Comparisons of vegetation recovery post fire, logging and salvage logging in the Victorian Central Highlands

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A thesis submitted for the degree of Doctor of Philosophy at The Australian National University

Candidate's declaration

This thesis contains no material that has been accepted for the award of any other degree or diploma in any university. The research, analysis and writing in the thesis are substantially (>90%) my own work. To the best of my knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

10 November, 2018

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Date

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ABSTRACT

Disturbance is an important ecological driver of plant community composition and adaption. My research was in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands in Victoria where the primary forms of disturbance are wildfire and clearfell logging. Three large conflagrations in 1939, 1983 and 2009 resulted in uniformly aged stands of *Eucalyptus regnans*. My research, comprising four interrelated studies, uses these major fire events and recent logging, to compare the recovery attributes of the plants in Mountain Ash forest.

Chapter one compares plant species richness and functional group responses to logging and fire of different intensities. I found species richness declined across a 'disturbance gradient' of low severity fire (30.1species/site), high severity fire (28.9spp/site), clearfell logging (25.1spp/site) and salvage logging (21.7spp/site). The greatest differences between the effects of fire and logging are on sprouting species including ferns and midstorey trees, with logging causing a simplification of the forest biota. Species losses are attributed to the mechanical disturbance of harvesting and the fire/logging disturbance sequence.

Chapter two studies growth rates of tree ferns, *Cyathea australis* and *Dicksonia antarctica.* Five years after the 2009 fires, I measured the new growth of 335 tree ferns and found *Cyathea australis* averaged 73(± 22)mm/year of growth, while *Dicksonia antarctica* averaged 33(± 13)mm/year. An unexpected finding was higher growth rates in taller tree ferns, increasing with height by 5-6mm/yr/m in both species. The non-linear growth is explained by the taller ferns being exposed to greater amounts of sunlight as the dense regeneration progressively shaded the shorter ferns over the five year period since the fire.

In **Chapter three**, I use a chronosequence from the major fire events of 2009, 1983, 1939 and 1851 to determine how species richness and functional groups differ in forests of different ages. Species richness is highest in the youngest cohort (17.1species/plot) when many early successional species are still present. The 1983 and 1939 cohorts have the lowest species richness (12.9 and 12.5 species/plot respectively) while the 1851 cohort has 13.4spp/plot. Sprouting species such as ferns and midstorey trees were most common in the older cohorts, while seeding species dominated the youngest. The presence of 12 species unique to the two oldest cohorts suggests Relay Floristics may best describe the successional pathway of this forest.

Chapter four examined how forest age prior to a disturbance affects subsequent regeneration cohorts. Using forest burned in 2009 that was 26, 70 and 158+ years of age at the time of the fire, I found species richness decreased with forest age (25.7, 22.7 and 20.7 species/site respectively). The diverse seeding species group, was most abundant in the youngest cohort, while sprouting species including ferns were the only functional group to increase with forest age.

My research concludes that Mountain Ash forests are resilient to fire, however, keystone species that resprout, like tree ferns and midstorey trees are susceptible to logging. Sprouting species

increase with time since disturbance and as with other biological legacies, sprouting species need to be carefully managed for during logging operations.

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DETAILS OF CHAPTER PAPERS

CHAPTER 1

Disturbance gradient shows logging affects plant functional groups more than fire

Authors: Blair, D. P., L. M. McBurney, W. Blanchard, S. C. Banks, and D. B. Lindenmayer.

Contributions: Study concept DB (60%), DL, SB; Data collection DB (90%), LM; Authorship of original manuscript DB (95%), DL, WB, SB; Statistical analysis WB, DB (10%); Edits and revision DB (70%), DL, SB, LM, WB.

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CHAPTER 2

Non-linear growth in tree ferns, *Dicksonia antarctica* and *Cyathea australis*

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CHAPTER 3

Testing succession theory using a chronosequence study of Australian Mountain Ash forest following wildfire

Authors: Blair, D. P., D. B. Lindenmayer, W. Blanchard, S. C. Banks, and L. M. McBurney.

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CHAPTER 4

Does pre-disturbance forest age influence recovery after fire in Mountain Ash?

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INTRODUCTION

The research for this thesis was conducted in the Mountain Ash forests in the Victorian Central Highlands region, in south-eastern Australia, 60-90km east/north-east of Melbourne. The forests being studied are some of the most politically contentious forests in Australia. For over a century, the Mountain Ash forests in this region have been prized for their water, wood and scenic beauty, and more recently their biodiversity and high carbon storage capacity. The forests are also the primary habitat of the Critically Endangered Leadbeater's Possum (*Gynobelideus leadbeateri*), one of Victoria's faunal emblems and endemic to the State.

Eucalyptus regnans (Mountain Ash) is the tallest flowering plant in the world, commonly growing to 55-75m tall, and historically over 100m tall. Wildfire is the major natural disturbance in these forests, with high severity fires burning the region, on average, every 75-150 years. *Eucalyptus regnans* is an obligate seeder, dying *en masse* in high severity wildfire and regenerating as a single age cohort. Despite the overstorey and many other seeding species regenerating in these key disturbance events, many understorey species within the Mountain Ash forests survive fires, often through biological legacies that re-sprout, allowing many of the plants to be far older than the overstorey eucalypts. When fires burn these forests at low severity the overstorey survives, but another regeneration cohort is typically initiated, leading to multi-aged forests.

The other major type of high-severity disturbance in these forests is logging. The Mountain Ash forests have provided an important supply of wood products to the native forest industry in Victoria for over a century and the main silvicultural system has been clearfelling. In this method, all merchantable trees are cut and removed and the remaining biomass from non-commercial species and tree crowns is burned in a high severity regeneration burn. The area is then seeded with the overstorey eucalypt species. Another common logging practice after every major wildfire in the last century has been salvage logging, where trees that have died from high severity wildfire are then extracted in clearfell operations.

My research has focused on the responses of vascular plants to the major forms of disturbance, fire and logging within the Mountain Ash forests.

Chapter 1, *Disturbance gradient shows logging affects plant functional groups more than fire*, asks two questions: (1) What is the response of plant species richness to a gradient of disturbance severity from undisturbed forest through to post-fire salvage logging? And (2) Are there differences in response to the disturbance gradient from different plant functional groups? In this study I compare forest burned at low and high severity to forest logged using standard clearfelling techniques (of unburned forest) and salvage logging (clearfelling of forest burned at high severity) to determine if there is a difference in recovery. I examined the responses of the different life forms and reproductive strategy groups to different kinds of disturbance.

In **Chapter 2**: *Non-linear growth in tree ferns, Dicksonia antarctica and Cyathea australis,* I studied the growth of the two most common tree fern species after being burned by wildfire in 2009. I asked three questions: (1) What are the rates of growth of *D. antarctica* and *C. australis* and do rates of growth vary between these two species? (2) What factors, including environmental variables, influence the rate of growth of *D. antarctica* and *C. australis*? And (3) Are we able to devise a simple equation of dividing height by annual growth rate to estimate tree fern age?

Chapter 3: *Testing succession theory using a chronosequence study of Australian Mountain Ash forest following wildfire* took advantage of two features of the Mountain Ash forests. Firstly, the discrete age classes created by high severity wildfires in 2009, 1983, 1939 and 1851 which allow comparison of successional change. Secondly, some areas of the Central Highlands forests have been protected in closed water catchments for over a century and as such, human disturbance in these forests has been very limited. As such, what is observed in these forests should be close to natural succession. By studying these four distinct age classes as a chronosequence, I was able to ask two questions relating to succession theory: (1) What succession theory, or group of theories, best explains observed differences in species richness between the age cohorts? And (2) What trajectories do the functional groups (based on life form and reproductive strategy) follow and how does that relate to successional theory? With this information, it should be possible to detect whether recovery trajectories from either logging or in response to climate change are different from how these forests would naturally have recovered after disturbance.

In **Chapter 4** *Does forest age influence recovery after fire?*, I explored the effect of forest age before a large wildfire on the subsequent regeneration after the fire. Specifically, I ask two questions: (1) Does forest age at the time of high severity fire affect the species richness of the subsequent regenerating forest? And (2) How does forest age at the time of high severity fire affect the different plant functional groups ability to persist?

The Mountain Ash forests of the Central Highlands are subjected to some of the most severe and intense wildfires anywhere in the world and part of their geographic range also is subject to intense clearfell logging. Understanding the effects of the different disturbance types and how they influence the forest's structure and diversity through the various functional groups is critical for managing these important forests.

CHAPTER 1

Disturbance gradient shows logging affects plant functional groups more than fire

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ABSTRACT

Understanding the impacts of natural and human disturbances on forest biota is critical for improving forest management. Many studies have examined the separate impacts on fauna and flora of wildfire, conventional logging and salvage logging, but empirical comparisons across a broad gradient of simultaneous disturbances are lacking. We quantified species richness and frequency of occurrence of vascular plants, and functional group responses, across a gradient of disturbances that occurred concurrently in 2009 in the Mountain Ash forests of southeastern Australia. Our study encompassed replicated sites in undisturbed forest (~70 years post-fire), forest burned at low severity, forest burned at high severity, unburned forest that was clearcut logged, and forest burned at high severity that was clearcut salvage logged post-fire. All sites were sampled two and three years post-fire.

Mean species richness decreased across the disturbance gradient from 30.1 spp/site on low severity burned sites and 28.9 spp/site on high severity burned sites, to 25.1 spp/site on clearcut sites and 21.7 spp/site on salvage logged sites. Low severity burned sites were significantly more species-rich than clearcut sites and salvage logged sites; high severity burned sites supported greater species richness than salvage logged sites.

Specific traits influenced species' sensitivity to disturbance. Resprouting species dominated undisturbed Mountain Ash forests, but declined significantly across the gradient. Fern and midstory trees decreased significantly in frequency of occurrence across the gradient. Ferns (excluding Bracken) decreased from 34% of plants in undisturbed forest to 3% on salvage logged sites. High severity burned sites supported a greater frequency of occurrence and species richness of midstory trees compared to clearcut and salvage logged sites. Salvage logging supported fewer midstory trees than any other disturbance category, and were distinctly different from clearcut sites. Plant life form groups, including midstory trees, shrubs and ferns, were dominated by very few species on logged sites.

The differences in biotic response across the gradient of natural and human disturbances have significant management implications, particularly the need to reduce mechanical disturbance overall and to leave specific areas with no mechanical disturbance across the cut area during logging operations, to ensure the persistence of resprouting taxa.

Key words: *wildfire, regeneration strategies, plant attributes, post-disturbance, clearcut logging, species richness, Eucalyptus regnans.*

INTRODUCTION

Disturbance is a primary driver of forest dynamics around the world, with species composition and vegetation structure influenced by the type, scale, intensity and frequency of the disturbances (Shugart 1984, Ross et al. 2002, Baker et al. 2004, Shea et al. 2004, Leverkus et al. 2014, Zhang et al. 2014). Because of this, the regeneration and species recovery processes following natural disturbances such as fire or wind have been well studied (Turner et al. 1998, Lindenmayer and Franklin 2002) as have the same processes following logging, including salvage logging (Lindenmayer et al. 2008, Neyland and Jarman 2011).

Understanding biotic responses to various disturbance regimes is becoming increasingly important around the world given the extent and frequency of human disturbance such as logging (Millennium Ecosystem Assessment 2005, Hansen et al. 2013, Mackey et al. 2014) as well as increases in the frequency and severity of ‘natural’ disturbances due to climate change (Allen et al. 2010, Williams et al. 2013, Seidl et al. 2014b). To address key questions associated with the effects of disturbance on biodiversity, we took advantage of a combination of circumstances that allowed us to compare both fire (at two intensities) and logging (clearcutting of green forest and salvage logging of burned forest). With extensive stands of even aged forest in the study area (regeneration from large fires in 1939), we were able to select sites where the overstory age was uniform, thereby controlling for forest age. Due to the broad scale of the fires, yet with continued logging across this period in unburnt areas, we were also able to select sites where the disturbances across all treatments occurred simultaneously. This led to a powerful analysis of different disturbance types and allowed us to make inferences relating to general disturbance theories and the conservation significance of such impacts while controlling for many factors that can otherwise influence plant responses. Our work focused on the response of vascular plants in the Mountain Ash (*Eucalyptus regnans*) forests of south-eastern Australia. An extensive wildfire in 70 year-old even aged stands in 2009, and ongoing logging in the area, enabled us to document plant responses on sites subject to different kinds of disturbances, including: (1) **undisturbed** forest, (2) forest burned at **low severity**, (3) forest burned at **high severity**, (4) unburned forest subject to conventional (green) **clearcut** logging, and (5) forest burned at high severity and then clearcut by post-fire **salvage** logging. We quantified plant species richness and the frequency of occurrence of plants in reproductive functional groups and life forms which allowed us to consider disturbance theory implications and to address two inter-related questions:

Question 1: What is the response of plant species richness to a gradient of disturbance severity from undisturbed forest through to post-fire salvage logging?

We hypothesised that overall plant species richness would not decline significantly in response to wildfire, irrespective of severity. However, we expected the impacts of logging to differ qualitatively and quantitatively from those of fire. This is because plants that persist in Mountain Ash forests are broadly adapted to infrequent but severe fire (Ashton and Martin 1996). Nearly all the late successional species that are found in the cool temperate rainforests further south in Tasmania, have already been extirpated from the forests of Victoria by previous fires over thousands of years (Read and Hill 1985). Indeed, following more closely to initial floristic composition theory (Wilson et al. 1992), we predicted overall species richness would increase when compared to undisturbed forest due to the influx of early successional species which may be largely absent from long unburnt forest (Martín-Queller et al. 2013, Leverkus et al. 2014).

Our predictions about the impacts of logging were more tentative. We expected the absence of some persistent species that may return in the longer term (Purdon et al. 2004, Lang et al. 2009), while transitory, early colonising species may appear in sufficient numbers to replace these species (Fedrowitz et al. 2014). We predicted similar results for post-fire salvage logging, but with additional persistent species lost due to the order of the rapid double disturbance of mechanical logging occurring when the forest is in the early stages of regenerating post wildfire (Van Nieuwstadt et al. 2001, Lindenmayer and Ough 2006, Brewer et al. 2012). This would lead to more homogeneous forest stands (D'Amato et al. 2011) although Kurulok and Macdonald (2007) found this not to be the case in boreal forests in Canada, nor did several other studies where wind was the main form of natural disturbance (Elliott et al. 2002, Laing et al. 2011).

Question 2: Are there differences in response to the disturbance gradient from different plant functional groups?

All plant species within Mountain Ash forests have evolved in the presence of fire as a major form of natural disturbance (Smith et al. 2014). Two key plant response strategies to fire are resprouting and germination from seed stored in various locations (e.g. on the plant, in the soil or off site) (Pausas and Keeley 2014). We postulated that these different regeneration strategies may make some species susceptible to the effects of mechanical disturbance associated with logging, with resprouting species in particular more likely to be negatively affected by conventional logging and salvage logging than by fire (McIver et al. 2000, Lindenmayer and Ough 2006, Cannon and Brewer 2013).

Not all disturbances in natural forests are equal in terms of their potential effects on plant biota (Shea et al. 2004). Salvage logging following disturbances such as fire is common (Lindenmayer et al. 2008), and likely to increase in future (Seidl et al. 2014b). Our study is therefore important for informing forest managers about the response of plant biota to different kinds of disturbances, including those of high intensity such as salvage logging.

METHODS

Study area and forest management

We conducted this study in the Mountain Ash (*Eucalyptus regnans* F. Muell) forests of the Victorian Central Highlands, 60-120km east of Melbourne in south-eastern Australia (Figure 1). These forests receive high rainfall (750-1700mm per annum) and are found at altitudes ranging from 150-1100m (Boland et al. 2006). Mountain Ash forests are characterised by hot and periodically dry summers, and are subject to infrequent, severe wildfires (Victorian Government DELWP 2014). Large stand-replacing wildfires in these forests have historically had an average return interval of 75-150 years (McCarthy et al. 1999).

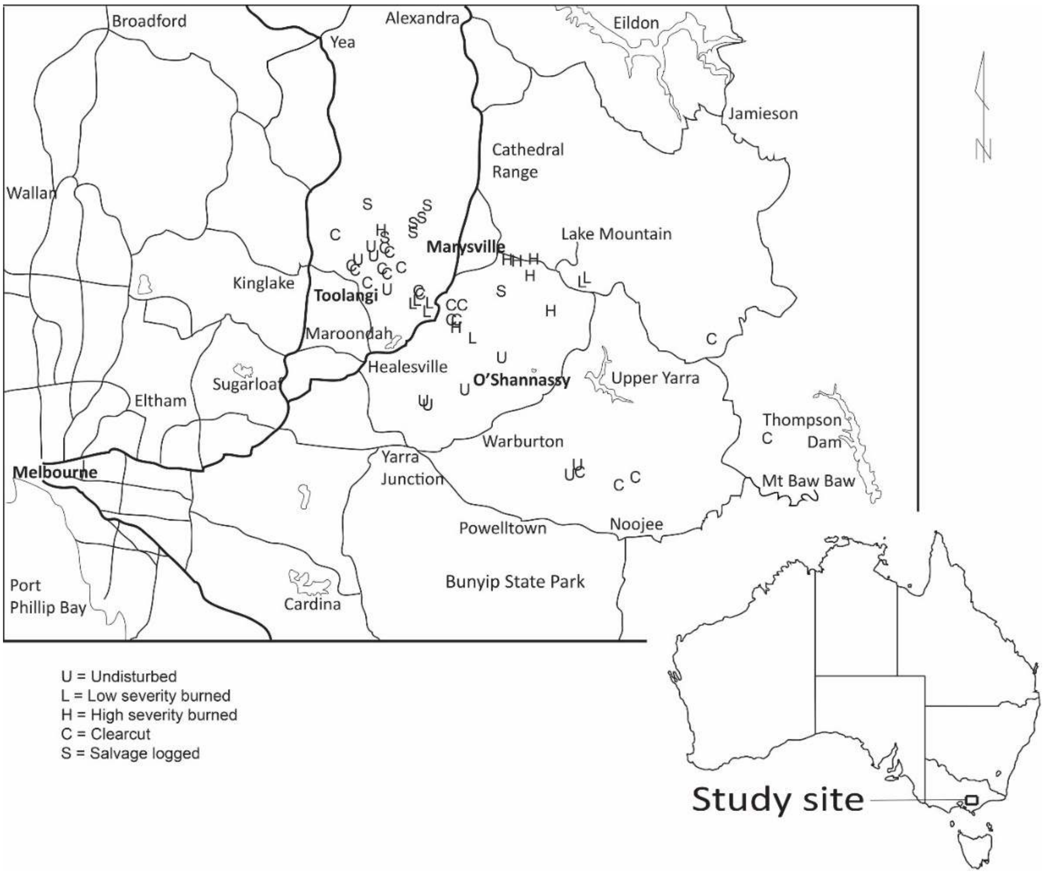

Figure 1: Maps of study area showing location of sites

Mountain Ash is an obligate seeder, with individuals usually killed by large crown fires and seedlings establishing in the nutrient rich ash bed (Attiwill and Leeper 1987). One such fire in 1939 was severe and widespread, burning 79% of the Central Highlands region (Land Conservation Council 1994) leading to numerous and widespread stands of trees that are now ~76 years old. In February 2009, wildfire burned large areas of forest which had previously burned in 1939 (Cruz et al. 2012, Burns et al. 2015a).

The usual silvicultural technique applied in Mountain Ash forests is clearcut logging. This involves the cutting of all overstory trees (eucalypts) usually by mechanical harvesters. De-barked and de-limbed logs are then dragged along skid trails to a central landing where they are loaded onto trucks. The remaining slash (tree heads, bark and non-commercial species) is left broadcast across the cutblock and allowed to dry, typically for 6 months, before being burnt in a high intensity 'regeneration burn'. The cutblock is then sown with seed of the overstory eucalypt species, usually by helicopter (Bassett et al. 2015, Victorian Government VicForests 2015).

Salvage logging has been conducted in Mountain Ash forests following every major fire since 1926 (Noble 1977, Lindenmayer and Ough 2006). Salvage logging is clearcut logging which directly follows a high severity wildfire. The harvest method is the same with the exception that slash is not burnt if regeneration from the initial wildfire is adequate; if it is not, then a broadcast burn is applied along with aerial seeding. Slash is not windrowed or heaped. All of our salvage logged sites were harvested within 18 months of the 2009 fire.

Study design

We designed our study around sets of replicate sites in five broad categories of disturbance. These were: (1) **undisturbed** (unlogged and unburned for 70 years); (2) burned at **low severity** in 2009; (3) burned at **high severity** in 2009; (4) green **clearcut** (not burned before harvesting in 2009); and (5) **salvage** logged after being burned at high severity in the 2009 wildfire.

We selected our undisturbed and burned sites from amongst 175 long term monitoring sites from a larger project, selecting those with uniform eucalypt overstory tree species and age class (regrowth from a fire in 1939) and where fire severity was uniform across a given site. We measured fire severity on the ground at all sites within two months of the fire in 2009. High severity fire resulted in tree death from scorch or the consumption of the majority of the overstory canopy while in low severity fire, the overstory canopy remained green. Logged sites also were chosen for uniform age class as well as those harvested closest to the date of the fire.

The 57 sites selected for this study were surveyed between March and June in 2011 and again in the same months in 2012 (Table 1).

Table 1: Descriptions of disturbance classes and number of sites per class.

Description	Undisturbed/ Unburnt	Low severity	High severity	Clearcut	Salvage
No. sites	14	7	7	22	7
Burnt 2009	No, still green	Yes, low severity	Yes, high severity	No	Yes, high severity
Logging	None	None	None	Clearcut in 2009	Clearcut in 2009 or 2010 post fire

A key strength of our research was that we controlled for forest age, which is important as forest structure and species composition can vary with forest age (Lindenmayer et al. 2000, Lindenmayer and Franklin 2002, Trotsiuk et al. 2012).

Site design and survey methods

Each of our 57 field sites was established in an identical way. Each site was 1 hectare in size (100m x 100m) with a central 100m long transect running perpendicular from the middle of the site's front edge. All sites were buffered around the transect by a minimum of 100m of uniform forest disturbance to reduce edge effects from adjacent forest with different disturbance history. We established three 10m x 10m plots straddling this transect between 10-20m, 50-60m and 90-100m. The first plot (10-20m) was set back from the site's edge to reduce edge effects. (See Appendix S9 for details of the environmental variables of the sites.) We recorded the presence or absence of each species from these plots as well as any species within 5m of either side of the central transect. We counted only live plants. For logged sites, the 100m transect was located away from uncut edges and the log landing, and was positioned without consideration of skid trails, but in a proportion that was representative of the overall cut area.

Plant species richness

To measure species richness, we recorded the presence of all vascular plant species 5m either side of the permanent 100 m transect on each site in 2011 and again in 2012. Thus, for the 57 sites, the maximum number of occurrences recorded for any particular species could be 114 (57 sites x 1 transect x 2 years).

Regeneration strategy functional group

Overall species richness was the count of the total number of species. However, we are aware that this measure can be strongly influenced, for example, by a pulse of short-lived invasive species immediately post disturbance (Alba et al. 2015). For this reason, we quantified frequency of occurrence within functional groups. We examined the responses of plants characterised by different reproductive strategies and physical life forms to determine if any particular groups of taxa was impacted disproportionately.

We assigned plant species to one of nine functional groups based on regeneration strategy (including dispersal) and whether they were persistent species (usually capable of persisting for decades post disturbance without additional disturbance) or transitory species (flourish with disturbance but do not usually persist beyond several years, otherwise known as ruderal species). These groups were: (1) **transitory, blow-in seed**; (2) **transitory, on-site seed**; (3) **persistent, blow-in seed**; (4) **persistent, on-site seed**; (5) **persistent, 'none'** (no defined strategy); (6) **persistent, seed and sprout**; (7) **persistent, sprout**; (8) **exotic**; and (9) **edge** (see Appendix S7). Seed and sprout species regularly reproduce from both seed and resprouting. Due to the low numbers in this group (7 species), and not wanting to dilute the sprout-only group, we combined them into the larger 'persistent on-site seed' group. The forests of these areas have very few weeds or alien species. All species in groups 1-7 above, are locally native species, including all the ruderals (Mueck 1990). The 'exotic' group included every exotic (not locally native) species (12 species) irrespective of reproduction method. The two 'edge' species were excluded from analysis as they occur only on roadsides and not more broadly across forested sites. We assigned plant species to categories by field observation, consultation with staff from the Melbourne Botanical Gardens and literature review (Walsh and Entwisle 1994, 1996, 1997, Costermans 2009, Bull and Stolfo 2014).

Life form/physical functional groups

We assigned plants to functional groups according to their physical life form, including: (1) **Eucalypts** (overstory); (2) **Acacia**; (3) **midstory trees**; (4) **shrubs**; (5) **ferns**; (6) **herbs**; (7) **climbers**; (8) **graminoids;** and (9) **exotic**. Again, all species in all groups except 'exotic' are locally native species. These nine groups were based on classifications by the Victorian State Government Department of Environment, Water, Land and Planning (DELWP) Highlands – Southern Fall Bioregion Ecological Vegetation Class (EVC) (Victorian Government 2015). Eucalypts (represented by species within genera *Eucalyptus*) and *Acacia* are not life forms as such. However, we used these groups because *Eucalyptus* is the sole genus represented in the overstory, and while Acacias are a midstory tree, they are often taller than other midstory trees and, more importantly, have specific ecological roles, such as nitrogen fixation, that we determined would be valuable to identify for this study.

To facilitate analysis of life form and regeneration strategy functional groups, we used data gathered at the plot level for each site in 2011 and 2012. This was presence/absence data for each species, collected across 3 plots (10m x 10m) per site, to give a measure of frequency of occurrence. We did not count individual plants within these plots because we were surveying all vascular plant species and, for many species, this would not be feasible due to counts in the hundreds or thousands on each plot (e.g. grasses, herbs, ground ferns, seedlings). We then divided the number of occurrences of plants within any particular life form group by the overall plant occurrences for that disturbance category to estimate the proportion of plants within each group.

