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What factors influence the occurrence and abundance of midstorey *Acacia* in Mountain Ash forests?

Abstract

The midstorey is a critical structural component of many forests globally. Using statistical models, we quantified the influence of two sets of variables on the percentage cover and basal area of two dominant *Acacia* spp. (Montane Wattle [*Acacia frigescens* and Silver Wattle [*Acacia dealbata*]) in the midstorey of Mountain Ash (*Eucalyptus regnans*) forests in mainland south-eastern Australia. Specifically, we focused on the influence of: **(1)** the age of the overstorey eucalypts (corresponding to the time since the last stand-replacing disturbance), and **(2)** environmental drivers (aspect, topographical wetness index, slope, elevation).

We found evidence for generally non-linear relationships between stand age and percentage cover and the basal area of both Silver Wattle and Montane Wattle. Silver Wattle had the highest values for percentage cover, and Montane Wattle the lowest, in stands regenerating from fire in 2009. The basal area of Silver Wattle was highest in stands that regenerated after the 2009 wildfires and after disturbance that occurred between 1960 and 1990s. For Montane Wattle, basal area was lowest in stands that regenerated in 2009 but values did not differ among stands of other ages. Both *Acacia* species were a midstorey component in old growth Mountain Ash forest.

No environmental covariates influenced the percentage cover of Montane Wattle or Silver Wattle. However, our model for the basal area of Montane Wattle contained evidence of a positive relationship with topographic wetness. The general paucity of environmental drivers in most of the models we constructed is likely due to the fact that both tree species occur well beyond our study region. Hence, the set of environmental conditions modelled

may not be limiting the percentage cover or basal area of these midstorey tree species. Disturbance appears to be the key driver of dynamics of Montane Wattle and Silver Wattle in Mountain Ash forests.

Keywords: Disturbance, wattle, ash-type eucalypt forest, wildfire, logging, succession, south-eastern Australia

Introduction

Many forests globally support multiple layers of vegetation, including a midstorey and an understorey of trees, shrubs and other plant species (e.g. tree ferns) (Brock et al. 2020; Franklin et al. 2002; Perry et al. 2008). These layers are a critically important component of stand structural complexity (*sensu* Lindenmayer and Franklin 2002) and have many key ecological roles. For example, the midstorey contributes to vertical heterogeneity (Brokaw and Lent 1999) which, in turn, creates more niches for more species in groups such as birds (MacArthur 1964; Recher 1969) and bats (Brown et al. 1997). Indeed, the midstorey is a key foraging substrate for many kinds of animals (Morrison et al. 2006) ranging from mammals and birds (Smith 1984; Whelan and Maina 2005) to invertebrates (Schultz 2002; Woinarski and Cullen 1984). Other key roles of midstorey plants include providing sites for animals to nest (Beruldsen 2003), acting as nitrogen fixers for other plants such as overstorey trees (Chaer et al. 2011; May and Attiwill 2003), and providing a substrate for the establishment of other plants such as epiphytes and bryophytes (Pharo et al. 2013).

In forests subject to stand-replacing disturbances, overstorey trees may be killed, but midstorey and understorey plants may persist and recover through resprouting (Blair et al. 2016; Bradstock et al. 2012; White and Vesk 2019). This may mean that some elements of the midstorey and understorey may be of markedly different age to that of the dominant trees in the overstorey (Fedrigo et al. 2019; Mueck et al. 1996). In other cases, the overstorey trees may survive a disturbance (see McCarthy and Lindenmayer 1998) with some midstorey tree species killed but then regenerating from seeds in the soil seed bank (Blair et al. 2016; Bowd et al. 2018). These include *Acacia* spp. trees which can occur as a key midstorey element in many eucalypt forests in Australia (Boland et al. 2006; Specht and Specht 1999), as well as other forests around the world (New 1984). *Acacia* spp. are an iconic component of Australia's flora with over 1000 species occurring on the continent (Burrows et al. 2018). They form long-lived, persistent soil seed banks that increase annually and which can be viable for multiple decades (Burrows et al. 2018; Strydom et al. 2017). The size of the *Acacia* spp. seed bank in the soil can increase with standing stem diameter, which when triggered by fire or other forms of soil heating (>60° C), can produce prolific germination of some species (Passos et al. 2017; Strydom et al. 2017). These reproductive strategies and traits allow *Acacia* spp. trees to persist in ecosystems for long periods (Passos et al. 2017; Strydom et al. 2017). However, *Acacia* spp. tree populations may be limited by pollinator availability (Cunningham 2000), recruitment issues, small seed set, and senescing stands in small, fragmented populations (Broadhurst and Young 2006).

Given the importance of midstorey vegetation, including that comprising *Acacia* spp. trees, it is important to quantify its response to: **(1)** temporal drivers such as disturbances (e.g. stand-replacing fire and logging), and **(2)** spatial drivers like environmental conditions (e.g. slope, aspect, elevation and topography (Huggett and Cheeseman 2002; Lindenmayer et al. 2000b). In this study, we quantified the factors influencing the occurrence and abundance of *Acacia* spp. in the Mountain Ash (*Eucalyptus regnans*) forests of mainland south-eastern Australia.

