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Time lags in provision of habitat resources through revegetation

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ABSTRACT

Broad-scale land use changes are occurring rapidly in rural landscapes worldwide, within which revegetation with native plant species to increase the area of suitable habitat is a key activity. Current models for planning revegetation are based solely on the spatial arrangement of new and remnant vegetation. Making wise decisions about revegetation requires projective models of ecological responses to revegetation, but there are few appropriate data. Substantial time lags are expected in the availability of many habitat resources because different resources are realised at different stages of vegetation maturation. Here we present results of surveys of 72 revegetation sites established over a range from 5 to more than 130 yr from the slopes and plains of central Victoria, Australia. We surveyed vegetation provision of habitat resources essential for many birds and arboreal and scansorial mammals (e.g. canopy, large boughs, tree hollows and fallen timber). Predictive models were developed for habitat resource provision as functions of time since planting, planting density and other covariates. Different habitat resources developed at different rates. While dense canopy and various forms of bark resources developed in about 10 yr, large boughs, tree hollows and fallen timber loads required at least 100 yr to develop. The development of these key habitat resources was delayed in revegetated sites with high stem densities. Habitat resources that are essential for many birds and arboreal and scansorial mammals have long time lags that models for planning offsets or landscape reconstruction should account for. Management has substantial effects: planting at high densities greatly reduces tree girth growth rates and delays the occurrence of large boughs, tree hollows and fallen timber by decades.

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1. Introduction

In many regions including Europe, North America and parts of Australia, de-intensification of land use and rehabilitation of agricultural lands is occurring with allocation of much hu-

man, biological and economic resources (Madsen, 2002; Stan-turf and Madsen, 2002; Vallejo et al., 2006). Most effort has been directed towards restoration and afforestation using woody vegetation. While passive restoration (management to encourage recruitment from persistent mature individuals

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or from seed banks) is often desirable, active replanting with seed or seedlings is frequently required (Honnay et al., 2002; Vallejo et al., 2006; Vesk and Dorough, 2006). In Australia, recent years have seen significant replanting of native trees and shrubs in rural landscapes (National Heritage Trust, 2005). In 2006, the community-based organization Greening Australia planted 2.6 million seedlings and direct seeded 1776 km of rows of native species (Greening Australia, 2007). While most revegetation is multifunctional in purpose, and control of soil salinity and provision of shelter for stock have been primary aims for much Australian revegetation, a key goal has been the conservation of native biodiversity. However, little is known about the ecological benefits of revegetation (Vesk and Mac Nally, 2006), information that is crucial for effective revegetation planning. Frequently, monitoring focuses on implementation, with tenuous links to ecological outcomes (Lake, 2001; Freudenberger et al., 2004; Vesk and Mac Nally, 2006). More useful are monitoring of fauna occupancy and abundance or using space-for-time substitutions of sites revegetated at differing but relatively short time frames (5–25 yr) (Biddiscombe, 1985; Ryan, 1999; Fisher, 2001; Martin et al., 2004; Cunningham et al., 2007; Kavanagh et al., 2007; Loyn et al., 2007). Both approaches fail to provide robust predictions of the long-term responses (50–200 yr) because most revegetation activities are recent.

There is scope for exploring development of revegetation over longer timeframes. Historical plantations date back to the late 1800s in Victoria (Bannear, 1997), albeit not intended specifically for biodiversity benefits. One approach is survey fauna in these plantations to assess the ecological outcomes of current revegetation efforts. However, this assumes that such plantations are a good proxy for current revegetation such that faunal responses would be expected to be similar between the historic and current revegetation at equivalent ages. There are reasons why this may not be valid. Some of the ways in which historical plantations differ from contemporary ones include: intention (shelter, woodlots); landscape context (isolated versus adjacent to remnants); tree species (many early plantings were *Eucalyptus cladocalyx*, which has a highly restricted natural range); planting designs (stem densities, understorey, spatial configuration). For these reasons, historical plantations may make for poor habitat that is unlikely to support populations of fauna. Many plantings, both historical and contemporary, are small, isolated from remnant native vegetation and have high perimeter to area ratios (Freudenberger et al., 2004; Radford and Bennett, 2007), properties commonly associated with low probabilities of occupancy (Mac Nally et al., 2000b; Westphal et al., 2003a), population persistence (Fahrig and Merriam, 1994; Mac Nally, 2007b), and dominance by aggressive, territorial species (e.g. noisy miners, *Manorina melanocephala*) (Clarke and Oldland, 2007; Maron, 2007).

An alternative is to focus on change in vegetation structure, with the eventual aim of modelling habitat resources, independent of spatial configuration of the planting and the surrounding landscape (Dennis et al., 2003). Many fauna are known to have strong associations with habitat resources such as boughs or hollows for nesting (Sedgwick and Knopf, 1986; Gibbons and Lindenmayer, 2002), flowers for nectar provision (Mac Nally and McGoldrick, 1997; Wilson and Bennett,

1999), and fallen timber for both foraging and shelter (Mac Nally, 2006; Mac Nally and Horrocks, 2007a). There is extensive literature on provision of timber resources in relation to time and silvicultural practices in managed forests (Smith et al., 1997). However, there has been limited research on the habitat resources provided for fauna by revegetation (Hobbs et al., 2003) and none has examined how these resources may change as vegetation matures. Knowledge about the provision of habitat resources over time can be incorporated into habitat suitability models for the purpose of projecting suitability beyond the ages of empirical datasets of faunal occupancy in revegetation (Mac Nally, 2007a). Here, we present results of a survey of habitat resources within revegetated areas of known age ranging from about 5–130 yr. We have three main aims: to demonstrate the timelags in the process of habitat restoration; to assess the effects of management, namely planting density, on this process; and to assess the functionality of the replanted habitat.

2. Methods

2.1. Study location and site selection

Surveys were conducted on the inland slopes and adjacent plains of the Great Dividing Range in south-eastern Australia from October 2005 to August 2006. The area lies within the 300–700 mm annual rainfall zone (Fig. 1). All sites were on sedimentary soils. Sites affected by past mining disturbance were avoided. Sites <1 ha and shelter-belt style plantings (linear strips) were excluded.