Statistical analyses

The analysis for species richness and frequency of occurrence were modelled at the site level with values at this level compared among disturbance classes. We quantified overall species richness among the five disturbance categories using a Generalised Linear Mixed Model (GLMM) with a Poisson distribution and log link to species richness with site as a random effect. The site-level random effect allowed for over-dispersion relative to the Poisson distribution. The analysis was completed in R (version 3.0.2) (R Core Team 2015) using the lme4 package (Bates et al. 2014).

A separate analysis (using GLMM with binomial distribution and logistic link function) was completed for frequency of occurrence within each functional group where we performed the analysis at the plot level within each site (as opposed to transect level as was used for species richness), collapsing two years of observations together, resulting in the number of occurrences of the species for each site to be a value out of six (3 plots x 2 years).

We did not formally include model aggregation and spatial dependence in our models; rather we assessed the degree of spatial dependence present in the residuals of our model fits. We did this by inspecting the variogram (Schabenberger and Gotway 2005) of the residuals for evidence of sill effects. Visual inspection of the variograms of the residuals did not reveal any evidence of sill effects. We took this as evidence of there not being any appreciable effect of aggregation. We employed Fisher's Least Significant Differences (LSD) to assess significant differences among disturbance classes. Formally, this means, we assessed the effect of the disturbance gradient overall and if the results were significant at this first stage, we then determined which levels of disturbance were different from each other. If the overall effect of the disturbance gradient was not deemed significant, we concluded there were no differences among levels of disturbance.

RESULTS

Species richness and disturbance

We identified 121 plant species across the 57 sites in our five disturbance classes (Appendix S7). A gradient in overall species richness was apparent for the four disturbance categories (i.e. excluding stands of undisturbed 1939 regrowth) (Figure 2). Sites subject to low severity fire supported the most species (30.1 ±4.2 species/site on average ±SD), followed by sites subject to high severity fire (28.9 ±4.1), then clearcut sites (25.1 ±2.1) and salvage logged sites (21.7 ±3.5).

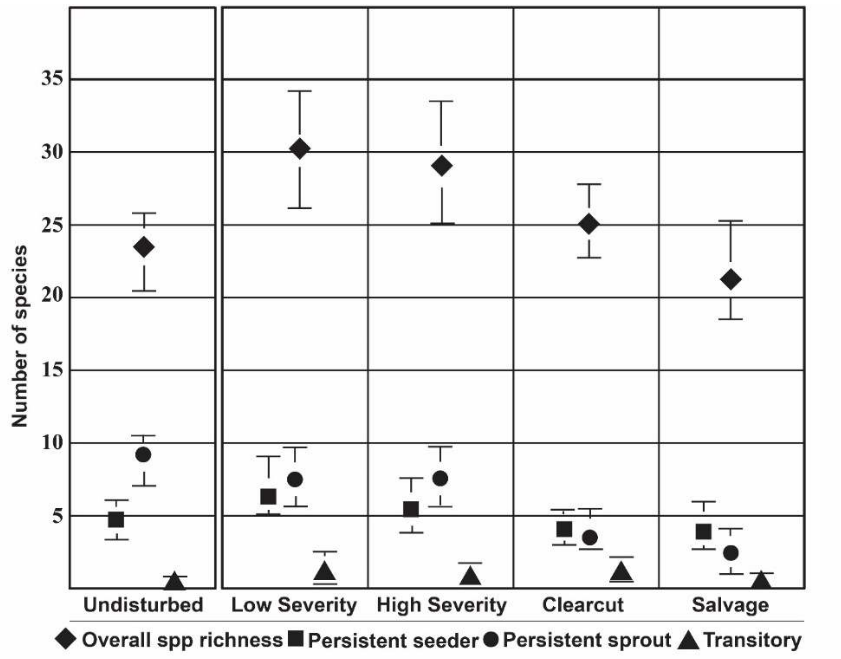

Figure 2: Average species richness with 95% confidence intervals of vascular plants per site across a gradient of increasing disturbance intensity showing total species richness and species richness for functional groups including persistent seeder, persistent sprouter and transitory species.

We identified no significant differences in species richness between low severity burned and high severity burned sites, but differences in species richness were significant between low severity burned sites and clearcut sites (p=0.045) and low severity burned sites and salvage logged sites (p=0.006) (Appendix S2). There also was a significant difference between high severity burned and salvage logged sites (p=0.019). Undisturbed sites supported an average of 23.5 (± 2.6) species/site and were significantly less species-rich than sites subject to low severity fire (p=0.012) and high severity fire (p=0.042), but not significantly different from either clearcut or salvage logged sites.

With the exception of the undisturbed sites, we identified a clear disturbance gradient for the persistent re-sprouting and seeding groups (Figure 2). While transitory species were abundant on burnt and clearcut logged sites, the group was not diverse. All disturbance categories were represented by relatively few species on average, but the burnt and clearcut sites had greater species richness than undisturbed and salvage logged sites (Figure 2; Appendix S1).

Species frequency of occurrence of life form

The occurrence of eucalypts was uniform with no significant differences between any of the disturbance classes, although the physical size of the trees varied from 2-3 year old (3-6m tall) saplings (high severity burnt and logged sites) to 75 year old, 65m tall mature trees (undisturbed and low severity, see Figure 3 and Figure 4 and Appendix S3 and S4). Acacia spp. trees were significantly more abundant on clearcut sites than on low severity burned sites or undisturbed sites (p<0.05), see

Figure 5. The frequency of occurrence of midstory tree species (which includes tree ferns) exhibited a significant decline across the disturbance gradient (Figure 6) with high severity burned sites supporting a greater proportion of midstory trees than sites subject to either clearcutting ($p=0.0005$) or salvage logging ($p=0.0001$). Salvage logged sites also supported significantly ($p<0.05$) fewer midstory trees than all other disturbance categories (other than sites which had been clearcut; Figure 3). Shrubs showed no significant differences in frequency of occurrence across the sites except for those subject to salvage logging (Figure 7), which supported a greater frequency of occurrence of shrubs than undisturbed sites ($p<0.05$). Ferns comprised a high proportion of the undisturbed forest species composition and showed the strongest decline across the disturbance gradient (Figure 3 and Figure 8). Differences in the frequency of occurrence of ferns between the undisturbed category and all other disturbance categories were significant ($p<0.05$). When Bracken (*Pteridium esculentum*) was excluded, high burn severity and conventionally clearcut sites supported significantly fewer ferns compared from sites that were undisturbed or subject to low severity fire ($p<0.05$). Salvage logged sites supported significantly fewer ferns than all other disturbance categories ($p<0.05$) including clearcut sites. Bracken was excluded from some analysis (ferns and resprouters) due to it being a “weedy colonizer” of open ground, where it can tolerate full sunlight and be extremely abundant (Walsh and Entwisle 1994). This is quite different to the other ground ferns which tend to require shading. Given the dominance of Bracken on clearcut sites and salvage logged sites, for comparison, we removed it from the overall sprouting and fern functional groups to allow us to quantify responses without Bracken, particularly when examining fern frequency of occurrence. Herbs were significantly less abundant on undisturbed sites (see Figure 9) compared to all other disturbance categories ($p<0.0001$). Low severity burn sites were characterised by a significantly greater ($p<0.05$) frequency of occurrence of herbs relative to high severity, clearcut or salvage logged sites. There was no significant difference between these last three of the disturbance categories. Climbers were more common in low severity burned sites than either undisturbed or clearcut sites ($p<0.05$) and salvage logged sites had more than clearcut sites ($p=0.04$, see Figure 10). Graminoids were more abundant on high severity burned sites than undisturbed sites ($p=0.007$, see Figure 11). Exotic species are discussed in the following section.

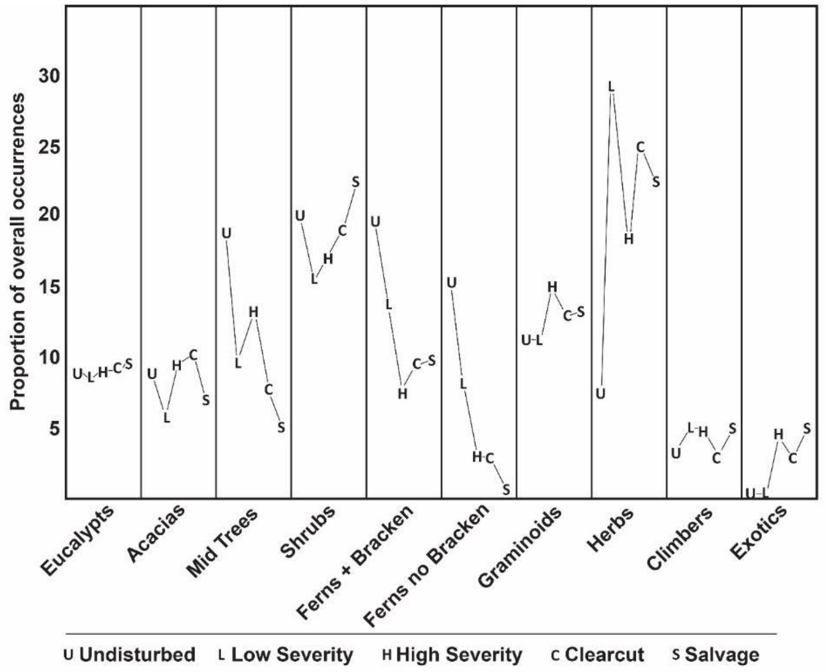

Figure 3: Frequency of occurrence of each life form group within each disturbance class as a proportion of the total frequency of occurrence (of all functional groups combined for that disturbance class)

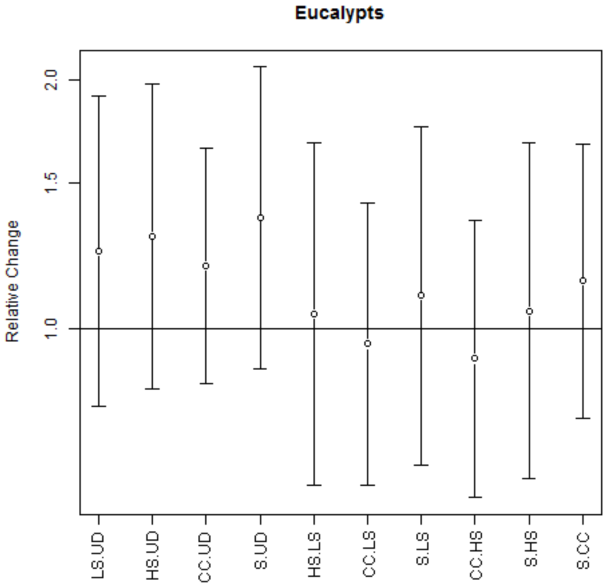

Figure 4: Relative change for Eucalypt life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

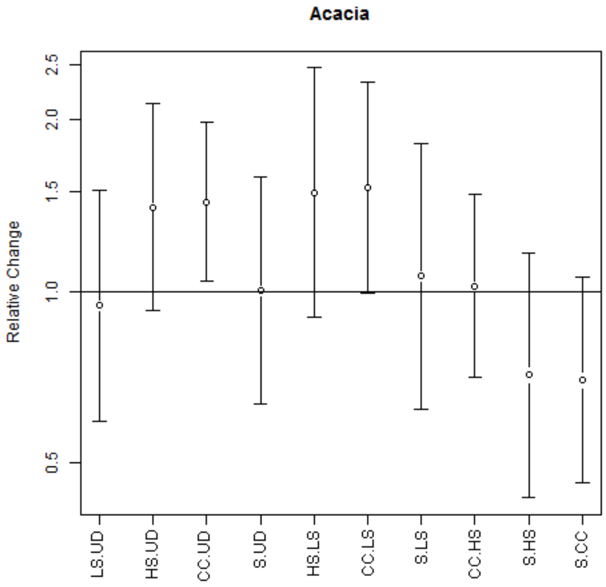

Figure 5: Relative change for Acacia life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

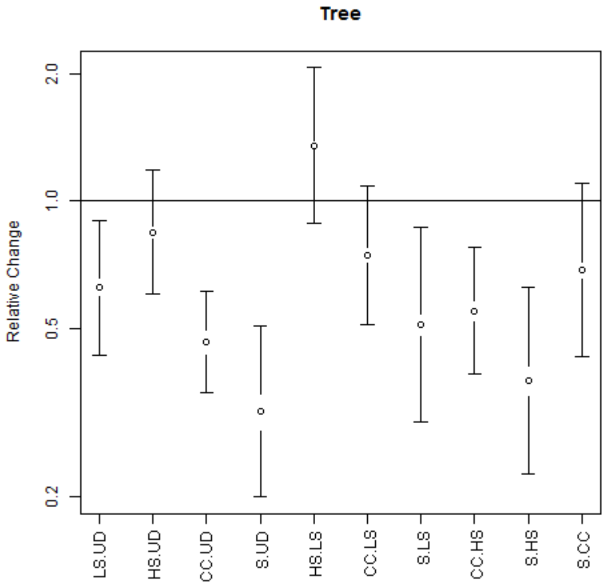

Figure 6: Relative change for Midstory Tree life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

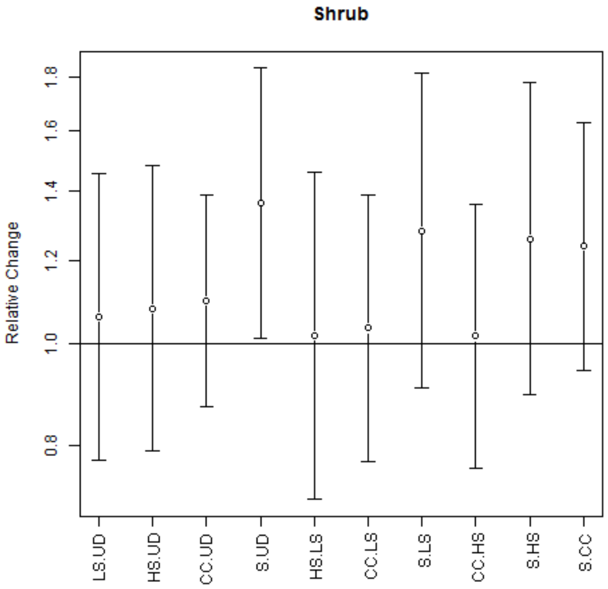

Figure 7: Relative change for Shrub life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

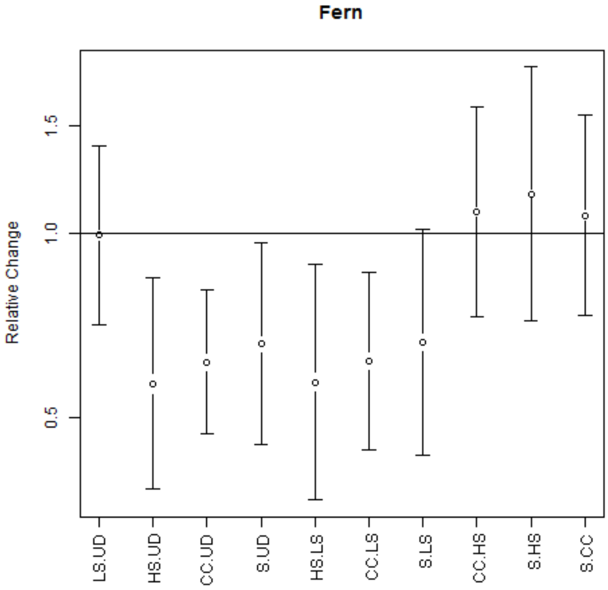

Figure 8: Relative change for Fern life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

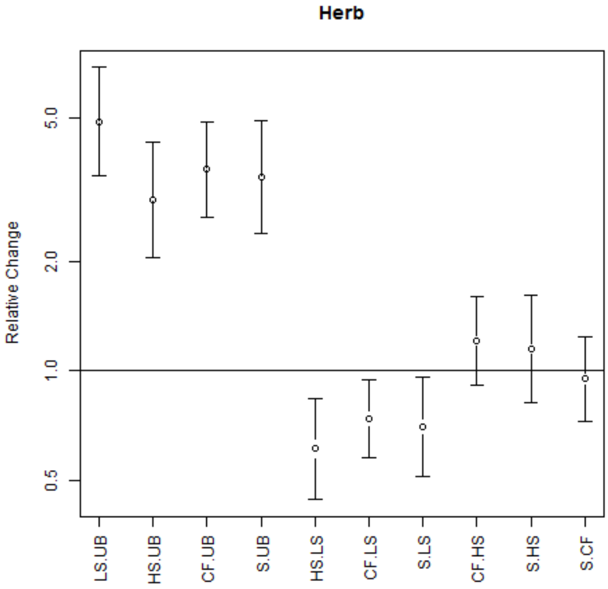

Figure 9: Relative change for Herb life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

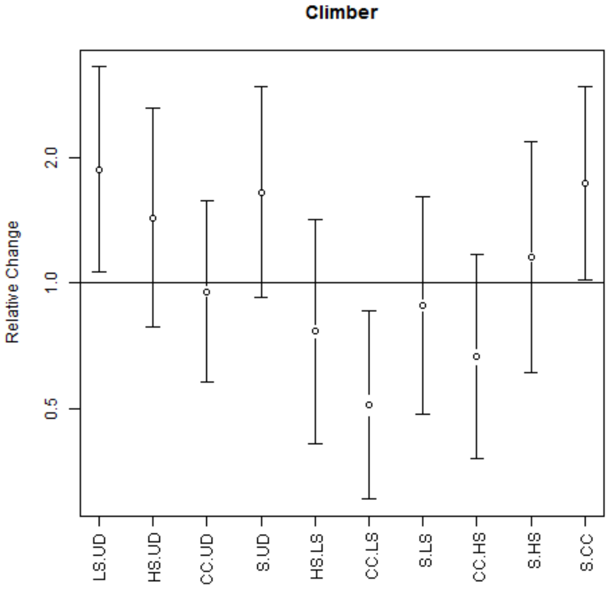

Figure 10: Relative change for Climber life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

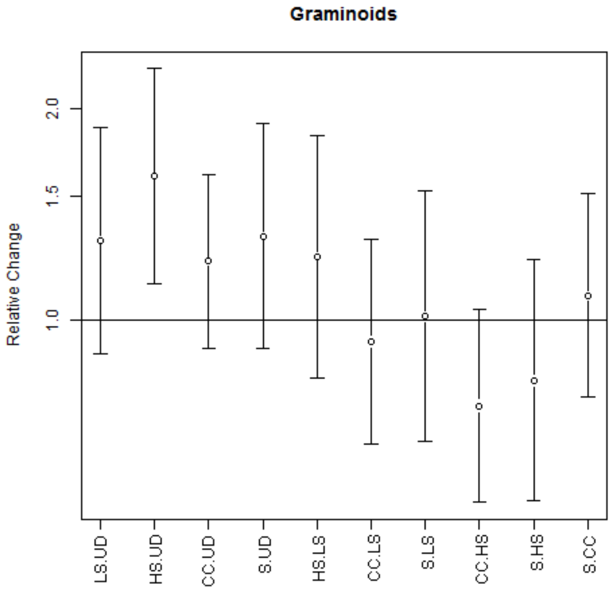

Figure 11: Relative change for Graminoid life form group with statistical differences between disturbance classes indicated by 95% confidence intervals

Species frequency of occurrence by regeneration strategy

We found that plants in the persistent resprouting functional group dominated undisturbed forest and members of this group were likewise highly abundant on sites subject to either low or high severity fire (Figure 12 and Figure 13; Appendix S5). Sites in non-logged disturbance classes (undisturbed, low severity and high severity burned) were characterised by a significantly ($p<0.0001$) greater frequency of occurrence of persistent resprouting species when compared to the two logged classes (clearcut and salvage logged sites). Clearcut sites supported significantly greater numbers of resprouting species than salvage logged sites ($p=0.003$). Despite such significant results, effects within the sprouting group were masked by the occurrence of Bracken. Bracken was only moderately common in long unburnt forest (accounting for 13% of all fern occurrences, compared to 64% on clearcut sites and 93% on salvage logged sites). When we removed Bracken from the analysis of persistent sprouting species, the overall decline in ferns across the gradient was far more pronounced than when Bracken was included (see the comparison with and without Bracken, Figure 12). The frequency of occurrence of persistent on-site seeding species varied little between sites in different disturbance classes (Figure 14) with the only significant result being on sites subject to high severity fire which were characterized by supporting a greater frequency of occurrence of this group than undisturbed sites ($p<0.05$). Persistent 'other' species were favoured by low severity burns, and were significantly ($p<0.05$) more abundant on sites in this disturbance class than on sites that were undisturbed or subject to clearcutting and salvage logging (see Figure 15). Persistent blow-in species showed no variation across disturbance classes for frequency of occurrence (Figure 12 and Figure 16).

Exotic species were significantly ($p<0.05$) more abundant on the logged and high severity burnt sites than undisturbed sites and sites subject to low severity fire (Figure 17).

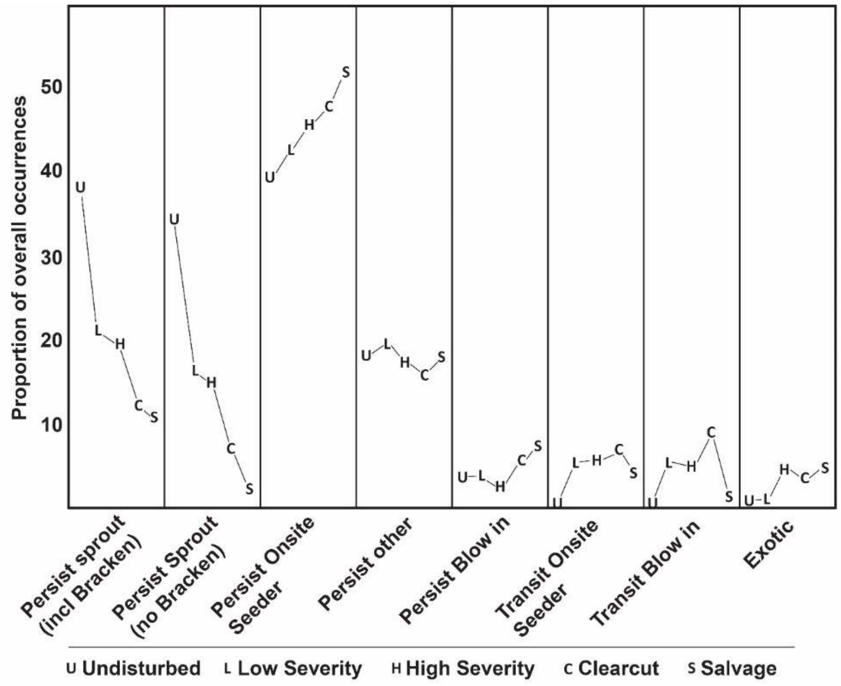

Figure 12: Frequency of occurrence of each regeneration strategy functional group within each disturbance class as a proportion of the overall frequency of occurrence (of all functional groups combined for that disturbance class)

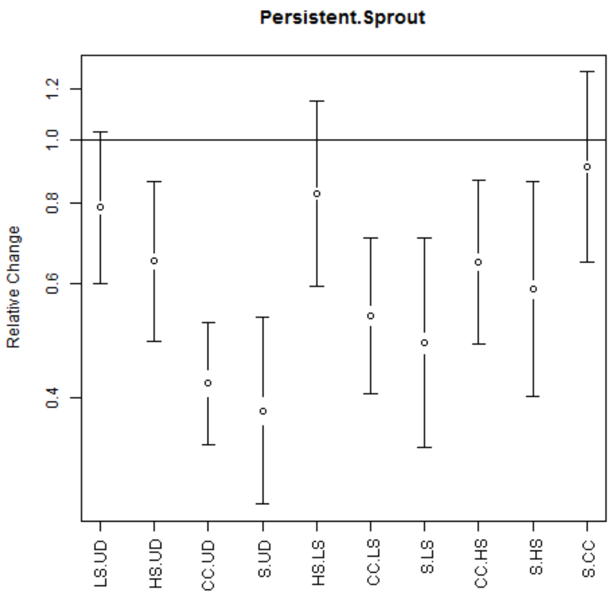

Figure 13: Relative change for Persistent sprout reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

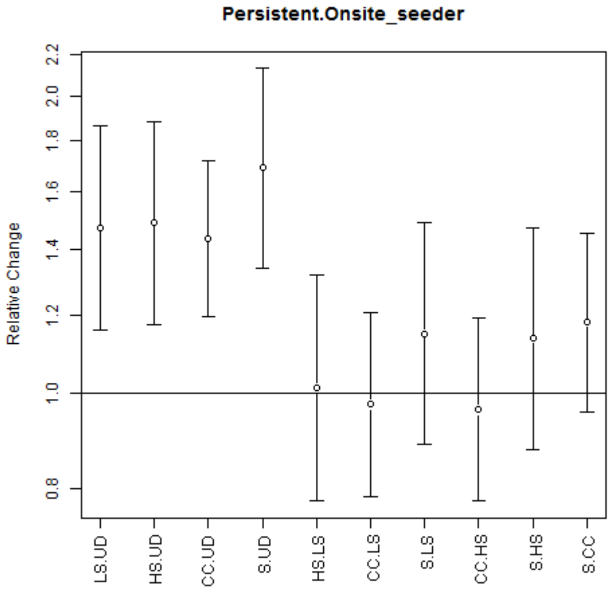

Figure 14: Relative change for Persistent on-site seed reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

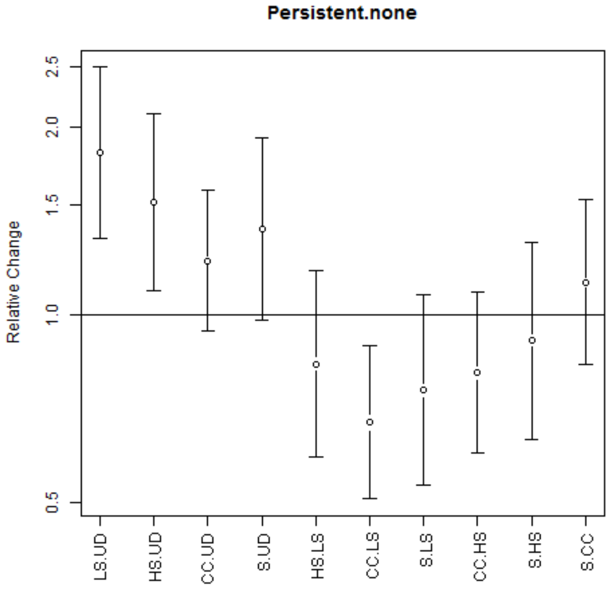

Figure 15: Relative change for Persistent ‘none’ (no defined strategy) reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

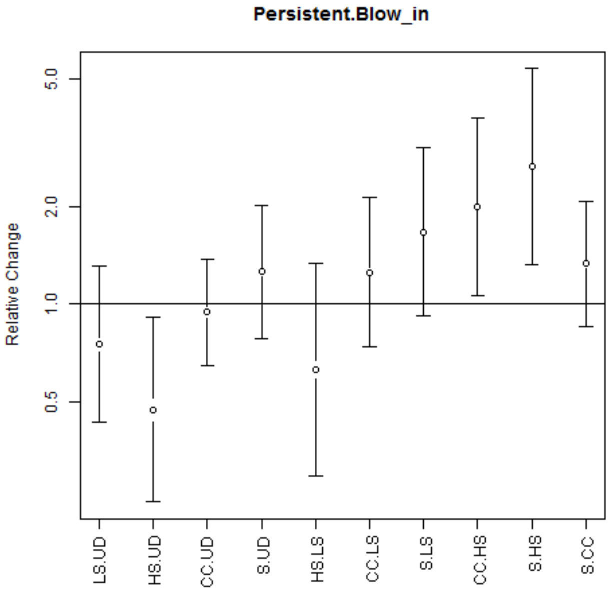

Figure 16: Relative change for Persistent blow-in seed reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

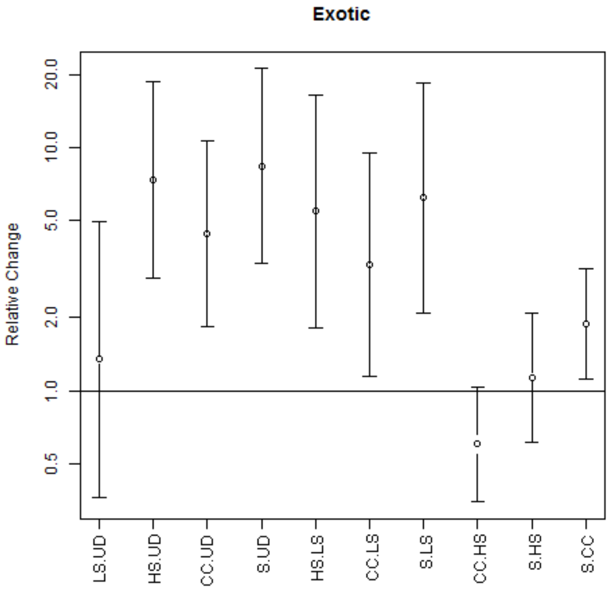

Figure 17: Relative change for Exotic reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

Results were very similar for the two groups of transitory species, onsite seeders (Figure 18) and blow-in seeders (Figure 19)(see also Figure 12). Transitory species (blow-in and on-site seeders), were virtually absent on undisturbed sites (0.8% of all plants observed), and were significantly less abundant than on the disturbed sites (p<0.0001). We found significantly fewer transitory blow-in seeders on salvage logged sites ($p<0.05$) compared to other disturbed sites, while clearcut sites supported the highest proportional frequency of occurrence of these species.

