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ORIGINAL ARTICLE

Alternative Silvicultural Systems Maintain Multiple Values in Tall Eucalypt Forest

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Abstract
Accelerating the development of more heterogeneous forest structures is an important goal of many contemporary forest management regimes. However, long-term silvicultural experiments that compare different approaches to generating structural complexity are rare. We took advantage of a replicated silvicultural experiment that was established in mountain ash (*Eucalyptus regnans*) forests in southeastern Australia in the late 1980s. We evaluated multi-decadal forest development responses to seven different silvicultural treatments: clearfelling (clearcutting), seed tree, three gap sizes (0.25, 0.5, and 2 ha), and two levels of overstorey retention (30% and 50%), plus unharvested controls. We compared a range of stand structural and compositional attributes, non-timber values (e.g., sequestered carbon, total sapwood area [a proxy for stand water-use]), and habitat features in 53 study plots replicated across all of the silvicultural treatments. Thirty years after the experiment was initiated, three treatment groups were apparent: 1) the gap (0.25-2 ha) treatments were dominated by small-diameter mountain ash, a greater abundance of *Acacia*, and relatively low basal area; 2) the clearfell and seed tree treatments had moderate basal area of mountain ash and the most uniform size-class distributions; and 3) the overstorey retention treatments had the largest trees across all treatments, as well as the greatest basal area and size inequality. Our findings indicate that alternative silvicultural systems could be used to accelerate the development of large trees and complex forest structures and support a broader range of forest values than the standard clearfell, burn, and sow silviculture prescriptions historically applied in mountain ash forests.

Keywords *Eucalyptus* · Southeastern Australia · Silviculture · Overstory retention · Restoration

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Introduction

Silvicultural prescriptions that emulate natural disturbances are the basis of ecosystem management and are fundamental to the practice of contemporary sustainable forest management (Nitschke 2005; Palik et al. 2021). In principle, when silvicultural systems recreate the heterogeneity generated by natural disturbances, they are more likely to provide the multiple forest values, such as wildlife habitat, carbon sequestration, and ecosystem resilience, associated with the natural disturbance regime (Attiwill 1994a; Bergeron and Harvey 1997; Seymour et al. 2002; Puettmann et al. 2012; Churchill et al. 2013). However, in practice, one or a few silvicultural systems is applied to a particular forest type to maximise production of preferred high-value timber species (*e.g.*, Burns and Honkala 1990; Florence 2004). When applied widely, this may have the effect of homogenising the structure and composition of forested landscapes (Tang and Gustafson 1997; Puettmann et al. 2012; Young et al. 2017). While this approach may promote a consistent supply of relatively uniform trees for wood and wood products, it often fails to provide for other forest values (Lydersen et al. 2013). In actively managed forested landscapes, many of the desirable features associated with natural disturbances—including size-class diversity, legacy structures, large trees, and vertical stratification—have become absent or rare (McRae et al. 2001; Lindenmayer and McCarthy 2002). Consequently, there is growing interest in silvicultural approaches that can promote more heterogeneous stand structures, accelerate the development of critical ecological features, and restore more complex forested landscapes (Miller and Emmingham 2001; Bauhus et al. 2009; Dodson et al. 2012; Gustafsson et al. 2012; Sullivan and Sullivan 2016; Kern et al. 2017; Willis et al. 2018). While a particular silvicultural system may produce some desirable ecological features, no single silvicultural treatment can reproduce the full spectrum of structures and patterns that would exist under a natural disturbance regime. To generate variability within a landscape, forest managers need to consider applying a more diverse range of stand-scale silvicultural prescriptions across the landscape (Bergeron et al. 2002).

For many forested ecosystems, there have been few opportunities to compare long-term stand development associated with different silvicultural systems. While there has been considerable research on thinning (Miller and Emmingham 2001; Bradford and Palik 2009; Ares et al. 2010; Comfort et al. 2010; Dodson et al. 2012; Sullivan and Sullivan 2016; Dagley et al. 2018), group selection (Neuendorff et al. 2007; Arseneault et al. 2011; Gray et al. 2012; Kern et al. 2013; Walters et al. 2016), and variable retention harvesting (Palik et al. 2014; Puettmann et al. 2016; Berrill et al. 2018; Willis et al. 2018, 2021), most has focused on comparing different intensities or configurations of the same silvicultural treatment, rather than comparing different silvicultural systems. Few empirical studies have applied silvicultural systems to emulate the full range of disturbance severity to the same forest type (but see Beese and Bryant 1999; Mitchell et al. 2004; Neyland et al. 2012; Lafleur et al. 2019). Those that do have primarily focused on regeneration outcomes over the first decade or two after treatment. While this has provided important insights into how the intensity and configuration of harvesting influences regeneration success, the long-term consequences on stand structure and composition, as well as various non-timber values, are less well understood. There is a need for more empirical studies and longer periods of monitoring to validate hypotheses about forest development and better understand how different silvicultural systems might be deployed across a landscape to accomplish the many management goals that define contemporary sustainable forest management.

In southeastern Australia, fire is the dominant natural disturbance that impacts forests. In the montane ash forests of the Central Highlands of Victoria, catastrophic, stand-replacing fires are particularly important in driving stand- and landscape-scale patterns in forest structure and composition (Ashton 1976, 1981; Attiwill 1994b; Simkin and Baker 2008). Clearfelling (or clearcutting) and seed tree silvicultural systems have long been justified on the basis that they create regeneration conditions that are similar to those produced by a catastrophic bushfire (Attiwill 1994b). These silvicultural systems remove all or most of the trees in the stand, then burn the slash to prepare the seed bed for sowing. They create a single-cohort stand and have been applied across the Central Highlands landscape for more than 60 years (Lutze et al. 1999; Flint and Fagg 2007). Given the success that the clearfell and seed tree systems have had in regenerating productive stands for wood and wood fibre in southeastern Australia, there has been little incentive to explore other silvicultural systems. Indeed, since 1950 clearfell and seed tree systems have been used for 93% of the forested area harvested in Victoria (Department of Jobs, Skills, Industry and Regions 2023). However, for several decades, there has been growing concern that this approach has had negative impacts on habitat for threatened species, water provision in catchments, and carbon sequestration in the montane ash forests (Lindenmayer et al. 1990; Keith et al. 2014; Taylor et al. 2019). While much criticism has focused on stand-level impacts of intensive silvicultural systems, a less discussed concern is that they homogenise landscapes. While large bushfires do have catastrophic impacts in parts of the landscape, they typically create a wide range of stand structures and development pathways (*e.g.*, Turner et al. 2009; Tepley et al. 2013; Merschel et al. 2024). A silvicultural regime that ignores this variability in the natural disturbance regime will make a landscape less resilient to future stressors.

Over the past decade, there has been a shift toward retention-based silviculture in southeastern Australia (Baker and Read 2011; Baker et al. 2017; Scott et al. 2019; VicForests 2019), but this too can create large (>5-15 ha), contiguous patches of relatively homogeneous forest. When any silvicultural system is applied broadly, including retention-based systems, it will have an homogenising effect at the landscape scale. Understanding how forests respond to different silvicultural systems would provide managers with a greater range of options for restoring structural complexity to forests that have been managed with the same intensive systems for long periods. This would lead to forests that are more closely aligned with the structural and compositional patterns generated by natural disturbance regimes.

This study takes advantage of a long-term, replicated experiment that tested seven different silvicultural treatments and two site-preparation techniques in mountain ash (*Eucalyptus regnans*) forests in southeastern Australia. The experiment was initiated in the late 1980s to assess the regeneration potential of various alternatives to clearfelling. The regeneration response was closely monitored for the first decade after treatment; however, by the early 2000s the experiment was no longer actively monitored. Now, three decades later, the experiment provides a unique opportunity to better understand long-term stand development patterns in response to different silvicultural treatments.

Here we address two specific questions related to the long-term consequences of alternative silvicultural systems:

1. What is the range of variability in stand structure and composition across the gradient of disturbance severity generated by the silvicultural treatments?
2. How do different silvicultural treatments influence non-timber values such as carbon sequestration, stand water-use, and habitat features?