Mountain Ash forests are wet-sclerophyll forests, dominated by the tall, obligate-seeder tree species, Mountain Ash. The forests support a diverse and well-developed midstorey consisting of *Acacia* spp. trees and other midstorey and understorey trees, broad leaved shrubs, tree ferns and a mesic ground layer rich in fern and herb species (Blair et al. 2016; Bowd et al. 2018; Mueck 1990). Prominent midstorey tree species include a range of *Acacia* spp. such as Silver Wattle (*Acacia dealbata*), Montane Wattle (*Acacia frigescens*) (sometimes also called Forest Wattle or Frosted Wattle), Mountain Hickory Wattle (*Acacia obliquinervia*), and Blackwood (*Acacia melanoxylon*) (Lindenmayer et al. 1994). Other midstorey tree species include the cool temperate rainforest trees, Myrtle Beech (*Nothofagus cunninghamii*) and Southern Sassafras (*Atherosperma moschatum*) that often occur in the cooler, wetter and more sheltered parts of the landscape (Lindenmayer et al. 2000b). Soils in these forests predominantly consist of well-drained, acidic, deep, dermosols derived from granitic rock (Bowd et al. 2019). In dominant stands, soil pH ranges from 3.4-5.2, nitrate and phosphorus content averages approximately 23 mg/kg and 50 mg/kg respectively, and organic carbon content typically exceeds 5 % (Bowd et al. 2019).

We sought to identify relationships between overstorey stand age (which is a function of the time elapsed since the last stand-replacing disturbance [typically logging or fire]), environmental factors, and the percentage cover and basal area of *Acacia* spp. trees. We focused on *Acacia* spp. trees because they are key components of the midstorey in Mountain Ash forests (Ashton 1981; Serong and Lill 2008; van der Meer and Dignan 2007). *Acacia* spp. trees contribute to the known habitat requirements of the critically endangered Leadbeater's Possum (*Gymnobelideus leadbeateri*) (Lindenmayer et al. 1991b) and provide food and movement pathways not only for this species (Lindenmayer et al. 1994; Smith 1984) but also for other species of arboreal marsupials (Seebeck et al. 1984) and birds (Lindenmayer et al. 2009; Loyn 1985). *Acacia* spp. trees in Mountain Ash forests also contribute to carbon stocks (Fedrigo et al. 2019; Keith et al. 2009) and form symbiotic relationships with nitrogen-fixing microorganisms (May and Attiwill 2003).

Past studies (e.g. see Adams and Attiwill 1984; Blair et al. 2016; Trouvé et al. 2019) in Mountain Ash forests have examined the occurrence of some *Acacia* spp. trees in eucalypt forests. However, there has been limited quantification of the factors influencing both percentage cover and basal area of *Acacia* spp. in Mountain Ash forests. Here, we sought to close this knowledge gap by testing two broad hypotheses at the outset of this investigation.

Stand age hypothesis*:* We hypothesized that the percentage cover and basal area of midstorey *Acacia* spp. trees would exhibit a non-linear relationship with the age of overstorey trees. Mountain Ash forests are subject to stand-replacing disturbances in which the overstorey trees, and the majority of midstorey and understorey plants (including *Acacia* spp. trees), are killed (Ashton 1981; Simkin and Baker 2008). This triggers the germination of *Acacia* spp., which form a dominant component of early-successional forest regrowth (Blair et al. 2016; Kasel et al. 2017; Bowd et al. 2018). Based on such prior knowledge of the biology of *Acacia* spp. trees, we therefore anticipated that values for percentage cover and basal area would be low soon after disturbance, then increase 20-80 years after disturbance, before declining again as *Acacia* spp. trees senesce and die (Adams and Attiwill 1984; Trouvé et al. 2019).

Environmental drivers hypothesis: We hypothesized that the percentage cover and basal area of midstorey *Acacia* spp. trees would be greatest in areas with the highest available moisture as reflected by broad environmental attributes such as topographic wetness, slope and aspect. That is, percentage cover and basal area values would be highest in areas with high values for topographic wetness, on flat terrain, and on sheltered aspects. We hypothesized this response because of well-known relationships between topography and moisture availability (Huggett and Cheeseman 2002), coupled with moisture effects on the balance of overstorey and midstorey vegetation cover (Crombie 1992; Specht and Morgan 1983). That is, after controlling for factors like stand age (and associated structural attributes like tree height and stocking rate), we hypothesized that percentage cover and basal area of *Acacia* spp. trees would be highest where there is greater site productivity (Larson et al. 2008) including available moisture (Crombie 1992; Yamaura et al. 2020).