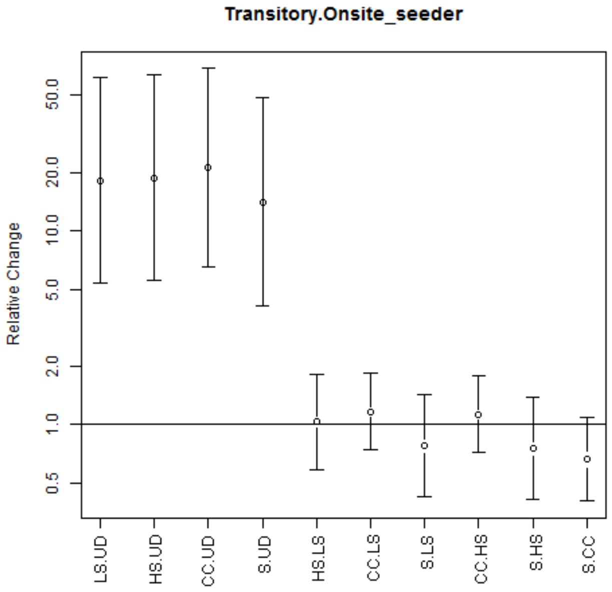

Figure 18: Relative change for Transient on-site seed reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

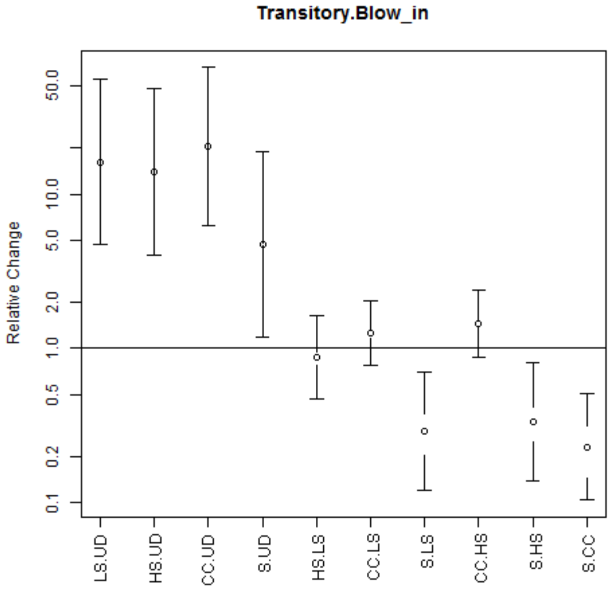

Figure 19: Relative change for Transient blow-in seed reproductive strategy group with statistical differences between disturbance classes indicated by 95% confidence intervals

DISCUSSION

The relationship between disturbance and measures of diversity is a central theme for our understanding of ecology and management of natural systems. Disturbance is often complex and multi-faceted and Diversity-Disturbance Relationships (DDRs) have been found to encompass a range of different relationship curves (Miller et al. 2011). The most recognised of these, the ‘peaked’ curve of the Intermediate Disturbance Hypothesis where maximum diversity comes from intermediate levels of disturbance (Bongers et al. 2009), has a long history (Connell 1978), but also many critics (Mackey and Currie 2001). One of the difficulties with determining a DDR is identifying which factors are genuinely influential and to which species or functional groups (Shea et al. 2004). Within the context of a constant fire history (uniform 70-year most recent inter-fire interval), variation in severity of a natural fire event had no significant impact on plant diversity, but disturbance type had significant impacts on species richness, functional groups and life forms of plants. Our findings have important implications for understanding the ecological impacts of logging, particularly in ecosystems affected by fire, and how they relate to variation in disturbance severity within natural forest disturbance regimes.

Disturbance gradient and plant species richness

Through this investigation, we found the existence of a forest disturbance gradient with ecological impacts increasing from low severity fire, high fire severity fire to clearcut logging of unburnt forest and finally salvage logging. Species richness declined across this gradient with salvage logging having the most pronounced negative effect of all the disturbance types we examined. The result was an overall simplification of the forest ecosystem due to logging and salvage logging in particular.

As is often the case, our results did not fit neatly into a single DDR, but rather needed a range of explanatory factors. These included frequency, intensity and type of disturbance, and also order in which disturbances occurred.

Our study did not test the effects of variation in long-term disturbance frequency, but our findings of lower species richness on sites subjected to rapid double disturbance (logging classes) were consistent with disturbance theory (Roxburgh et al. 2004). However, frequency alone should have resulted in both burned categories being equal and both logged categories being equal, which they were not.

Intensity of the disturbance resulted in a minor separation of the fire severity categories. However, the effect of intensity for the two logging categories is far more subjective as we did not directly measure this. Both involved clearcutting the forest and a high intensity fire, so it is likely disturbance intensity was similar for these two categories.

Despite the two logging categories having similar disturbance frequencies, disturbance types (fire and logging) and presumably intensity, our results clearly showed them to be different. We believe the critical difference between green clearcutting and salvage logging was the order in which the disturbances occurred. In the Mountain Ash forests, germination is primarily triggered by fire. On our green clearcut sites, fire came after the mechanical disturbance of logging so, once triggered, the regeneration was then left undisturbed. On the salvage logged sites however, fire triggered a regeneration cohort, which was subsequently mechanically disturbed. It appears this, rather than any particular DDR, has separated the two logged categories, as found by others (Greene et al. 2006, Lindenmayer and Ough 2006, Palik and Kastendick 2009, D'Amato et al. 2011).

The decrease in species richness in relation to disturbance intensity appears to be common in other ecosystems. For example, Rao et al. (1990) found decreasing diversity and increasing dominance by fewer species across human-induced disturbance gradients of clearing for agriculture in Indian forests. Brewer et al. (2012) found limited decreases in species richness but a shift from persistent species to ruderals after salvage logging post tornado disturbance in Mississippi, USA. Leverkus et al. (2014) found decreases in species richness, Shannon diversity, and cover in plant communities as a result of salvage logging in the Sierra Nevada of southern Spain. In other forests, salvage logging has been used as a management tool to select for certain species (Palik and Kastendick 2009) or forest characteristics such as the creation of high stem densities (Greene et al. 2006) or homogeneous stands (D'Amato et al. 2011). Similar findings for reduced species richness have been quantified in Australian grasslands in response to a gradient in grazing pressure by domestic livestock (Fensham et al. 1999).

The fundamental difference between fire and the physical disturbance of logging may explain why results from salvage logging after fire disturbances are generally more consistent in the literature compared to the highly variable impacts of wind storms and subsequent salvage logging. Some studies show negative impacts of salvage logging compared to unlogged areas (Foster and Orwig 2006, Rumbaitis del Rio 2006), others are characterized by increased values for some diversity measures (Elliott et al. 2002, Laing et al. 2011, Morimoto et al. 2011), while yet others show no difference between the two disturbance types (Nelson et al. 2008, Lang et al. 2009, Palik and Kastendick 2009, Kramer et al. 2014).

Our data indicated that overall plant species richness increased with fire and logging when long-term persisting species were joined by a pulse of ruderal species that either blew in from outside, or were present in the seedbank prior to disturbance. However, the presence of these transitory species masked the losses of several persistent species, particularly ferns (other than Bracken fern) and midstory trees, which were lost primarily from clearcut and/or salvage logged areas (see Appendix S3). This is the result of greatest conservation significance as in such tall forests, having midstory trees mostly absent creates a vertical gap between overstory eucalypts (with canopies generally 40-70m above the ground) and the shrub layer (which is generally 5m tall or less). It also reduces food variability and availability. This shows that while overall species richness is a useful metric, it does not capture changes in plant community composition in response to disturbance type, nor does it explain changes that may occur in the dominance of different functional groups or life forms.

We suggest that high levels of plant species richness on low severity burned sites was probably due to fern dominance being reduced while strong suppression from the tree regeneration cohort seen on high severity and logged sites was largely missing from low severity burned sites. Both factors allowed the diverse groundstory plants to flourish with reduced competition for light and moisture (Walsh and Entwisle 1994, North et al. 2005).

Disturbance gradient, functional groups and frequency of occurrence

The magnitude of effects of disturbance became more pronounced when we separated plants into life forms (Figures 3 to 11) and functional groups based on regeneration strategy (Figures 12 to 19).

Acacia, herbs, graminoids and climbers

Acacia occurred least frequently on sites where disturbance was insufficient to trigger a new cohort (Figure 5). Undisturbed sites and low severity burned sites had fewer Acacia than the other three disturbance classes, and the Acacias on these sites tended to be large old mature trees that were senescing. The herb layer appears to respond positively to disturbance, and in particular, intermediate levels of disturbance. Long undisturbed sites had fewest herbs present with the ground layer dominated by ferns. In contrast, low severity burned sites consistently had the highest herb abundance. On these sites, fern cover was reduced and light infiltration increased, but the moderate level of disturbance allowed herbs to persist in forms that could rapidly recolonise or recover. High disturbance classes of clearcut, high severity burned and salvage logged sites fell between these two extremes (see Figure 9). Graminioids were little affected by the different disturbance classes (Figure 11) with flushes of common post disturbance grasses such as *Dryopoa* occurring across the majority of disturbed sites. Climbers were represented by only 4 species in these forests and showed limited trends in response to the different disturbance levels (Figure 10).

Transitory and persistent seeding species

Transitory species by definition are short lived and do not generally persist on sites in the long term. It was unsurprising both the transitory on-site seeding and transitory blow-in seed species were significantly less common on the undisturbed sites compared to all other disturbance classes. For the on-site seeding species (which were mostly herbs), there were no significant differences between the disturbed sites (Figure 18), indicating tolerance to a range of disturbance levels. However, in the blow-in transitory species group, in addition to undisturbed sites, sites subject to salvage logging also supported significantly fewer of these species than other disturbance classes (Figure 19). All species within this group were *Senecio* (fireweeds) and are usually a strong colonisers of disturbed land. This unexpected result may have been due to *Senecio* plants not being in seed when the salvage logged coupes were harvested.

Persistent species generally became more common on the four disturbed site classes due to a new cohort having germinated on these sites. On-site seeders all fared equally well across the disturbance gradient (Figure 14), while those that blew in (Figure 16) tended to be favored by the more highly disturbed sites, presumably those with the greatest reduction in competition. This group was represented by five species, all of which are shrubs that behave in an invasive manner, including *Cassinia* and *Oleria phlogopappa*. Surprisingly, high severity burned sites did not support large numbers of these species (similar to undisturbed sites), which may have been due to competition with other shrub and midstory species that survived better on these sites than on the logged sites (see section below). The persistent 'none' group (Figure 15) is a highly diverse group with over 30 species and covering all life forms except eucalypts and acacias and, as such, it is difficult to draw strong conclusions other than, similar to herbs, they seem to benefit from intermediate disturbance given low severity burned sites were the only sites to have significantly greater numbers of this group.

Exotic species

Exotic species are relatively uncommon in these forests, but as with transitory species, exotic species generally favoured disturbance with lowest occurrences on undisturbed and low severity burned sites and high severity burned, salvage logged and clearcut sites all having greater abundance of the range of exotic weed species.

Midstory trees, ferns and persistent sprouting species

Persistent sprouting species (Figure 13), ferns (Figure 8) and midstory trees (Figure 6) were significantly negatively affected across the disturbance gradient, with several species such as *Nothofagus cunninghamii* and *Pittosporum bicolor* that were present in all unlogged categories being totally absent from logged areas. Salvage logging had particularly noticeable impacts on otherwise common midstory trees such as *Bedfordia arborescens, Cyathea australis, Hedycarya angustifolia, Lomatia fraseri, Notelaea ligustrina* and *Tasmannia lanceolata*. The loss of these midstory trees from logged areas fundamentally changes the structure of the forest; however, provided they are still in the surrounding area, these 'missing species' may colonize such areas after a period of decades, which would be consistent with other studies showing the impact of logging disturbance decline over time (Purdon et al. 2004, Lang et al. 2009). Each of these species was absent from salvage logged sites but present on sites in all other disturbance classes. Even common ground ferns like *Blechnum wattsii* that were present on all sites, were absent from areas subject to salvage logging. We suggest these results are due to the physical uprooting of these species during logging which then makes them prone to desiccation or burning in post-logging regeneration burns (Ough and Murphy 2004). This is a similar result to what Stuart et al. (1993) found in Douglas-fir *(Pseudotsuga menziesii)* forests in California, USA, Purdon et al. (2004) found in Quebec, Canada, and Van Nieuwstadt et al. (2001) found in Indonesian East Kalimantan, all involving salvage logging after fire. Such susceptibility to salvage logging may occur in many forest ecosystems around the world, particularly those where fire is the primary type of disturbance.

We found that the impacts of both clearcutting and salvage logging on particular functional groups of plants became increasingly apparent when a range of measures of biotic response were explored.

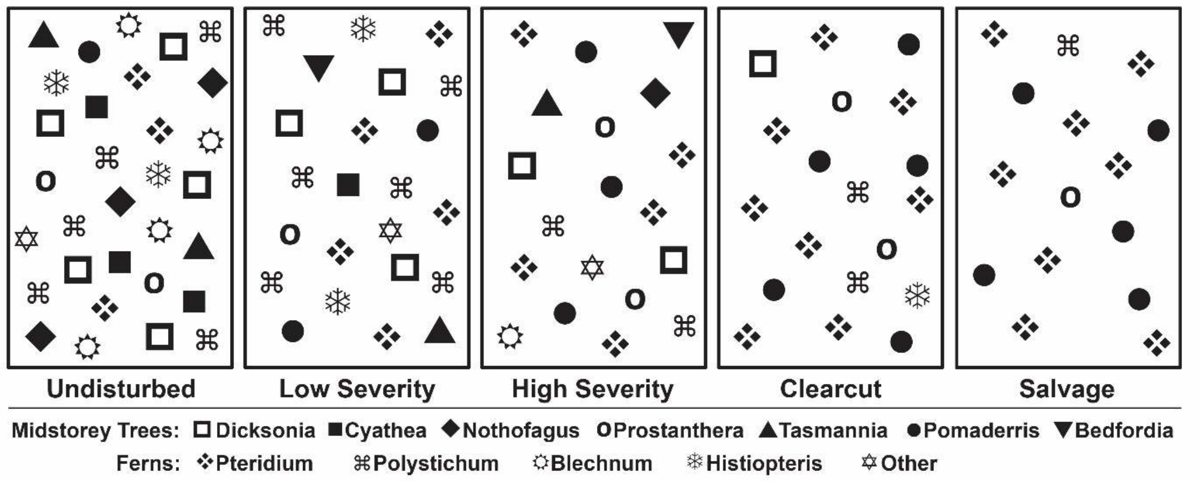

Figure 20: Fern and Midstory Tree proportional frequency of occurrence and species richness comparison for each disturbance class (conceptual diagram based on our data). The diagram shows the simplification of the fern and midstory strata through the loss of species such as *Blechnum, Tasmannia, Cyathea* and *Nothofagus* when the forest is clearcut or salvage logged compared to burnt and undisturbed forest. It also shows the increased relative abundance of a small number of species such as *Pteridium* (Bracken) and *Pomaderris* on the logged sites that become highly dominant when compared to their moderate abundance on burnt and undisturbed sites.

Figure 20 is a conceptual diagram of the disturbance classes showing the relative frequency of occurrence of the dominant fern and midstory tree species, and highlights the primary conservation concern drawn from this study, that of simplification of forest across the disturbance gradient. There also was a marked shift across the disturbance gradient from species that regenerate by resprouting to those that regenerate from seed. On unlogged sites (i.e. those that were undisturbed, or subject to low severity and high severity fire) midstory trees were represented by 18 different species with a maximum frequency of occurrence of any one species being a quarter (27%) of all plants in this life form (Table 2). However, on logged sites, a single species, *Pomaderris aspera*, accounted for over half (56%) of all midstory trees on clearcut sites and more than three-quarters (79%) on salvage logged sites. Almost half (45%) of the species on the clearcut sites were represented by a single occurrence (i.e. just one individual), while on salvage logged sites, all of these species had been lost with the midstory tree group represented by only 3 species, and one of those (*Dicksonia*, which is the only resprouter of the three), by a single individual. Sites in all other disturbance classes supported a minimum of 10 midstory tree species. The other common tree fern, *Cyathea australis*, was present on sites in all other disturbance classes (except salvage logged), although it was reduced on clearcut sites – a finding consistent with Ough and Murphy (2004). A similar result characterised the shrub category, where logged sites supported a higher frequency of occurrence of shrubs, but the high frequency of occurrence was dominated by very few species.

Table 2: Percent frequency of individual midstory tree species, by disturbance classes

Disturbance	Midstory tree species	% Frequency
Undisturbed	*Dicksonia antarctica*	27%
	Nothofagus cunninghamii	15%
	Cyathea australis	14%
	Prostanthera lasianthos	7%
	Tasmannia lanceolata	7%
	Pomaderris aspera	4%
Low Severity	*Dicksonia antarctica*	25%
	Pomaderris aspera	21%
	Bedfordia arborescens	11%
	Cyathea australis	11%
	Prostanthera lasianthos	11%
	Tasmannia lanceolata	11%
High Severity	*Pomaderris aspera*	26%
	Prostanthera lasianthos	17%
	Dicksonia antarctica	17%
	Lomatia fraseri	9%
	Hedycarya angustifolia	6%
	Nothofagus cunninghamii	6%
Clearcut	*Pomaderris aspera*	56%
	Prostanthera lasianthos	20%
	Dicksonia antarctica	10%
	Cyathea australis	5%
Salvage	*Pomaderris aspera*	79%
	Prostanthera lasianthos	16%

We suggest that the simplification of plant biota observed in this investigation is likely to be repeated in other the forest ecosystems globally, where resprouting species comprise an important part of the plant assemblage. This includes wet tropical forests such as Brazilian Amazonia (Balch et al. 2013), dry tropical forests of India (Mondal and Sukumar 2015) and many other nations (Pérez-Harguindeguy et al. 2013). In contrast, some resprouting species such as Aspen (*Populus tremuloides*) in the boreal forests of North America can respond positively to salvage logging (Boucher et al. 2014), provided mechanical disturbance of the soil is limited, otherwise stem densities can deline (Fraser et al. 2004).

Implications for forest management and plant conservation

Our findings have several important implications for forest management around the world. First, our study demonstrates that the disturbance effects on plant assemblages from logging, and in particular those from salvage logging, often simplifies forest structure and species composition, particularly when it follows wildfire. This is likely to be the case for other forest ecosystems affected by wildfire (Lindenmayer et al. 2008) and, to a lesser extent, is likely for some other natural disturbances such as wind (Foster et al. 1997, Brewer et al. 2012). There will of course be exceptions where intense natural disturbances (for example volcanic eruptions) cause far greater impacts on diversity than any form of logging (Dale et al. 2005).

Despite some studies concluding that the impacts of logging may be congruent with the impacts of wildfire (Attiwill 1994, Baker et al. 2004, Perera et al. 2007), the disproportionate loss of ferns and midstory trees and overall reduction in species richness indicates this is not the case in Mountain Ash forests. Post-fire salvage logging resulted in greater simplification of the forest when compared to conventional green forest clearcutting (Figure 20).

Our study uncovered strong evidence of a large reduction in midstory trees from clearcutting and salvage logging. The midstory is a critical component of forest structure, providing many faunal species such as mammals (Seebeck et al. 1984, Grelle 2003, Lindenmayer et al. 2004) and birds (Laiolo 2002, Lindenmayer 2009) with food resources, nesting sites and a conduit for movement through the forest. Mechanical disturbance of the midstory and understory appears to be the primary factor leading to plant species loss in Mountain Ash forests when we compared logged sites to those burned by wildfire. Therefore, a key management strategy to limit impacts on potentially vulnerable plant functional groups would be to implement machinery exclusion zones that leave areas of forest undisturbed within and between cutblocks (Ough and Murphy 2004, Baker and Read 2011). Such undisturbed areas could have a secondary function of buffering old trees with cavities to enhance protection of these important habitat elements (Gustafsson et al. 2012, Lindenmayer et al. 2014) where they exist. We also recommend that post-logging assessments be broadened to include measures of species composition and monitoring of vulnerable species of the functional groups most affected by logging. In Mountain Ash ecosystems, there is a greater proportion of ruderal species compared to species which will return to a site only after a prolonged period post disturbance. Yet, when we closely examined plant functional group responses to determine which species were absent from all logged sites, none were transitory species, all were persistent species. Given the limited dispersal abilities of some of these persistent species, we predict that it may be many years before these species return, if ever. The large decrease in plant species richness following salvage logging is consistent with numerous studies from around the world (Van Nieuwstadt et al. 2001, Swanson et al. 2010, Leverkus et al. 2014).

Climate-induced natural disturbances are becoming more frequent and severe (Allen et al. 2010, Seidl et al. 2014b) which is resulting in salvage logging becoming increasingly common worldwide. Environmental regulations for salvage logging are often less stringent than for traditional logging (Lindenmayer et al. 2008). This is the case in many countries around the world, as well as in important international forest certification schemes (Forest Stewardship Council 2015). Given the disproportionately high levels of ecological impact on plant biota from this form of harvesting, we suggest that levels of environmental regulation associated with continued widespread salvage logging require serious reconsideration.

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CHAPTER 2

Non-linear Growth in Tree Ferns, *Dicksonia antarctica* and *Cyathea australis*

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ABSTRACT

Tree ferns are an important structural component of forests in many countries. However, because their regeneration is often unrelated to major disturbances, their age is often difficult to determine. In addition, rates of growth may not be uniform, which further complicates attempts to determine their age. In this study, we measured 5 years of growth of *Cyathea australis* and *Dicksonia antarctica* after a large wildfire in 2009 in south-eastern Australia. We found growth rates of these two species were unaffected by aspect and elevation but slope had a minor effect with *D. antarctica* growing 0.3mm faster for each additional degree of slope. Geographic location influenced growth in both species by up to 12 - 14mm/yr. The most consistent factor influencing growth rate, however, was initial height at the time of the 2009 fire; a finding consistent in both species and all geographic locations. For both tree fern species, individuals that were taller at the commencement of the study had greater overall growth for the duration of the study. This effect did not decrease even among the tallest tree ferns in our study (up to 6 metres tall). Overall, *Cyathea australis* averaged 73 (± 22)mm/year of growth (± 1SD), with the rate increasing 5mm/yr per metre of additional height. *Dicksonia antarctica* averaged 33 (± 13)mm/year, increasing by 6mm/yr/m. Growth rates dependent on initial height were unexpected and we discuss possible reasons for this finding. Variable growth rates also suggest that common age estimation methods of dividing height by average growth rate are likely to underestimate the age of short tree ferns, while overestimating the age of tall tree ferns, particularly if they have been subject to a fire.