Methods

Study Area

The study was conducted at the Tanjil Bren Silvicultural Systems Project (SSP) site located in the Central Highlands of Victoria, southeastern Australia. The site was originally selected because it was considered to be broadly representative of mountain ash forests in the Central Highlands that established in the wake of the 1939 Black Friday fire. The climate is cool and wet with mean annual rainfall of ∼1900 mm. The soils are deep, well-drained, and relatively nutrient-rich and support highly productive wet eucalypt forests. Elevation at the site ranges from 650 to 1000 m above sea level with slopes of 0-40°. Fire is the primary natural disturbance in these landscapes. In 1939 the study area burned in the Black Friday fire, a major regional fire event. This led to the establishment of a largely even-aged forest dominated by mountain ash with scattered surviving or regenerating *E. cypellocarpa*. At the time of treatment establishment, stands were approximately 50-years old and characterized by a tall closed canopy with high aboveground biomass typical of mature regrowth mountain ash forests. Midstorey tree species include *Acacia* spp., *Pomaderris aspera*, *Olearia argophylla*, and *Polyscias sambucifolia*. The forest has a dense lower stratum of tree ferns, including both *Dicksonia antarctica* and *Cyathea australis*, as well as diverse shrubs and ground ferns.

Silvicultural Treatments

The Tanjil Bren SSP was established in the late 1980s to assess regeneration responses to different silvicultural systems proposed as alternatives to clearfelling. The silvicultural treatments were selected to represent two axes of silvicultural intensity: the size of harvested area and the amount of overstorey retained. For the first, all trees were harvested in small gaps (0.25 ha and 0.5 ha), medium gaps (2 ha), and clearfells (6-8 ha). For the second, the amount of overstorey retained ranged from 0-50%. Clearfell treatments retained 0% of the overstorey, seed tree treatments retained 5% of the overstorey, and the two shelterwood treatments retained 30% and 50% of the overstorey. We refer to the shelterwood treatments as retention treatments because the second harvest of a traditional shelterwod in which the residual overwood is removed was never undertaken. As such, they are better described as dispersed retention harvests of differing intensity. The study also included untreated controls; we treated these as having an opening size of 0 ha and overstorey retention of 100%. Altogether there

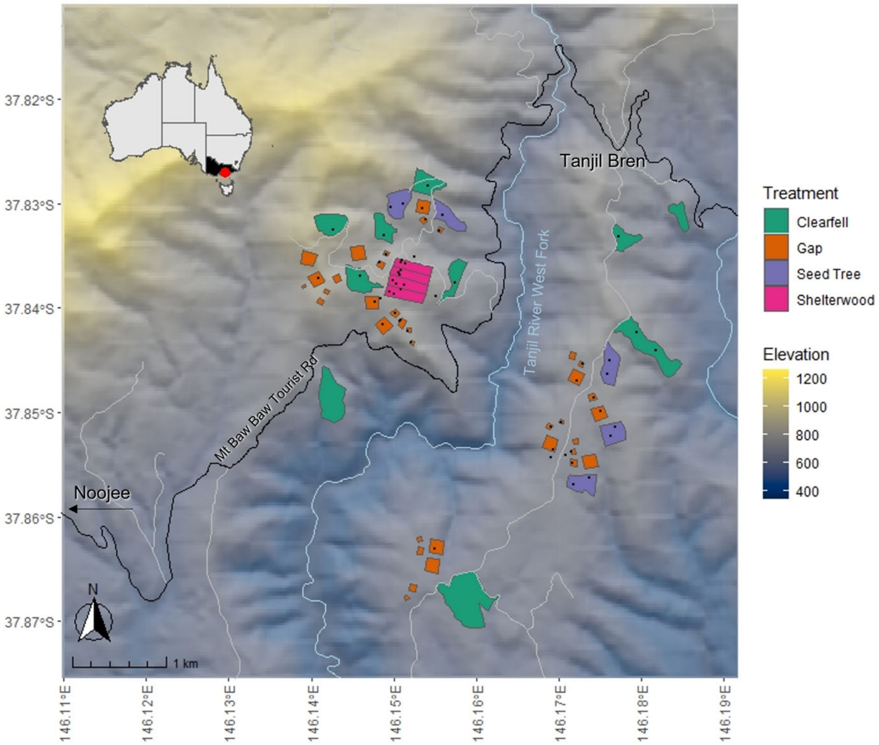

Fig. 1 The Tanjil Bren Silvicultural Systems Project site. Dots indicate plot locations

were seven silvicultural treatments: clearfelling, seed tree, two retention prescriptions (30% and 50% retained overstorey, which equated to ~16 and ~24 m^2 ha^{-1} residual basal area, respectively), and three patch clearfell prescriptions (canopy gap sizes of 0.25, 0.5, and 2 ha). Mean pre-harvest basal area across the site was estimated to be 37.4 m^2/ha (standard deviation 6.4 m^2/ha) and mean tree height was estimated to be 47.5 m (standard deviation 2.6 m^2/ha). Analysis of Variance (ANOVA) comparing pre-harvest basal area of treatment units revealed no significant differences ($p = 0.76$).

The total area of treatments varied amongst the silvicultural systems. There were 10 clearfell coupes (harvest units) covering 61 ha, five seed tree coupes covering 25 ha, and two 5 ha coupes for each level of overstorey retention. The gap treatments had four replicates for each combination of gap size and understorey treatment (see below). The treatments were randomly dispersed across the project site (Fig. 1).

All trees were harvested by the Victorian Forest Commission between 1988 and 1990. Each replicate within each silvicultural treatment was randomly assigned one of two site preparation methods: burning or mechanical disturbance by bulldozer. The exception was the retention systems, which were only mechanically disturbed (slash piled and left onsite) due to concerns about potential fire damage to the residual overstorey trees. Prepared sites were then seeded in autumn (April–May) at an average rate of 382,500 seeds per ha (38 seeds m^{-2}, Dignan et al. 1998). The number of 20 x 20 m plots belonging to each combination of treatment and site preparation can be found in Appendix S1.

Data on regeneration in the different treatments were collected for the first 8 years following harvest (Saveneh and Dignan 1997; Dignan et al. 1998; Van Der Meer et al. 1999; Van Der Meer and Dignan 2007). No additional measurements were undertaken until 2019. During the period between harvest and 2019, no fires nor major windthrow events were recorded at the study site, and no evidence of fire or wind damage was observed during subsequent field assessments (*e.g*., wind damage observed in trees or woody debris). Although the Millennium Drought occurred during the broader study period, it followed the initial regeneration phase and is therefore unlikely to have substantially influenced early regeneration dynamics. While unmeasured influences cannot be entirely excluded, there is no evidence of disturbance events or differential exogenous factors that would reasonably explain the observed treatment differences.

Data Collection

In 2019, we established 3-5 20 x 20 m (400 m^2) plots in each combination of silvicultural treatment and site preparation method for a total of 53 plots (Table 1). Plot size was selected as the maximum size that could be reasonably fit into the smallest treatment (the 50 x 50 m gap), ensuring standardisation across treatments. Plot locations were randomly assigned using GIS prior to commencement of field work and were positioned such that all plots were at least 20 m from the treatment edge. This 20 m buffer ensured that plots were fully contained within the treated area and reduced direct physical edge influences (*e.g*., damage from falling branches). However, edge effects cannot be fully eliminated: variation in proximity to surrounding forest is a key mechanism through which treatments are expected to differ.

For each plot, we recorded the species and diameter at breast height (DBH) of all live and dead standing trees >5 cm DBH and measured the height and crown area of four dominant canopy trees. We also counted and recorded the species and height of all tree ferns. We established two perpendicular transects and measured all coarse woody debris (CWD) >2 cm diameter using the line intersect method of Wagner (1968) (total transect length per plot = 40 m). Each piece of CWD was assigned one of three decay classes. We also used the transect lines to assess litter cover. At 5-m intervals along the transect lines, we established a 1-m^2 plot and measured litter depth and estimated percent litter cover. We measured the height, diameter, and percentage decay of all stumps >20 cm diameter within each plot. Finally, we compiled a list of all tree, shrub, and herbaceous species present in each plot.