Site selection was based primarily on replanting age. We aimed to sample representatively with respect to age of planting and to sample the oldest possible sites. Establishment years ranged from 1876 to 1999, with most sites established after 1970. Most selected sites were planted with seedling tubestock (59 sites, 6 for farm forestry). Eleven sites were directly seeded into plough lines. Two naturally regenerated sites were included where landholders were confident of establishment date (i.e. germination year). Many more naturally regenerated sites exist, but accurate information about establishment dates was unavailable. Informants were asked of the possible range of establishment dates where records were unavailable. The greatest uncertainty was ± 7 yr, for a 111 yr old site. Most sites were confidently ascribed to a particular year (59 sites) or ± 1 yr (7 sites). One site was ± 3 yr, and 11 sites were ± 5 yr. One site was nominally 36 ± 5 yr, all other sites for which an establishment date could not be determined more confidently than ± 5 yr (10 sites) were older than 60 yr. In all cases, we used the middle of the year range. Greater uncertainty in older plantations is reduced in importance because ages were log scaled for all analyses. Planting age was calculated at 2006.

Growth of revegetation and provision of habitat resources was measured using 0.1 ha plots. Given that our aim was to maximize number of sites for broader inferences rather than to precisely characterize individual sites, we used one plot per site as the standard. However, if the site exhibited distinct vegetation or environmental heterogeneity, up to three plots were employed. Large sites were sampled with multiple plots (two plots for sites >10 ha, three plots for sites >100 ha). We

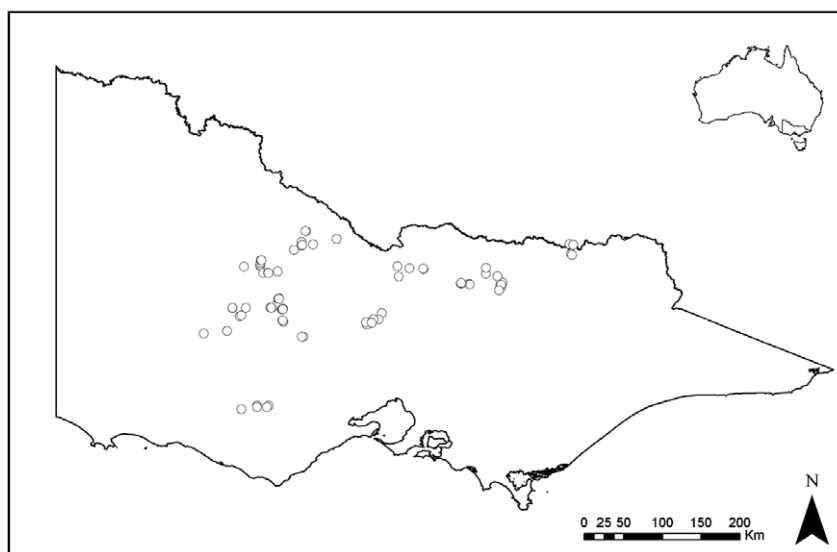


Fig. 1 – Study region and site locations.

aimed to maintain sampling of one edge and interior areas to sample the edge effects likely in more linear sites. Plots were laid from one edge of the revegetation site, and dimensions differed according to site width. For sites with width <30, 30–60, 60–120 and >130 m, plot dimensions (along edge \times into site) were 100 m \times 10 m, 40 m \times 25 m, 25 m \times 40 m and 10 m \times 100 m, respectively. Sites were georeferenced with a handheld GPS (Garmin GPS 60) to mesh with spatial datasets. For this study we investigated: establishment age, elevation, slope, aspect and net primary productivity ($\text{kg C m}^2 \text{ yr}^{-1}$), from a data layer based on the BiosEquil model predicting for 0.05°, about 5 km sides (Raupach et al., 2001).

2.2. Growth of revegetation and provision of habitat resources

Data were collated from three vegetation strata: trees, shrubs and ground layer (Table 1). For trees, we collected data on contemporary stem density, species, height and girth, canopy width and cover, trees likely to be present before revegetation, dead trees, and evidence of any subsequent recruitment, as well as resources on trees, such as boughs, hollows and bark features. For shrubs, density and species were recorded along with evidence of regeneration or senescence. Data on cover abundance of plant growth-forms, leaf litter and the amount of fallen timber were collected for the ground layer. We did not have information on stem densities at planting so we used contemporary densities as a proxy. Contemporary densities are subject to site-specific mortality, which we could not estimate. We checked for collinearity between age and density to assess the ability of our models to separate their effects.

2.3. Data analyses

Most continuous data were \log_{10} -transformed because there was left skew in most variables. Age was our main predictor variable. We analysed at the plot level for environmental

stratification (e.g. slope, aspect, planting style), meaning that several of the 72 sites contributed two or more plots to the dataset of 84 plots. Site random effects were included in predictive model to account for this potential non-independence (see below). Averaging stratified sites would dilute environmental relations. SigmaPlot v7.0 (Systat Software, Inc. 1735 Technology Drive, San Jose, CA, USA) was used for linear-regression modelling.

2.4. Predictive modelling

We built predictive models for selected response variables: average height, average diameter at breast height and the probability of trees bearing boughs or hollows. We focused on three predictors: age, stem density and net primary productivity. We used semi-parametric regression to model each response as non-linear functions of \log_{10} -transformed age (logAGE) and density (logDENSITY) and net primary productivity (NPP). We assumed normal error distributions for \log_{10} -transformed diameter at breast height (logDBH) and height (logHEIGHT) and binomial distributions with logit links for probability of bearing hollows [Pr(hollows)] and boughs [Pr(boughs)].

The models were of the form

$$\eta = \beta_0 + f_1(\logAGE) + f_2(\logDENSITY) + f_3(NPP) + e_{\text{site}}.$$

Here η is the linear predictor of the response, $f(\cdot)$ denotes a smooth function, and e_{site} is the site level random error to account for spatial correlation among plots within sites. The smooth functions $f(\cdot)$ were estimated as penalized cubic splines (Crainiceanu et al., 2005) with five knots:

$$f_n(x) = \beta_n + \sum_{k=1}^5 u_k |x - \kappa_k|^3,$$

where β_n , and u are regression coefficients and $\kappa_1 < \kappa_2 < \kappa_3 < \kappa_4 < \kappa_5$ are fixed knots. Penalized splines employ a relatively large number of knots to provide flexibility but penalize the coefficients to avoid overfitting (Crainiceanu et al., 2005).