INTRODUCTION

Tree ferns are found in wet forests worldwide, from tropical regions to cool temperate forests (Conant et al. 1995, Korall and Pryer 2014). Tree ferns are generally considered to be slow-growing, long-lived plants that do not require disturbance for reproduction, and as such, become increasingly common in the late successional stage of older forests (Ashton and Willis 1982, Lindenmayer et al. 2000). Tree ferns often fill important physical and ecological roles. In many forests, including those in Costa Rica, New Zealand and Australia, tree fern trunks host a wide range of epiphytic ferns and bryophytes (Roberts et al. 2005, Pharo et al. 2013, Brock et al. 2016), often supporting a greater diversity of such kinds of plants than the other trees in the same forest (Moran et al. 2003). Tree ferns influence the presence of other species both positively and negatively, for example, in the forests of south-eastern Australia there are positive relationships between the abundance of tree ferns and the occurrence of arboreal mammals such as the Mountain Brushtail Possum *Trichosurus cunninghami* (Lindenmayer et al. 1993) with these plant species providing both habitat structure and a food source (Seebeck et al. 1984), while in southern New Zealand, tree ferns have been found to negatively influence the regeneration success of other trees (Coomes et al. 2005).

In the cool temperate forests of south-eastern Australia where we completed this study, tree ferns are well adapted to the prevailing regime of infrequent but high severity fire (Hunt et al. 2002), resulting in these midstorey species often being older than the overstorey eucalypts, the majority of which are obligate seeders in this investigation (Mueck et al. 1996, Lindenmayer and Ough 2006). The tree fern species in this study can grow to over ten metres in height (Walsh and Entwisle 1994) and have been estimated to live more than 500 years (Mueck et al. 1996), while other species in Australia have been recorded growing in excess of 15m, including the Norfolk Tree Fern, *Cyathea brownii*, which can grow to 20m (Large and Braggins 2004). Tree ferns also may be an indicator of past disturbance history given their ability to survive fire, but susceptibility to logging (Peacock and Duncan 1995, Ough and Murphy 2004, Blair et al. 2016b). Because tree ferns regularly survive fire but do not require fire to regenerate, their age is not easily determined from the dates of previous major fires. While there have been several studies examining the conditions required for tree ferns to persist, there have been relatively few investigations of the effects of tree fern age, growth rates, or the environmental factors on growth rates, particularly in Australia (Ferwerda 1981, Mueck et al. 1996, Hunt et al. 2002, Volkova et al. 2010, 2011).

We studied the short-term growth rates of the two most common species of tree fern occurring in south-eastern Australia, the Rough Tree Fern (*Cyathea australis*) (R. Br.), family Cyatheaceae and Soft Tree Fern (*Dicksonia antarctica*) (Labill), family Dicksoniaceae. The genus *Cyathea* has Pan-Tropical origins (Page and Clifford 1981) with approximately 700 species globally (Walsh and Entwisle 1994) in the tropics, subtropics, and southern temperate zones (Korall and Pryer 2014) and includes 11 species in Australia. The genus *Dicksonia* is of Gondwanan origin (Page and Clifford

1981) with 50 species found in south-eastern Australia, New Zealand, south-east Asia and Central and South America. There are three species of *Dicksonia* in Australia (Walsh and Entwisle 1994). In our study region, the distributions of *D. antarctica* and *C. australis* overlap, with both found predominantly in cool, wet gullies. *Cyathea australis* is more tolerant of drier micro-climates, and commonly found in the mid to lower elevations where it is warmer and drier and away from streams; *D. antarctica* is most often found at mid to higher elevations where annual rainfall is greater, particularly at cold, wet sites close to streams (Dignan and Bren 2003).

Tree ferns grow by producing new fronds which extend from the centre of the apical trunk, extending and growing to the outside edge of the trunk. Over a period of 6-12 months, the older fronds gradually deteriorate and die, to be replaced by new layers of fronds with each new layer adding to the overall height of the fern's trunk. The older fronds eventually drop off and leave the base of the stipe on the trunk. In the study reported here, we quantified the short-term growth rates of *D. antarctica* and *C. australis* immediately following the Black Saturday wildfires in 2009 in Victoria. Thus, all tree ferns were burnt (with all fronds removed) with trunks of tree ferns blackened to the height they were at the time of the fire. New growth was easily distinguishable in the subsequent years and it was the height of this new growth that we subsequently measured. Previous investigations have measured fern growth following fire (Ferwerda 1981) and made estimates of maximum age (Mueck et al. 1996) by focussing on the largest individuals, while other studies examined the physiological effects of different temperatures and amounts of light on the photosynthetic abilities of tree ferns (Volkova et al. 2009, Volkova et al. 2010), although these factors were not then related to resulting changes in growth rate. No previous studies in the wet forests of Victoria, and few investigations internationally (Tanner 1983, Arens 2001, Schmitt and Windisch 2006, Nagano and Suzuki 2007), have measured the growth of tree fern trunks in field conditions, spanning a wide range of heights (and therefore ages) to determine if growth rates of overall trunk height vary with age.

We posed three key questions with related hypotheses: What are the rates of growth of *D. antarctica* and *C. australis* and do rates of growth vary between these two species? What factors, including environmental variables, influence the rate of growth of *D. antarctica* and *C. australis?* Finally, from our results: Are we able to devise a simple equation of dividing height by annual growth rate to estimate tree fern age? Given there is no clear consensus within the literature on which species grows faster, and at the leaf scale both have equivalent photosynthetic capabilities (Volkova et al. 2011), we hypothesised that *C. australis* would have similar growth rates to *D. antarctica* and that growth of both species of tree ferns will be affected by environmental variables. We postulated both species of tree ferns will grow most rapidly at higher elevations. In our study area, elevation is strongly positively correlated with rainfall and temperature. Previous field studies of these two species revealed a lack of effect of seasonal water use efficiency (Volkova et al. 2011), leading us to postulate that rainfall would not be a determining factor for growth in this area (which receives some of the highest and most consistent rainfall in mainland Australia (Australian Bureau of Meteorology 2017a, b)). Temperature has been found to affect tree fern growth in these two species. Lower elevations (our lowest sites were 275m ASL) are subject to periodic very high temperatures during summer, with temperatures in excess of 40ºC. While Volkova et al (Volkova et al. 2009) found no change in photosynthetic capacity in *D. antartica* with high temperatures (35ºC) under shade, when combined with high irradiance, severe photoinhibition was witnessed. On our burned sites, high irradiance was common, thus the higher temperatures at these lower altitudinal sites were expected to reduce growth. Conversely, the lowest temperatures in winter are recorded on our highest sites (up to 985m ASL), with snow falling most winters. Such low temperatures were also found to inhibit photosynthesis (Volkova et al. 2011). Snow could potentially retard growth by reducing solar interception, however snow does not persist for long periods (usually days at most, not weeks). On balance, we postulated it was most likely the greater reduction in quantum yield, leading to overall lower trunk height growth, would come from the higher temperatures in summer when photosynthetic activity is greatest and is the time of year when the tree ferns have their greatest period of growth (Lee et al. 2009, Volkova et al. 2011). We further postulated tree ferns growing on sites on hotter and drier northerly aspects were likely to grow more slowly than on sites on cooler aspects due to slower growth associated with hotter temperatures (Volkova et al. 2009). We did not expect geographic location to affect growth. Given most studies on tree ferns in Australia assume a constant growth rate through time (Ferwerda 1981, Mueck et al. 1996), we expected to be able to develop a relatively simple growth equation based on annual growth increments, however several international studies on other tree fern species suggest this may not be possible due to variable growth over the life of the tree ferns (Tanner 1983, Arens 2001, Schmitt and Windisch 2006, Nagano and Suzuki 2007).

METHODS

Our study focused on the forests of the Central Highlands of Victoria, 60-120km east of Melbourne in south eastern Australia (Fig 1).

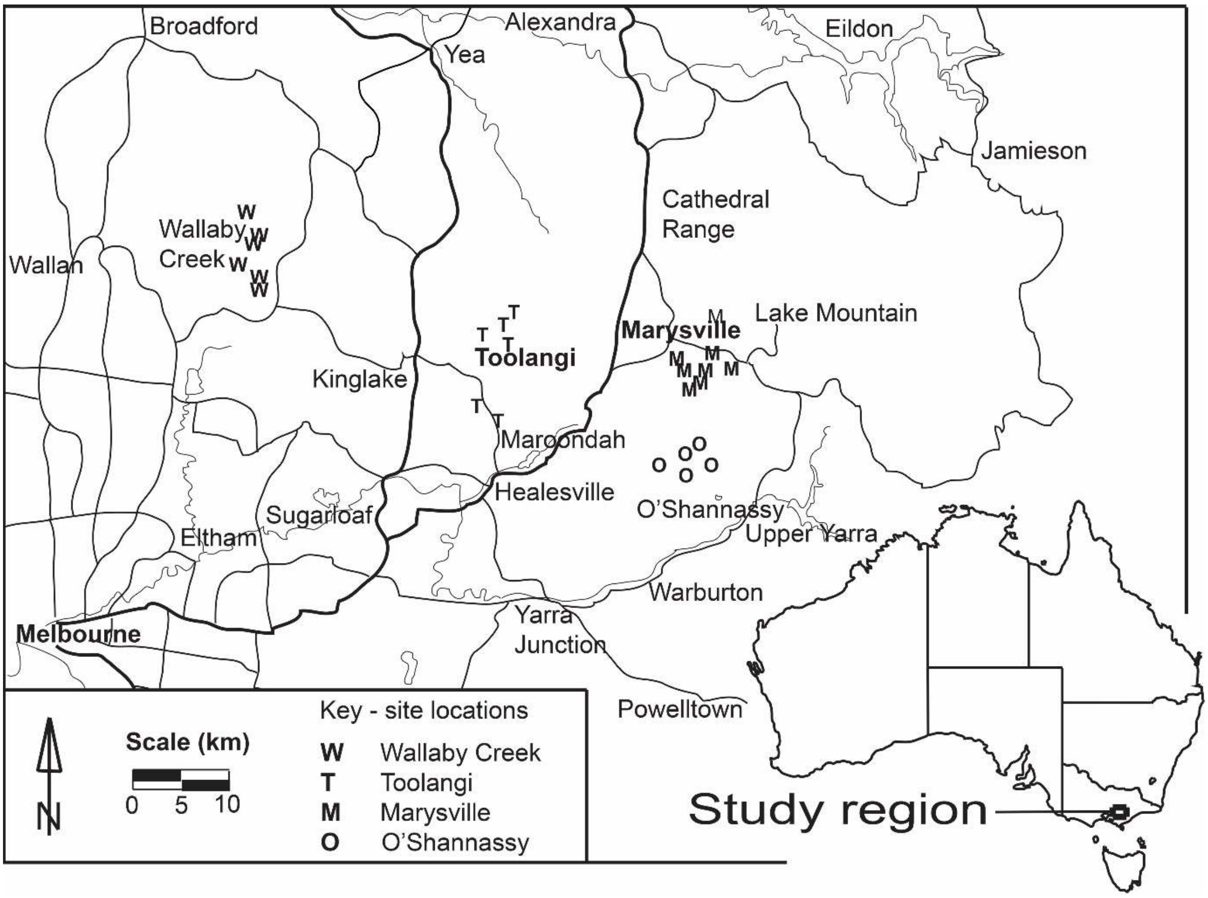

Figure 1: Map of study region showing location of sites

Sample areas and fern selection

We measured tree ferns at 25 sites within four separate geographic locations: Marysville State Forest, O'Shannassy water catchment, Toolangi State Forest, and Wallaby Creek water catchment (see Fig 1). At each geographic location, we selected 5-8 sites, and then measured up to ten tree ferns of each species at each site. In total, we measured 163 stems of *Cyathea australis* ranging in pre-fire height from 0.37m to 6.20m and 172 stems of *Dicksonia antarctica,* with heights between 0.28m to 5.03m (Table 1). Each site was selected to allow 10 tree ferns to be measured close to each other (each site having a maximum 25m radius) and with limited variation in slope, aspect and elevation. While there was uniformity of environmental variables *within* sites, we specifically chose sites around each geographic location that would cover a wide range of environmental variables (aspect, slope and altitude) *between* sites. Each site was a minimum of 1 km apart to minimise the potential for spatial depencence to influence our results.

Table 1: Summary of attributes for *C. australis* and *D. antarctica* at geographic area and site level

	C. australis	***D. antarctica***	**Total for study**
Number of geographic areas	3	4	4
Number of sites	16	17	25
Number of ferns measured	163	172	335

Height range (time of fire)	0.37 – 6.20m	0.28 – 5.03m	0.28 – 6.20m
Altitude range	275m – 975m	395m – 985m	275m – 985m
Slope range	0^{o} – 32^{o}	1^{o} – 28^{o}	0^{o} – 32^{o}

The dominant forest types where our sites were located included mixed (eucalypt) species foothill forest dominated by Messmate (*Eucalyptus obliqua*), Peppermints (*E. radiata* and *E. dives*) and Stringybarks (predominantly *E. macrorhyncha*), and at higher elevations, forests dominated by Mountain Ash (*E. regnans*) and Alpine Ash (*E. delegatensis*). The majority of our sites (21 of our 25 sites), were in the ash forests. Large wildfires dominate the ecology of these forests with intense, stand replacing fires historically occurring on average every 75 – 150 years (McCarthy et al. 1999).

To ensure all tree ferns had had their trunks burnt at the same time (February 2009) and physically blackened uniformly up the trunk (up to 6m tall), we selected sites that had burned at moderate to high severity in the 2009 wildfires. We used fire severity maps from the Victorian Government GIS layer and local knowledge to identify suitable locations. On the Victorian Government fire severity scale, this included areas burned at severity 1-3 (on a scale of 1-6, where 1 is highest severity) and in which the midstorey was fully scorched (Jemison 2012, Benyon and Lane 2013).

At each site, we measured 10 tree ferns of each species unless insuffiicent tree ferns of either species were able to be found. Eight of the 25 sites supported 10 individuals of both tree fern species. We measured 10 of the tree ferns nearest to the centroid of each site, ensuring that ferns of differing heights were measured. We elected not to measure ferns with multiple trunks, tree ferns with any section of the trunk leaning at an angle of 30^{o} or greater, or ferns that had fallen over and continued to grow. We located the centre of each site away from road edges to reduce potential effects of additional light, temperature differences or water run off.

Determining growth rates

To determine the growth rates of tree ferns, we located tree ferns with trunks that showed clear delineation between the lower part of the trunk which had been burnt by the February 2009 wildfires and the unburnt upper section of trunk resulting from subsequent growth in the following 5 years, when the ferns were measured between February and April 2014. We measured the overall height of each tree fern using a tape measure, while the new growth was measured using callipers. We then divided the new growth from the last five years (post fire growth) by five to give an overall annual average rate of growth for each individual tree fern.

We took more than two thousand photographs of the study region progressively over the 5 years between the time of the fires to the time of measurement and by looking at these and through field observations, we were able to determine the majority of tree ferns had visible new fronds within 1-4 months of the 2009 fire, indicating growth typically did not appear to have paused due to the fires, despite rare occurrences where some individuals took up to a year after fire to re-sprout.

Statistical analyses

We used a linear random effects model to explore relationships between annual growth rate and geographic region, elevation, slope, aspect and initial height of the tree fern post 2009 wildfire. Aspect of each site was allocated to the nearest of the eight major compass points (north, north east, east etc.). North, north-west and north-east were collated as 'northerly aspects' and analysed against all other aspects combined. This was done to ascertain whether the hotter, drier conditions of the northerly aspects effected tree fern growth. Rainfall within the study area is highly positively correlated with elevation with the summer (November-March) rainfall correlation being 0.910 and winter (April – October) being 0.717. The analysis for both altitude and rainfall resulted in similar findings, therefore we excluded rainfall from subsequent analyses. Site was treated as a random effect to account for potential correlation among the tree ferns at the same site. We used the MCMCglmm package (Hadfield 2010) to fit the models in R 3.2.1 (R Core Team 2015). The model parameters are summarized by the posterior mean, 95% credible intervals and Btail, which gives the fraction of the posterior distribution that is to the left or right of zero conditional on whether the posterior mean was greater or less than zero, respectively. Small values of Btail indicated support for non-zero parameter values, that is, posterior distributions that are shifted away from zero.

We did not perform model selection, but rather chose to interpret the full model for each tree fern species. We also performed a diagnostic analysis to assess the underlying assumption of normality and to assess the need to include a site-level random effect. There was very little support for the inclusion of the site-level random effect, and hence our results show the models without this term.

Ethics statement

Our research required no ethics approvals as we were undertaking non-destructive vegetation measuring without collection of any vegetation samples and we were not studying fauna. Our sites were all in publicly accessible locations on public land controlled by the Victorian Government, and therefore no special permission was required.

RESULTS

Overall tree fern growth rates

From our field data, we calculated the overall average growth of *C. australis* to be 73 (+/- 22)mm/year of growth (+/- 1 SD) and 33 (+/- 13)mm/year for *D. antarctica* (Table 2).

Table 2: Summary of growth rates of C. australis and D. antarctica, for all ferns measured on all sites

	C. australis	***D. antactica***
Number of tree ferns measured (n)	163	172
Average growth (mm/yr)	73	33

Standard Deviation (mm/yr)	22	13
Maximum growth of an individual fern (mm/yr)	135	75
Minimum growth of an individual fern (mm/yr)	19	7
Additional growth per m of height (mm)	5	6

Growth rates and initial height

For both *C. australis* and *D. antarctica*, initial height in 2009 was the most significant (Btail <0.001) determinant of growth rates. *Cyathea australis* grew an additional 5mm each year for every additional meter in height the tree fern was at the time of the fire. For *D. antarctica*, the increase in growth for taller ferns was even greater with an additional 6mm of additional growth measured each year for each meter taller the ferns were at the time of the fire (Table 2).

Growth rates and environmental variables

Environmental variables had limited influence on growth rates in *C. australis* with no significant effect identified for slope, elevation or aspect. In contrast, *D. antarctica* grew more rapidly on steeper slopes at a rate of 0.3mm/year for each additional degree in slope (Btail = 0.010). Elevation and aspect had no influence on the growth rate of *D. antarctica* and *C. australis*.

Growth rates and geographic location

Other than initial height in 2009, geographic location had the largest effect on growth rates. *Cyathea australis* grew most rapidly in the Toolangi region, with the growth rate being 13.8mm/yr faster than tree ferns in Marysville (Btail = 0.002). Tree ferns in Wallaby Creek grew 11.7mm/yr faster than in Marysville (Btail = 0.009) (Fig 2). There were insufficient numbers of *C. australis* in the O'Shannassy water catchment for statistical analyses of geographic location effects.

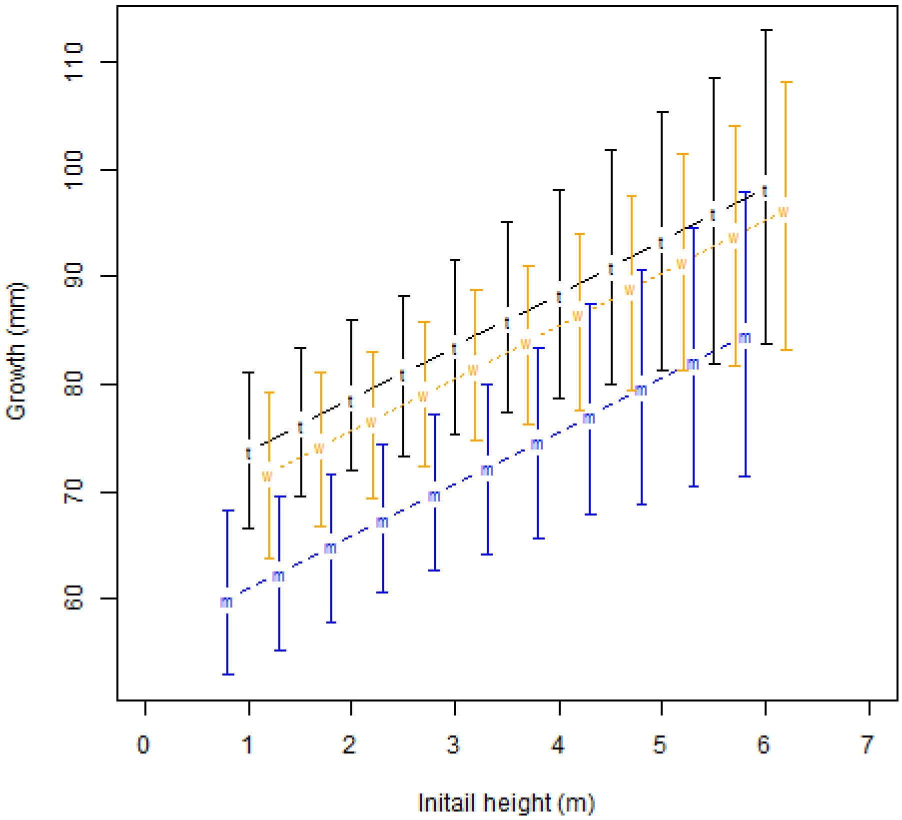

Figure 2: Annual growth of *C. australis* by initial height and geographic area (note that height has been slightly offset for each geographic region to improve readability), based on modelled data. m = Marysville State Forest, t = Toolangi State Forest, w = Wallaby Creek water catchment

Dicksonia antarctica grew most rapidly in the Wallaby Creek water catchment and was 12.5mm/yr faster than in Marysville State Forest (Btail = 0.002), 10.2mm/yr faster than in Toolangi State Forest (Btail = 0.002), and 8.8mm/yr faster than in O'Shannassy water catchment (Btail = 0.004). There was no significant difference in growth rates between the other three geographic locations for this species (Fig 3).

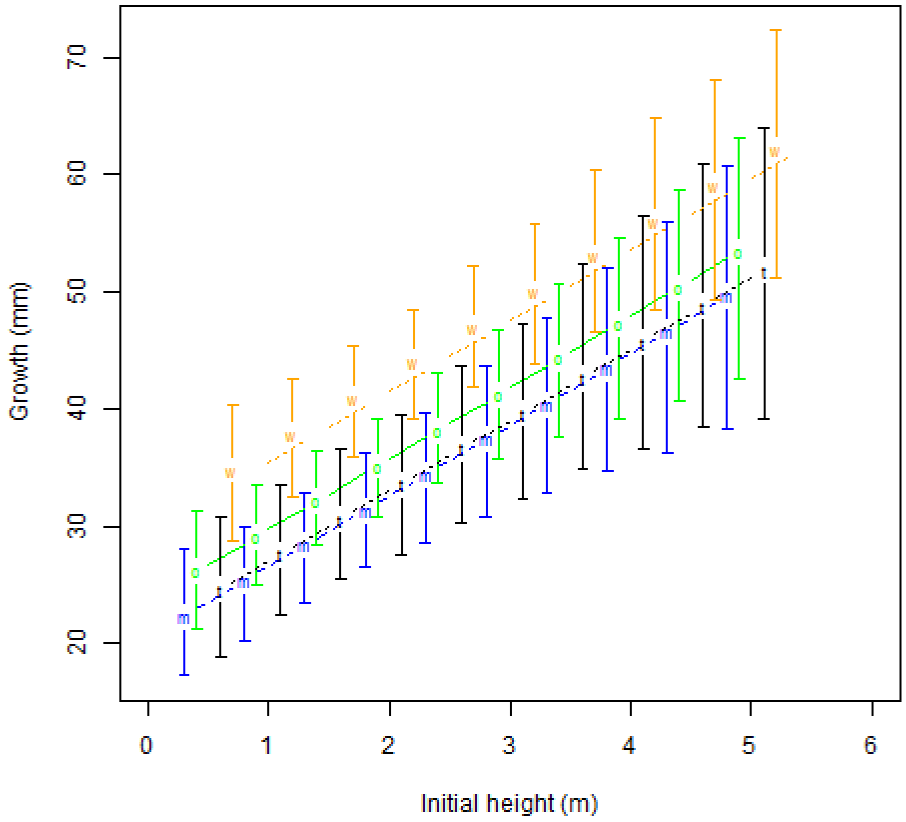

Figure 3: Annual growth of *D. antarctica* by initial height and geographic area (note that height has been slightly offset for each geographic region to improve readability), based on modelled data. m = Marysville State Forest, o = O'Shannassy water catchment, t = Toolangi State Forest, w = Wallaby Creek water catchment

DISCUSSION

We posed a series of questions relating to the growth of the two most common tree fern species in south-eastern Australia, *D. antarctica* and *C. australis,* and the factors that influenced their growth. We expected that the environmental variables we measured would influence growth with the more favourable conditions being in areas at higher elevation, where temperatures are lower. Snow falls are common in winter at sites at higher elevation but this was thought to be of little consequence due to its limited persistence and occurrence at the time of year when tree ferns grow the least (Lee et al. 2009). At lower elevations, high temperatures and drier conditions throughout the summer are common which are likely to affect growth rates, especially when combined with high irradiance (Volkova et al. 2009). At the outset of this investigation, we expected growth of both species to be lower on the hotter and drier northern and western aspects compared to cooler southern and eastern aspects. With the forests of the four geographic areas having broadly similar rainfall (long term average between 1194-

1393mm per annum for the 4 areas,(Australian Bureau of Meteorology 2016)), we expected similar growth rates across the different geographic locations where other environmental variables such as aspect, elevation and slope were the same.

We found growth rates varied in unexpected ways with initial height at the time of the fire being the strongest determinant of growth rate. In the following sections, we discuss possible explanations for our findings.