Structural, Compositional, and Functional Metrics

We calculated a number of commonly used area-based metrics that describe forest structure, composition, and functional attributes. These included basal area of all live and dead stems, basal area of *Acacia* spp. and *Pomaderris aspera*, stem density, quadratic mean diameter (QMD) of all live stems and of all eucalypts, the Gini coefficient for DBH, species richness, and Shannon's diversity index for understorey

Table 1 Mean and standard deviation (in parentheses) of structural, compositional, and functional attributes associated with the different silvicultural systems assessed at the Tanjil Bren SSP. Metrics referencing trees were calculated for trees >5 cm DBH. Mean values followed by the same letter are part of the same group as indicated by the Tukey-Kramer post hoc test

Variable	Small Gap $n = 7$	Medium Gap $n = 8$	Large Gap $n = 8$	Clearfell $n = 8$	Seed tree $n = 8$	30% retention $n = 5$	50% retention $n = 5$	Control $n = 4$	p value: site preparation	p value: treatment	ω^2, 95% CI
DBH_{50}	35.5^{a} (7.0)	42.9^{a} (8.0)	51.7^{a} (8.6)	50.3^{a} (6.6)	61.8^{a} (27.7)	104.7^{b} (30.5)	121.6^{b} (62.5)	98.2^{b} (16.3)	<**0.05**	<**0.05**	0.55 (0.42, 1.00)
Basal area of live stems (m^2/ha)	26.8^{a} (5.6)	34.3^{a} (6.2)	40.8^{ab} (6.9)	41.5^{ab} (7.3)	49.5^{ab} (9.6)	101.2^{bc} (62.4)	80.9^{c} (26.5)	79.2^{bc} (14.9)	>0.05	<**0.05**	0.51 (0.28, 1.00)
Basal area of snags (m^2/ha)	4.7 (2.7)	4.7 (1.4)	4.5 (2.5)	13.0 (18.5)	6.6 (2.6)	7.6 (1.5)	5.7 (5.4)	17.8 (24.3)	>0.05	>0.05	-
Basal area of *Acacia* spp. (m^2/ha)	9.6^{ab} (7.9)	12.7^{ab} (7.9)	10.9^{ab} (7.1)	10.7^{ab} (3.9)	14.9^{a} (4.8)	10.7^{ab} (4.1)	8.4^{ab} (5.2)	0.5^{b} (1.1)	>0.05	<**0.05**	0.18 (0,1.00)
Basal area of *Pomaderris aspera* (m^2/ha)	7.6 (6.8)	6.2 (8.4)	4.0 (5.5)	0.7 (1.1)	3.0 (2.8)	0	0.5 (0.7)	1.7 (2.6)	>0.05	>0.05	-
Density (stems/ha)	1900^{a} (600)	2000^{a} (1300)	1600^{ab} (900)	1000^{b} (300)	1700^{ab} (400)	1300^{ab} (200)	1200^{ab} (500)	1100^{ab} (400)	>0.05	<**0.05**	0.997 (0.262)
Quadratic mean diameter (cm)	14.1^{a} (3.2)	16.2^{ab} (3.7)	19.7^{abc} (4.8)	23.8^{bcde} (3.9)	19.4^{abcd} (3.1)	30.4^{de} (9.7)	30.9^{cde} (7.6)	30.9^{e} (5.0)	>0.05	<**0.05**	0.56 (0.35, 1.00)

Table 1 continued

Variable	Small Gap $n = 7$	Medium Gap $n = 8$	Large Gap $n = 8$	Clearfell $n = 8$	Seed tree $n = 8$	30% retention $n = 5$	50% retention $n = 5$	Control $n = 4$	p value: site preparation	p value: treatment	ω^2, 95% CI
Gini coefficient for DBH	0.27^{a}	0.30^{ab}	0.35^{bc}	0.36^{bc}	0.37^{bc}	0.43^{cd}	0.43^{cd}	0.49^{d}	>0.05	**<0.05**	0.65 (0.48, 1.00)
Shannon's diversity index for understorey species	0.97	0.96	1.14	1.29	1.17	1.28	1.39	1.16	>0.05	>0.05	-
Mean tree fern age (years)	24.4^{ab} (16.0)	28.2^{ab} (18.4)	29.1^{b} (15.6)	28.0^{ab} (15.3)	22.6^{a} (15.1)	30.2^{b} (18.0)	27.8^{ab} (14.8)	47.9^{c} (26.8)	>0.05	**<0.05**	0.11 (0,1.00)
Mean tree fern abundance	16.75 (14.9)	25.8 (23.6)	27.9 (21.7)	45.0 (36.6)	28.9 (23.0)	21.8 (15.4)	10.6 (4.2)	44.8 (28.9)	>0.05	>0.05	-
Eucalypt sapwood area (m^2/ha)	2.8^{a} (2.7)	4.8^{abc} (2.8)	6.3^{abc} (3.0)	7.7^{bc} (1.5)	8.0^{c} (1.5)	9.2^{abc} (1.7)	6.6^{abc} (4.3)	2.2^{ab} (4.4)	**<0.05**	**<0.05**	0.36 (0.01, 1.00)
Hollow-bearing tree density (hollows/ha)	0.01^{a} (0.01)	0.03^{a} (0.01)	0.1^{a} (0.1)	1.7^{ab} (4.5)	1.3^{abc} (1.8)	7.1^{bc} (4.7)	10.9^{c} (11.3)	7.8^{bc} (9.8)	>0.05	**<0.05**	0.49 (0.26, 1.00)

species. All area-based metrics are reported on a per hectare scale. To compare tree size amongst treatments, we calculated the mean and standard deviation of DBH for the largest 50 trees per hectare (DBH_{50}). We calculated sapwood area index (SAI) of eucalypts as a proxy for tree water use; we used the regression equations for mountain ash and *A. dealbata* stems >10 cm DBH developed by Pfautsch et al. (2010). All metrics and sources can be found in Appendix S1.

Hollow-Bearing Trees

To calibrate a hollow–DBH model for *Eucalyptus regnans*, we used data from the Victorian State Forest Resource Inventory (SFRI, DNRE 1999), following a similar framework to Fox et al. (2008) but fitting a simplified DBH-only model suitable for applications where additional tree-level variables are unavailable. The inventory employed relascope sampling (basal area factor = 3) across major forest management areas (FMAs) recording species, DBH, live/dead status, and hollow presence by ground-based visual assessment for each tree with a DBH of 20 cm or greater.

Analyses were restricted to three FMAs (Central, Dandenong, and Central Gippsland) representing our Central Highlands study area. We retained only plots where *Eucalyptus regnans* comprised more than 80% of live basal area, approximating monoculture mountain ash forests. From these plots we retained live *E. regnans* stems only.

Hollow presence (0/1) was modelled as a function of DBH using a generalised linear mixed-effects model with a binomial error distribution and logit link:

$$logit(p_{ij}) = \beta_0 + \beta_1 \ln(DBH) + b_j \tag{1}$$

where p_{ij} is the probability of hollow presence for tree i in plot j, and b_j is a plot-level random intercept drawn from a normal distribution. The random intercept accounts for spatial clustering and unmeasured stand-level heterogeneity. Models were fitted using the R package *lme4*.

We used Eq. 1 to predict hollow abundance for each plot in the Tanjil Bren experiment. For each tree, we estimated the probability of hollow occurrence and then summed these probabilities across all trees within a plot, then scaled the result to hollows per hectare.

Biomass Estimation

To estimate aboveground biomass (AGB), we used existing allometric equations that calculate total stem, bark, branch, and leaf biomass. Our analysis was limited to aboveground biomass and did not include root biomass or soil carbon. For live trees, we used species-specific equations for *Acacia* spp. from Bi et al. (2004) and equations for *Eucalyptus* spp. and eucalypt forest understorey species from Dean et al. (2012). For standing dead trees (*i.e.*, snags), we calculated biomass using species-specific equations, but adjusted for density using a decay multipler of 0.77 (the wood density ratio of weakly to moderately decayed classes for eucalypt forest based on Fedrigo et al. 2014). Tree fern biomass was estimated using the height-only equation described by Fedrigo et al. (2019). To estimate tree fern age, we used the species-specific, height-based models described by Fedrigo et al. (2019). When individual tree fern heights were outside the range used to develop the models (56 – 425 cm for *Dicksonia antarctica* and 23 – 436 cm for *Cyathea australis*), we assumed a constant growth rate based on the growth rates for the minumum and maximum values. For CWD, decay multipliers for each decay class were based on the density values for five decay classes calculated by Fedrigo et al. (2014). Because we only measured three decay classes rather than the five identified by Fedrigo et al. (2019), we adapted the decay multipliers to a three class system by averaging decay multipliers 1 and 2 for the first class and 4 and 5 for the third class. We estimated stump biomass by multiplying the cylindrical volume of the stump by the estimated percentage remaining and then applied the decay multiplier used for standing dead wood.