In addition to testing the two above hypotheses, given that the percentage cover and basal area of *Acacia* spp. trees were measured on the same sites, we sought to quantify statistical relationships between these two attributes of stand structure. Values for percentage cover may be similar for stands with quite different measures for basal area such as those with a high density of stems versus those with a low density of stems (Curtis et al. 2019). Nevertheless, at the outset of this study, we hypothesized there would be high levels of correlation between percentage cover and basal area. Thus, both measures also would exhibit similar responses to stand age and environmental drivers. We also explored patterns of co-occurrence among *Acacia* spp. trees and hypothesized that where values of percentage cover and basal area were high for a given species, they would be low for other species. Finally, we tested whether stand age or environment factors influenced the patterns of co-occurrence of *Acacia* tree species that were observed.

Methods

Study area

We focused our study on the Mountain Ash forests of the Central Highlands of Victoria. The region lies about 120 km north-east of the city of Melbourne and covers approximately 1/2 degree of latitude and one degree of longitude (378200–378550S and 1458300–1460200E) (Fig. 1). The region experiences mild, humid winters with occasional periods of snow. Summers are generally cool. There is approximately 140 000 ha of Mountain Ash forest in our study area and this tree species typically occurs at altitudes between 400 and 900 m (Boland et al. 2006; Costermans 1994).

We conducted surveys of midstorey *Acacia* spp. trees on 156 long-term monitoring sites in Mountain Ash forests. These sites measured 1 ha in size and they covered a wide range of environmental conditions including stand age, slope, aspect, elevation and topographic position (Supporting Information Table S1).

Vegetation surveys

We visually estimated the projective (percent) foliage cover (%) of *Acacia* spp. in six 10 x 10 m quadrats at 20 m increments along a 110 m transect in each site. Specifically, we made these estimates from the centre of each quadrat proportionate to the quadrat area (e.g. $1m^2$ of foliage cover = 1% of cover) in the summer of 2019-2020.

In 2017 at each site, we measured the diameter at breast height (DBH) of all live *Acacia frigrescens*, *Acacia dealbata* and eucalypt stems greater than 2 m in height across three 10 m x 10 m plots, 10 m, 50 m and 90 m along a central 100 m transect. We counted the number of stems of each *Acacia* spp. and all eucalypts. We grouped the results into eleven DBH size categories: 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-60 cm, 60-80 cm, 80-100 cm, 100-140 cm, 140-180 cm and 180 cm+. For each stem, we computed the basal area at breast height using the DBH in metres via $BA = \pi\,(DBH/2)^2$ (the mid-point of each diameter interval was used in this calculation and 200 cm used for the highest category). We then summed the individual basal areas at breast height across all the stems of a particular species and then converted a measure per hectare by multiplying the total by $10{,}000m^2/300m^2$. We summed all eucalypt species at a site to get a total measure of Eucalypt basal area. To account for the potential influence of overstorey eucalypts on *Acacia* spp. (Trouvé et al. 2019) we included the basal area and percent cover of all eucalypts in all respective statistical models.

Environmental and other variables

We calculated values for a suite of covariates at each site for subsequent use in constructing statistical modelling. We assigned the age of the forest at each site to one of five age classes: 1 = old-growth dominated by trees that germinated before 1900 (7 sites), 2 = 1939 regrowth (dominated by trees that regenerated as a result of the 1939 wildfires) (75 sites), 3 = 1960–1990s regrowth (i.e. trees that regenerated between 1960 and 1990) (15 sites), 4 = sites were regenerated after the 2009 wildfire (31 sites), and 5 = mixed-aged forest (in which there were two or more distinct age cohorts of trees in the stand) (28 sites). Our age class classification was based on the dominant age cohort of living overstorey trees in a stand (>85%). We also have made extensive measurements of the diameter of trees and using tree diameter-age relationship developed by Ashton (1976) to confirm stand age for any given site. We note that the vast majority of the mixed-aged stands supported an old-growth component with a number of individual large old living trees.

We interrogated a 20 m resolution Digital Elevation Model to extract data on slope, northerly aspect (aspect angles between 67.5 and 292.5 were assigned to a non-northerly aspect and the remainder were assigned northerly aspect) and elevation for the centroid of each site. We also calculated values for a Topographic Wetness Index (TWI) (Moore and Hutchinson 1991) for each site. TWI is a measure of relative position in the landscape and thus potential water distribution. Calculation of TWI requires a Digital Elevation Model (DEM) that has hydrological integrity; we used the ANUDEM algorithm (Hutchinson 2011) to generate a DEM of our study region at a grid resolution of 20 m. For each cell, the size of the catchment that flows to it was divided by its width, adjusted geometrically by the aspect of inflow direction. This ‘specific catchment’ was then divided by the cell’s local slope. Lower values indicate ridges and upper slopes that have little to no contributing catchment, with values increasing for lower slopes, valley bottoms, and drainage lines. We present the range of values for key covariates in Table S2.