Comparison of tree fern growth rates

Values for the average growth rate of *C. australis* and *D. antarctica* were broadly within the range of two other earlier studies in south-eastern Australia (Ferwerda 1981, Mueck et al. 1996) (Table 3). Mueck et al (Mueck et al. 1996) used radiocarbon dating from the base of tall specimens of *C. australis* and *D. antarctica*, dividing height by age to give an average growth rate. Their findings were highly variable for *D. antarctica* with both the highest and lowest growth rates outside 2 standard deviations of our result. Mueck et al (Mueck et al. 1996) concluded the higher end of their results for *D. antarctica* were probably overestimates. Ferwerda (1981) measured tree fern frond spacing on coastal bluffs and new growth after fire in forests similar to our study. Despite the results of Ferwerda (1981) being 1.8 standard deviations higher than our own, all of the post-fire measurements from that study were taken from tall specimens, for which our study indicates growth rates to be above average.

Table 3: Summary of tree fern growth studies in Victoria, south-eastern Australia

Study	Location	Method	Species	Growth rate
Ferwerda (1981)	Western Port	Frond spacing	*C. australis*	105 mm/yr (n=5)
Ferwerda (1981)	Ferntree Gully NP	Regrowth after fire	*C. australis*	113 mm/yr (n=6)
Mueck et al (1996)	Toolangi	Radio carbon dating	*C. australis*	22-38 mm/yr (n=2)
Mueck et al (1996)	Toolangi	Radio carbon dating	*D. antarctica*	5-88 mm/yr (n=6)
This study	Central Highlands	Regrowth after fire	*C. australis*	73(+/-22) mm/yr (n=163)
This study	Central Highlands	Regrowth after fire	*D. antarctica*	33(+/-13) mm/yr (n=172)

Environmental variables

We found only limited effects of environmental variables on growth rates, despite at the outset of the study predicting all three variables (elevation, slope and aspect) would be important based on results from other studies (Jones et al. 2007, Brock et al. 2016). Our analyses revealed that elevation had a very limited effect, with growth rates increasing marginally with increased elevation. This may indicate that temperature and rainfall, both of which are highly correlated with elevation in our study area, did not have an effect, or that there were additional factors that masked these effects. A lack of effect was unexpected due to temperature, in particular, having been shown to alter quantum yield (Volkova et al. 2009, Volkova et al. 2011). In addition, both variables have been identified as important determinants of the distribution of *C. australis* and *D. antarctica* (Neyland 1986, Fedrigo et al. 2014, Brock et al. 2016). It therefore appears that what affects the distribution of tree ferns may not influence growth rate.

Geographic location

We did not measure sufficient or appropriate additional variables to determine why the growth rate of tree ferns would vary between different geographic locations. Different local factors are important as Toolangi State Forest was the area of fastest growth for *C. australis*, but slowest growth for *D. antarctica.* Wallaby Creek water catchment seemed very favourable to both species with *D. antarctica* growing significantly more rapidly relative to other locations. In New Zealand, Brock et al (Brock et al. 2016) found tree fern growth increased with decreasing latitude. In contrast, the geographic range of our study was far more restricted, but also spread more east-west with minimal difference in latitude. As such, latitude was unlikely to be a factor affecting our results.

Cyathea grow faster than *Dicksonia*

We confirmed that *C. australis* grows faster than *D. antarctica*. This is perhaps not surprising given *Cyathea* as a genus has many very fast growing species and, on average, have larger crown spread than *Dicksonia* (Large and Braggins 2004).*This* may in part be due to *C. australis* having a greater specific leaf area of 10.4m^2/kg compared to 8.6m^2/kg for *D. antarctica* (Volkova et al. 2011) which provides for greater photosynthetic capability. Physiologically, *Cyathea australis* also has leaf hairs that may reduce UV-B exposure in the post-fire high growth irradiance environment. It is thought these leaf hairs also may explain why *C. australis* has a broader climatic niche that *D. antarctica* (Dignan and Bren 2003, Volkova et al. 2011). Interspecific differences in growth rates also may be due to differences in rooting structure or due to resources extracted by bryophytes and epiphytes, which are in greater numbers on the moister fibrous trunks of *D. antarctica* than on the drier stipe shielded trunks of *C. australis* (Ashton 1986). The difference in microclimatic conditions of locations where these tree fern species are found also may effect growth rates.

Taller ferns grew more

Contrary to our expectations at the outset of this investigation of uniform growth rates for ferns of different height, we found that taller *C. australis* and *D. antarctica* had grown more than shorter individuals during the 5 year period of measurement. We considered four possible reasons for this: 1) The size and spread of the rosette of fronds, which increase in diameter as ferns become established; 2) shorter ferns being more negatively affected by the fire and being less capable of using fire released nutrients; 3) growth rates for these species were exponential; and 4) following increases in light availability due to overstorey canopy removal by fire, taller ferns being exposed to these increased light levels for longer as shorter ferns are over taken and shaded by regrowing tree species for a greater proportion of the study period. We examine these four explanations in detail below.

Our first proposition suggested the larger rosettes of older ferns may allow for greater growth due to increased capture of light (and therefore photosynthetic capacity) and re-direction of rainfall compared to shorter ferns with smaller crowns. Interception of rainfall by tall tree ferns may further limit rainfall reaching short individuals when they are situated beneath taller ones. New fronds pointing upwards funnel water into the top of the trunk where aerial roots surround the fronds, as well as fronds themselves being capable of direct uptake of moisture (Hunt et al. 2002). However, higher growth rates achieved through the effect of greater interception of both light and rainfall should taper once maximum crown diameter is reached, which from our observations, occurs when ferns are approximately one metre in height.

Given we measured growth following a major wildfire, the second possible explanation for our observation of taller ferns growing faster than short tree ferns, was the change in photosynthetic capability due to loss of fronds, potentially counter-balanced by a positive effect of increased growth due to increased availability of nutrients in the ash bed following fire (Attiwill and Leeper 1987). Physical damage from fire could have greater effects on short ferns which have their crown closer to ground level and where fuel loads are generally highest. If fire damage was a factor affecting growth rates, we would expect aspect and slope to have been important covariates in our models because they have a strong influence on fire severity (Berry et al. 2015). It also seems unlikely such effects would be influential beyond the first year unless the fire delayed post-fire re-sprouting in shorter ferns. We checked for such effects by viewing several hundred post-fire photographs of burned stands but found no evidence of retarded resprouting of short ferns compared to tall ones. Increased nutrients may be a factor underpinning changes in growth rates pre and post fire. However, as all our measurements were post-fire, this does not explain the greater rates of growth among taller ferns, unless dominant individuals were able to monopolize resources, which seems unlikely.

A third possible explanation for our results was that we had measured exponential growth, or that taller tree ferns inherently grew faster. Given that initial height of the tree ferns at the time of the 2009 fire determined how much they grew, and that this apparent increased growth rate did not seem to taper over the duration of our investigation (Figs 2 and 3), a possible conclusion was that we had discovered exponential growth throughout a plant’s life, a very unusual pattern for any plant species. The only example in the literature for tree ferns that suggested this may be possible was a Jamaican study on *Cyathea pubscens* that found stipe interval increased with trunk height, indicating possible growth acceleration with time (Tanner 1983), although this was not directly measured. To test this explanation, we modelled exponential equations from our data. However, given the longevity of these two species, our equations provided highly unrealistic results for old tree ferns with heights over 50 metres tall, suggesting another explanation was needed.

A fourth possible explanation for our results was canopy removal by fire of the surrounding trees and shrubs and subsequent sequential shading by dense regeneration. In the forests of the Central Highlands, following a high severity fire such as the one at the start of our study period, all strata have foliage removed (Lindenmayer et al. 2015) leading to greatly increased light availability. This is followed by a pulse of vigorous regrowth of eucalypts and *Acacia* germinating from seed. From other unpublished vegetation data we collected on post fire regrowth, measured across the same period as our study, we know the growth rate of this dense cohort of trees is rapid but is relatively uniform (Blair et al. 2016a). After a year to establish, the regrowth grows at approximately 1-1.5m/year. The regrowth is very dense and provides almost complete shade to plants beneath the canopy. The loss of overstorey canopy shading due to the fires created a period of greatly increased light penetration reaching the tree ferns, which may have led to an accelerated growth rate (Ash 1987, Brock et al. 2016). For the shortest ferns in our study, the period of increased light availability due to absence of overstorey canopy may have lasted less than 12 months, while the tallest ferns studied would have had such conditions for three to five years, giving them more favourable growing conditions for longer.

Differential growth of individuals in sun, compared to those located in shade, has been observed in tree fern studies in Columbia (Arens and Baracaldo 2000). Observations from New Zealand found different tree fern species occupy niches along a shade-light spectrum where growth varied, but importantly, where recruitment was also effected by shade levels (Bystriakova et al. 2011). A series of studies on the physiology of both *D. antarctica* and *C. australis,* in greenhouse and field conditions, showed high irradiance caused decreases in photosynthetic capacity (Volkova et al. 2009, Volkova et al. 2010, 2011). However, these same studies also showed varying ability of these species to acclimatise to such changes in irradiance over periods up to 3 months. The one field-based study of the three, which was the only one studying tree ferns more than a year old, found the ability for seasonal acclimation (Volkova et al. 2011). Lower temperatures in winter were shown to reduce photosynthetic capacity, so it may be that the additional warmth of full sun exposure during winter allowed additional growth in our study despite our study finding temperature not to be influential. Actual growth rates were not measured in these studies. The results from Ferwerda (1981) would support our concept of variable growth rates in tree ferns as it was the tallest ferns burnt by fire (and therefore exposed to more light for longer) that had the greatest growth rates in that study.

If tree ferns grow faster with increased available light, this may assist interpretation of the results of other studies. For example, a study in Costa Rica which concluded growth rates were related to whether the surrounding habitat was primary or secondary forest (Bittner and Breckle 1995), only briefly mentioned light levels. Our study would suggest that increased light levels may have been important, with tree fern growth in open secondary forest being up to three times that of closed primary forest. The concept of greater growth rates in sun compared to shade was found to hold true in a study from the Andes, where *Cyathea caracasana* grew more rapidly when exposed to full sun compared to closed forest (Arens 2001). The conclusion was that *C. caracasana* was a species that was able to take advantage of gaps in the forest to grow rapidly and produce large volumes of spores, then slow down again but persist as shading increased. It would appear that tree ferns in Australia may follow a similar ‘sit and wait’ life strategy. However, our findings showing an increase in growth rate as ferns became taller was in contrast to a study of five *Cyathea* species in Costa Rica where growth remained constant over time (Bittner and Breckle 1995), or in Japan where growth of *Cyathea spinulosa* slowed gradually over time (Nagano and Suzuki 2007). It was also counter to the assumption (without evidence) made by Ferwerda (1981) that growth rates of *C. australis* would slow as the ferns increased in height.

We do not know if tree ferns in Australia produce additional spores during times of increased light exposure and accelerated growth, but if this is the case, it could have significant implications for forest management if an aim is to encourage tree fern recruitment in areas where they have been reduced in number (such as logged stands or areas where tree fern harvesting occurs). In New Zealand, tree ferns rapidly colonise open areas with suitable conditions, however this does not appear to be the case in Australia (Pope 1926, Brock et al. 2016). Improved recruitment of tree ferns across logged areas may be possible by retaining them around the edge of cutblocks, in undisturbed islands of forest retained across harvested areas where they are more likely to survive and where possible, within the cut area. By retaining tree ferns in multiple directions, this is likely to enhance post-disturbance recruitment because the tree fern’s spores are wind dispersed.

We did not specifically measure light interception, canopy cover or spore production by tree ferns. Further research measuring tree ferns in areas subject to different light regimes is required. Given *D. antarctica* tends to grow to a height of ~ 5-6m before collapsing, it should be possible to test whether it is age or height (and therefore access to light) that most strongly influences growth rate. If old fallen tree ferns grow at the same rate as much younger ferns which are the same height, this would lend weight to light being significant driver of growth rates. If however, they continue to grow at similar rates to those of the same age, it would indicate age is a more important driver of growth rates.

CONCLUSIONS

Tree ferns are an important element of stand structure and species composition of many forests worldwide. They have numerous key ecological roles such as providing food, nesting sites and movement pathways for animals and being host sites for a wide diversity of epiphytic plants. Tree ferns are long lived and are commonly found in old growth forests. The factors that determine where tree ferns persist appear to be different from those that determine growth rates. Accurate estimation of their age remains difficult due to growth rates varying through a plant’s life, preventing the development of simple equations such as those that divide height by growth rate. Given our measurements were taken across a period when increased growth rates due to the increased light availability seems likely, the average growth rate for the two species of tree ferns are likely to be above longer term averages when greater shading is the norm. Despite being well adapted to fire, tree ferns are highly susceptible to logging (Ough and Murphy 2004, Blair et al. 2016b) and if spore production in these species is found to increase with increases in available light, this may have important implications for forest management. Our research, while a relatively short term cross-sectional study of these long-lived organisms, increases our understanding of their ability to grow rapidly following fire and may assist with the management of these important species.

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SUPPORTING INFORMATION

S1 Table. Summary of locations, number of ferns and variables measured.

Geographic Region	**Location**	**# ferns measured**		**Aspect**	**Altitude**
		Cyathea	**Dicksonia**		
Marysville	Yellow dog	10		S	500
	Yellow dog + 1k	10	10	S	605
	Olsens		10	SW	840
	Lady Talbot bottom	10	2	flat	395
	Tommys Bend		10	W	985
	Tommys Bend/Yellow dog	1	10	W	975
	Site 805	10	10	N	924
	Paradise Plains Rd, 1.8km below Keppel Lookout	10		N	640
O'Shannassy	Poley/Paradise Plains		10	SW	940
	Rd 9	1	10	flat	860
	Rd 9 / 7		10	W	945
	Site 512	1	10	flat	770
	Rd 9 1km from Rd 7		10	flat	830
Toolangi	Nolans	10	10	flat	690
	Chum Creek -5km	10		SW	275
	Chum Creek -3km	10		SW	355
	Blowhard at 277	10		NW	640
	Starlight Rd	10	10	flat/E	715
	Klondyke/Mt Klondyke	10	10	NE	682
Wallaby Creek	Rd 3, 200m from Rd 10	10		flat/S	530
	Rd 3, 1km from Rd 10	10		S	590
	Rd 3, 0.5km W of Rd 15	10	10	S	670
	Rd 3, 0.7km S of Rd 12	10	10	S	685
	Rd 3 / Rd 14 intersection	10	10	flat	690
	Rd 14, 0.2km E of Rd 2 at the creek		10	flat/NE	660

S1 Table 2. Modelling results for the two fern species. Where L-95% CI and U-95% CI are the lower and upper end points of the 95% credible interval and Btail is a measure of support (see Methods for more detail).

Cyathea australis

	Posterior Mean	L-95% CI	U-95% CI	Btail
GR: Marysville, Aspect: North	37.923	15.766	62.391	**0.002**
GR:Toolangi vs Marysville	13.856	5.630	22.474	**0.002**
GR: Wallaby Creek vs Marysville	11.686	2.055	21.191	**0.009**
Elevation	0.019	-0.006	0.044	0.066
Slope	-0.016	-0.443	0.404	0.460
Aspect: Other	5.502	-4.142	15.134	0.126
Initial Height (m)	4.902	2.015	7.696	**<0.001**
GR: Toolangi vs Wallaby Creek	2.17	-8.914	12.660	0.343

GR = Geographic Region

Dicksonia antarctica

	Posterior Mean	L-95% CI	U-95% CI	Btail
GR: Marysville, Aspect: North	3.662	-16.762	24.794	0.360
GR: O'Shan vs Marysville	3.745	-2.374	9.95	0.118
GR:Toolangi vs Marysville	2.261	-4.799	9.559	0.273
GR: Wallaby Creek vs Marysville	12.514	5.934	20.201	**0.002**
Elevation	0.016	-0.005	0.036	0.061
Slope	0.333	0.069	0.637	**0.010**
Aspect: Other	-0.195	-5.273	5.105	0.475
Initial Height (m)	6.000	3.188	8.889	**<0.001**
GR: O’Shan vs Toolangi	1.484	-6.333	9.329	0.357
GR: O’Shan vs Wallaby Creek	-8.769	-15.393	-2.305	**0.004**
GR: Toolangi vs Wallaby Creek	-10.253	-16.241	-3.855	**0.002**

GR = Geographic Region

CHAPTER 3

Testing succession theory using a chronosequence study of Mountain Ash forest following wildfire

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ABSTRACT

The study of succession within forest ecosystems has a long history with the development of many explanatory theories over the last century. It is increasingly unusual however, for an ecosystem to be free from confounding effects of human disturbance. We studied vascular plants in parts of the Mountain Ash (*Eucalyptus regnans*) ecosystem of the Victorian Central Highlands in south-eastern Australia, where major disturbances (other than natural wildfires) have been minimal prior to and since European settlement of the region. Using sites in forest of four age classes that regenerated following high severity fires (in 2009, 1983, 1939 and 1851), we constructed a 'space-for-time' chronosequence to quantify differences in overall species richness and the species richness of different plant functional groups. We used these to test a range of theories associated with forest succession.

Overall species richness was highest in the youngest forest (3 years of age) with 17.1 species/plot and lowest in regrowth forests of 29 and 73 years of age, with 12.9 and 12.5 species/plot respectively. Our oldest cohort (161+ years old), supported intermediate numbers of species (13.4 species/plot). Sprouting species, ferns and midstorey trees were most species rich in the oldest cohort, and lowest in the young regrowth forest, indicating Relay Floristics and inhibition succession by these groups as they most likely supressed other species. Seeding species such as eucalypts, *Acacia*, herbs, shrubs and graminoids all exhibited a decline in species richness with increasing forest age, indicating Initial Floristic Composition may be the most likely successional theory to explain changes in these functional groups. Biological legacies were important to all groups. With different functional groups described most accurately by a range of successional theories, this suggests it may be an oversimplification to try and explain the patterns of species richness for all plants in an ecosystem using only a single successional theory.

Our results provide an important baseline showing succession in Mountain Ash forests in areas with minimal human disturbance. This allows comparisons to be made with human disturbances or future changes in regeneration trajectories due to climate change. Our results also suggest the need for careful management of sprouting species as these are the slowest to recover after disturbance.

Key words: functional group, life form, species richness, *Eucalyptus regnans*, Initial Floristic Composition (IFC), Relay Floristics, disturbance, plant traits.

INTRODUCTION

Succession within forest ecosystems has been studied for over a century (Clements 1916, Egler 1954, Cremer and AB 1965, Connell and Slatyer 1977, Pulsford et al. 2014). As succession theory has developed, there has been recognition of complexity in plant responses arising from differences in recovery trajectories. The range of recovery trajectories are influenced by an array of factors (Roxburgh et al. 2004). The state (e.g. age) of an ecosystem at the time of a disturbance can have important effects on species composition and trajectories post disturbance (Drury and Nisbet 1973, Phillips 2011, Swanson et al. 2011). The frequency of disturbance also can change the recovery path, particularly if multiple disturbances occur in a relatively short timeframe (Bowman et al. 2014b, Bowd et al. 2018a). Also of fundamental importance is the type of disturbance, whether it is natural (e.g. a windstorm, wildfire, eruption, landslide etc.) or human induced (e.g. logging, grazing) (Foster et al. 1999, Blair et al. 2016, Sass et al. 2018).

An understanding of natural succession without such human influences is required to better understand forest succession, including differences in succession between infrequent, natural disturbances and human disturbance, or the effects of rapid multiple disturbance events. Unfortunately, this is increasingly difficult to achieve given so much of the world's natural forests have been subject to human disturbance (Hansen et al. 2010, Mackey et al. 2015, Watson et al. 2018).

Here, we document succession in response to wildfire in the iconic wet temperate forests of the Victorian Central Highlands of south-eastern Australia. Substantial areas of these forests have been subject to significant human disturbance, however some areas have had very little human interference. We focused our studies on parts of the Mountain Ash forests that have been subject to minimal indigenous or European human disturbance. Before European settlement, indigenous people travelled through or hunted within these forests, but did not live permanently within them (Griffiths 2001). Unlike much of Australia, burning by indigenous people was not done in a deliberate and systematic way in the Mountain Ash forests (Griffiths 2001), and at most, limited burning may have occurred around the margins (Gammage 2011). After European settlement and before the forests were impacted by logging or mining, substantial areas of water catchment were set aside and protected for water supply, resulting in very limited human disturbance in these areas including being closed to public access. Such protection continues to the current day (Viggers et al. 2013). This provided a rare opportunity to quantify natural patterns of succession with minimal human influence, and before climate change potentially alters these unusual examples of undisturbed forests (Allen et al. 2010, Mok et al. 2012).

We studied vascular plants in a chronosequence of four age classes after major wildfires in 2009, 1983, 1939 and 1851 or older; resulting in forests that were 3, 29, 73 and 161+ years old at the time of our surveys. We compared changes in species richness with predicted patterns derived from the diverse range of succession theories (Figure 1 and Table 1). We also quantified the response patterns of specific functional groups of plants including those with different life forms and reproductive strategies. In this way, we aimed to determine which, if any, of the numerous successional theories best explained the key successional drivers within this ecosystem.

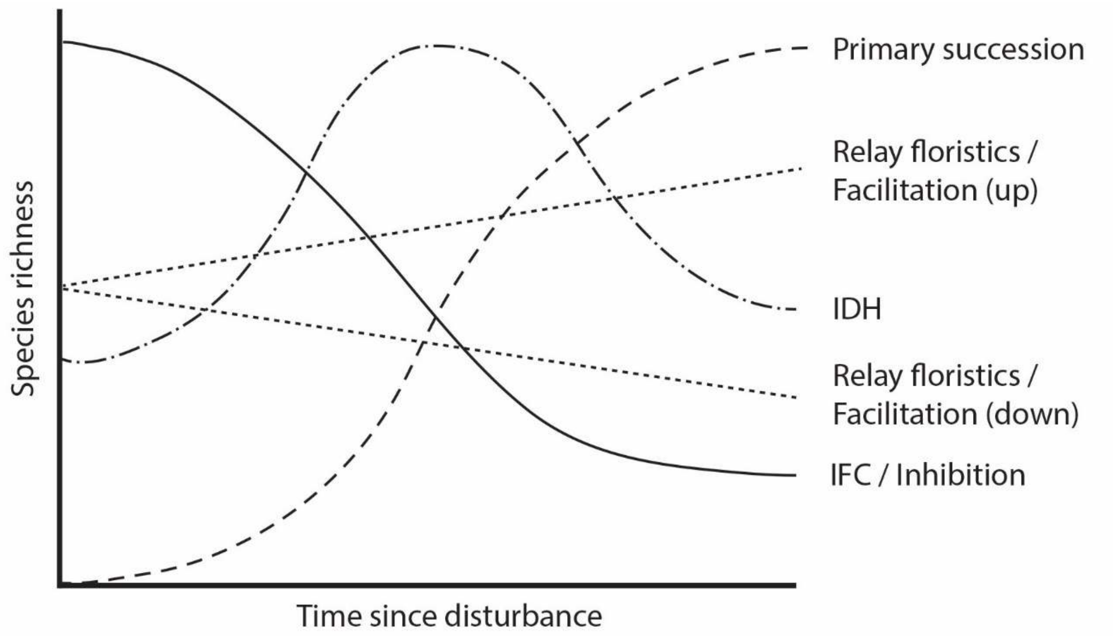

Figure 1: Conceptual diagram showing possible trends in species richness described by different succession theories. Many succession theories are not explicit with respect to species richness change through time and species richness can vary due to a wide range of influences within each ecosystem in question. For several theories, including relay floristics, whether the overall species richness increases or not over time depends on each successive cohort and whether they are more species rich than the last. Time on this diagram is also highly variable, depending on the ecosystem being described. IDH = Intermediate Disturbance Hypothesis. IFC = Initial Floristics Composition.

Table 1: Succession theories and our hypothesis for our results.

Successional theory	**General description**	**Species richness curve**	**Hypothesis for this study**
Primary succession (Walker and Del Moral 2003)	Building of an ecosystem from substrates initially lacking soil, eg. glacial retreat, lava flow, sand dunes.	Begins with no life forms, usually builds slowly as soil forms, then species additions are more rapid before tapering.	Not relevant to our study (included for completeness only), our study is secondary succession.
Facilitation	Early successional species make conditions unsuitable for themselves and/or more suitable for subsequent species, leading to series of invasions through to late successional species.		
Climax community (Clements 1916)	Early species facilitate later species along a predictable course until a final stable climax or equilibrium plant community is established.	Variable, depending on number of species in successional stages.	Facilitation partially describes our study, however, climax theory poorly describes multiple disturbance or disturbance of different types and the end state in our study area can vary from rain forest to Acacia scrub depending on disturbance history.
Initial Floristics Composition (IFC)/Relay floristics (Egler 1954)	IFC: All species are present at the time of disturbance, early dominant species facilitate subsequent species, then drop out. Relay floristics: Series of invasions, species enter a site progressively as conditions become appropriate and as other species are lost.	Variable, depending on number of species in each successional stage.	The majority of species are present at the time of disturbance, but not all. Major change is in dominance of species groups, not in whether they are present or not. Some early successional species are lost as conditions become unsuitable.
Tolerance	Resource levels dictate species composition, with those more tolerant of low resources levels able to outcompete established species over time		
Tolerance (Connell and Slatyer 1977)	Species compete, those more tolerant of lower resource availability able to replace less tolerant species.	Variable, depending on number of species in each successional stage.	Highly productive forests with deep rich soil and high rainfall, light is limiting factor so expect tall species to dominate shorter until canopy opens in older stages if disturbance sufficiently infrequent.