Data Analysis

Our analyses focused on comparing the structural, compositional, and functional metrics of the different silvicultural treatments to assess whether and how they differed after 30 years of stand development. Due to the large number of variables that we measured across all of the plots, we used principal components analysis (PCA) to reduce dimensionality and illustrate the relationships between different treatments. To account for spatial clustering by harvest unit, we first fit linear mixed-effects models for each variable with harvest unit as a random effect and then conducted PCA on the model residuals. This allowed for the comparison of treatment-level multivariate response after removing variation attributable to harvest unit. This approach allowed treatment-related patterns to be more clearly identified in the ordination.

To assess differences in individual response variables amongst treatments, we used mixed-effects models, incorporating harvest unit as a random effect to account for the spatial structure of the data. This approach explicitly accounts for non-independence of plots within harvest units and appropriately partitions variance at the plot and unit levels. Mixed-effects models inherently reflect the available replication in their estimation of standard errors; treatments with fewer independent units are associated with greater uncertainty and are therefore penalised in hypothesis testing through wider confidence intervals and more conservative inference. For count-based response variables, we used Poisson generalised linear mixed models (GLMMs).

After checking model assumptions, we used linear mixed-effects models to test for an interaction between site preparation method and treatment, with harvest unit included as a random effect to account for spatial clustering. We tested for effects of site preparation method (burnt vs mechanically disturbed) and its interaction with silvicultural treatment using linear mixed-effects models. Because two treatments (control plots and retention treatments) were implemented under only one site preparation method (no preparation for the controls, mechanical disturbance for the retention treatments), these were excluded from the interaction analysis. The interaction term was only significant for one response variable—DBH_{50}. Post-hoc comparisons indicated that the mechanically-disturbed seed tree treatments had significantly larger diameters than the other treatments included in this analysis (Appendix S1). Given that post-harvest burning can damage the retained trees in a seed tree system, this difference likely reflects mortality of the retained stems in the burnt seed tree harvest units. The main effect of site preparation was only significant for one variable—eucalypt sapwood area—which tended to be greater in the burnt plots than the mechanically disturbed plots (Appendix S1). The limited influence of site preparation is consistent with the findings of Van Der Meer et al. (1999) and Van Der Meer and Dignan (2007) who found that burnt plots had significantly larger saplings at year 3, but by year 8, this difference was no longer apparent, and suggested these initial differences may be associated with the short-term increase in nutrients associated with slash burning. We therefore pooled burnt and mechanically disturbed plots within each silvicultural treatment to simplify the model structure and increase statistical power, increasing the number of plots per treatment from 3-5 to 4-8. This gave us eight silvicultural treatments (including the control) and approximately eight plots per treatment, rather than the initial 14 unique combinations of site preparation and silvicultural treatment.

To compare treatment groups, we calculated estimated marginal means (also known as least-squares means) using the "emmeans" package (Lenth 2024). These represent model-adjusted treatment means, providing the average response for each treatment while averaging over the effects of other variables in the model. We then used compact letter displays (cld) to identify statistically significant group differences, adjusting for multiple comparisons using Tukey's method. We report Omega-squared (ω^2) for treatment for the linear mixed-effects models and R^2 for the GLMMs.

To assess patterns in species composition we used non-metric multidimensional scaling (NMDS, Oksanen et al. 2019) based on species presence/absence data. Differences between silvicultural treatments were tested using Permutational Multivariate Analysis of Variance (PERMANOVA) with Jaccard's distance measure. To account for the random effect of harvest unit, permutations were constrained within harvest units. All analyses were conducted in R (R Core Team 2024).

Results

We established 53 plots that included 4424 trees from 18 species across the range of treatments at the Tanjil Bren SSP. Eighteen percent of the trees were eucalypts; however, the eucalypts represented 68% of the basal area in the plots. Only four of the 4424 trees appeared to have initiated before the 1939 bushfires. Each of these four trees was found in a different plot in a different silvicultural treatment, which means that they did not substantially contribute to the basal area or biomass of any treatment. Stem diameters ranged from 5-184 cm for *Eucalyptus* spp., 5-49 cm for *Acacia* spp., and 5-26 cm for other understorey species. Tree heights ranged from 3 to 73 m. Plot-level standing biomass ranged from 34 to 821 Mg ha^{-1} and coarse woody debris ranged from 2 to 110 Mg ha^{-1}. Species richness of non-eucalypt plants varied from 10 to 29 species across the plots.

Principal Components Analysis

The first two principal components (PCs) explained 73% of the variance in the full dataset of measured attributes (Fig. 2). PC1 represented structural metrics, while PC2

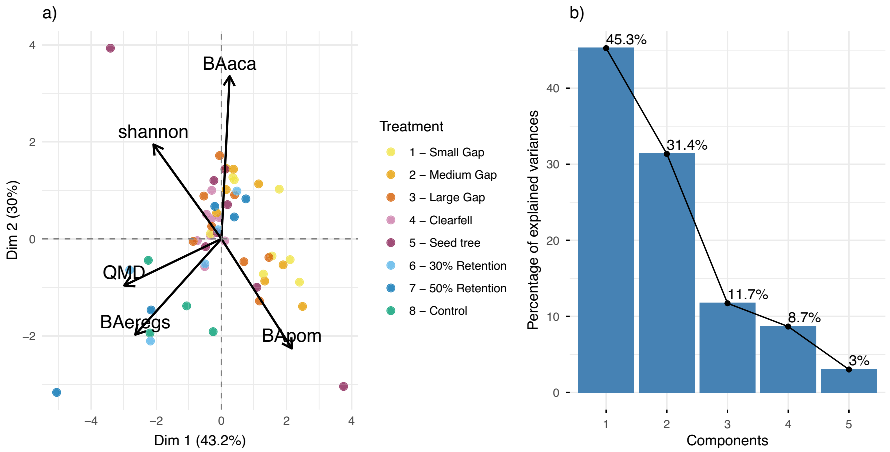

Fig. 2 Principal components analysis of structural, compositional, and functional metrics derived from the Tanjil Bren SSP plots. The left panel (**a**) shows the first two principal components and all plots organised by silvicultural treatments. BAeregs = basal area of mountain ash, BApom = basal area of *Pomaderris aspera*, BAaca = basal area of *Acacia* spp., shannon = Shannon's diversity index for understorey tree species in each plot, QMD = quadratic mean diameter of all trees >5cm diameter. Arrows point in the direction of increasing values for each variable. The right panel (**b**) shows the percentage of variation explained by the first five principal components in the analysis

was associated with compositional metrics. PC1 explained 43% of the variance and had a negative association with basal area of mountain ash, quadratic mean diameter (QMD), and Shannon's diversity index for understorey tree species (Appendix S1). PC2 explained 30% of the variance and had a negative association with basal area of *Acacia* spp. and a positive association with basal area of *Pomaderris aspera*. The distribution of individual plots within the PC1/PC2 ordination space was strongly associated with silvicultural treatment. Both of the retention treatments were clustered with the control plots, reflecting the greater size inequality and basal area of mountain ash in those plots. In contrast, the gap treatments were highly variable and were associated with higher basal area of either *P. aspera* or *Acacia* spp. and more uniform size distributions. The clearfell and seed tree treatments were clustered near the centre of the ordination with somewhat higher basal area of *Acacia* spp.