Statistical analyses

Models of percentage cover and basal area

We modelled the percentage cover of each *Acacia* species using a Bayesian hurdle-beta regression model (Ospina and Ferrari 2012). We calculated the mean percent cover across the six plots on each site and used the proportion data as the beta distribution is restricted to lie in the open interval (0,1) and the hurdle portion of the model was used to accommodate absences on a plot of a given species. In the literature, these models are typically called zero-inflated beta models. However, the name zero-inflated-beta is a misnomer, as zeros and ones are not part of the support of the beta distribution. To avoid confusion, we do not use the standard nomenclature and refer to these models as hurdle-beta models. Specifically, the model we employed was the following:

$$PC_i \sim HB(\mu_i, \Phi)$$

$$\mu_i = Intercept + EPC_i + StandAge_i + Slope_i + NortherlyAspect_i + TWI_i + Elevation_i$$

$$HU_i = Intercept + EPC_i + StandAge_i + Slope_i + NortherlyAspect_i + TWI_i + Elevation_i$$

where PC_i is the average percentage cover on the ith site, HB refers to the hurdle-beta model, μ_i, is the mean of the hurdle-beta distribution, Φ is the precision parameter of the beta distribution, EPC_i is the eucalypt percent cover, Stand Age (a categorical variable with levels: Old growth, 1939, 1960-1990s, 2009, mixed age), slope, northerly aspect, TWI, elevation are covariates and HU_i is the hurdle component of the model. Both model components use the logistic link function. As the likelihood function for hurdle models factor in two independent components, we performed model selection for each component of the model independently. We fit each of the 32 possible combinations of the five covariates for each component of the zero-inflated beta regression model and chose the simplest model within two Widely Applicable Information Criterion (WAIC) units (see Gelman et al. 2014; Vehtari et al. 2016) of the best fitting model for each component. We note that eucalypt percent cover was included in all models.

We modelled site-levelbasal area data using a Bayesian hurdle-gamma regression model with an identical set of predictor variables as employed for the analysis of site-level average percentage cover described above. We employed a gamma distribution for basal area, as it is a positive variable, which has a gamma distribution. Specifically, the model was as follows:

$$BA_i \sim HG(\mu_i, \theta)$$

$$\mu_i = Intercept + log(EBA_i) + StandAge_i + Slope_i + NortherlyAspect_i + TWI_i + Elevation_i$$

$$HU_i = Intercept + log(EBA_i) + StandAge_i + Slope_i + NortherlyAspect_i + TWI_i + Elevation_i$$

where the covariates are the same as described previously except $log(EBA_i)$ is the basal area of all eucalypts, HG is the hurdle gamma, is the shape parameter of the gamma distribution. The logistic link function was used for the hurdle component of the model, while the gamma mean component of the model was modeled with a log link function. We employed the same model selection strategy as for the hurdle-beta regressions described above.

The models for percentage cover and basal area were fit with using the brms (Bayesian regression models using Stan) package (Buerkner 2017) in R version 3.6.1 (R Core Team 2019). We used the default priors in brms for all model parameters. Specifically, we used student-t priors with three degrees of freedom with zero mean and scale parameter ten for the regression parameters and a half student-t with three degrees of freedom with zero mean and scale parameter 10 for the standard deviation of the site random effect. We ran four Markov chains for 2,000 iterations, discarding the first 1,000 iterations as warm-up leaving 4,000 posterior samples for inference. We assessed convergence using the Gelman-Rubin statistic, $\hat{R}$ (Gelman and Rubin 1992). Note, in all cases the $\hat{R}$ was less than 1.01 indicating adequate mixing of the chains. We present posterior medians and 95% credible intervals for model parameters. We present R^2 values for each model for each species and also provide some basic residual diagnostics for each species.

Relationships between percentage cover and basal area

For each *Acacia* species, we used Spearman's correlation coefficients to investigate the associations between percentage cover and basal area.

Co-occurrence patterns between Silver Wattle and Montane Wattle

We defined co-occurrence as a binary variable, indicating whether or not pairs of species occurred together (1=if species A and B occur together, 0=if not) (see Table S2, Fig. S1). We modelled each of the binary variables on the previously mentioned covariates using a Bayesian logistic regression to determine whether or not co-occurrence was associated with the covariates. We used an identical model selection strategy as previously described.

Results

We recorded six species of *Acacia* as midstorey components on our 156 survey sites in Mountain Ash forests. These species were: Silver Wattle, Dwarf Silver Wattle (*Acacia nanodealbata*), Mountain Hickory Wattle, Montane Wattle, Blackwood, and Prickly Moses (*Acacia verticilliata*). Of these, only two species, Montane Wattle and Silver Wattle were recorded at a sufficient number of sites (> 30) to enable subsequent analyses and the construction of robust statistical models.

Silver Wattle occurred on 94 of our 156 sites surveyed in 2019 with percentage cover values ranging from 1 to 37% on the sites where it occurred. Using basal area, we gathered in

2017, Silver Wattle occurred on 83 sites and when it did occur, values for basal area ranged from 0.02 to 29.52 m^2 ha^{-1}. Montane Wattle occurred on 64 of our 156 sites surveyed in 2019 with values for percentage cover ranging from 1.7 to 63.3% on sites where it occurred. Using basal area data gathered in 2017, Montane Wattle occurred on 57 sites and when it did occur, values for basal area ranged from 0.02 to 30.79 m^2 ha^{-1}. We developed separate models for percentage cover and basal area for both species.