Table 1 – Summary of variables used to assess vegetation growth and provision of habitat resources within revegetated sites

	Vegetation attribute	How assessed
Ground level	Exotic flat leaf herb cover	Percent cover of each of these variables visually estimated to the nearest 10% in four 1 m ² quadrats under tree canopies, and four more away from tree canopies
	Native herb	
	Grass, origin unclear	
	Native grass tussock cover	
	Native grass tussock number	
Ground level	Leaf litter	Counted in each of the above quadrats
	Leaf litter	Percent cover visually estimated to the nearest 10% in five 1 m ² quadrats, haphazardly distributed.
	Fallen timber	Length of fallen timber >10 cm diameter measured, multiplied by diameter at midpoint to yield volume. Fallen timber originating from remnant (exogenous) and planted (endogenous) trees were kept apart
Shrub level	Species richness and density	Species identified and number of individuals recorded within 0.1 ha plot
	Senescence	Proportion of counted shrubs senesced
	Shrub regeneration	Observation of recruits either from seed or clonal reproduction (0–10, 10–100, >100 stems per 0.1 ha plot)
Tree level	Species composition and density	Each tree within the plot was identified and counted. Measurements and observations were made on up to 50 trees per plot covering the size range at the site, with ≥10 trees per species, where possible. For remaining unmeasured trees, site medians for the species were used to estimate sizes. Occasionally, additional stems outside the plot were measured, to increase sample size of the site or of individual species
	Senescence	Each senesced stem was counted and, where possible, identified
	Size	Height was measured with a clinometer, diameter at breast height of all stems at breast height (1.3 m), projected diameter at breast height of multistem trees was calculated from cross-sectional areas using $2\sqrt{\frac{\sum \text{areas}}{\pi}}$
	Canopy width	Measured to nearest 10 cm on individual trees
	Foliage projective cover	Visually estimated to nearest 10% on individual trees
	Canopy leaf area index	The sum product of canopy width and foliage projective cover across all trees on the plot, divided by the plot area
	Bark architecture	Presence/absence of fissures (characteristic of heavily textured barks, e.g. ironbark eucalypts), ribbons (strips of bark sloughing from upper limbs) and splits (between bark and lower trunk) on individual trees
	Boughs	Count of branches >10 cm diameter, >60° from vertical, on individual trees
	Mistletoe	Presence/absence on individual trees
	Hollows	Presence/absence of hollows >10 cm diameter on individual trees
	Tree regeneration	Observation of recruits either from seed or clonal reproduction (0–10, 10–100, >100 stems per 0.1 ha plot)

All models were fitted as Bayesian mixed models in WinBUGS software (Spiegelhalter et al., 2003). Theoretical and technical details about fitting penalized spline models in WinBUGS are given by Crainiceanu et al. (2005). For a more general introduction to Bayesian modelling, see Link et al. (2002). We gave all fixed effects (β_0 and β_n) uninformative normal prior distributions $N(\mu = 0, \sigma^2 = 10^6)$ and all random effects (u and site random errors) normal prior distributions with common variances as appropriate. Thus $u_k \sim N(0, \sigma_n^2)$ for each u_k associated with spline function f_n , and $e_{\text{site}} \sim N(0, \sigma_{\text{site}}^2)$. For uninformative priors for variance parameters, we used uniform prior distributions for standard deviations (Crainiceanu et al., 2005; Gelman, 2006).

For each response variable, we used the deviance information criterion (DIC) (Spiegelhalter et al., 2002), a Bayesian measure of model fit and complexity analogous to Akaike's information criterion, to compare models with the following combination of predictors: logAGE, logAGE + logDENSITY, logAGE + NPP and logAGE + logDENSITY + NPP. Within each combination of predictors, we also tested whether individual predictors could be included as simple linear terms

rather than as spline functions, again using the deviance information criterion to compare models. We confirmed the adequacy of fit of lowest deviance information criterion models using posterior predictive P-values (PPP) which can be interpreted as the probability that the observed data could have come from the specified model (Gelman et al., 1996).

For each response variable, we also fitted boosted regression tree models (Leathwick et al., 2006) that included additional candidate predictors (slope, aspect, elevation) and allowed for interactions among predictors. Boosted regression tree results always were consistent with Bayesian models that had the lowest deviance information criterion and provided no evidence of strong interactions among predictors or for important effects of variables other than age, density and net primary productivity. Therefore, we present only Bayesian model results.

Regeneration of planted trees and shrubs (recruitment after the plantation reached reproductive maturity) was modelled using Bayesian linear models assuming Bernoulli distributions with the logit link.

3. Results

Planting tubestock has been the most common method of active revegetation and direct seeding also has long been employed (Fig. 2). Sites ranged in size from 0.3 to 235 ha (median 2.9 ha, mean 13.8 ha).

3.1. Plot variables and stand structure

After about 25 yr the majority of stems were >20 cm diameter at breast height (Fig. 3). Large trees (>60 cm diameter at breast

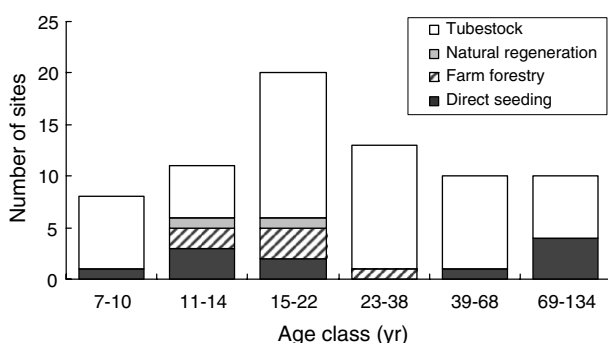


Fig. 2 – Age class and establishment of 72 surveyed revegetation sites. Successive age classes, after the youngest two classes, are double the interval of the preceding class.