Structural Metrics

Analysis of the structural variables revealed a gradient of differences amongst the silvicultural treatments, broadly corresponding to the severity of harvesting disturbance (Table 1). The control and retention treatments clustered together at one end of the spectrum, followed by the seed tree and clearfell treatments, with the gap treatments forming a group at the opposite end. The most notable difference amongst treatments was the mean DBH of the 50 largest trees per hectare (DBH_{50}, Fig. 3). The control and retention treatments had significantly larger trees than the other treatments. The DBH_{50} was nearly twice as large (mean = 108 cm) in the retention treatments and

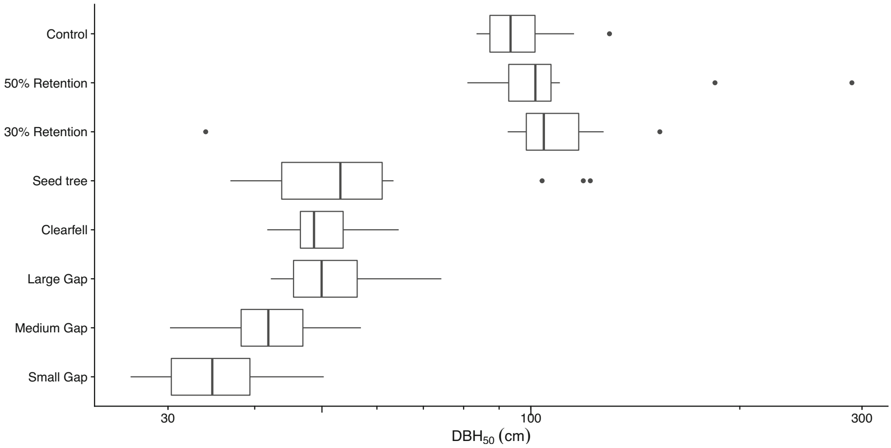

Fig. 3 Boxplots of the mean DBH of the largest 50 trees per hectare (DBH_{50}, in cm) by treatment. Vertical lines in each boxplot indicate the median value. X-axis is shown on a log scale

control plots than in any other treatments. This difference was also reflected in higher values for QMD and the Gini coefficient in the retention treatments and controls than in the other silvicultural treatments. Greater size inequality was also apparent in the diameter distributions, with the retention treatments and control plots having the greatest range in diameters across the various treatments (Fig. 4). Mean live basal area was higher in the retention treatments and controls and lower in the small and medium gaps. Diameter distributions became wider and more skewed as disturbance severity

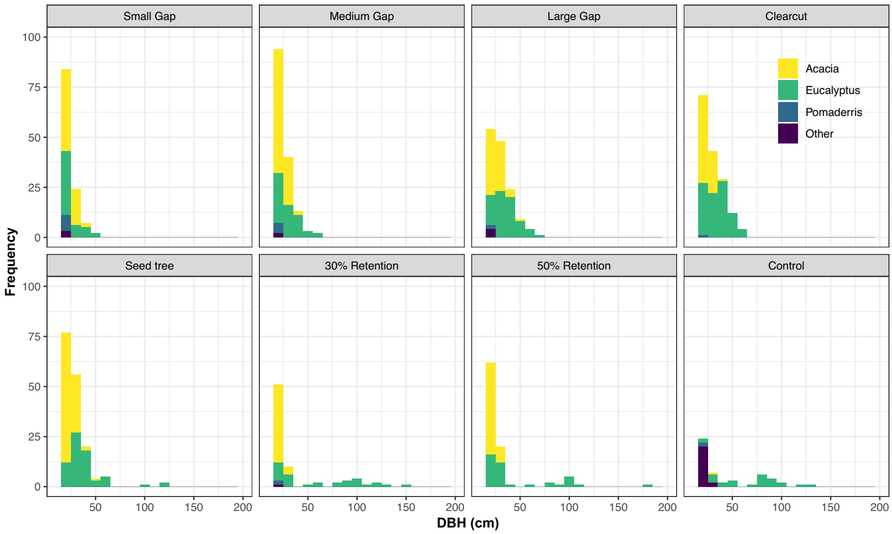

Fig. 4 Distributions of diameter at breast height (DBH) for all live stems in sample plots across the seven silvicultural treatments and the unharvested control. The upper row shows treatments in increasing order (left to right) of opening size; the lower row shows treatments in increasing order (left to right) of overstorey retained

decreased (Fig. 4). The number of stems per hectare was greater in the small and medium gaps than the other treatments. While there were significant differences in tree size and variability in tree size across the treatments, we did not find any significant differences amongst treatments for other structural metrics, such as snag basal area or abundance or litter cover and depth (results not shown).

Compositional Metrics

We found no differences in species richness or Shannon's diversity index for understorey tree species across the treatments. The NMDS and PERMANOVA analysis revealed no patterns in species presence associated with silvicultural treatment or site preparation method (all $p > 0.05$). The control plots had significantly lower basal area of *Acacia* spp. than the plots that received silvicultural treatments. There were no differences in *Pomaderris aspera* presence or basal area across the treatments. We recorded substantial variability in tree fern abundance amongst the study plots, but found no patterns associated with the silvicultural treatments. The mean age of tree ferns was greater in the controls but similar across all of the silvicultural treatments ($\sim$27 years), which reflected the timing of harvesting.

Functional Metrics

Forest water-use, as measured by total eucalypt sapwood area index (SAI), was lowest in the small gaps and control plots, highest in the clearfell and seed tree treatments, and intermediate in the medium and large gap and retention treatments.

Hollow-Bearing Trees

The final hollow dataset for the DBH-only model contained 2,590 live trees from 187 plots (mean DBH = 77.6 cm; range 20.6-387.8 cm), of which 7.4% had hollows. Hollow occurrence increased strongly with tree size. The estimated population-level relationship was:

$$p_{hollow} = \frac{1}{1 + exp(-(-31.49 + 6.23\ln(DBH)))} \tag{2}$$

The intercept was -31.49 (SE = 2.07) and the slope for $\ln(DBH)$ was 6.23 (SE = 0.43). The standard deviation of the plot-level random effect was 1.1.

Predicted probabilities were $<$1% below 75 cm DBH, approximately 6% at 100 cm, and increased steeply to $\sim$50% at 150 cm and $\sim$95% at 250 cm. Observed proportions of hollow-bearing trees per DBH class closely matched model predictions across the full range of observed sizes (Fig. 5).

When applied to the sample plots, the estimated density of tree hollows was very low in the small and medium gaps (less than one hollow per ha), moderate for the clearfell and seed tree treatments, and highest in the retention treatments and control plots due to the presence and relative abundance of larger trees.

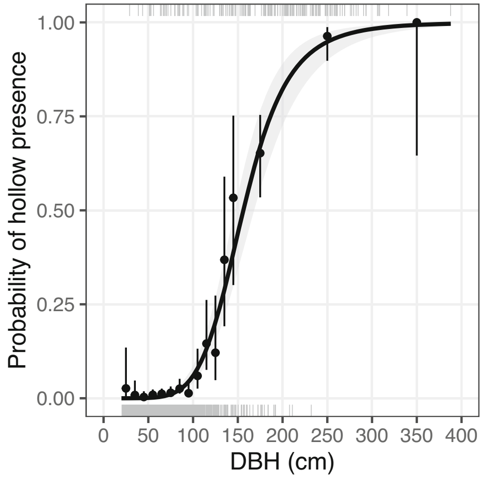

Fig. 5 Relationship between DBH and hollow occurrence in live *Eucalyptus regnans*. Grey rugs along the bottom and top of the panel show hollow-bearing tree absence and presence observations, respectively. Points show the observed proportion of hollow-bearing trees per DBH class with 95% Wilson binomial confidence intervals. The solid line shows the population-level model prediction (2) with 95% confidence interval (shaded area)

Biomass

Total biomass in the retention treatments and controls was nearly twice that of all other treatments, primarily due to the presence of large living trees with high biomass values (Fig. 6). Tree fern biomass was over four times higher in the controls than any of the silvicultural treatments. There were no significant differences in the other biomass components (*e.g.*, stem, branch, bark, or leaf) amongst the silvicultural treatments and controls.