Percentage cover of Acacia

The results of model selection for the hurdle and Beta component of the model for each species are given in Supporting Information Table S3. For the presence of Silver Wattle, we found a stand age effect but no eucalypt percentage cover or environmental covariate effects (Fig. 2a, Table S4, Fig. S2). After conditioning on the presence of Silver Wattle at a site, further analyses of percentage cover data revealed no environmental covariate effects but a stand age effect in which values were highest in stands that regenerated after the 2009 fire relative to other forest age classes (Table S4, Figure S2).

The presence of Montane Wattle was lowest in forest that germinated in 2009 and highest in forest that regenerated between 1960 and 1990 (Fig. 2a, Table S5, Fig. S3). No environmental factors, nor the percentage cover of eucalypts influenced the presence of Montane Wattle at a site (Table S5). After conditioning on the presence of Montane Wattle at a site, further analyses of percentage cover revealed a stand age effect but again no response to any environmental covariates (Table S5, Figure S3).

Basal area of Acacia

The results of the model selection for the hurdle and Gamma component of the model for the basal area of each species of *Acacia* are given in Table S6. There was a stand age effect, but no effect of eucalypt basal area or environmental covariate effects in the hurdle component of the model for the basal area of Silver Wattle (Table S7). After conditioning on the presence of Silver Wattle at a site, we found evidence of a stand age effect on basal area; values were highest in stands that regenerated after the 2009 wildfires and after disturbance that occurred between 1960 and the 1990s (Table S7, Fig. S4). There also was evidence of a eucalypt basal area effect in which values for the basal area of Silver Wattle were lower with increasing basal area of eucalypts (Table S7).

Our model for the basal area of Montane Wattle contained evidence of a stand age effect for the presence of the species (Fig. 2, Table S8, Fig. S5) with the lowest values being in forests burnt in 2009. There were no environmental covariate effects, nor a eucalypt basal area effect for this (hurdle) component of the model (Table S8). After conditioning on the presence of Montane Wattle at a site, we found no stand age effects or basal area effects or environmental effects.

Relationships between percentage cover and basal area

We found a high level of correlation, as measured by Spearman's correlation coefficient, between percentage cover and basal area for both Silver Wattle (0.66) (Fig. 3a) and Montane Wattle (0.70) (Fig. 3b).

Co-occurrence patterns between Silver Wattle and Montane Wattle

Table 1 gives the breakdown of the presence/absence co-occurrence pattern of Silver Wattle and Montane Wattle for percentage cover and basal area and Fig. 4 shows the results graphically. Model selection results for the Bayesian logistic regression for percentage cover (Tables S9 and S10) revealed no association with any of our covariates. However, there was evidence of a stand age effect for basal area co-occurrence of the two *Acacia* spp. (Tables S9 and S11).

Diagnostics

We present residual diagnostic plots (residuals versus fitted values and response versus fitted values) for the percentage cover and basal area analysis in Fig. S6. We give Bayesian R^2 measures for percentage cover, basal area and co-occurrence in Table S12.

Discussion

Midstorey vegetation is a critical component of many forests globally and plays a wide range of important ecological roles in ecosystem dynamics and biodiversity conservation (Perry et al. 2008). A key finding from our work was that time since disturbance (as reflected by the age of the overstorey eucalypt trees) was an important factor influencing the percentage cover and the basal area of both Silver Wattle and Montane Wattle, although there were marked inter-specific differences in responses (Fig. 2). Previous studies in Mountain Ash forests have found a decline in the prevalence of *Acacia* spp. with an increase in the age of the eucalypt overstorey (e.g. Forrester et al. 2011; Trouvé et al. 2019). However, in this study and in the case of Montane Wattle, the lowest percentage cover values were for stands that regenerated after the 2009 fire (Fig. 2), but there were limited differences in percentage cover among other age classes (except for mixed aged forests relative to stands that regenerated after the 1939 wildfire). Thus, there was a generally non-linear percentage cover-stand age relationship that was broadly consistent with what we hypothesized would occur at the outset of our study. The highest values for the percentage cover of Silver Wattle were for stands regenerating after the 2009 fire with markedly lower levels of cover in other age classes (Fig. 2). The stand age relationships that we identified for basal area were broadly congruent with those recorded for percentage cover, again with marked inter-specific differences in responses between Silver Wattle and Montane Wattle (Fig. 2). Such similar responses for percentage cover and basal area were consistent with the high levels of correlation between these two measures (as discussed further below).