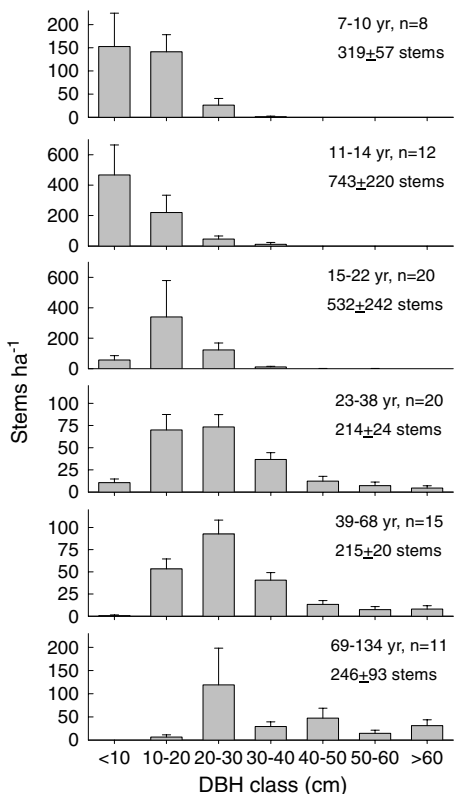


Fig. 3 – Stand structure as a function of age. Means (+SEM) of total stem densities are provided with the number of plots for each age class.

height), which many studies assume provide the bulk of tree-related habitat resources for many vertebrates (Bennett et al., 1994; Mac Nally et al., 2000a), were absent for the first 20 yr and did not form a substantial proportion of stems until about 100 yr (Fig. 3).

Plot measurements of basal area, canopy leaf area index and fallen timber all increased with age but model fit generally was poor (Fig. 4). There was 10-fold variation in stand basal area and canopy leaf area index between similarly aged sites. The volume of endogenous fallen timber varied up to 100-fold between similarly aged sites (Fig. 4c). There was no fallen timber observed in 38 of 84 plots. The median and mean fallen timber loads were 2.5 and 4.2 m³ ha⁻¹, respectively.

While trees of greater girth and height were more common on older sites (Fig. 5a and b), variation between plots of similar age was similar to that explained by the range of ages, about 5-fold for diameter at breast height and about 3-fold for height. The best model for logDBH was a linear function

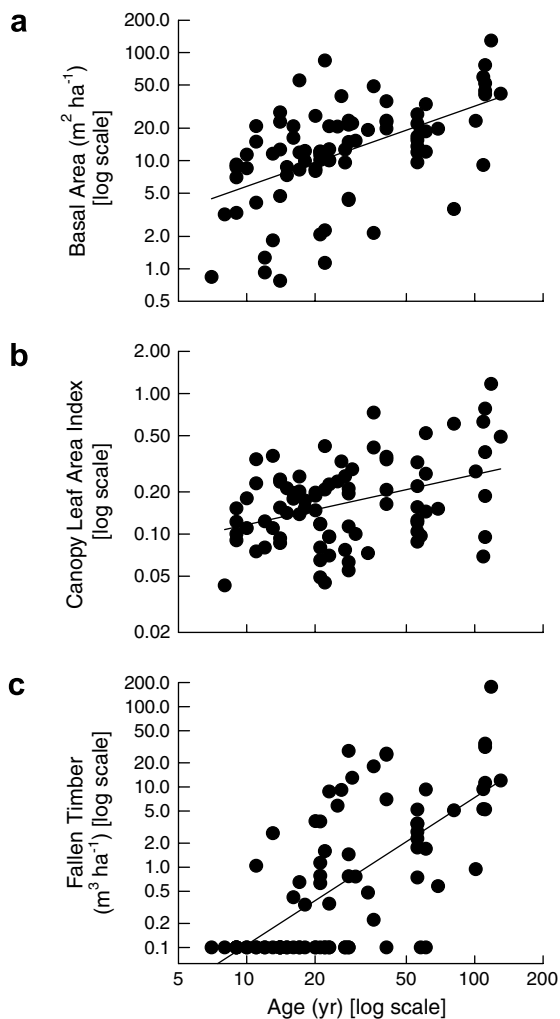


Fig. 4 – Aggregate vegetation structure as a function of age, with linear trend lines: (a) plot living basal area (BA); log BA = 0.74 logAGE – 0.98, $r^2 = 0.28$; (b) canopy leaf area index (LAI); log LAI = 0.36 logAGE – 1.29; $r^2 = 0.15$; (c) fallen timber; log(fallen timber + 0.01) = 1.83 logAGE – 2.80, $r^2 = 0.46$.

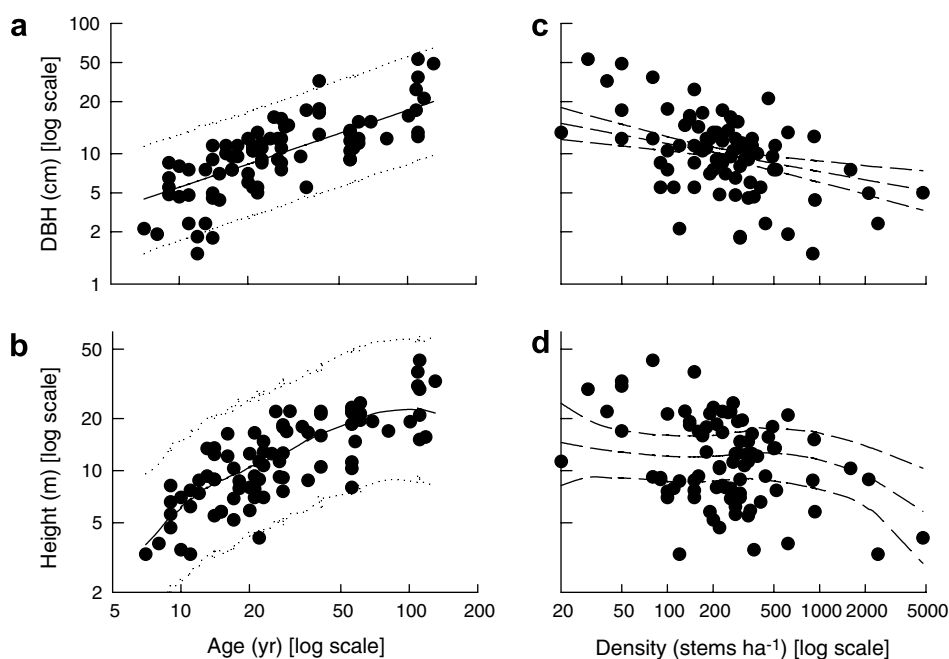


Fig. 5 – Average tree size as a function of age (a,b) and planting density (c,d). Plot average diameter at breast height (logDBH) as a linear function of (a) logAGE and (c) logDENSITY, with modelled predictions. Credible bounds in (a) include uncertainty about parameter estimates, site effects and random variation (see Table 3 for parameter estimates), credible bounds in (c) represent uncertainty about parameter estimates only. Plot average height (logHEIGHT) as a spline function of (b) logAGE and (d) logDENSITY, with modelled predictions. Credible bounds in (b) include uncertainty about parameter estimates, site effects and random variation (see online supplement for marginal plots), credible bounds in (d) represent parameter uncertainty only.

