective forest management strategies where complex conservation objectives exist. This is particularly the case in landscapes impacted by disturbance, fragmentation, and forest loss, where the transient structures that threatened or endangered species depend upon are less likely to co-occur in space and time.

Acknowledgements

This work was supported by the Australian Research Council (ARC), DELWP and VicForests through an ARC Linkage Project (LP140100580). P.J.B. was also supported by an Australian Research Council Future Fellowship (FT120100751).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2019.05.055.

References


of Natural Resources and Environment.