An interesting observation from our datasets was that, similar to Montane Wattle, Silver Wattle was a midstorey component in old growth Mountain Ash forest (Fig. 2). This is consistent with earlier studies that revealed that *Acacia* spp. trees characterize the midstorey of old growth montane ash forests (Lindenmayer et al. 2000a). An allied investigation (see Lindenmayer et al. 1999) showed that very few old growth stands supported strictly one age of overstorey trees, but rather there was strong empirical evidence of the presence of at least two (and sometimes more) age classes (see also Fedrigo et al. 2019). It is possible that partial stand-replacing disturbances or site-specific environmental changes (increases in light from gaps in the understorey and canopy) may have triggered the germination and subsequent growth of *Acacia* spp. midstorey in stands of old growth forest (Fedrigo et al. 2019; Lindenmayer et al. 2000a). Notably, detailed dendrochronology of a limited number of large old Mountain Ash trees provides evidence of multiple fires which have not killed these trees (Banks 1993). This is consistent with both the presence of fire scars on many living trees, and the occurrence of multi-aged stands in montane ash forests in the Central Highlands of Victoria (Lindenmayer et al. 1991a; McCarthy and Lindenmayer 1998). Furthermore, while measures like percentage cover and basal area of *Acacia* spp. may exhibit a general decline with stand-age, seed stores increase (Passos et al. 2017; Strydom et al. 2017), which in the event of high-severity fire can result in a high abundance of *Acacia* spp, that exceeds that of younger forests (Bowd et al., unpublished data, 2020).

As outlined above, our analyses contained evidence of inter-specific differences in percentage cover and basal area relationships with stand age. We have not explored the underlying mechanisms for such inter-specific differences in responses. However, they may be associated with inter-specific competition or, alternatively, differences in life history attributes such as the regeneration niche and/or subsequent growth patterns following disturbance. Further studies, specifically targeted at quantifying between-species competition would be required to provide additional insights into the differences in stand age relationships for percentage cover and basal area that we have identified.

The influence of environmental factors on the midstorey

Unexpectedly, we found no evidence of effects of environmental factors such as slope, aspect and topographic wetness on the percentage cover of neither Montane Wattle nor Silver Wattle. This suggests their influence is limited relative to the impacts of disturbance. In contrast, we found a positive relationship between the basal area of Montane Wattle and topographic wetness. Thus, there was some support for our second postulate that *Acacia* spp. midstorey would be best developed in the wettest parts of Mountain Ash landscapes. The findings of this part of our study of *Acacia* spp. were broadly similar to those of previous work on other midstorey components of Mountain Ash forests (see also Kasel et al. 2017) such as Myrtle Beech. That study revealed that strongly influenced by environmental attributes (e.g. slope (Lindenmayer et al. 2000b)).

The reasons for general paucity of environmental effects in most of the models we developed for percentage cover and basal remain unclear. Both Montane Wattle and Silver Wattle species have somewhat broader distributions (that encompass a wider range of environments) than the Central Highlands region where we completed this study. Hence, the relatively restricted set of environmental conditions that we modelled are a subset of the overall environmental domains occupied by these species, and may therefore not be limiting for either species.

Relationships between percentage cover and basal area and co-occurrence patterns

We found broadly similar responses to stand age and environmental drivers for percentage cover and basal area for both species. That is, the shapes of the response curves for stand age for both measures were broadly congruent (compare Fig. 2 and Fig. 3). This result was perhaps not surprising given the high level of correlation between these measures, particularly for Montane Wattle.

Given the broad similarity of responses of percentage cover and basal area to stand age, the findings reported here will be generally relatable to past work such as that on animal responses to the basal area of *Acacia* (Lindenmayer et al. 1991b). However, because there were differences between percentage cover and basal area in responses to environmental factors, there are benefits in measuring both attributes of stand structure.

Co-occurrence patterns

While we have not explicitly sought to complete a formal statistical comparison of the post-disturbance trajectories of Montane Wattle and Silver Wattle, it is important to note that sites with high values of percentage cover for one species often were characterized by an absence of the other species (Fig. 4). This result may, in part, be an outcome of examining compositional data where the total amount of cover has a maximum (capped) value (100%). However, our findings also may reflect interspecific competition or physiological differences which can influence germination and dispersal success (Brown et al. 2008; Forrester et al. 2011). Notably, no factors influenced the co-occurrence of the two species based on percentage cover data. By contrast, our, analysis of basal area data indicated there was a stand age effect, with Silver Wattle and Montane Wattle less likely to co-occur in forests regenerating after the 2009 wildfires. The reasons for the limited co-occurrence of both species (as reflected by basal area values) in young post-fire forests remain unclear, but this effect may be related to the general rarity of Montane Wattle in forests of this age.

Caveats

We modelled the factors influencing the percentage cover and basal area of two key species of *Acacia* in the understorey of Mountain Ash forests. We recognize the factors in addition to the ones we analyzed may have had an important effect. These include soil type.

Further studies in which detailed soil data are gathered would be a useful adjunct to the work reported here. In addition, our study did not include early post-regeneration stands, such as those that were between one and nine years old. We recognize that there would be value in completing additional field surveys to capture information on such early successional forests. Finally, we did not explore the effects of interactions between variables such as stand age and environmental attributes such as topographic wetness. This was because stand age was the sole main effect for the vast majority of models that we constructed. Moreover, a larger dataset than we had available to us would be required to build robust models comprising interactions among a suite of variables.

Concluding comments

We provide insights into the temporal and spatial dynamics of two dominant *Acacia* tree spp. in the Mountain Ash forests of mainland Australia highlighting the critical role of disturbance, and subsequent stand age on their levels of cover and basal area. As *Acacia* spp. trees have important functional roles in forests (e.g. as a foraging substrate, for habitat connectivity, and nitrogen fixation), our findings provide important insights for forest management, including understanding where and when suitable amounts of this kind of vegetation will occur. Indeed, our findings suggest that the dynamics of a given dominant midstorey tree species cannot be well understood in the absence of insights into the dynamics of other relatively common midstorey species in the ecosystem.