of logAGE and logDENSITY (Table 2 and Fig. 5a, c). The best model for logHEIGHT was a spline function of logAGE, logDENSITY and net primary productivity (Table 2, Fig. 5b, d, and online supplement). Sites of greater stem density supported slower DBH growth (Fig. 5a, b). Stem density also broadly reduced height growth rates, but to a lesser degree and not so simply (Fig. 5b). Net primary productivity had a positive effect (online supplement).

3.2. Stem densities

Older sites had fewer live stems ($\log\text{DENSITY} = 1.96 - 0.41\log\text{AGE}$; $r^2 = 0.12$, $P < 0.02$) possibly due to mortality but possibly by differences in initial plant densities. If mortality is the primary mechanism, this corresponds to a best estimate of the number of stems halving between 10 and 50 yr after establishment. However, 10-fold variation in live stem density was observed at both young (<20 yr) and old sites (>100 yr), which is about half the range in stem densities. Hence, we are confident that collinearity between age and density is not critical, and that our models accurately reflect the effects of both age and density.

3.3. Tree-borne resources

Resources borne by individual trees increased with age: the proportion of trees bearing hollows (Table 3), boughs and different bark structures (Figs. 6 and 7). No trees had hollows before 60 yr, and few had them before 100 yr

(Fig. 6a). The best model for the probability of bearing hollows was a linear function of logAGE and logDENSITY (Tables 2, 3 and Fig. 6a, c). Sites with more stems per plot had lower probabilities of trees bearing hollows (Fig. 6c). This probably was due to the smaller size of trees in sites planted with higher stem densities (Fig. 5a and c). Including residuals of logDBH regressed on logAGE (logDBHres) to this model substantially reduced the apparent effect of density on the probability of bearing hollows. A model with linear functions of logAGE and logDBHres only, had a lower deviance information criterion (48.5) than any other model for the probability of bearing hollows (Table 2), including a model with logDBH alone (deviance information criterion = 135.2). We do not consider these results further because it uses an outcome of the process as a predictor: larger trees develop because of site effects. Nevertheless, these results imply that hollow formation depends both on tree age and size.

The youngest tree to bear a bough was 15 yr, yet many trees did not bear boughs even at 100 yr (Fig. 6b). The best model for the probability of bearing boughs >10 cm diameter was a spline function of logAGE, logDENSITY and NPP (Table 2 and Fig. 6b, d). Pr(boughs) increased with logAGE (Fig. 6b), was reduced by increased logDENSITY (Fig. 6d) and increased with NPP (supplementary material). At one site with only two trees in the plot, both trees bore boughs at a relatively young age of 22 yr (see also Fig. 6b). The effect of NPP on Pr(boughs) increased to about $1.5 \text{ kg m}^{-2} \text{ yr}^{-1}$ and was relatively flat at higher NPP values (online supplement).

Table 2 – Comparison of models for tree size and incidence of hollows and boughs

Model	Spline	Linear
<i>Dependent variable: logDBH</i>		
logAGE	–33.9	–31.1
logAGE + logDENSITY	–41.7	–51.5
logAGE + NPP	–37.1	–35.9
logAGE + logDENSITY + NPP	–50.5	–51.1
Linear logAGE + spline(logDENSITY)	–40.6	
Linear logAGE + linear logDEN + spline(NPP)	–50.9	
<i>Dependent variable: logHEIGHT</i>		
logAGE	–67.4	–69.4
logAGE + logDENSITY	–69.9	–70.3
logAGE + NPP	–84.4	–80.4
logAGE + logDENSITY+NPP	–86.8	–82.5
linear logAGE + spline(logDENSITY) + spline(NPP)	–82.5	
<i>Dependent variable: Pr(hollows)</i>		
logAGE	100.5	112.5
logAGE + logDENSITY	53.3	50.4
logAGE + NPP	84.6	86.3
logAGE + logDENSITY + NPP	63.9	77.1
logAGE + spline(logDENSITY)	51.6	
<i>Dependent variable: Pr(boughs)</i>		
logAGE	249.6	230.5
logAGE + logDENSITY	194	192
logAGE + NPP	211.3	
logAGE + logDENSITY + NPP	180.5	192.8
Linear AGE + spline(logDENSITY)	182.3	
Linear AGE + spline(logDENSITY) + spline(NPP)	175.5	

The model with the lowest deviance information criterion (Spiegelhalter et al., 2002) (in bold) is the model that has the greatest probability, of the candidate models, of generating the observed data. Spline column refers to penalized spline models, linear refers to linear models. Deviance information criterion values for combined spline and linear models appear in spline column.

Table 3 – Posterior estimates of linear parameters for best models of diameter growth and incidence of hollows

	Mean	SD	2.5%	Median	97.5%
<i>logDBH</i>					
Intercept	1.30	0.02	1.26	1.29	1.33
logAGE effect	0.19	0.02	0.15	0.19	0.24
logDENSITY effect	–0.08	0.02	–0.13	–0.08	–0.04
Residual variance	0.03	0.01	0.02	0.03	0.05
Residual SD	0.18	0.01	0.16	0.18	0.21
<i>Pr(hollows)</i>					
Intercept	–6.74	0.76	–7.80	–7.01	–5.21
logAGE effect	5.16	0.39	4.33	5.22	5.81
logDENSITY effect	–0.82	0.15	–1.14	–0.82	–0.54

SD is standard deviation. 2.5% and 97.5% are the lower and upper 95% credible bounds, respectively.

Mistletoe was present on trees in only 8 of 84 sites, with one of these sites the result of deliberate grafting (D. Millsom, personal communication). Thus, natural colonization by mistletoe occurred in 8% of sites, all >11 yr, but only two of the 22 sites older than 50 yr had mistletoe. The proportion of trees bearing different types of bark architecture or decortication

increased with age, but with much spread probably related to species-specific differences in bark form within and between sites (Fig. 7). By 10–20 yr, most sites displayed a range of forms of bark architecture.