Intermediate Disturbance Hypothesis (IDH) (Connell 1978)	Species richness is highest with intermediate levels of disturbance intensity and duration between disturbance events.	Increases after disturbance, but peaks then falls towards steady state.	We are not studying frequency or intensity of disturbance, but expect opposite species richness curve with highest richness soon after disturbance, dropping when forest is young, then increasing again as it becomes old due to canopy gaps opening to provide more variable environmental conditions.
Inhibition	Early species inhibit later species from establishing until they die or are damaged		
Inhibition (Connell and Slatyer 1977)	Early species inhibit later species until they die or are damaged.	Variable, but likely decline unless dominant pioneer species gives way to multiple replacement species.	In an ecosystem dominated by access to light, early rapid pioneers may be able to inhibit successive species. Predict this to be of only minor importance.
Other			
Biological legacies (Franklin et al. 2000)	Secondary disturbance leaves living plant legacies and structural legacies that influence the successional path.	Highly variable, depending on legacies and range of other factors.	This theory does not predict species richness trajectory, however it has influence in our study as there are many biological legacies in the post-fire environment, in particular, species that re-sprout.
Stochastic community drift, Markovian (Horn et al. 1975)	Successional path to the next state is determined wholly by the current state, and is not determined by states prior to that.	Highly variable depending on current state and stochastic events.	Model does not predict species richness trend as it is determined by stochastic events and each site may have a different starting state.

Through quantifying plant species richness in different age cohorts, we aimed to answer two interrelated questions.

Question 1. What succession theory, or group of theories, best explains observed differences in species richness between the age cohorts?

Early studies of the Mountain Ash forests in Victoria suggested Egler's Initial Floristic Composition (IFC) theory (Egler 1954) best explained succession in this forest type (Attiwill 1994, Pulsford et al. 2014). To maximise diversity across the landscape, Attiwill (1994) suggested intermittent disturbance (from fire or logging) as per the Intermediate Disturbance Hypothesis (IDH) (Connell 1978), stating that old growth forests have the lowest species diversity. More recently, Pulsford et al. (2014) suggested succession in Mountain Ash would be best represented by a range of theories, depending on the frequency and intensity of the disturbances, but primarily IFC and facilitation theories. Pulsford et al. (2014) also suggested that biological legacies (sensu (Franklin et al. 2000)) are important drivers of post-disturbance recovery and by 'anchoring' species to sites, may reduce the likelihood of ecosystems shifting to a different state (Zielke et al. 2008). Biological legacies include structures remaining after natural disturbances such as seed or living structures capable of re-sprouting that form part of the new stand that develops on a perturbed site (Franklin et al. 2000, Johnstone et al. 2016).

Question 2. What trajectories do the functional groups (based on life form and reproductive strategy) follow and how does that relate to successional theory.

Due to early successional ('ruderal') species being short lived early colonisers, and ground herbs generally favouring sunlit positions (Chazdon and Pearcy 1991, Chazdon et al. 1996), we predicted that the species richness of functional groups of plants on sites burned in 2009 would be dominated by herbs and short-lived species. Sprouting species and ground ferns were predicted to be present, but with low richness due to inhibition successional characteristics that allowed dominance to develop over time (Purdie and Slatyer 1976). We predicted that the sites burned in 1983 and 1939 would be physically dominated by dense stands of eucalypts and *Acacia* (Ashton 1976, Wang 1997), and as such, the dense shading from such regrowth would support the fewest short-lived early successional species. As dominance by eucalypts and *Acacia* reduced through senescence and self-thinning over time (Ashton 1976), we predicted increasing numbers of long-term persistent species such as sprouting species, shrubs and midstorey trees would increase in richness. If these predictions are correct, it follows that our oldest sites, burned in or before 1851, would have more sprouting species, ferns and midstorey trees than the younger cohorts. Minor disturbances from tree and branch fall may create areas of bare soil and an opportunity for re-entry of some early successional species and herbs, able to take advantage of the increased solar radiation due to periodic canopy and understorey gaps found in this older age of forest (Ashton and Chinner 1999). Consistent with Relay Floristics (Egler 1954), we expected that some additional species in the oldest sites may appear for the first time in this chronosequence, such as rainforest species, epiphytic ferns and mistletoe (Ashton and Chinner 1999, Loyn and Kennedy 2009).

We hypothesised that species richness would be highest within the first few years after natural disturbance as per Initial Floristics Composition, declining in the middle periods when canopy density is greatest and ground layers (which are the most diverse (Gilliam 2007)) are most supressed. Then as canopy density reduces with more substantial gaps becoming larger and increasingly common in the oldest forest due to natural self-thinning, we expect an increase in species richness again due to light availability at ground level stimulating ground cover species. A summary of successional theories and the likely association to this study are shown in Table 1.

By measuring species richness of different functional groups, we sought to gain important insights into how the presence and composition of different plant groups differ at different points in time, and identify whether a single succession theory is appropriate, or if a number of theories is required to describe the trajectories of different functional groups of species. By understanding how a forest ecosystem that is largely free from human disturbance recovers naturally following a major disturbance event, we are better able to recognise alternative recovery trajectories from other disturbance regimes such as logging or future climate change.

METHODS

Study area, forest type, site selection and survey years

We conducted our study in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, 60-100km east of Melbourne in south-eastern Australia (Figure 2). *Eucalyptus regnans* persists at an altitudinal range of 150m-1100m (Boland et al. 2006) and the forests of this region receive high annual rainfall (750-1700mm per annum). *Eucalyptus regnans* is the tallest flowering plant in the world, typically growing 55-75m tall (Boland et al. 2006) and historically, in excess of 100m (Walsh and Entwisle 1996, Ashton 2000). The forests have a tall luxuriant midstorey/understorey of shrubs, tree ferns and trees, including *Acacia dealbata*, which grow to 30m tall (Walsh and Entwisle 1996, Costermans 2009) and dense ground coverage of herbs, graminoids and/or ferns (Ashton 2000). *Eucalyptus regnans* is an obligate seeder, with seed stored in capsules in the canopy, which is released following large stand replacing fires (Ashton 1976). As a result, *E. regnans* usually regenerate as a stand of uniform age. In contrast, many other species in the Mountain Ash forests survive fire and as such may be a century or more older than the overstorey eucalypts (Mueck et al. 1996, Blair et al. 2017). The large wildfires that burn these forests typically do so when *El Nino* conditions periodically create strong drought conditions in summer. Historically the return interval of high-severity fires has been every 75-150 years (McCarthy et al. 1999).

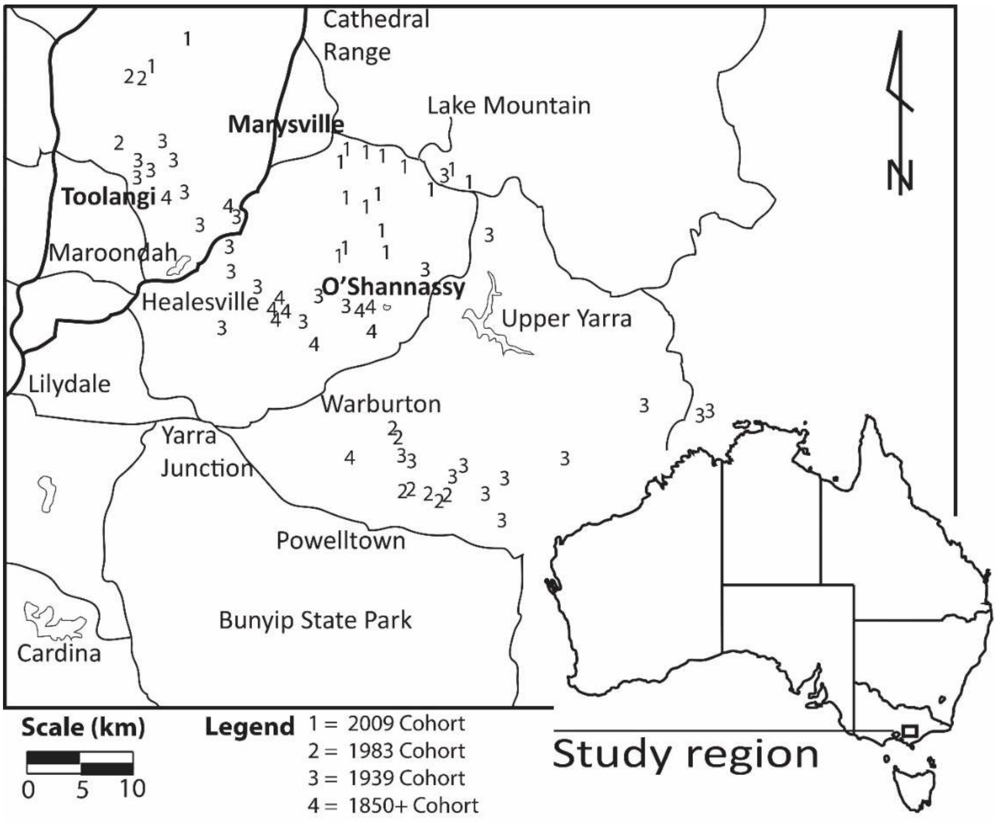

Figure 2: Victorian Central Highlands showing location of sites containing forest of the (1) 2009 cohort, (2) 1983 cohort, (3) 1939 cohort and (4) 1851 cohort.

To quantify the functional group species richness of the Mountain Ash ecosystem and how it may vary with forest age, we studied stands of four overstorey ages on 67 sites selected from 181 long term monitoring sites (Table 2). We measured the presence of vascular plant species in forest stands that regenerated after large wildfires in 1851, 1939, 1983 and 2009. We surveyed all 67 sites on three separate occasions, in 2009/10, 2012 and 2015. The 2009 'Black Saturday' fires burned 34% of the Central Highlands (Burns et al. 2015b) and trees regenerating from this fire were 1-6 years old when surveyed. The 1983 'Ash Wednesday' fire also was a major fire, but it primarily burned other regions of the state, with 9% of the Central Highlands region burned (Taylor 2018). Regrowth from this fire was 26-32 years old at the time of surveys. The 1939 'Black Friday' fire was widespread, with the fire footprint covering 79% of the Central Highlands region (Noble 1977, Macfarlane 1988), with trees from that conflagration 70-76 years old at the time of our three survey years. The oldest of our sites were burned in 1851 or earlier, being a minimum 158 years old. Due to the difficulty in correctly identifying species within months of a fire, the first survey year for the 2009 cohort was in 2010 instead of 2009. For this youngest age cohort, at the time of the 2009 fire, 65% of the sites we surveyed were forest that had regenerated after the 1939 wildfire (so this was the second fire in 70 years); the remainder were old growth sites at the time of the 2009 fire. For this study, we tried to select sites with as few recorded fire events prior to the fire that created our cohorts as possible. This is because multiple fires can effect species composition, with multiple fires reducing on-site seeding species richness and abundance, including overstorey eucalypts (Bowd et al. 2018a).

Table 2: Site survey summary for forest cohorts

Forest cohort	Survey year	Age at time of survey	Number of sites
2009	2010	1	17
	2012	3	17
	2015	6	17
1983	2009	26	10
	2012	29	10
	2015	32	10
1939	2009	70	29
	2012	73	29
	2015	76	29
1851+	2009	158	11
	2012	161	11
	2015	164	11

Compounding disturbance and multi-age forests

Logging affects the species composition of Mountain Ash forests in a fundamentally different way to wildfire, and that effect is likely to persist for several decades (Turner and Kirkpatrick 2009, Blair et al. 2016). To reduce the effects of historical human disturbance on our sites, we selected sites either in closed water catchments (which have never been logged), or sites where no records or obvious signs of past harvesting were evident.

Some stands of Mountain Ash forests are multi-aged, formed by low severity fire triggering a regeneration cohort while individuals in the overstorey survive (McCarthy and Lindenmayer 1998). We avoided surveys of multi-aged stands for this study as we wanted to reduce variability in the disturbance. Therefore, we selected sites that had only burned at high severity, indicated by uniform stand replacement of the overstorey. Also to reduce variability, we selected sites that were uniform in overstorey species composition, avoiding mixed (eucalypt) species stands.

Elevation and aspect effects

We measured the elevation and aspect of all sites, as these affect temperature and topographic wetness and thus influence the available niches for different plant species (Pausas and Austin 2001). Aspect was divided into two groups, 'north' being the hottest and driest aspect was taken from north-west (315°) to north-east (45°). All other aspects (southerly, easterly and westerly) were combined.

Geographic spread

Given our study was based on sites burned at high severity by four major wildfires, the location of our sites was constrained by the geographic location of each high severity fire. This resulted in clustering of sites of some age cohorts (Figure 2). Kasel et al. (2017) found geographic distance influenced beta-diversity within a range of forest types in the same region, but environmental variables including climate and soil were found to have greater effects than geographic spread. To limit the effect of environmental variables, we accounted for aspect and elevation (which is highly correlated with rainfall and temperature in these forests (Blair et al. 2017)) within our modelling.

Site layout and survey methods

Each of the 67 sites was a 100m x 100m square, with a 100m long central transect running perpendicular from the middle of the front edge, bisecting the site. Along the transect were three 10m x 10m plots, located between 10-20m, 50-60m and 90-100m, symmetrically straddling the transect. The first plot was set back from the front edge of the site to reduce edge effects (see Appendix A).

We measured the presence or absence of all vascular plant species within each of the three plots. The same sites were used in each of the survey years and surveying was between February and May in any given year. We did not measure the abundance of each plant species as this would be extremely time consuming for many species due to very high numbers or indistinct growth forms. To ensure consistency of data collection over the study period, all data were collected by two field ecologists, with one (DB) collecting 90% of the data.

Life form and reproductive strategy functional groups

To develop a more detailed picture of successional drivers, each plant species on our sites was categorised into one of eight life forms and one of five reproductive strategies (see Appendix B). The life forms categories related to physical form of the plants and included: (1) eucalypt (overstorey), (2) *Acacia*, (3) midstorey tree, (4) shrub, (5) fern, (6) graminoid, (7) herb and (8) climber. The eucalypt category was dominated by a single species, *Eucalyptus regnans*, which grow densely before rapidly self-thinning from 380 stems/ha at age 40 to 40 – 80 stems/ha in ecologically mature forest (Ashton and Attiwill 1994). The *Acacia* category included four species that are midstorey trees (*Acacia dealbata, A. obliquinervia, A. frigesens* and *A. melanoxylon*), growing to 15-30m tall (Costermans 2009) and generally living to 30-80 years old. These were separated from other midstorey tree species as they are usually taller and also because they have long established unique ecological roles that are likely to be of interest for other research, such as nitrogen fixation (Adams and Attiwill 1984, Polglase and Attiwill 1992), associations with birds (Lindenmayer et al. 2009), or as feed trees for arboreal marsupials(Lindenmayer et al. 1990, Lindenmayer et al. 1991). The two species of tree ferns, *Dicksonia antarctica and Cyathea australis* were listed as midstorey trees, not ferns, due to their size and importance for structure in the midstorey.

We assigned each plant species to one of five reproductive strategies. The categories were broadly split into species that are short-lived ‘early successional’ species and ‘persistent’ species: (1) Early Successional Seeders (ESS), (2) Persistent External Seed (PES), (3) Persistent On-site Seed (POS), (4) Persistent Sprout (Sprout) and Persistent None (Pnone). Early Successional Seeder (ESS) species, or ruderals, are disturbance specialists. They regenerate rapidly from seed within the first few years after fire, then are typically visually absent within a decade unless additional disturbances occur, which may include small localised disturbances. Despite being visually absent, ESS species may still be present on site, having moved from the above ground (visually apparent) pool, to the below ground soil seed bank. Persistent species by contrast, remain in an extant state beyond the initial successional stage of recovery after fire. Persistent External Seed (PES) species have highly mobile seed, brought into the site from vectors such as wind or birds. In contrast, Persistent On-site Seed (POS) species originate from seed that was either in the soil or canopy and survived the fire. Persistent Sprout (Sprout) species recover by re-sprouting from a surviving part of the plant such as shooting from the trunk, lignotubers or rhizomes. Persistent None (Pnone) species have no clearly defined reproductive strategy. This may mean reproduction is undefined or, more commonly, consists of multiple reproductive methods without a single dominant strategy. The assignment of species into these various groups was done from field observations, literature reviews (Walsh and Entwisle 1994, 1996, 1997, Costermans 2009, Kattge et al. 2011, Bull and Stolfo 2014) and through consultation with staff from the Melbourne Botanical Gardens (Walsh 2013).

Statistical analysis

We modelled overall species richness at the plot level (that is, the data from the three years at the plot level were used in computing site level richness) accounting for elevation (standardized) and four age cohorts. We used a Bayesian generalized linear mixed model (GLMM) with a Poisson distribution and log link with site as a random effect. The site level random effect allowed for correlation among the plots on each site. We completed our analysis in R (R Core Team 2017) using the brms package (Bürkner 2016). We used the default priors provided in the package and ran four Markov Chains for 2000 iterations discarding the first 1000 as burn-in. Standard MCMC diagnostics were employed to check for convergence of the chains and all were found to show adequate mixing (Gelman and Rubin 1992). We report posterior mean estimates and 95% credible intervals. The species richness from each of the 13 functional groups (eight life form groups and five reproductive strategies) were analysed in a similar fashion.

Qualitative comparison analysis of succession response curves

The generalised curves of species richness for different succession theories are shown in Figure 1. To determine which of the succession theories best explained observed changes in overall species richness and plant functional groups in the Mountain Ash forests, we drew inferences from the pattern of our chronosequence data points in a qualitative comparison with the succession theories trends.

RESULTS

Overall species richness

We found a significant trend in species richness (Figure 3, Appendix C). Sites burnt in 2009 supported significantly higher species richness than other age cohorts, averaging 17.1 (Lower CI 15.3, Upper CI 19.2) species per plot. The 1983 and 1939 cohorts had the lowest average species richness with 12.9 (LCI 11.0, UCI 15.1) and 12.5 (LCI 11.4, UCI 13.6) spp/plot respectively, with plots in 1851 aged stands supporting 13.4 (LCI 11.7, UCI 15.6) spp/plot. There was no significant difference in species richness between the older three age classes. There were a number of species found only in one age cohort. The 2009 sites supported seven species that were unique to that age cohort, 1983 cohort had one unique species, 1939 had eight species and the 1851 cohort had three species found only in those plots. We found species richness declined with increasing elevation, adjustments for elevation was therefore included in adjusting for analyses of overall species richness.

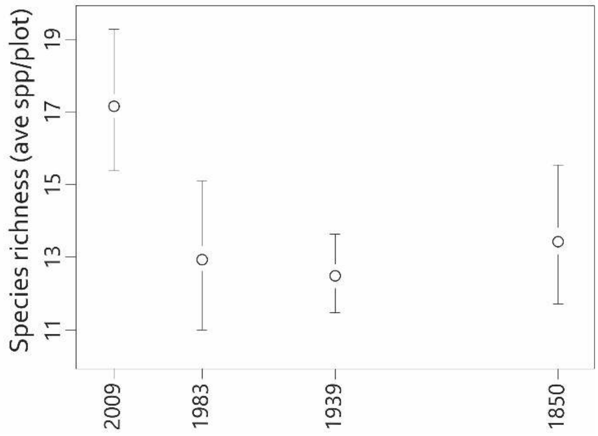

Figure 3: Overall species richness, average number of species per plot with 95% credible intervals for the four age cohorts that regenerated after fires in 2009, 1983, 1939 and 1851 for a site with average elevation.

Functional groups – life form

The following graphs (Figure 4) of life form show the average number of species per 10mx10m plot for the four age cohorts with 95% credible intervals. Modelling has the effects of elevation taken into account where elevation effects where significant.

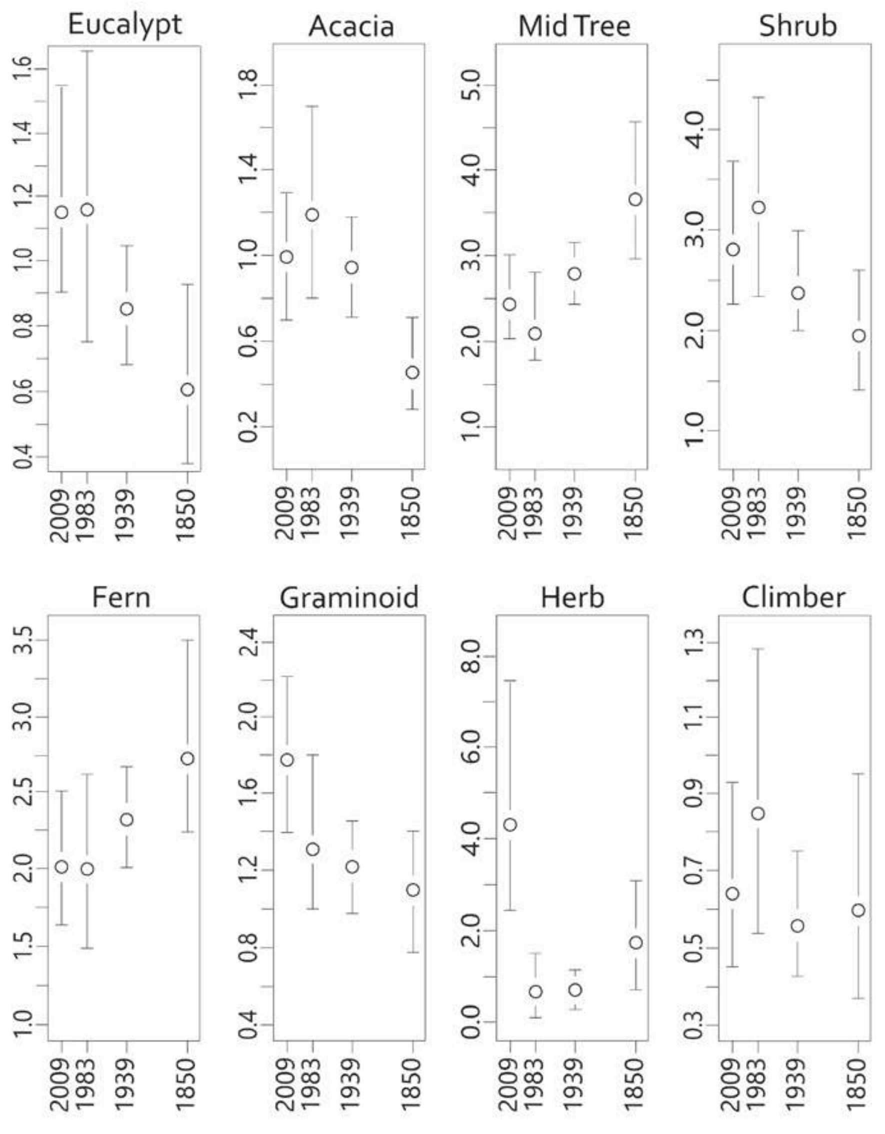

Figure 4: Life form species richness, average number of species per plot (y-axis) with 95% credible interval for the four age cohorts that regenerated after fires in 2009, 1983, 1939 and 1851 for a site with average elevation.

Eucalypts and **Acacias** generally diminished in the older cohorts. Eucalypts were significantly less species rich in our 1851 cohort compared to stands dating from 2009. Species richness of Acacia in the 1851 cohort was significantly lower than the other three cohorts.

Midstorey trees were most species rich in the 1851 cohort, significantly greater than the younger three cohorts of which, the 1983 cohort had the lowest richness. **Shrubs** by contrast, were a mirror image of midstorey trees, with the 2009 and 1983 cohort having the greatest species richness, significantly greater than 1851, which had the lowest.

Fern species richness increased in the older forest cohorts, with 1851 having the greatest richness, significantly more than 2009 and 1983. **Graminoid** species richness was high immediately post fire, with subsequent cohorts having reduced species richness. The 2009 cohort was significantly more species rich than the 1939 and 1851 cohorts. **Herb** species richness was also highest immediately post fire disturbance, with the 2009 plots having significantly greater richness than all three other age cohorts. Herb richness was lowest in the 1983 and 1939 age forest plots. **Climbers** are represented by three species and no significant differences were established between the four age cohorts.

Functional groups – reproductive strategy

The five graphs of reproductive strategy (Figure 5), show the species richness within each 10mx10m plot for the four age cohorts with 95% confidence intervals. Modelling has the effects of elevation taken into account.

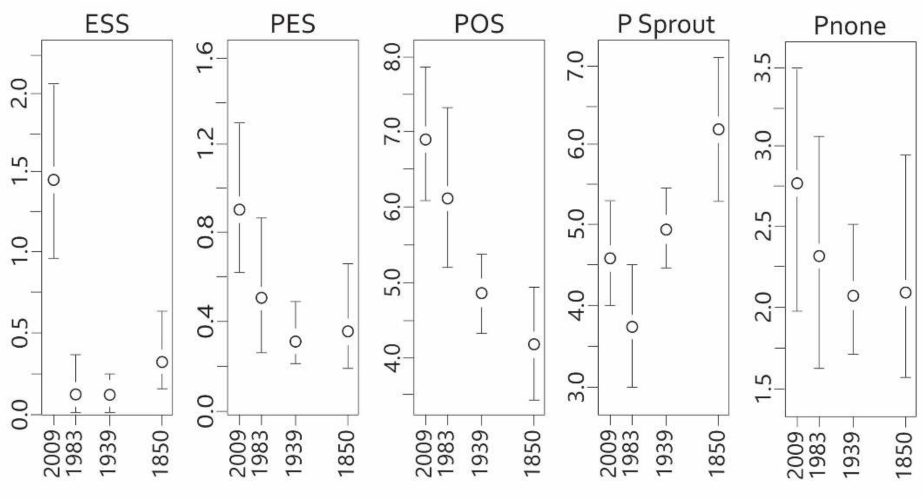

Figure 5: Reproductive strategy species richness, average number of species per plot (y-axis) with 95% credible interval for the four age cohorts that regenerated after fires in 2009, 1983, 1939 and 1851 for a site with average elevation. ESS = Early Successional Seed; PES = Persistent External Seed; POS = Persistent Onsite Seed; PSprout = Persistent Sprout, Pnone = Persistent None (no clearly defined strategy).