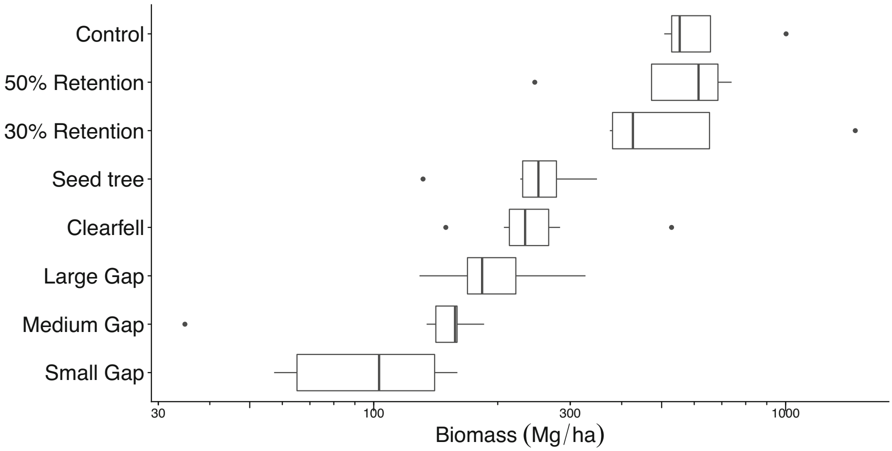

Fig. 6 Boxplots of total biomass (Mg/ha) by treatment. Vertical lines in each boxplot indicate the median value. X-axis is shown on a log scale

Discussion

The development and application of silvicultural systems around the world has historically focused on timber production. In recent decades forest management goals have diversified to accommodate a broader range of forest values, such as habitat diversity, carbon sequestration, and recreational use (Roxburgh et al. 2006; Fedrowitz et al. 2014; Baker et al. 2015). However, the operational application of silvicultural systems has not diversified in parallel. In part, this is because managers often lack guidance about the long-term consequences of different silvicultural systems on non-timber values. In this study we used a decades-long experiment to assess how a broad range of silvicultural systems shaped stand structure and composition, as well as associated values. We found that the different silvicultural treatments led to widely different structural outcomes, showed few compositional differences, and offered several potential alternatives to current silvicultural practices. A schematic summary of stand development under the different treatments can be found in Fig. 7. In particular, these results provide the silvicultural tools to restore the forest to a more complex and heterogeneous state. Here we consider how specific silvicultural systems initiated different stand development pathways, the various features associated with those pathways,

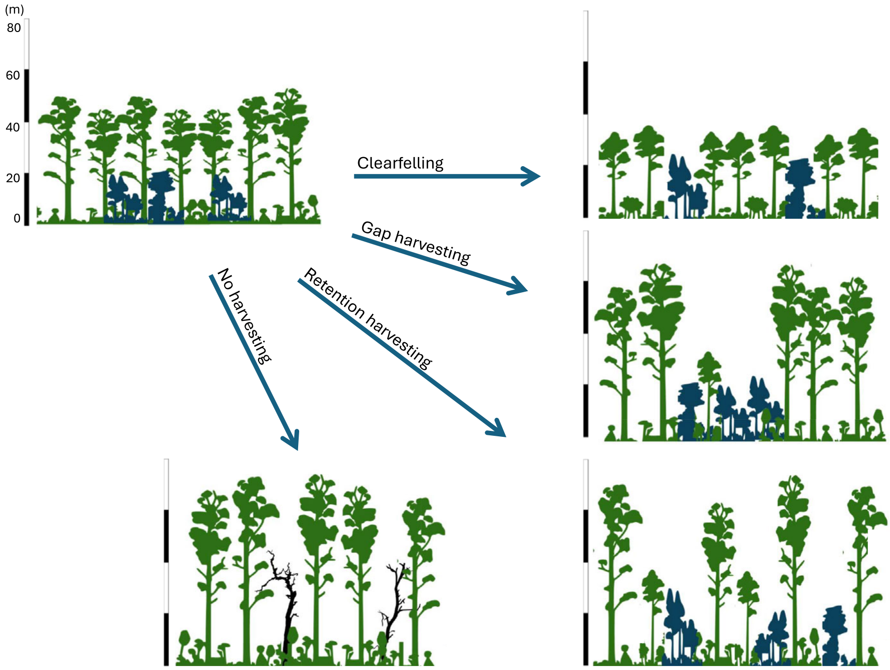

Fig. 7 Schematic summary of stand development in mountain ash (*Eucalyptus regnans*) stands after silvicultural treatment. The initial stand was 50 years old at the time the treatments were applied. The outcomes are 30 years post treatment. The silvicultural treatments include clearfelling, small gap creation, retention harvesting, and an untreated control. *Eucalyptus* species are in green; *Acacia* species are in blue. Understorey vegetation is a diverse mix of non-eucalypt species

and the implications for landscape-scale forest restoration efforts that more closely approximate natural disturbances.

Structural Complexity and Composition

Thirty years after the silvicultural prescriptions were applied there were distinct differences amongst the treatments in structure, but relatively small differences in species composition. The gap treatments were dominated by small, relatively shade-tolerant tree species (*i.e.*, *Acacia* and *Pomaderris*) and had low overall basal area. The clearfell and seed tree treatments had greater eucalypt basal area and a more uniform distribution of tree sizes. The retention treatments had the highest basal area, the greatest size inequality, and the largest trees. These differences are primarily driven by the relative shade-tolerance of the tree species. Mountain ash grows rapidly when substantial direct sunlight is available, but poorly where only diffuse sunlight occurs (Ashton 1976). When the SSP study was initiated, the forest at Tanjil Bren was approximately 50 years old and the canopy was nearly ~50 m tall (Van Der Meer et al. 1999); it is now 70-75 m tall. For direct sunlight to reach the forest floor at this latitude (38°S), gaps in the forest canopy would need to be quite large. The silvicultural prescriptions created gaps in the forest canopy that were 50 x 50 m, 75 x 75 m, and 150 x 150 m. In the smallest gaps, a few eucalypts established on the southern side of the gap, but the rest of the harvested area was dominated by the more shade-tolerant *Acacia* species. As gap size increased from the smallest gap (0.5 ha) to the clearfell (6-8 ha), greater numbers of eucalypts established and a greater proportion of the harvested area supported eucalypt regeneration rather than *Acacia*. In the silvicultural prescriptions that retained a proportion of the overstorey, the number of new recruits and the proportion of eucalypts increased as the proportion of overstorey retained decreased. Much like the regeneration response to gap size, this was driven by light availability and relative shade tolerance of the tree species initiating after the harvesting. In all cases, germination of *Acacia* from the soil seed bank was stimulated by harvesting operations and subsequent site preparation (whether fire or mechanical scarification; Van Der Meer et al. 1999). Where sufficient shade was cast by the retained overstorey or, in the case of the small gaps, by shade from the forest edge, *Acacia* established and often outcompeted the more shade-intolerant mountain ash.

While the silvicultural treatments differed in the relative proportion of the dominant tree species (specifically, the *Acacia* and *Eucalyptus*), we found no evidence of differences in plant community composition or measures of diversity between any of the silvicultural treatments and the unharvested controls after 30 years of stand development. Many studies have compared species assemblages in harvested and naturally disturbed plots (*e.g.*, Bassett et al. 2000; Ough 2001; Bowd et al. 2018; White and Vesk 2019), but most are limited to a short period post-harvest and are conducted on clearfelled forest, which represents one extreme on the gradient of silvicultural intensity. As our results demonstrate, different silvicultural systems and prescriptions will have different influences on the many biotic and abiotic factors affecting plant growth and development, particularly in the long term.

Fire has been used for decades as the site preparation tool of choice in the mountain ash forests of southeastern Australia because studies had shown that mountain ash requires a burnt seedbed for successful regeneration (Ashton and Chinner 1999). In the first decade of the Tanjil Bren SSP regeneration surveys showed an early increase in the number of mountain ash seedlings at sites that had been burned in preparation for sowing (Dignan et al. 1998; Van Der Meer et al. 1999). However, the difference in regeneration success between the mechanical and fire site-preparation techniques was small and transient; within eight years of the initial treatments, it had disappeared (Van Der Meer and Dignan 2007). Thirty years later, there are minimal detectable differences in stand composition or structure associated with site preparation method. While there was considerable operational inertia for using fire to prepare the post-harvest seedbed, community concerns about the negative impacts of smoke from regeneration burns dramatically reduced the use of fire for site preparation. Our results extend those of Dignan et al. (1998) and Van Der Meer et al. (1999) and suggest that mechanical scarification may be an acceptable substitute for fire when trying to regenerate mountain ash forests. This may afford land managers greater flexibility in site preparation where other operational considerations, such as fire risk, public health, and potential fire damage to residual trees, exist (Hindrum et al. 2012; Puettmann et al. 2015; Johnston et al. 2021).