3.4. Natural regeneration of plantings: recruitment

Natural regeneration of trees and shrubs (>100 stems ha⁻¹) was observed in 28% and 17% of planted sites, respectively (Table 4). Models to predict high recruitment (>100 stems ha⁻¹) generally were poor, but the best predictor was stem density. A binary classification into low (≤250 stems ha⁻¹) and high density (>250 stems ha⁻¹) was at least as good a predictor of high recruitment as logDENSITY (Table 5). Dense sites were less likely to support natural recruitment of trees than open sites (Table 4). The probability of high tree recruitment at open sites was 0.37 (95% CI: 0.24–0.57), which is 2.8 times as likely as at dense sites (odds ratio, 95% CI: 1.0–8.4), where the probability of high rates of tree recruitment was 0.18 (95% CI: 0.08–0.31). The probability of high shrub recruitment also was reduced by planting density. Sparser sites had a probability of shrub recruitment of 0.26 (95% CI: 0.14–0.40), 4.8 times as likely as at dense sites (odds ratio, 95% CI: 1.3–24.2), where the probability was 0.08 (95% CI: 0.02–0.17). Neither age nor net primary productivity had a substantial effect on the probability of high rates of recruitment when models were compared with the deviance information criterion (Table 5). The effect of age was inconsistent between tree and shrub recruitment: with increasing age the probability of high tree recruitment tended to decrease, but the probability of shrub recruitment tended to increase (not shown).

3.5. Ground level

No ground-level habitat variables, except for fallen timber loads, were related to establishment age or stem density ($r < 0.22$, $P > 0.05$ for each of cover of grass, flat weeds, native herbs, leaf litter and native grass tussocks, for age or density). Cover values for ground plants were usually slightly higher away from trees than under canopies. The average (\pm SEM, $n = 81$) percent cover of ground plants was: grass, 28 ± 2.9 ; native herbs, 1.6 ± 0.60 ; native grass tussocks, 0.31 ± 0.12 , flat weeds, 0.16 ± 0.07 ; litter, 62 ± 2.3 . Native grass tussocks were rare and were detected under tree canopy in 9% of plots, and 15% of plots away from tree canopies.

4. Discussion

Our data extends to much older sites than any other published study of revegetation in Australia. The three major contributions are: (1) documentation of the time course of provision of habitat resources necessary for faunal (specifically birds and mammals) occupation of these sites; (2) analysis of the effect of management, through planting density, on this time course; and (3) analysis of the functionality of planted sites in terms of recruitment and life form diversity.

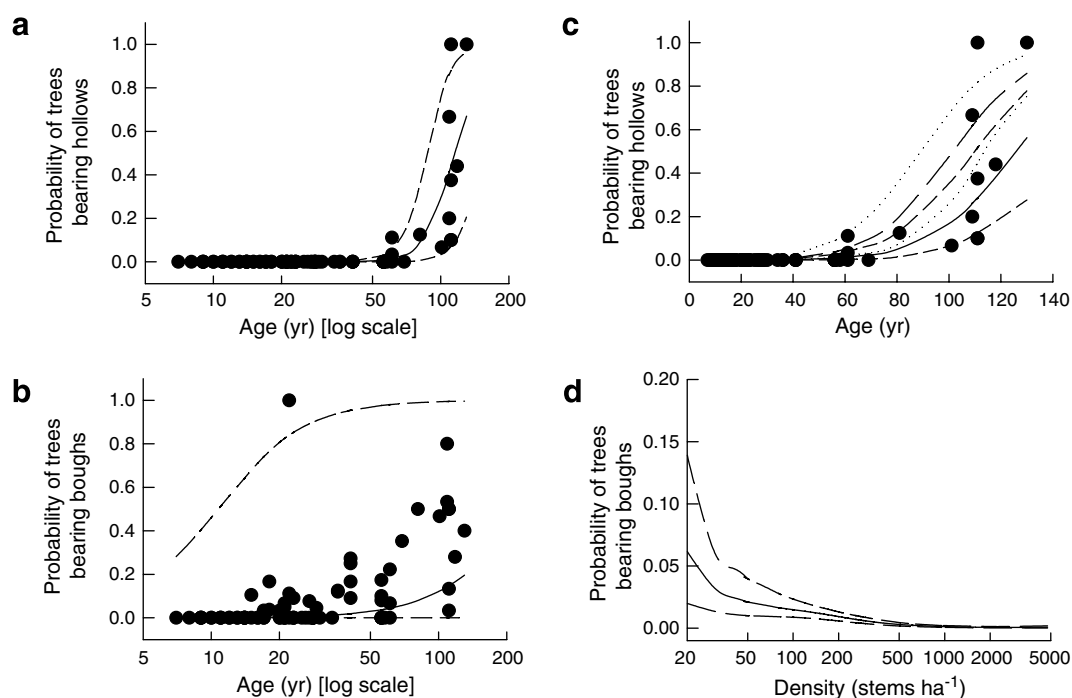


Fig. 6 – Probability of trees bearing hollows (a,c) and boughs (b,d) as functions of age and planting density, with observed proportions: (a) the proportion of trees that had hollows; (b) the proportion of trees that had boughs as functions of logAGE, each with predictions of Pr(Hollows) or Pr(Boughs), respectively, evaluated for the mean logDENSITY (~ 380 stems ha^{-1} , credible bounds represent parameter uncertainty and site variation); (c) the effects of logDENSITY on Pr(Hollows): solid line represents high density (1000 stems ha^{-1}), short dashed lines are credible bounds around parameter estimates. Long dashed line represents low density (100 stems ha^{-1}), dotted lines represent credible bounds about parameter estimates. Note age is on arithmetic scale in this graph; (d) modelled effect of logDENSITY on Pr(Boughs), evaluated at mean logAGE (~ 27 yr) and mean NPP. Credible bounds only incorporate parameter uncertainty.