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Table 1. Cross-tabulation showing the number of sites for the co-occurrence of Silver Wattle and Montane Wattle as reflected by percentage cover and basal area.

		Montane Wattle		
Attribute	Silver Wattle	Absent	Present	**Total**
Percentage cover	Absent	34	28	62
	Present	58	36	84
	Total	92	64	156
Basal area	Absent	53	24	77
	Present	49	30	79
	Total	102	54	156

Figure legends

Fig. 1. Location of the field survey sites where vegetation measurements of Acacia spp. were completed.

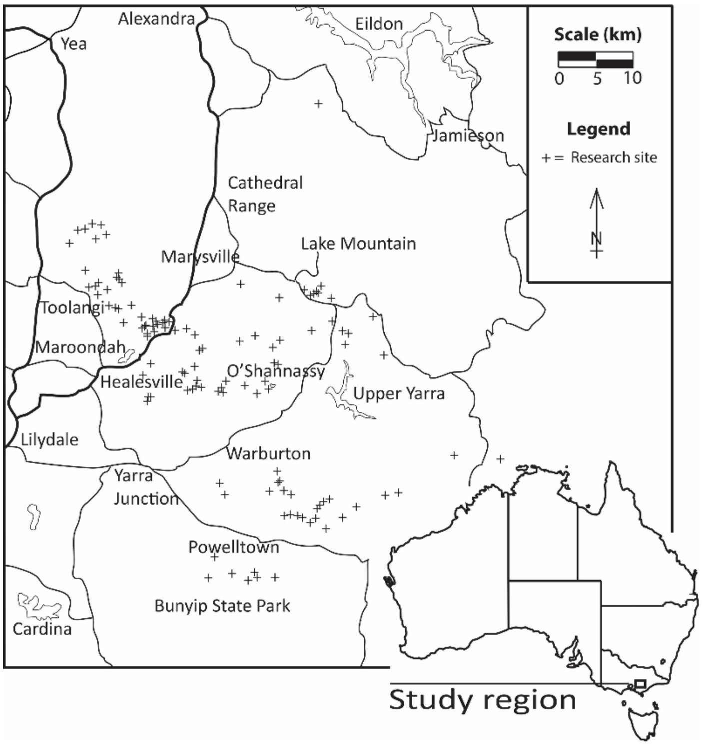

Fig. 2. Panel A: Percentage cover of Montane Wattle and Silver Wattle in stands of Mountain Ash forest of different age in the Central Highlands of Victoria. Panel B: Basal area of Montane Wattle and Silver Wattle. The age categories were: 1 = old-growth (dominated by trees that regenerated before 1900), 2 = 1939 regrowth (dominated by trees that regenerated as a result of the 1939 wildfires), 3 = 1960–1990s regrowth (dominated by trees that regenerated between 1960 and 1990), 4 = 2009 regrowth (dominated by trees that regenerated from 2009 wildfire), and 5 = mixed-aged forest (in which there were two or more distinct age cohorts of trees in the stand). The percentage cover is a combination of the proportion of zeros (obtained from the hurdle part of the model) and the beta (conditional abundance) part of the model, basal area is a combination of the proportion of zeros and gamma (conditional abundance) part of the model. The model estimates are plotted as 95% credible intervals

(closed circles) and the individual data points are plotted as open circles. The number of zeros, for each species and measurement, are indicated at the bottom of each plot and the overall number of plots in each group are also indicated in the labels for each age class.