Biomass, Tree Ferns, and Sapwood Area

Live trees constituted the greatest proportion (66-84%) of total biomass in all plots. The retention treatments, which had the highest basal area of all the treatments, had significantly more total biomass and live tree biomass than the other treatments. The mean total and live tree biomass in the retention treatments were approximately 3-4 times greater than in the small- and medium-sized gaps. Of the seven silvicultural treatments only the two retention treatments had levels of total and live tree biomass (mean total biomass: 551-652 Mg ha^{-1}) that were similar in magnitude to the control plots (mean total biomass: 654 Mg ha^{-1}). These values are similar to or slightly lower than published values of aboveground biomass in mountain ash forests in Victoria's Central Highlands (Ximenes et al. 2018). The high biomass values in the retention treatments are largely due to the overstorey trees that were retained in the initial harvests 30 years ago. These trees would have benefited from sharply reduced competition as a result of the harvesting. Their crowns would have been free to expand laterally and the base of the live crown would not have needed to recede upwards. The larger crown would have increased photosynthetic production and overall growth substantially. The retained overstorey trees would be equivalent to individual trees that persist as biological legacies after a natural disturbance. The surviving trees store the majority of on-site carbon (Fedrigo et al. 2014), particularly immediately after the disturbance, and would provide significant structural heterogeneity as the younger cohort of trees develops below them.

It is worth noting the degree to which the biomass of the two retention treatments had returned towards the undisturbed control plots. The retention treatments had 70% and 50% of their basal area removed at the time of treatment. Thirty years later they had regained all of the lost basal area, such that there were no significant differences between the retention treatments and the unharvested control plots, although the mean values were 27% and 2% more basal area than the control plots, respectively (Table 1). They also have 120% and 97% of the live tree biomass and 101% and 84% of the total biomass of the control plots, respectively.

Large snags that were created by or before the 1939 fire and fallen logs that resulted from the silvicultural treatments made a substantial contribution to the biomass pool in some of the study plots. However, they were randomly distributed through the SSP area and contributed to much of the variability within and amongst treatments. Of the other biomass components that we measured or estimated, only tree fern biomass differed amongst treatments. It was nearly five times higher (29.7 vs 5.8 Mg ha^{-1}) in the control plots than in the 50% retention treatment, which was the silvicultural treatment with the greatest tree fern biomass. Tree fern biomass was nearly 20 times greater in the control plots than in the gap (1.2-1.8 Mg ha^{-1}) and clearfell (1.4 Mg ha^{-1}) plots. The lack of treatment differences amongst the other biomass components is primarily due to the considerable within-treatment variability that we observed.

Overall, we found that the two retention treatments, in which a substantial proportion of the forest biomass was removed at the time of treatment, had already surpassed the control plots in basal area and were rapidly converging on the biomass levels of the unharvested controls. In the 30 years since the experiment was initiated, the retention treatments had recovered all of their harvested biomass and most of the additional growth in biomass of the controls. The other silvicultural treatments had not (Table 2). Our results appear consistent with Keith et al. (2009) who found higher biomass values in forests that had been partially disturbed in the past than in forests that were undisturbed. While harvesting is often seen to compromise carbon stocks, our results indicate that retention systems could reduce disparities in aboveground carbon storage between natural and silvicultural disturbances and result in a rapid return to pre-disturbance levels of aboveground carbon storage within a few decades. Importantly, retention harvesting systems may also have a net positive carbon outcome relative to “no management" scenarios if the harvested wood is used for high-quality wood products with long-term carbon storage potential.

Tree ferns are an important component of the wet sclerophyll forests of southeastern Australia and New Zealand. They make significant contributions to biomass storage, influence recruitment dynamics, and are an important substrate for epiphytes (Fedrigo et al. 2019). Tree ferns are also sensitive to physical disturbances because they are slow-growing and do not resprout. The Tanjil Bren SSP provides useful insights into how tree fern populations respond to different levels of harvesting intensity. We found that tree fern biomass was much lower in the harvested plots than in the controls; however, tree fern abundance was similar, although quite variable across the plots. Ough and Murphy (2004) and Bowd et al. (2018) found that tree fern abundance decreased after harvesting and had not returned to pre-harvest levels after 6-8 years. Our results demonstrated that tree ferns are able to return to pre-harvest levels of stem numbers within 30 years, but that they will require substantially longer to reach pre-harvest levels of biomass. This is consistent with the findings of Fedrigo et al. (2019) who found that tree ferns recruit continuously following disturbance, but are slow growing. The tree ferns at Tanjil Bren were estimated to range in age from 1 to

Table 2 Mean aboveground biomass (Mg/ha) components for the different silvicultural treatments. Standard deviations in parentheses. Mean values followed by the same letter are part of the same group as indicated by Tukey's HSD test

Component	Small Gap	Medium Gap	Large Gap	Clearfell	Seedtree	30% retention	50% retention	Control	p	ω^2, 95% CI
Live trees	81.4^{a} (37.4)	114.6^{ab} (41.7)	172.4^{b} (59.8)	189.1^{bc} (41.9)	219.4^{bcd} (57.3)	$627.7.3^{cd}$ (464.5)	503.7^{cd} (193.0)	521.1^{d} (116.2)	<**0.05**	0.65 (0.48, 1.0)
Snags	11.7 (5.8)	11.1 (5.0)	11.3 (7.7)	48.2 (94.0)	15.4 (7.6)	19.4 (5.0)	18.0 (23.6)	85.3 (122.2)	>0.05	-
Tree ferns	1.0^{a} (1.1)	2.7^{a} (4.1)	4.3^{ab} (4.6)	4.2^{ab} (3.8)	1.75^{a} (1.8)	2.3^{ab} (1.3)	5.8^{ab} (4.8)	29.7^{b} (21.8)	<**0.05**	0.23 (0, 1.0)
Stumps	1.6 (1.8)	1.2 (0.9)	1.8 (2.0)	1.4 (2.4)	3.4 (7.8)	1.4 (1.3)	1.1 (0.5)	0	>0.05	-
Coarse woody debris	12.0 (8.0)	15.7 (15.5)	15.5 (8.9)	26.6 (35.3)	15.7 (10.4)	14.3 (11.1)	29.3 (18.4)	23.2 (12.7)	>0.05	-
Total	105.1^{a} (41.8)	141.6^{ab} (45.6)	202.1^{b} (64.4)	263.9^{bc} (1154.0)	252.3^{bc} (64.0)	662.0^{cd} (469.3)	551.6^{cd} (197.9)	654.2^{d} (233.7)	<**0.05**	0.67 (0.51, 1.0)

200 years. The oldest tree ferns were predominantly individuals in the control plots that had survived the 1939 fire. However, all of the silvicultural treatments had tree ferns that were approximately 80 years old (*i.e.*, they initiated after the 1939 fire), which indicates that at least some proportion of tree ferns had survived the harvesting operations in the late 1980s.

Tree water use in forested catchments influences water yields, drought responses, and a variety of other ecological functions (Vertessy et al. 2001; Benyon et al. 2015). The total sapwood area index for eucalypts was approximately 50% lower in the small and medium gaps and control plots ($\sim$3 m^2) than in the other silvicultural treatment ($\sim$8 m^2). Catchment level studies of even-aged mountain ash forests suggest that water yield decreases for approximately 30 years post-disturbance due to the increased water consumption of younger trees and then gradually returns to pre-disturbance levels over the following 150 years (Kuczera 1987). Our results indicate that, at the stand level, forest water use differed only slightly amongst the silvicultural treatments This is consistent with the predicted peak in water use that occurs at approximately 30 years. The lower values amongst the small gap treatments may reflect the relatively low abundance of eucalypts that established, the relatively small crowns (and associated leaf area), or the lower rates of photosynthesis and transpiration due to shading. In the control plots, the lower values may be due to the senescence of understorey trees. However, all of the values are within the range of SAI values from mountain ash forests in the Central Highlands described by Benyon et al. (2015).