4.1. Time lags

Some resources take a long time to develop. On average, neither boughs nor hollows are to be expected to have a probability of occurrence greater than 0.3 before 100 yr. Fallen timber loads equivalent to the mean observed from managed floodplain forests in a region that overlapped with this study (20 tonnes ha^{-1} using a conversion factor of 0.6 tonnes m^{-3} for timber density) (Mac Nally et al., 2002), would not be expected before 150 yr, on average. Even after 150 yr the fallen timber is likely to be different from that in mature forests, with few large logs from fallen trees and large boughs – most would be smaller logs. Lada et al. (2007) have reported on the responses of a small insectivorous marsupial, *Antechinus flavipes*, to flood proximity, availability of large trees and fallen timber on nearby floodplains in northern Victoria. They reported independent effects of all three components, suggesting a synergistic effect of tree size (age) and fallen timber loads, both of which are much greater than most of the replanted sites we report upon. This species is widespread throughout the box-ironbark region, but at very low densities compared to floodplains, perhaps reflecting the generally impoverished availability of key habitat resources.

We did not assess flowering and nectar provision by trees, upon which many birds depend [e.g. the two nationally endangered birds, the Swift Parrot *Lathamus discolor* (Mac Nally and Horrocks, 2000) and the Regent Honeyeater *Xanthomyza*

phrygia (Ford et al., 1993)]. Pertinent data from dry sclerophyll eucalypt forests in the same region are available (Wilson and Bennett, 1999; Wilson, 2002). Data from flowering over 3 yr in trees ranging from 5 to over 80 cm diameter for seven eucalypt species showed that the frequency of flowering among years, relative flowering intensity (per unit canopy) and, particularly, the amount of floral resource (per tree) increased with tree diameter. Trees smaller than 20 cm diameter contributed little to availability of floral resources while those greater than 40 cm flowered consistently and heavily. Stands younger than 50 yr will not provide substantial eucalypt floral resources, which are especially important winter nectar source across inland southeast Australia (McGoldrick and Mac Nally, 1998). Recent work in commercial eucalypt plantations on farmland in the same region (Loyn et al., 2007) showed a paucity of nectarivores, in support of the poor nectar resource expected from trees under rotation of less than 30 yr.

Some habitat resources accumulate rapidly dense canopies and bark architecture. Dense canopies can develop in about 10 yr, which is important to small birds, whether for shelter or to glean foliage for insects. Dense shrubs may also provide nectar sources, but trees will not for decades. By 10–20 yr, most trees provided the various forms of bark resources upon which many birds forage (Marchant and Higgins, 1990–2002; Vesik et al., in press) and that microbats use for roosting (Lumsden et al., 2002). Loyn et al. (2007) found bark foraging

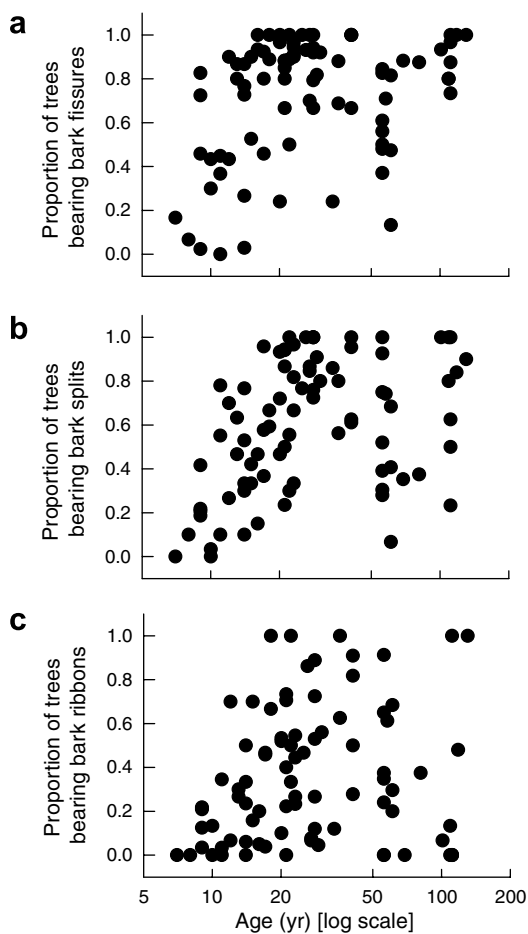


Fig. 7 – Proportions of trees bearing different forms of bark characteristics at different ages: (a) fissures in rugose bark; (b) split bark, including decorticated bark and (c) ribbons of bark stripping away from trunk and limbs.

birds made little use of plantations, though this was partly explained by the preponderance of smooth-barked eucalypts.

Our results demonstrate that models for planning restoration, such as calculating offsets required for habitat destruction (Bruggeman et al., 2005; Harper and Quigley, 2005) or optimal landscape reconstruction (Westphal et al., 2003b; Westphal and Possingham, 2003), that assume immediate equivalence of native and restored vegetation are flawed. Models must account for this delay in resource provisioning

because population viability of fauna depends upon continuity of resource supply as a necessary, yet insufficient, requirement. Time lags in provision of habitat resources can lead to population bottlenecks with potentially disastrous consequences (Martinez-Garza and Howe, 2003; Vesk and Mac Nally, 2006; Mac Nally, 2007a). Offset calculations incorporating time discounting are more defensible (Moilanen et al., in press), and our data can be used to estimate such time lags.

4.2. Density and management

Management choices strongly affect the trajectory of resource provision. Planting at high densities substantially delays resource provisioning. Density was negatively related to diameter growth, the development of boughs and hollows, accumulation of fallen timber and the likelihood of natural regeneration. While our density data were not for initial stem densities at establishment, which largely are unknown, we showed that the effect of density and age could be distinguished. Absolute values for the effect of density on growth and development of resources may be inaccurate, but we are confident in their relative magnitude. Boughs were unlikely in plots of high stem density – closely spaced stems cannot develop open spreading crowns (Vesk and Mac Nally, 2006). This is important because broken boughs are the major precursor to tree hollow formation (Gibbons and Lindenmayer, 2002) and also the major provider of fallen timber. Provision of tree hollows could be delayed by several decades by high-density planting. The time taken for a site of mean density to reach a probability equivalent to 20% of trees bearing hollows was about 87 yr. If the density were reduced to 100 stems ha⁻¹, the time taken would be marginally shorter, 80 yr. However, if the density were increased to 1000 stems ha⁻¹, then the time taken would be about 105 yr. Boughs would not simply be delayed under high density, they may not develop.