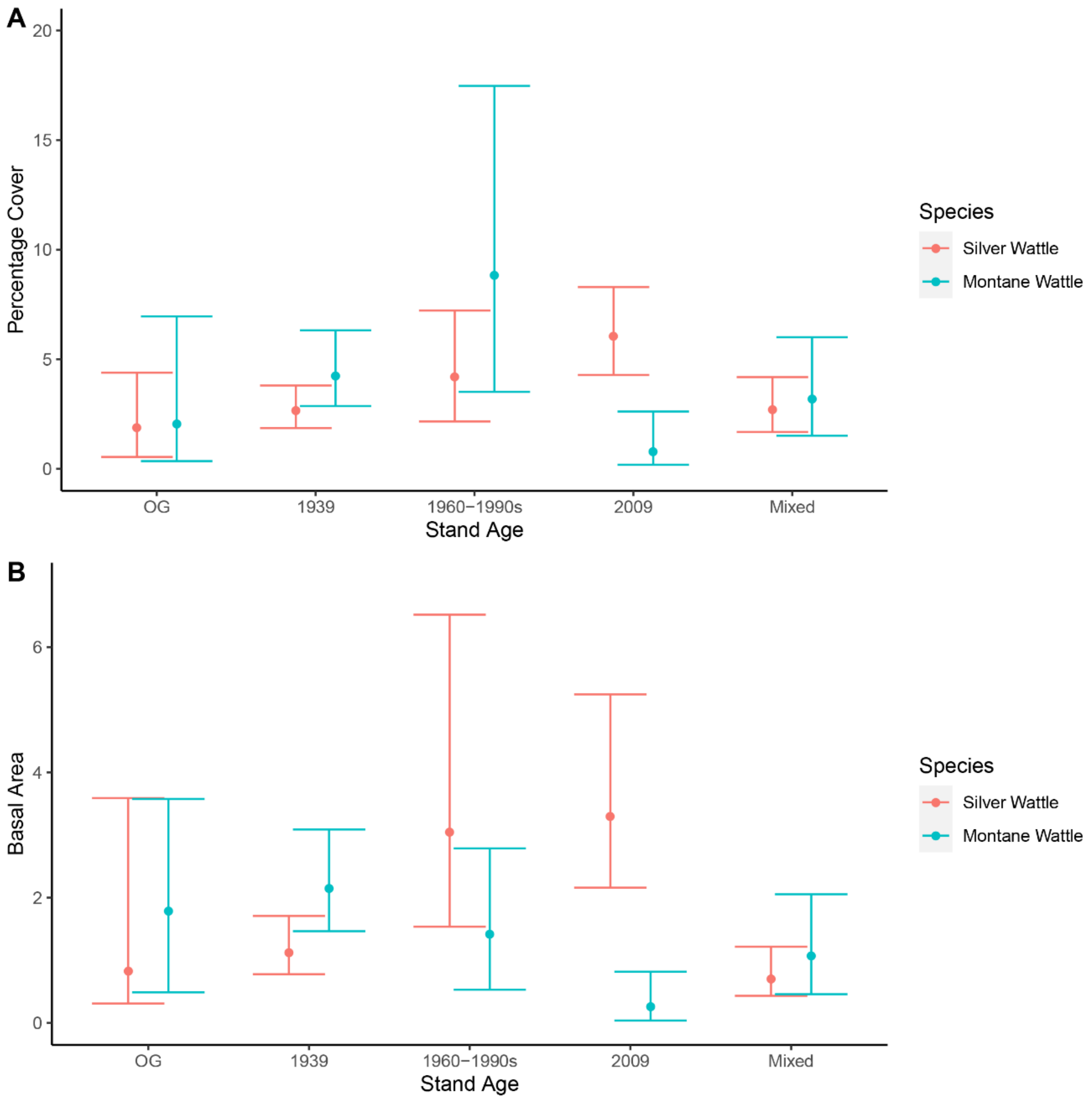

Fig. 3. Scatter plots of percentage cover versus basal area for A. Montane Wattle and B. Silver Wattle. The Spearman correlation coefficients are 0.70 and 0.66, respectively, for Montane Wattle and Silver Wattle.

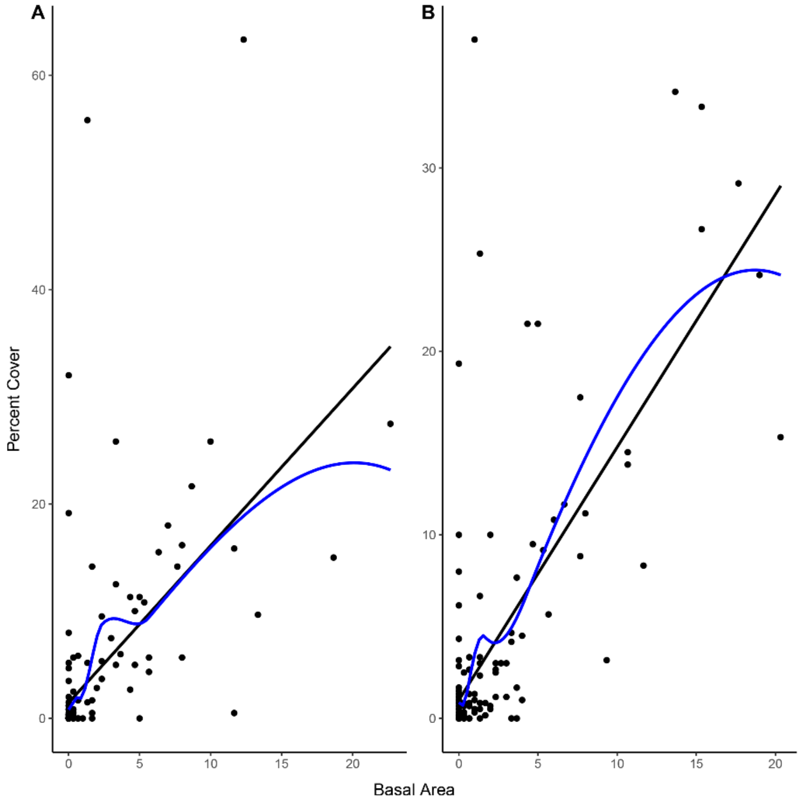

Fig. 4. Scatter plots of Silver Wattle versus Montane Wattle for percentage cover (panel A) and basal area (panel B).