Tree Hollows

Hollow-bearing trees are an important habitat element for many arboreal animals. Because hollows are typically associated with large and old trees, their abundance is often greatly reduced in landscapes with a long history of logging or high-intensity natural disturbances. In southeastern Australia hollows typically begin to form once a tree reaches 100 cm DBH, which may take from 70-150 years depending on the tree species and growing conditions (Fox et al. 2008). Lindenmayer et al. (1991) have suggested that it takes approximately 120 years for hollows to form in mountain ash forests. The standard silvicultural system applied to these forests—clearfell, burn, and sow—typically has rotation lengths of 80 years or less. This means that sites harvested under this system are unlikely to have or produce hollow-bearing trees. Results from the Tanjil Bren SSP showed that the density of hollow-bearing trees was very low in the gap treatments, but similar to the controls in the other silvicultural treatments. The mean number of hollows per hectare was more than six times higher in the retention plots than in the seed tree and clearfell plots. This suggests that retaining even a few large trees in the overstorey can accelerate the development of hollow-bearing trees in the post-harvest stand. The reduction in canopy density leads to accelerated branch, stem, and crown growth of the residual trees, which may allow them to reach the threshold size associated with hollow formation decades sooner. In addition, partial harvesting may damage some of the residual trees, which may accelerate hollow creation within the stand (Gibbons and Lindenmayer 2002). At Tanjil Bren estimates have suggested that approximately half of the retained mountain ash were damaged as the harvested trees were hauled out or afterwards during site preparation activities (T. Fairman, *personal communication*).

Some Caveats

The Tanjil Bren SSP provides a unique opportunity to assess forest development following silvicultural interventions that have not been implemented operationally across the broader landscape. Nonetheless, there are a few caveats to this study that must be acknowledged. First, the silvicultural trials were not replicated across the larger landscape, which limits our ability to assess any differences associated with topography or landscape position. Second, the retention treatments were only implemented in two harvest units, which reduces independent replication at the harvest-unit scale. In our mixed-effects framework, this is explicitly accounted for through the inclusion of harvest unit as a random effect, such that uncertainty associated with limited replication is reflected in wider confidence intervals and more conservative inference. Despite this constraint, we detected statistically significant treatment differences, indicating that the observed effects were sufficiently strong to be identified under a conservative analytical structure. Despite these limitations, this study is the first to assess the multi-decadal consequences of the full range of silvicultral systems on stand development and various non-timber values in mountain ash in southeastern Australia. While replication of the treatments at additional locations would have strengthened inference, the experiment represents a rare, landscape-scale silvicultural study established under operational harvesting conditions. The sites were selected to be representative of actively managed mountain ash forests, and the treatments were implemented at a spatial scale that reflects real-world forest management. As such, despite limitations, the study provides valuable long-term insights into structural and compositional responses under operationally relevant conditions.

Management Implications

Over the past 150 years forest management in Australia and other parts of the world has focused primarily on the production of wood and wood products. However, modern society has grown to appreciate the many and diverse values that forests provide. As a consequence, the relatively intensive forest management practices that were developed for timber-based forest management have become increasingly contested because they simplify forest structure and composition and homogenise forests. This may reduce, compromise, or eliminate many of the other values that forests can provide. Concerted public action has led to changes in forest management practices (*e.g.*, ending logging of old-growth forests, limits on the size of clearfell coupes, restrictions on harvesting in riparian areas and steep slopes) and, in some places, the cessation of logging. In Australia, the governments of Western Australia and Victoria have recently ended commercial logging of native forests on public lands. However, more than a century of timber harvesting, fires, and land-use change has altered and fragmented these forests. This has led to calls from a wide range of stakeholders to restore these forests.

Two broad strategies are commonly proposed to restore the forests and the ecological values that have been diminished by historical harvesting: long-term protection and active management. Long-term protection focuses on eliminating the key stressors that have impacted and degraded the forest. Typically, this involves removing human disturbances (*i.e*., logging) from the landscape and letting the current degraded forests recover. However, some have proposed even more extreme levels of protection, such as reducing or eliminating natural disturbances such as fire from the landscape through aggressive detection and suppression (Lindenmayer and Sato 2018; Lindenmayer et al. 2022). Long-term protection assumes that the current stands, which were created by disturbances that have degraded the forest (*i.e*., logging, high-intensity fires), are on developmental trajectories that will produce the desired ecological values some time in the future.

In contrast, active management identifies areas that have been either severely degraded or particularly homogenised and uses silvicultural tools to accelerate their recovery or generate heterogeneity at the landscape scale (Bennett et al. 2024). However, restoration through active management requires an understanding of how different silvicultural prescriptions may alter the structure, composition, and function of forests over time. The Tanjil Bren SSP provides the empirical foundation necessary to do this. Rather than the traditional approach in which a single silvicultural system that maximises timber production is applied everywhere (Attiwill 1994a), the Tanjil Bren SSP shows that different silvicultural prescriptions, applied to the same forest type across a landscape, can create more structurally diverse stands, generate a broader range of ecological values, and more closely emulate the broad-scale spatial patterns generated by the natural disturbance regime (Mönkkönen et al. 2014; Ashton and Kelty 2018).

In areas of the landscape that have been heavily impacted by logging or high-intensity fires and in which large trees are currently rare, the application of retention-based treatments similar to those at Tanjil Bren could increase the number of large trees. Forest managers could prioritise mountain ash stands that are 40-60 years old with the expectation that trees > 100 cm would be available within the next 20-30 years. Because most existing large trees in these landscapes are close to riparian areas (Trouvé et al. 2024), managers might target areas that are more distant from riparian areas or would connect disjunct populations of large trees to improve landscape connectivity. This would increase the aboveground carbon stocks within the landscape and the resilience of that carbon to climate-driven stressors, particularly fire. While mountain ash is an obligate-seeding species that is relatively sensitive to fire, larger trees are less likely to be killed in fires, particularly of low to moderate intensity (Trouvé et al. 2021). Increasing the number and distribution of large mountain ash trees within the Central Highlands landscape would increase the probability of survival for a greater proportion of mountain ash trees and the persistence of the carbon that they store in the landscape.

In the mountain ash forests of Victoria's Central Highlands, the critically endangered Leadbeater's possum has been a central focus of concerns about the ecological impacts of logging. Leadbeater's possum has two key habitat requirements: a relatively dense, connected understorey of *Acacia* and hollow-bearing trees (Smith and Lindenmayer 1988; Baker et al. 2021). This presents a conservation conundrum because the

Acacia are short-lived and require disturbance to germinate and establish, whereas hollow-bearing trees require a century or more to develop (Baker et al. 2021). We found that the *Acacia* component had disappeared from the control sites at the Tanjil Bren SSP. Given the basal area of the mountain ash in the canopy (~80 m^2/ha) and the time since the last disturbance (80 years), the probability of *Acacia* occurring in the undisturbed stands in the SSP is zero (Trouvé et al. 2019). Consequently, the control sites are no longer suitable habitat for Leadbeater's possum. In contrast, the sites that received silvicultural treatments all resulted in the germination and establishment of *Acacia*. If hollow-bearing trees are present within the stands or adjacent to the stands with regenerating *Acacia*, the treated stands would be more suitable habit for Leadbeater's possum than the controls. Depending on the current structure and composition of a stand, silvicultural treatments may improve habitat quality. In stands with existing hollow-bearing trees, creating small gaps ($\leq$2 ha) will lead to a pulse of *Acacia* and other understorey species that will increase connectivity in the understorey. In stands without hollow-bearing trees, retention prescriptions that accelerate the growth of the retained canopy trees and stimulate germination of a new cohort of *Acacia* will increase the abundance of both required habitat features. However, a more comprehensive landscape-scale strategy that establishes a mosaic of silvicultural prescriptions that encourage understorey development in areas adjacent to existing hollow-bearing trees and promote the development of hollow-bearing trees where they are absent is likely to be more successful in supporting populations of Leadbeater's possum at the landscape scale.

While this study provides important insights into how different silvicultural treatments can influence the stand development pathways that a single forest type can follow, further investigation is needed into how they might be applied at the landscape scale to align with the natural heterogeneity of the large fires that shape these ecosystems. Patch size, spatial configuration, and cumulative harvested area all need to be considered when developing long-term sustainable forest management plans for multiple forest values at landscape scales. Identifying an appropriate mixture of stand-level silvicultural prescriptions to apply within a managed landscape presents a significant challenge to forest managers. The analyses presented here provide the empirical foundations for developing and assessing the consequences of a more varied – and more naturalistic – silviculture in complex landscapes.

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Availability of data and materials Code available at https://github.com/kaitlynhammond/Code-for-Aternative-silvicultural-systems-maintain-multiple-values. Data available on request.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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