Early Successional Seeder (ESS) species had the same pattern of as the overall species richness and as herbs, with the 2009 cohort having the highest species richness, significantly greater than the other three age cohorts. The 1983 and 1939 cohorts had fewest early successional species.

Persistent External Seed (PES) species richness declined with increasing forest age. We recorded a significant difference between the 2009 plots and those of 1939 and 1851.

Persistent On-site Seed (POS) species richness declined with increasing forest age with plots from both the 2009 and 1983 cohorts having greater species richness than the older 1939 and 1851 cohorts.

Persistent sprout (Sprout) was the only reproductive strategy group to increase with forest age. The 1851 cohort had significantly greater species richness than all younger cohorts. The 1939 cohort had greater species richness than the forest of 1983 age, which had the lowest species richness.

Persistent none (Pnone) species richness trended slightly down with forest age but there were no signifcant differences betweeen the four cohorts.

Functional group proportions of overall species richness

Figure 6 illustrates the relative contribution of each functional group to the overall species richness of the Mountain Ash forest for the four age cohorts. Life forms are the top half of the chart and reproductive strategy the bottom half. The graphics are graduated from the functional groups that contribute most to overall species richness to the least (up for life form, down for reproductive strategy). From this graphic we see Midstorey Trees and Ferns increasingly dominate the overall species make up of the forest, with Herbs diminishing from the life form providing the greatest species richness in the 2009 cohort, to only minor representation in the 1983 and 1939 cohorts. For reproductive strategy, Persistent On-site Seed species contribute the most species to overall richness in the 2009 and 1983 cohorts before diminishing in the older forests, replaced by the increasing number of Persistent Sprouting species that increase their share of overall species richness with each age cohort. Early successional species contribute almost 9% of species richness in the 2009 cohort before reducing to 1 or 2% in the other cohorts.

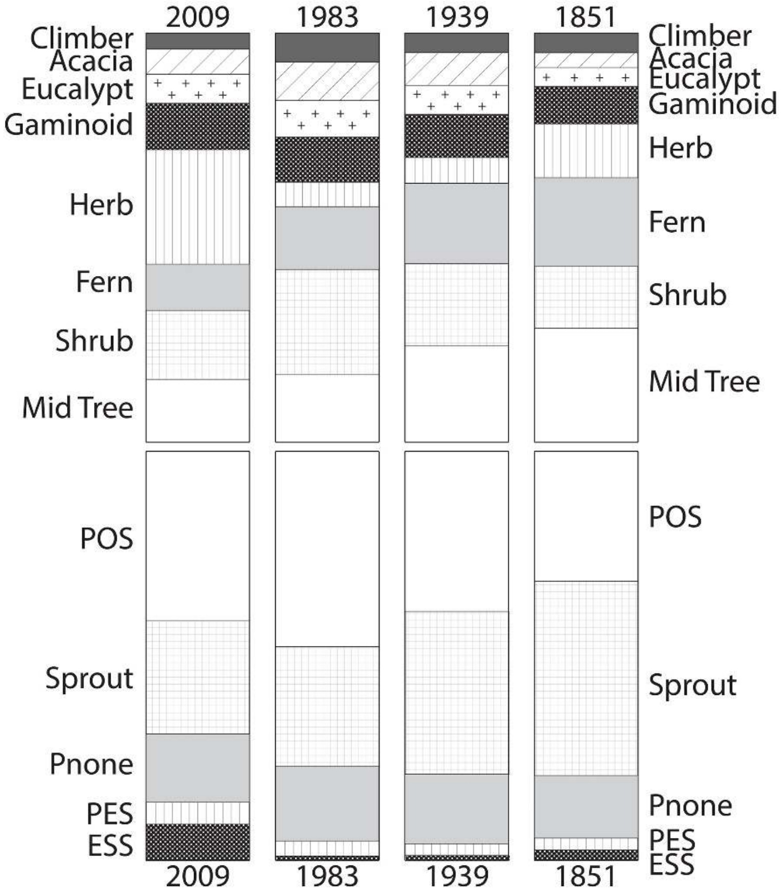

Figure 6: Proportion of overall species richness contributed by different functional groups – life forms in the top half and reproductive strategy below in four age cohorts of Mountain Ash forest. Note, this graphic does not show abundance of any functional group, but what proportion of the overall species richness each group contributes. (POS = Persistent On-site Seed. Sprout = Persistent Sprouting species, PES = Persistent External Seed, Pnone = Persistent none/no defined strategy ESS = Early Successional Seeder.)

DISCUSSION

Disturbance within a range of ecosystems, including forests, has been studied for over a century (Clements (1916) reviewed by Pulsford et al. (2014)). Disturbance brings changes which benefit some species and negatively influence others at different times, creating shifts in the composition of plant species in a forest (Noble and Slatyer 1980, Lavorel and Garnier 2002). While the original theories from Clements (1916) of orderly transitions to a final ‘climax’ state have been superseded (Sousa 1984, McIntosh 1999, Moore et al. 2009), there is still a wide range of theories to explain successional change through time (Pulsford et al. 2014), and theories which fit one ecosystem may not explain changes in others. However, understanding the disturbance recovery trajectories within largely natural ecosystems such as the studied areas of this temperate forest, assists with comparative analyses of temperate forest biomes at larger scale, including from climate change influences (Sommerfeld et al.

2018). Our chronosequence study within the Mountain Ash forests, was developed to examine the congruence between predictions from a range of succession theories and the observed patterns within this forest ecosystem.

Stochastic community drift

Disturbance history is important in wet temperate forests around the world. In the North American Rocky Mountains, historic fire and insect attack affected the regeneration trajectory of forests due to changes in severity of subsequent fire (Bigler et al. 2005). In north-western Canada, disturbance history affected stand basal area (Johnstone and Chapin 2006), which in turn, altered fire frequency (Bergeron et al. 2001). Fire is rare in the forests of the European Alps. Where it has occurred, it has radically changed the resulting vegetation community (Tinner et al. 2005), and when it interacts with drought it can also affect recovery pathways (Moser et al. 2010). In the temperate and boreal forests of northern China, fire affects stand age which is correlated to carbon storage (Wei et al. 2013). Early work by Ashton (1981) and more recent work by Bowd et al. (2018a) in the Mountain Ash forests in Victoria, has showed combinations of stochastic events such as fire, with the deterministic disturbance of logging and post-fire salvage logging, can shift the plant community, with losses of species within some functional groups after particular types of disturbance. For example, multiple fires resulted in losses of persistent on-site seeding species, while logging, and in particular salvage logging, greatly reduced the number of sprouting species (Blair et al. 2016, Bowd et al. 2018a). Given we specifically avoided sites with complex human-generated disturbance histories, we are unable to establish evidence of stochastic community drift from this study.

Question 1. What succession theory, or group of theories, best explains observed differences in species richness between the age cohorts?

The major form of natural disturbance of Mountain Ash forests is wildfire. Following wildfire, a wide range of biological legacies remain (Franklin et al. 2000) and secondary succession is the dominant process (Walker and Del Moral 2003). Legacies that help establish the recovering forest include sprouting rhizomes and lignotubers (Murphy and Ough 1997), seed and even nutrients (Johnstone et al. 2016). Earlier work in the Mountain Ash forests suggested the Initial Floristic Composition (IFC) model of plant succession best explained changes in plant species richness through time (Attiwill 1994) or a combination of IFC, State Transitions and Biological Legacies (Pulsford et al. 2014). However, the species richness at different points in time in our study indicate the shape of the species richness curve for this forest may be better explained (at least in part) by Relay Floristics than by IFC, with reduced levels of species richness in the 1983 and 1939 cohorts, but increased overall species richness in older forest (see Table 1 and Figure 3). Our identification of 19 species that occurred in only one of the age cohorts, and 11 of these being in the oldest two cohorts, further supports the concept of relay floristics. While beta-diversity due to possible edaphic differences between our sites may partially explain our findings (Kasel et al. 2017), it should also be noted there are plants known to be uncommon in younger regrowth forests, including Mistletoe (Lindenmayer 2009, Loyn and Kennedy 2009) and epiphytic ferns (Hickey 1994), further supporting a Relay Floristics model. Additionally, seed storage effects result in some species that may be present in the below ground seed bank, not being recorded on some surveys due to not being visually observable.

Question 2. What trajectories do the functional groups (life form and reproductive strategy) follow and how does that relate to successional theory.

It is difficult to state definitive trends from 4 points in time as per our chronosequence. However, some trends through time are more likely than others. The changes in species richness for the life form and reproductive strategy functional groups that seem most plausible, could be generalised into four main trends (Figure 7).

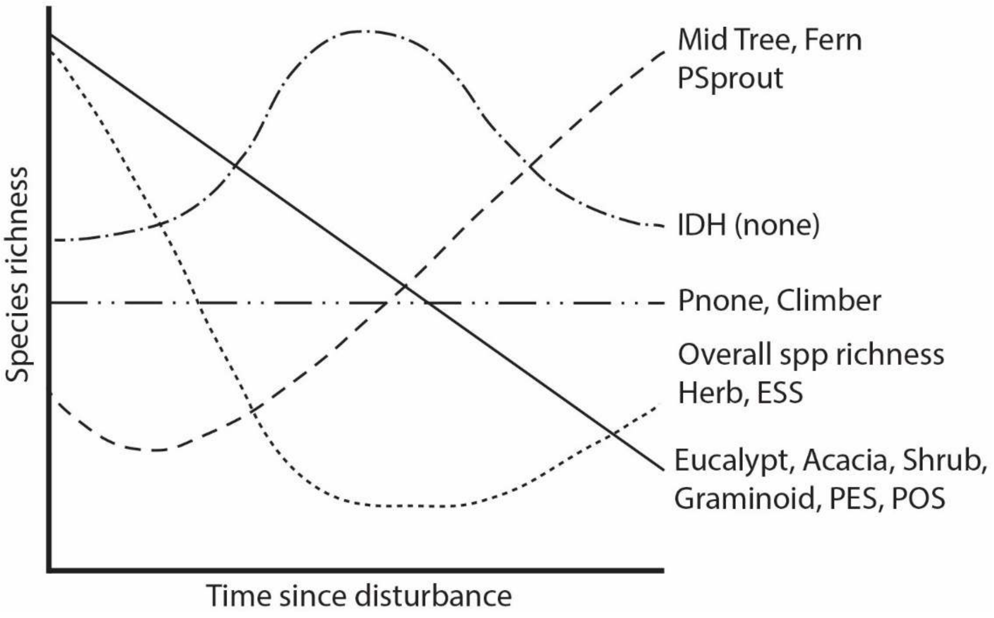

Figure 7: Generalised trends from our results for overall species richness and species richness of the functional groups. IDH = Intermediate Disturbance Hypothesis, no functional groups followed this trend. ESS = Early Successional Seed; PES = Persistent External Seed; POS = Persistent On-site Seed; P Sprout = Persistent Sprout, Pnone = Persistent None (no clearly defined strategy).

As can be seen in Figure 7, the functional group species richness fitted into four broad trends across the forest age cohorts: (1) trending up, (2) trending down, (3) a flattened 'U' shape and (4) flat. None were the inverted-U shape characteristic of IDH.

Upward trending species richness with increasing forest age was seen in the Persistent Sprouting species, midstorey trees and ferns (the majority of which are sprouting species). This most closely follows Relay Floristics succession theory where inhibition is playing an increasing role through the sprouting species. This appears to be at the expense of other groundstorey seeding species (herbs, graminoids, Figure 6). By definition, sprouting species arise from biological legacies (Franklin et al. 2000) that persist after the major disturbance by fire (although in reduced numbers soon after fire), so this theory is clearly of importance in the recovery of these species. The concept of biological legacies describes pathways of recovery, including through sprouting species, but it is not necessarily a predictor of trends in species richness.

Downward trending species richness with increasing forest age was common. Eucalypts, *Acacia*, shrubs, graminoids, Persistent External Seed and Persistent On-site Seed species all followed this trend, which is best explained by Egler's Initial Floristics Composition. Declines in seeding species richness over time since disturbance can be attributable to plants senescing and moving from the above ground (visible) pool to the below ground seed store. If they require disturbance to re-establish above ground, there could be very extensive periods without these species visually apparent. Another reason for their diminishing richness may be inhibition competition from the sprouting species.

The **'U' shaped trend** group, which included herbs and Early Successional Seed species, was similar to the downward trend, with large decreases in species richness from the 2009 cohort as forest age increased. However, the species richness of the oldest cohort for these functional groups rebounded slightly (Figure 4 and 5). The large decline in species richness in cohorts older than the 2009 age forest (6 years of age) was likely due to a number of factors. Many species, such as the Early Successional Seed species and several herbs, are gradually out competed, becoming visually unobservable over time and often transitioning to become part of the below-ground seed bank. Some species, such as *Dryopoa dives*, are capable to remaining in the seed bank for well over a century (Lindenmayer et al. 2015). This fits with many successional theories, including Relay Floristics, facilitation or tolerance models, depending on the plant dynamics moving into the secondary phase of succession. For both ESS and the herbs, there were elevated levels of early successional species that appear in the oldest forest age cohort, presumably making use of minor disturbances from branch and tree fall and the increased sunlight available at ground level. Given these forests have high consistent rainfall and deep, rich soils, sunlight is likely to be a limiting factor for many of the groundstorey species (Ashton and Martin 1996), particularly in the 1983 cohort, and to a lesser extent the 1939 and 1851 forests as stocking densities decrease (Ashton 1976). This leads to the dominance of some species by inhibition as mentioned previously, and tolerance by those that persist (Connell and Slatyer 1977). Most species with seed that enters the site from external sources (PES and ESS) require a receptive available seed bed for establishment, so as the forest becomes dense and closed, this may reduce the number of persistent blow-in species from establishing at a time subsequent to the initial establishment period. With the inability to establish within a dense existing stand, and short longevity, this explains why the1983 and 1939 stands had very few early successional species, although, as mentioned above, they increased in the oldest forest.

Finally, a **flat trends in species richness** was seen in the Persistent None and climbers groups. The Persistent None group includes a wide range of life forms and variable reproductive strategies, so it is perhaps not surprising there was no clear trend. In contrast, there are only three climber species (*Clematis aristata, Billardiera mutabilis and Parsonsia brownii*), all are Persistent On-site Seeders. By occupying an arboreal niche, it is likely much of the competition experienced by other understorey species (particularly for light) is avoided by these species.

We documented a shift in the **proportion of the overall forest species richness** for different functional groups with increasing forest age (Figure 6). Of the reproductive strategy groups, Persistent On-site Seed and Persistent Sprout species contributed the most to overall species richness in this forest ecosystem (Figure 6), but they trended in opposite directions; as the on-site seeders declined, the sprouters increased, leading to the overall species richness graph being ‘U’ shaped. The high species richness of both is due to these being diverse groups of species with a wide range of traits for survival in this forest type (Wang 1997, Blair et al. 2016). For life forms, herb species richness declined with forest age, while sprouting species and midstorey trees both increased. This is likely to be due to the low growth habits of the herbs favouring initial conditions after fire when light reaches the ground. In contrast, many ferns are shade tolerant (Ashton 2000) and are able to reproduce asexually from rhizome growth or frond tip bulbils (Walsh and Entwisle 1994). Eucalypts contributed little to overall species richness. This was as expected given sites were selected on the basis of being dominated by *Eucalyptus regnans*. It is likely the high level of competition for available light and water by the dense stands of eucalypts and Acacia, particularly in the 1983 and 1939 stands is a major contributing factor in the low overall species richness for those age cohorts. In the 1983 stands, eucalypts are generally 20-40m tall, averaging 500-800 stems/ha, are at or have maximised basal area, and are still growing rapidly (Ashton 1976, Blair et al. 2018). The persistence of *Acacia*, albeit at lower levels, in the oldest cohort is interesting as although *A. melanoxylon* may live in excess of 100 years (Attiwill 1994) most *Acacia* species senesce before that age. This indicates possible regeneration without disturbance, or regeneration from minor disturbances such as tree or branch fall, disturbance by lyrebirds or low severity fire in the interim since the last high severity fire.

Multiple succession theories for one ecosystem.

Our findings suggest the various functional groups of the Mountain Ash forest ecosystem have dissimilar recovery trajectories, and while they may interact (eg. ferns outcompeting herbs or graminoids), they follow different successional theories. Therefore, while Initial Floristic Composition may explain the majority of the seeding species well, sprouting species are better explained by Relay Floristics (Egler 1954) or Inhibition (Connell and Slatyer 1977). The finding that multiple successional theories may be required to describe the responses of different functional groups of plants in a single ecosystem is supported by others (Roxburgh et al. 2004, Pulsford et al. 2014).

The Intermediate Disturbance Hypothesis

The Intermediate Disturbance Hypothesis (Eggeling 1947, Grime 1973, Connell 1978) had been suggested by Attiwill (1994) to explain maximum species diversity in the Mountain Ash forests. Indeed, maintenance of diversity is used by Attiwill (1994) as an argument for logging within these forests, with the assumption that maintaining an 'intermediate' disturbance frequency would lead to greater species diversity on a landscape scale. What was probably poorly known at the time was the disturbance type of logging itself is deleterious to species diversity in these forests (Ough 2001, Blair et al. 2016). Many studies suggest that the peaked species richness curve that characterises IDH, may actually be uncommon (Mackey and Currie 2001, Fox 2013), or that it is a result of amalgamating a range of more complex interactions (Roxburgh et al. 2004). There are also differences in what is described, with IDH theory having been used to describe severity, frequency, or time since disturbance (Mackey and Currie 2001). Our findings of time since fire, were not of peaked species richness, rather the opposite, with minimum species richness occurring in the two middle age cohorts. Even when examining the results of all the individual functional groups (Figure 4), none of the functional groups had a species richness pattern consistent with predictions from the IDH theory. In fact not only do we know that logging fundamentally changes the species composition in a way that is different to natural wildfire (Ough 2001, Blair et al. 2016), but our species richness results (Figure 3) show species richness is at its lowest during the age at which forests would spend the majority of their time if logged at 60-80 years of age, as has occurred over the last couple of decades in the Mountain Ash forests. With only 1.16% of the Mountain Ash forests currently older than 80 years of age (Lindenmayer et al. 2012), these forests are not lacking disturbance. Greater diversity is likely to be achieved across the landscape through the natural spatial heterogeneity of periodic wildfire across variable topography than through a series of deliberate disturbances at set intervals from a disturbance type that in itself reduces diversity.

A baseline from undisturbed forests

Temperate forests around the world are subjected to a range of disturbances which are beginning to be influenced by climate change (Sommerfeld et al. 2018). Given their history includes very minor human disturbance in certain areas (Griffiths 2001), this study is able to provide an important baseline of how we would expect the various plant functional groups to respond following infrequent major natural disturbances. With this knowledge, it is now possible to contrast these baseline responses with human disturbance such as logging or altered regeneration responses under future climate change influences. Climate modelling has suggested most tree species within the study region may be unable to naturally self-sustain from seed by the 2080s and possibly as early as the

2050s in the majority of areas where they currently persist (Mok et al. 2012, Wang et al. 2016). A better understanding of the successional pathways is important to detect early warning signs that these forests are recovering in fundamentally different ways to how they do so currently or have done in the past.

Use of chronosequence

Some studies using the 'space for time' methodology employed by chronosequencing have been found to be invalid in some situations, including examples of primary succession on dunes and glacial retreat (Johnson and Miyanishi 2008). Others have generally endorsed the method with specific cautions, including drawing inferences on species richness (Foster and Tilman 2000), or between plots of different site quality (Ashton and Martin 1996), or not extrapolating from plot level to landscape level (Harmon and Pabst 2015).

Walker et al. (2010b) found chronosequencing an effective method for decade to millennial length studies, including for studying species richness, where sites of different ages are generally following the same trajectory. They also found optimal results when sites had low diversity, high species turn over, low severity disturbance and long intervals between disturbances. While our study sites were subject to high severity disturbance in the form of wildfire, the disturbance interval for the selected sites was long, 70 years as a minimum and well over 100 years for the majority of our sites. Given our study is at a decadal or longer scale and it is likely sites are on the same successional trajectory, we believe chronosequencing was an instructive method to compare stands of different ages.

CONCLUSIONS

Succession in the Mountain Ash forests of Victoria appears to most closely follow a combination of Initial Floristic Composition and Relay Floristics. We found the recovery trajectories of some functional groups, such as the on-site seeding species, herbs, eucalypts, *Acacia*, shrubs and graminoids can be largely explained through Egler's Initial Floristic Composition theory (Egler 1954). However, the ferns, midstorey trees and sprouting species, as well as the addition of 11 species found exclusively in the 1939 and 1851 cohorts indicates Relay Floristics may also have a role to play with the sprouting species appearing to be inhibitors, increasing in dominance over time. The sprouting species are also important examples of biological legacies (Franklin et al. 2000) that are able to survive fire. Biological legacies underpin regeneration of all secondary succession with legacies such as seeds and nutrients playing important roles in forest recovery (Johnstone et al. 2016). Sprouting species may help 'anchor' this forest community in the face of a changing climate or other disturbance shocks through their ability to survive a disturbance such as wildfire with already well established root systems, which is likely to increase their resilience to climate induced drought in the very early stages of establishment after wildfire when species regenerating from seed are particularly susceptible due to less substantial root mass (Pratt et al. 2008).

Our studies revealed the Mountain Ash forests of Victoria comprise a variety of functional groups with differing recovery trajectories, and as such, are best explained by different successional theories. The recovery trajectories of some functional groups, such as the on-site seeding species, herbs, eucalypts, *Acacia*, shrubs and graminoids can be largely explained through Egler's Initial Floristic Composition theory (Egler 1954). However, the ferns, midstorey trees and sprouting species, as well as the addition of 11 species found exclusively in the 1939 and 1851 cohorts indicates Relay Floristics may also have a role to play.

As examples of forest free from human disturbance become increasingly rare around the world (Hansen et al. 2010, Watson et al. 2018), and impacts of climate change begin to fundamentally alter global forests (Allen et al. 2010, Sommerfeld et al. 2018), gaining an understanding of how our forests function without these influences becomes increasingly important so variations to usual forest recovery are observable. This may include increased insect attack in Canada's boreal forests (Kurz et al. 2008), drought and associated fire in tropical forests including the Amazon (Laurance 1998) and Indonesia (Van Nieuwstadt and Sheil 2005), increased wind storms in the Congo (Whitmore 1998) or changes due to logging of native forests as occurs in many countries around the world. In our study region, modelling predicts most tree species will be unable to regenerate naturally from seed within 40-70 years across the majority of their current geographic ranges (Mok et al. 2012, Wang et al. 2016). Having descriptions of baseline recovery pathways following natural disturbance, means we are better equipped to detect changes in recovery due to human disturbance, multiple disturbances within a short time frame, or changes in regenerative capacity of the forest due to the more subtle effects of our changing climate.

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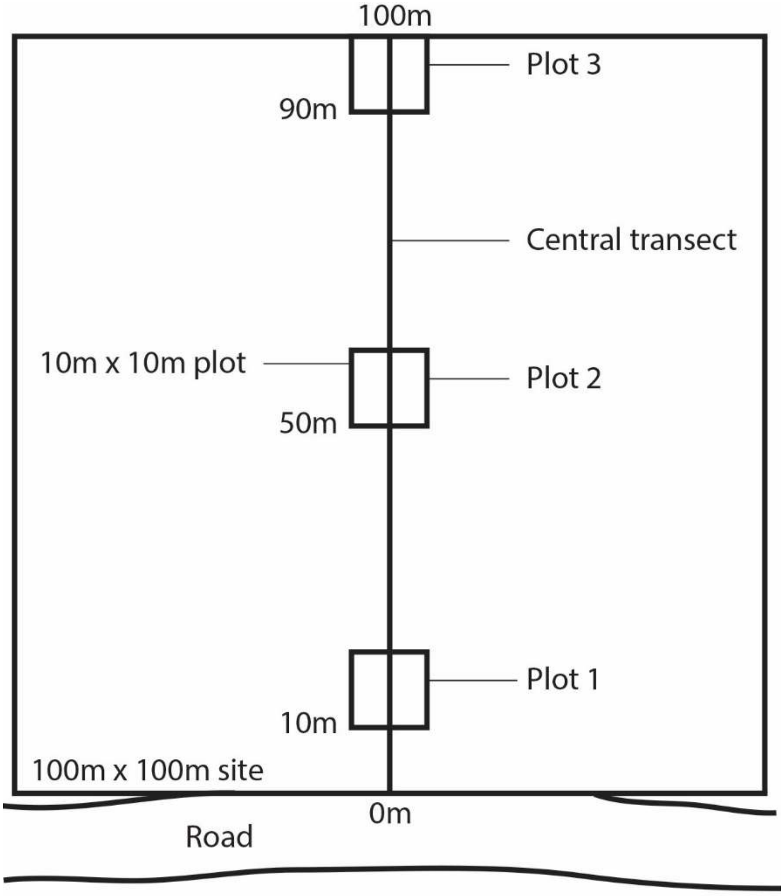
APPENDIX A

Site layout with plots



APPENDIX B

Plant species classification

Y = species observed on 2 or more sites, y = species observed on a single site.