Fallen timber volumes varied substantially across the plots and often were zero. We suspect that this is due to removal for firewood or for ‘cleaning up’ plots (Driscoll et al., 2000). Fallen timber loads in all but one plot were much below the mean of 20 tonnes ha⁻¹ observed for managed floodplain eucalypt forests in this region (Mac Nally et al., 2002). Perceptions that revegetation provides a source of timber and firewood and that fallen timber needs to be ‘cleaned up’ must be changed if revegetation sites are to provide useful habitat

Table 4 – Observed frequencies of tree and shrub regeneration cross-classified by plot age and density

Age	Density	Trees			Shrubs		
		Low regeneration	High regeneration	Totals	Low regeneration	High regeneration	Totals
Young	Low	8	6	14	11	3	14
Young	High	19	5	24	24	1	25
Old	Low	19	10	29	21	7	28
Old	High	13	2	15	12	3	15
Totals		59	23	82	68	14	82

Young plots were <21 yr, old plots greater than 22 yr. Low-density plots were <250 stems ha⁻¹, high density plots were >250 stems ha⁻¹. Low regeneration was defined as <100 trees or shrubs ha⁻¹, high regeneration was ≥100 trees or shrubs ha⁻¹. Two natural regeneration sites were omitted.

Table 5 – Comparison of models for tree and shrub recruitment

Model terms	Tree DIC	Shrub DIC
Null model, intercept only	99.3	77.0
Intercept, binary age	101.2	76.7
Intercept, continuous age	101.2	76.6
Intercept, binary density	97.5	73.6
Intercept, continuous density	98.4	77.7
Intercept, binary density, binary age	98.9	74.8
Intercept, binary density, binary age and interaction	101.1	76.6
Intercept, NPP	100.7	78.5

Tree recruitment, binary density and binary ages were defined as in Table 4. Best model is bolded (lowest deviance information criterion, Spiegelhalter et al., 2002); models with values that differ by less than about 2 U are of equivalent predictive value. Trees and shrubs both included for stem density calculation for tree recruitment, only tree stems counted for density effect on shrub recruitment.

for species which dwell in, around or forage among fallen timber (e.g. *A. flavipes*, Mac Nally and Horrocks, 2007b; *Climacteris picumnus*, Mac Nally, 2006).

Direct seeding presently dominates revegetation practice, and one of the claimed benefits is the high stem densities that can arise (Corr, 2003). Planted sites can achieve high densities and our observations suggest that high-density stands persist for decades. Mortality through self-thinning, if it does occur, is relatively slow and this retards provision of desirable habitat attributes, namely, large spreading canopies with large boughs, tree hollows, appreciable fallen timber loads, tree and shrub recruitment and diverse ground vegetation. The propensity to self-thin, or the converse – tolerance – differs among tree species, and generally is low in species from low-rainfall areas, such as ours (Florence, 1996). Reducing plant densities at the time of establishment is an easy remedy for this, but in situations of existing high density, managed thinning should be factored in to management plans (Reid, 2006).

Dense vegetation provides shelter for small birds (Watson et al., 2001), and in landscapes with almost no remnant vegetation, dense plantings will have relatively great value, compared with more vegetated landscapes. Several studies have demonstrated foraging use of plantings by birds (Ryan, 1999; Hobbs et al., 2003; Martin et al., 2004; Kavanagh et al., 2007; Loyn et al., 2007). Recent work in a subset of the current sites shows that many bird species breed and produce young in the replantings (Selwood et al., in Litt.). The most significant findings are that breeding is dominated by ‘open country’ species (e.g. white-plumed honeyeater *Lichenostomus penicillatus*, Australian magpie *Gymnorhina tibicen*, red-rumped parrot *Psephotus haematonotus*) and that core box-ironbark species such as the fuscous honeyeater (*L. fuscus*) are rare breeders, at least until replantings are >100 yr old. Law and Chidel (2006) found that microbat activity was significantly lower in denser plantings and was not much better than paddocks, possibly due to low manoeuvrability of most insectivorous bats. The proposed optimal spacing for microbats was about 20–30 ha⁻¹ (Lumsden and Bennett, 2005; Law and Chidel, 2006). A mix

of planting densities seems desirable, but presently this is not the norm in practice and high density is the standard.

4.3. Recruitment and ground storey

Recruitment of shrubs and trees was more likely in sparser plantings, which increased the chance of creating vegetation that is self-regenerating and open to natural recolonization. Shrubs were not planted routinely before 1990, so we have little information about their long-term dynamics. However, shrub mortality already is occurring in young plantations and attention needs to be given to how to produce self-sustaining populations. Many shrub species included in revegetation (e.g. species of *Acacia*, *Cassinia*) need disturbance (e.g. fire) for recruitment. Many woodland eucalypt trees also recruit more frequently following disturbance such as fire (Yates et al., 1994).

While our primary focus has been on habitat resources associated with trees, we note that ground-level variables do not show the same responses to time or density. We found that tussock grass ground stores were uncommon. Asymmetric competition from trees may affect negatively the understorey or establishment could be limited by high biomass of exotic perennial and annual grasses that frequently dominate the understorey of revegetation sites (McIntyre and Lavorel, 2007). Targeted planting for key ground-level growth forms may be required. More work is needed on potential conflicts between restoring overstorey and understorey.

4.4. The way forward

Broad design principles for revegetation can be found in the report by Bennett et al. (2000) and Salt et al. (2004). We advocate generally lower tree planting densities, although with spatial variation. Retaining logs and dead trees is important because these may tide over the time lags in hollows and fallen timber. Our data also illustrate the expected time lags expected from the considerable recent plantings established since the late 1980s. Future abundance and occurrence of fauna in these temperate Australian landscapes will be influenced not simply by the spatial arrangements of revegetation plantings. The data presented here can be integrated with habitat suitability models (Van Horne and Wiens, 1991; Vesk et al., in press) and spatial models of bird distributions (Thomson et al., 2007) to build projective models of habitat suitability for bird species of the Victorian Northern Plains region (Vesk and Mac Nally, 2006; Mac Nally, 2007a). This will enable the development of strategies for landscape-scale revegetation that are free from the simple assumption of equivalence of native and restored vegetation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2007.09.010](https://doi.org/10.1016/j.biocon.2007.09.010).

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