Species	Life form	Reproductive strategy	Cohort present in			
			2009	1983	1939	1851
Acacia dealbata	Acacia	POS	Y	Y	Y	Y
Acacia frigescens	Acacia	POS	Y	Y	Y	Y
Acacia melanoxylon	Acacia	POS		y	Y	Y
Acacia obliquinervia	Acacia	POS	Y	Y	Y	
Acacia verniciflua	Shrub	POS	y			
Acaena novae-zelandiae	Herb	POS	Y	y	Y	Y
Acrothamnus maccraei	Shrub	POS			Y	
Asperula euryphylla	Herb	POS	Y			y
Asplenium bulbiferum	Fern	Sprout				Y
Atherosperma moschatum	Midstorey Tree	Sprout			Y	Y
Australina pusilla	Herb	POS	Y	Y	Y	Y
Austrocynoglossum latifolium	Herb	POS				y
Bedfordia arborescens	Midstorey Tree	Sprout	Y	Y	Y	Y
Billardiera mutabilis	Climber	POS	y	Y	Y	
Blechnum cartilagineum	Fern	Sprout			Y	
Blechnum nudum	Fern	Sprout	y		Y	y
Blechnum wattsii	Fern	Sprout	Y	Y	Y	Y
Calochlaena dubia	Fern	Sprout		y		y
Carex appressa	Graminoid	Sprout	y			y
Cassinia aculeata	Shrub	PES	Y	Y	Y	Y
Cassinia longifolia	Shrub	PES	Y	y	y	y
Clematis aristata	Climber	POS	Y	Y	Y	Y
Coprosma hirtella	Shrub	POS	Y	Y	Y	Y
Coprosma quadrifida	Shrub	POS	Y	Y	Y	Y
Correa lawrenceana	Shrub	POS	Y	Y	Y	Y
Cyathea australis	Midstorey Tree	Sprout	Y	Y	Y	Y
Daviesia latifolia	Shrub	POS			y	
Dianella tasmanica	Graminoid	Sprout	Y	Y	Y	Y
Dicksonia antarctica	Midstorey Tree	Sprout	Y	Y	Y	Y
Drymophila cyanocarpa	Herb	Sprout		y	y	
Dryopoa dives	Graminoid	POS	Y	y	Y	Y
Eucalyptus cypellocarpa	Eucalypt	POS			Y	
Eucalyptus delegatensis	Eucalypt	POS	y		Y	
Eucalyptus nitens	Eucalypt	POS	Y	Y	y	
Eucalyptus regnans	Eucalypt	POS	Y	Y	Y	Y
Eucalyptus viminalis	Eucalypt	POS	y			
Gahnia radula	Graminoid	Sprout		y	Y	
Galium propinquum	Herb	POS	Y		Y	y
Geranium potentilloides	Herb	POS	Y	y	Y	Y
Gonocarpus humilis	Herb	POS	Y		Y	
Goodenia ovata	Shrub	POS	Y	y		
Goodia lotifolia	Shrub	POS	Y			
Grammitis billardierei	Fern	POS		Y	Y	Y
Hedycarya angustifolia	Midstorey Trees	Sprout	Y	Y	Y	Y
Histiopteris incisa	Fern	Sprout	Y	Y	Y	Y
Hydrocotyle geraniifolia	Herb	POS		y		
Hydrocotyle hirta	Herb	POS	Y	Y	Y	Y
Hymenophyllum sp	Fern	POS			Y	y

Hypolepis rugosula	Fern	Sprout	Y			
Leionema bilobum	Midstorey Tree	POS	y		Y	
Lepidosperma elatius	Graminoid	Sprout	Y	Y	Y	Y
Leptinella filicula	Herb	POS			Y	y
Leptospermum grandiflorum	Midstorey Tree	POS			Y	
Leptostigma reptans	Herb	POS	Y	Y	Y	y
Lomatia fraseri	Midstorey Tree	Sprout	Y		Y	y
Mentha australis	Herb	POS	y		y	y
Mentha laxiflora	Herb	POS	Y		y	Y
Microlaena stipoides	Graminoid	POS		y	y	y
Microsorum pustulatum	Fern	POS			Y	Y
Myrsine howittiana	Midstorey Tree	Sprout				y
Notelaea ligustrina	Midstorey Tree	Sprout	Y	y	Y	y
Nothofagus cunninghamii	Midstorey Tree	POS	Y	y	Y	Y
Olearia argophylla	Shrub	Sprout	Y	Y	Y	Y
Olearia lirata	Shrub	PES	y	Y	Y	Y
Olearia phlogopappa	Shrub	PES	Y	Y	Y	Y
Oreomyrrhis eriopoda	Herb	POS	Y			y
Oxalis exilis	Herb	POS	Y	y	Y	Y
Parsonsia brownii	Climber	POS		Y	Y	y
Persoonia arborea	Herb	POS	Y	Y	Y	Y
Pimelea axiflora	Shrub	POS	Y	Y	Y	Y
Pimelea ligustrina	Shrub	POS		y		y
Pimelea linifolia	Shrub	POS	y	y	Y	Y
Pittosporum bicolor	Midstorey Tree	Sprout	Y	Y	Y	Y
Poa ensiformis	Graminoid	POS	Y		Y	Y
Poa sieberiana	Graminoid	POS			y	
Polyscias sambucifolia	Shrub	POS	Y	Y	Y	Y
Polystichum proliferum	Fern	Sprout	Y	Y	Y	Y
Pomaderris aspera	Midstorey Tree	POS	Y	Y	Y	Y
Poranthera microphylla	Herb	POS	y			
Prostanthera lasianthos	Midstorey Tree	POS	Y	Y	Y	Y
Prostanthera melissifolia	Shrub	POS		Y	Y	
Pteridium esculentum	Fern	Sprout	Y	Y	Y	Y
Rorippa dictyosperma	Herb	ESS	Y	y		y
Rubus parvifolius	Herb	Sprout	Y		Y	y
Rumohra adiantiformis	Fern	Sprout	y			
Sambucus gaudichaudiana	Herb	Sprout	Y	Y	Y	Y
Senecio glomeratus	Herb	ESS	y			y
Senecio gunnii	Herb	ESS	Y		Y	y
Senecio minimus	Herb	ESS	Y		y	y
Senecio vagus	Herb	ESS	Y	y		y
Senecio velleioides	Herb	ESS	Y		y	Y
Solanum aviculare	Herb	ESS	Y			
Solanum prinophyllum	Shrub	POS			y	y
Stellaria flaccida	Herb	POS	Y	Y	Y	Y
Sticherus lobatus	Fern	Sprout			y	
Tasmannia lanceolata	Midstorey Tree	Sprout	Y	y	Y	Y
Tasmannia xerophila	Midstorey Tree	Sprout			y	
Tetrarrhena juncea	Graminoid	POS	Y	Y	Y	Y
Urtica incisa	Herb	POS	Y	y	y	y
Viola eminens	Herb	POS			Y	y
Viola hederacea	Herb	POS	Y	Y	Y	Y
Zieria arborescens	Shrub	POS	Y	Y	Y	Y

APPENDIX C

Posterior median and lower and upper 95% credible intervals are reported for each of the model effects. The cohort effects are given holding elevation fixed at the mean level. Also, note that elevation is standardized to have mean 0 and standard deviation 1. We also report relative effects comparing each of the cohorts, note that credible intervals that don't contain 1 indicate evidence that the rates are different from each other (displayed in bold).

Overall Species Richness

	est	lower	upper
2009	17.11	15.34	19.24
1983	12.95	11.01	15.1
1939	12.47	11.39	13.56
1850	13.4	11.7	15.64
Elevation	0.94	0.88	1
Aspect O	17.11	15.34	19.24
Aspect N	16.92	14.54	19.54
1983-2009	**0.76**	**0.62**	**0.91**
1939-2009	**0.73**	**0.64**	**0.84**
1850-2009	**0.78**	**0.66**	**0.94**
1939-1983	0.96	0.81	1.15
1850-1983	1.03	0.85	1.29
1850-1939	1.08	0.92	1.26
Aspect N – O	0.99	0.85	1.11

Life form

Significant results highlighted in **bold**.

Eucalypt species richness

	est	lower	upper
2009	1.18	0.9	1.56
1983	1.17	0.76	1.68
1939	0.86	0.67	1.06
1850	0.6	0.37	0.94
Elevation	1.06	0.9	1.25
Aspect O	1.18	0.9	1.56
Aspect N	1.07	0.74	1.56
1983-2009	0.99	0.61	1.53
1939-2009	0.72	0.52	1.04
1850-2009	**0.51**	**0.29**	**0.82**
1939-1983	0.73	0.48	1.13
1850-1983	**0.51**	**0.28**	**0.89**
1850-1939	0.7	0.42	1.16
Aspect N – O	0.91	0.63	1.28

Acacia species richness

	est	lower	upper
2009	0.95	0.66	1.29
1983	1.18	0.74	1.73
1939	0.93	0.72	1.16
1850	0.44	0.24	0.73
Elevation	1.14	0.96	1.34

Aspect O	0.95	0.66	1.29
Aspect N	0.98	0.63	1.43
1983-2009	1.24	0.76	2.1
1939-2009	0.98	0.67	1.46
1850-2009	**0.46**	**0.25**	**0.81**
1939-1983	0.79	0.5	1.29
1850-1983	**0.37**	**0.19**	**0.71**
1850-1939	**0.47**	**0.26**	**0.84**
Aspect N – O	1.03	0.71	1.47

Midstorey Tree species richness

	est	lower	upper
2009	2.48	2.03	3
1983	2.17	1.66	2.85
1939	2.74	2.37	3.12
1850	3.61	2.94	4.51
Elevation	0.86	0.78	0.94
Aspect O	2.48	2.03	3
Aspect N	2.19	1.7	2.86
1983-2009	0.87	0.62	1.21
1939-2009	1.1	0.88	1.41
1850-2009	**1.45**	**1.11**	**1.92**
1939-1983	1.26	0.95	1.71
1850-1983	**1.66**	**1.19**	**2.36**
1850-1939	**1.32**	**1.03**	**1.69**
Aspect N – O	0.88	0.7	1.12

Shrub species richness

	est	lower	upper
2009	2.84	2.21	3.74
1983	3.18	2.25	4.41
1939	2.43	2	2.96
1850	1.88	1.33	2.67
Elevation	0.89	0.78	1.02
Aspect O	2.84	2.21	3.74
Aspect N	2.88	2.1	4.01
1983-2009	1.12	0.74	1.66
1939-2009	0.85	0.62	1.2
1850-2009	**0.66**	**0.44**	**0.99**
1939-1983	0.76	0.52	1.08
1850-1983	**0.59**	**0.38**	**0.94**
1850-1939	0.78	0.52	1.12
Aspect N – O	1.02	0.76	1.35

Fern species richness

	est	lower	upper
2009	2.02	1.65	2.5
1983	1.99	1.48	2.65
1939	2.33	2.01	2.66
1850	2.8	2.21	3.5
Elevation	1.03	0.93	1.14
Aspect O	2.02	1.65	2.5
Aspect N	1.84	1.4	2.35

1983-2009	0.98	0.69	1.38
1939-2009	1.16	0.89	1.46
1850-2009	**1.39**	**1.02**	**1.82**
1939-1983	1.17	0.86	1.61
1850-1983	1.41	0.98	2
1850-1939	1.2	0.93	1.56
Aspect N – O	0.91	0.72	1.14

Graminoid species richness

	est	lower	upper
2009	1.77	1.41	2.23
1983	1.3	0.91	1.81
1939	1.21	0.98	1.46
1850	1.08	0.77	1.51
Elevation	0.92	0.81	1.04
Aspect O	1.77	1.41	2.23
Aspect N	1.98	1.45	2.61
1983-2009	0.73	0.5	1.1
1939-2009	**0.68**	**0.52**	**0.93**
1850-2009	**0.61**	**0.41**	**0.91**
1939-1983	0.93	0.66	1.38
1850-1983	0.83	0.54	1.31
1850-1939	0.89	0.59	1.29
Aspect N – O	1.12	0.86	1.51

Herb species richness

	est	lower	upper
2009	4.28	2.41	7.53
1983	0.7	0.29	1.62
1939	0.72	0.43	1.12
1850	1.57	0.72	3.08
Elevation	0.88	0.67	1.24
Aspect O	4.28	2.41	7.53
Aspect N	4.84	2.32	9.72
1983-2009	**0.16**	**0.06**	**0.44**
1939-2009	**0.17**	**0.08**	**0.34**
1850-2009	**0.37**	**0.17**	**0.96**
1939-1983	1.02	0.41	2.5
1850-1983	2.23	0.71	6.08
1850-1939	2.17	0.99	5.02
Aspect N – O	1.13	0.59	2.22

Climber species richness

	est	lower	upper
2009	0.65	0.43	0.96
1983	0.87	0.53	1.38
1939	0.57	0.42	0.76
1850	0.6	0.35	0.95
Elevation	0.89	0.72	1.07
Aspect O	0.65	0.43	0.96
Aspect N	0.62	0.38	1
1983-2009	1.33	0.73	2.35
1939-2009	0.88	0.55	1.4

1850-2009	0.93	0.5	1.59
1939-1983	0.66	0.38	1.1
1850-1983	0.69	0.37	1.33
1850-1939	1.06	0.61	1.87
Aspect N – O	0.96	0.61	1.44

Reproductive strategy

Significant results highlighted in **bold**.

Early Successional Seed (ESS) species richness

	est	lower	upper
2009	1.43	0.91	2.14
1983	0.13	0.03	0.35
1939	0.14	0.08	0.26
1850	0.33	0.16	0.62
Elevation	1.31	0.95	1.72
Aspect O	1.43	0.91	2.14
Aspect N	1.44	0.83	2.51
1983-2009	**0.09**	**0.02**	**0.26**
1939-2009	**0.1**	**0.05**	**0.19**
1850-2009	**0.23**	**0.11**	**0.46**
1939-1983	1.13	0.35	4.84
1850-1983	2.59	0.75	11.16
1850-1939	2.3	0.89	5.07
Aspect N – O	1	0.57	1.79

Persistent External Seed (PES) species richness

	est	lower	upper
2009	0.93	0.59	1.38
1983	0.51	0.26	1.02
1939	0.35	0.23	0.55
1850	0.39	0.18	0.69
Elevation	1.11	0.86	1.42
Aspect O	0.93	0.59	1.38
Aspect N	0.77	0.43	1.38
1983-2009	0.55	0.24	1.16
1939-2009	**0.38**	**0.21**	**0.64**
1850-2009	**0.43**	**0.21**	**0.9**
1939-1983	0.69	0.33	1.53
1850-1983	0.77	0.32	1.92
1850-1939	1.11	0.53	2.31
Aspect N – O	0.83	0.47	1.43

Persistent On-site Seed (POS) species richness

	est	lower	upper
2009	6.76	5.89	7.69
1983	5.92	4.94	7.12
1939	4.78	4.25	5.3
1850	4.08	3.31	4.95
Elevation	0.95	0.88	1.02
Aspect O	6.76	5.89	7.69
Aspect N	7.23	6.08	8.57

1983-2009	0.87	0.7	1.08
1939-2009	**0.71**	**0.6**	**0.84**
1850-2009	**0.6**	**0.48**	**0.76**
1939-1983	**0.81**	**0.66**	**0.99**
1850-1983	**0.69**	**0.54**	**0.9**
1850-1939	0.86	0.68	1.06
Aspect N – O	1.07	0.92	1.25

Persistent Sprout (Sprout) species richness

	est	lower	upper
2009	4.69	4.02	5.39
1983	3.87	3.16	4.77
1939	4.96	4.49	5.53
1850	6.33	5.32	7.39
Elevation	0.96	0.9	1.03
Aspect O	4.69	4.02	5.39
Aspect N	4.32	3.56	5.13
1983-2009	0.82	0.65	1.04
1939-2009	1.06	0.89	1.26
1850-2009	**1.35**	**1.09**	**1.64**
1939-1983	**1.28**	**1.02**	**1.58**
1850-1983	**1.63**	**1.27**	**2.12**
1850-1939	**1.28**	**1.06**	**1.54**
Aspect N – O	0.92	0.78	1.08

Persistent None (Pnone) species richness

	est	lower	upper
2009	2.76	2.14	3.52
1983	2.29	1.61	3.15
1939	2.09	1.73	2.52
1850	2.15	1.54	2.97
Elevation	0.81	0.71	0.92
Aspect O	2.76	2.14	3.52
Aspect N	2.76	2.03	3.79
1983-2009	0.83	0.54	1.21
1939-2009	0.76	0.56	1.03
1850-2009	0.78	0.53	1.16
1939-1983	0.92	0.62	1.29
1850-1983	0.94	0.6	1.51
1850-1939	1.03	0.72	1.49
Aspect N – O	1	0.76	1.33

CHAPTER 4

Does pre-disturbance forest stand age influence recovery after fire in Mountain Ash?

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ABSTRACT

The age of a forest prior to a large natural disturbance is important in determining the species composition of the post-disturbance regeneration cohort. Forest age broadly influences a range of biological legacies from which a new forest regenerates.

We quantified the recovery of vascular plants in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands in Victoria, south-eastern Australia. We compared the regeneration from forest of three age cohorts that were 26, 70 and 158+ years old when all were burned by high-severity wildfire in 2009. Overall species richness declined with forest age at the time of disturbance with 25.7, 22.7 and 20.7 species/site respectively. The youngest sites had greater richness of the seeding functional groups. In contrast, sprouting species, including ferns and most midstorey trees, were more species rich when older cohorts regenerated after fire.

We suggest the lower overall plant species richness in the regeneration of the 158+ year old forest burned in 2009 was likely due to a diminishing soil seed bank producing fewer seedlings, or seedlings failing to establish due to competition from an increased number of re-sprouting ground ferns, or both.

Our findings indicate that in forests where the overstorey eucalypts are reproductively mature, the age of a forest at the time it is subject to major wildfire has a moderate influence on the subsequent post-fire regeneration, but broadly does not impede the ability of this forest type to regenerate and support a representative diversity of plant functional groups.

INTRODUCTION

A wide variety of factors determine how forest vegetation recovers following major disturbances, such as large wildfires (Cohen et al. 2016, Kulakowski et al. 2017). These include characteristics of the landscape, the disturbance itself (Gill 1975, Keeley 2009), the resilience and resistance traits of the plant species (Duveneck and Scheller 2016), the pre-disturbance history including number and frequency of past disturbances (Bowd et al. 2018b), and stand characteristics before the disturbance (Foster et al. 1998).

In this investigation, we examined one of the pre-disturbance stand characteristics. We studied the effects that forest age prior to a disturbance has on the post-disturbance regeneration cohort. The age of a stand of forest at the time it is burned is likely to influence post-fire forest recovery for at least four key reasons. These include:

1. The age of individual plants can affect their resilience to fire through physical factors such as bark thickness (Clarke et al. 2013) and canopy height, especially for species where seed is stored in the canopy (e.g. species in the Myrtaceae family (Gill 1997)).
2. Older (and therefore larger) plants usually produce more seeds, which can in turn affect the soil seed bank and hence post-disturbance dynamics (Wenk and Falster 2015).
3. Forest age can influence disturbance severity. For example, fire tends to burn at higher severity in younger forests than in older stands in higher elevation areas in south-eastern Australia (Taylor et al. 2014, Zylstra 2017). This has implications for the survival of individual plants and may influence persistence of on-site seed (Ferrandis et al. 1999, Lindenmayer et al. 2010).
4. Individuals and species remaining after disturbance can strongly shape the structure and composition of recovering stands (Egler 1954, Franklin et al. 2002, Pulsford et al. 2014).

Numerous ‘time since disturbance’ studies have examined plant species richness and successional changes in the composition of plant assemblages in forests of different ages after major disturbances (Connell and Slatyer 1977, Johnson and Miyanishi 2008, Swanson et al. 2011). However, relationships between the age of a forest at the time it was disturbed and subsequent patterns of plant species richness and assemblage composition have rarely been quantified. This is a major knowledge gap because of its implications for forest biodiversity in response to recurrent large disturbances and recovery of particular species during inter-disturbance periods (Lindenmayer et al. 2017).

Here we report the results of a study of vascular plants in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, in south-eastern Australia. Widespread, high severity wildfires across the study region in 1851, 1939 and 1983 resulted in even aged stands of Mountain Ash in different parts of the landscape (Victorian Government DELWP 2018a). In 2009, another large wildfire burned stands of some of these respective age cohorts. The cohorts were 26, 70 and 158+ years old when burned by the 2009 fire. By selecting forest with no previous logging history, we took advantage of an important opportunity to determine whether the age of a forest prior to a large disturbance influenced post-fire plant species composition.

We posed two inter-related questions:

1) Does forest age at the time of high severity fire affect the species richness of the subsequent regenerating forest; and

2) How does forest age at the time of high severity fire affect the different plant functional groups ability to persist*?*

The species richness and composition of life forms in a forest stand regenerating after wildfire will depend largely on the plant propagules present (Leck 2012). This includes seed in the soil and canopy, seed that enters from outside the site, and the abundance of resprouting species with structures such as lignotubers, rhizomes and trunks. We made a series of predictions about how forest age is likely to affect each of these regeneration traits. We based many of these predictions on a detailed understanding of the ecology of Mountain Ash forests, including information from past studies of this ecosystem (Ashton 1976, 1981, Wang 1997, Ashton 2000).

Prediction 1: Overall species richness would be lowest in stands 158+ years old at the time of the 2009 fire.

Our prediction was based on the expected cumulative responses of the various functional groups within the Mountain Ash forests (see predictions below). We predicted overall species richness would be lowest in the 158+ year old forest burned in 2009 because of suppression from ground ferns (Coomes et al. 2005) (which we predict to be most abundant on old sites), and where seed bank viability may have reduced over time.

Prediction 2: Establishment of on-site seeding species will decline with forest age at the time of the 2009 fire.

This prediction corresponds to plant regeneration arising from seed originating on the site, either in the canopy (typified by many species in the Myrtaceae family, including *Eucalyptus regnans*) (Judd and Ashton 1991) or in a seed bank in the soil. For this prediction, we need to determine how seed banks change over time. Seed longevity varies between forest ecosystems. In tropical rainforests, competition is such that seed is constantly produced but generally short-lived (Vázquez-Yanes and Orozco-Segovia 1993). In the temperate deciduous forests of the Northern Hemisphere, it was found that seed banks are filled with an early deposition of large amounts of seed, that diminishes over time (Pickett 1989). Seed viability decline, seed loss through abiotic means (crushed, abraded, water logging etc) and biotic seed predation over time, particularly by ants (Ashton 1979) can deplete soil seed banks (Chambers and MacMahon 1994, Bossuyt et al. 2002). However, the soil seed banks of some species may persist for over a century (Leck 2012, Lindenmayer et al. 2015).

The on-site seeding functional group is likely to be an important component of overall species richness as it is a species-rich group (Murphy and Ough 1997, Blair et al. 2016). We predict the germination from on-site seeding species may decline with forest age due to seed predation and a decline in seed viability as well as increasing competition from ground ferns that are likely to be more abundant on older sites (Ough 2001).

Prediction 3: **The species richness of functional groups with highly mobile seed would be similar across all sites.**

The 'blow-in seed' group includes species with highly mobile seed dispersed by vectors including wind, birds and mammals that typically enter a burned site from unburned areas outside the perturbation boundary. Hence, we predicted this group would exhibit similar levels of species richness across all sites as the biological legacies remaining from the pre-disturbance forest should not have an effect on seed from these sources reaching the site. This group includes the 'climbers' life form group, represented by two species, *Clematis aristata* and *Billardiera mutabilis* which are wind and bird dispersed, respectively.

Prediction 4: The highest species richness of sprouting taxa would be forest regenerating from stands that were 158+ years old at the time of the disturbance.

Resprouting as a response to disturbance comes from retained living biological legacies within a forest such as rhizomes, lignotubers/root balls or trunks (Murphy and Ough 1997, Ough 2001). Such legacies are increasingly abundant as forests age (Ashton 2000, Ough 2001). Therefore, we predicted that sprouting species would be more common in forest regenerating from stands that were 158+ years old at the time it was burned. Given these sprouting plants usually have an established root system and are able to access resources beyond those available to newly germinated plants, they can grow rapidly soon after disturbance, and thus may out complete seeding species (George and Bazzaz 1999, Coomes et al. 2005). This group includes the majority of the midstorey trees and all but one of the ferns.

Prediction 5: Species richness of eucalypts would be even across sites and species richness of *Acacia* would be greatest on sites that were 158+ years old at the time of the fire.

Given we selected sites that were dominated primarily by *Eucalyptus regnans*, we predicted species richness for the eucalypts would be limited mainly to this one species with forest age prior to disturbance having little or no effect.

Acacias have very long lived seed with trees continuing to produce additional seed over many decades of the life of an individual tree (Wilson et al. 2011). This should increase seed abundance in the seed bank over time. However, *Acacia* seed is also targeted by ants (Ashton 1979). Ants consequently move seed to a wide range of depths within the soil profile (Wang 1997) which could increase the probability of successful germination under a variety of conditions. Due to expected increases in seed availability in both eucalypts and *Acacia* as forests age, we predicted the prevalence of these species in post-fire regeneration would be greatest on sites that were the oldest at the time of the 2009 fire.

Prediction 6: Shrubs, graminoids and herbs would regenerate with greatest species richness from sites that were young at the time of disturbance.

Shrubs are a diverse group with a range of reproductive strategies. In another study in these forests, they were the only life form that increased in probability of occurrence across a 'disturbance gradient' of fire, clearfall logging and salvage logging (Blair et al. 2016), indicating the potential to respond positively to severe and repeated disturbance. For this reason, we predicted that shrubs would be more common in stands regenerating on sites dominated by young (26 year old) forest at the time of the 2009 fire.

Many herbs and graminoids decline in abundance after the early successional stages following fire (Swanson et al. 2011) and we therefore anticipated that these species may not add significantly to the seed bank after that initial period. If this is the case, together with a predicted decline in seed bank viability over time, then we should observe greater species richness of graminoids and herb species in the resulting regeneration cohort when younger (26 year old) forest is burned. Additionally, their low growth habits are more likely to lead to greater competition with ground ferns, which we predict to be more common on older (70 and 158+ year old) sites.

METHODS

We conducted this study in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, 60-120km east of Melbourne in south eastern Australia (37°20'-37 ° 55'S and 145 ° 30'-146 ° 20'E) (see Figure 1). *Eucalyptus regnans* is an obligate seeder and the tallest flowering plant in the world, typically 55-75m in height (Costermans 2009). Our study sites were between 436m and 1175m in elevation and located within closed water catchments, where logging is excluded, and multi-purpose State Forest, which includes areas subject to timber harvesting. As we wanted to avoid the effects of logging, we selected areas within the State Forest that were unlogged.

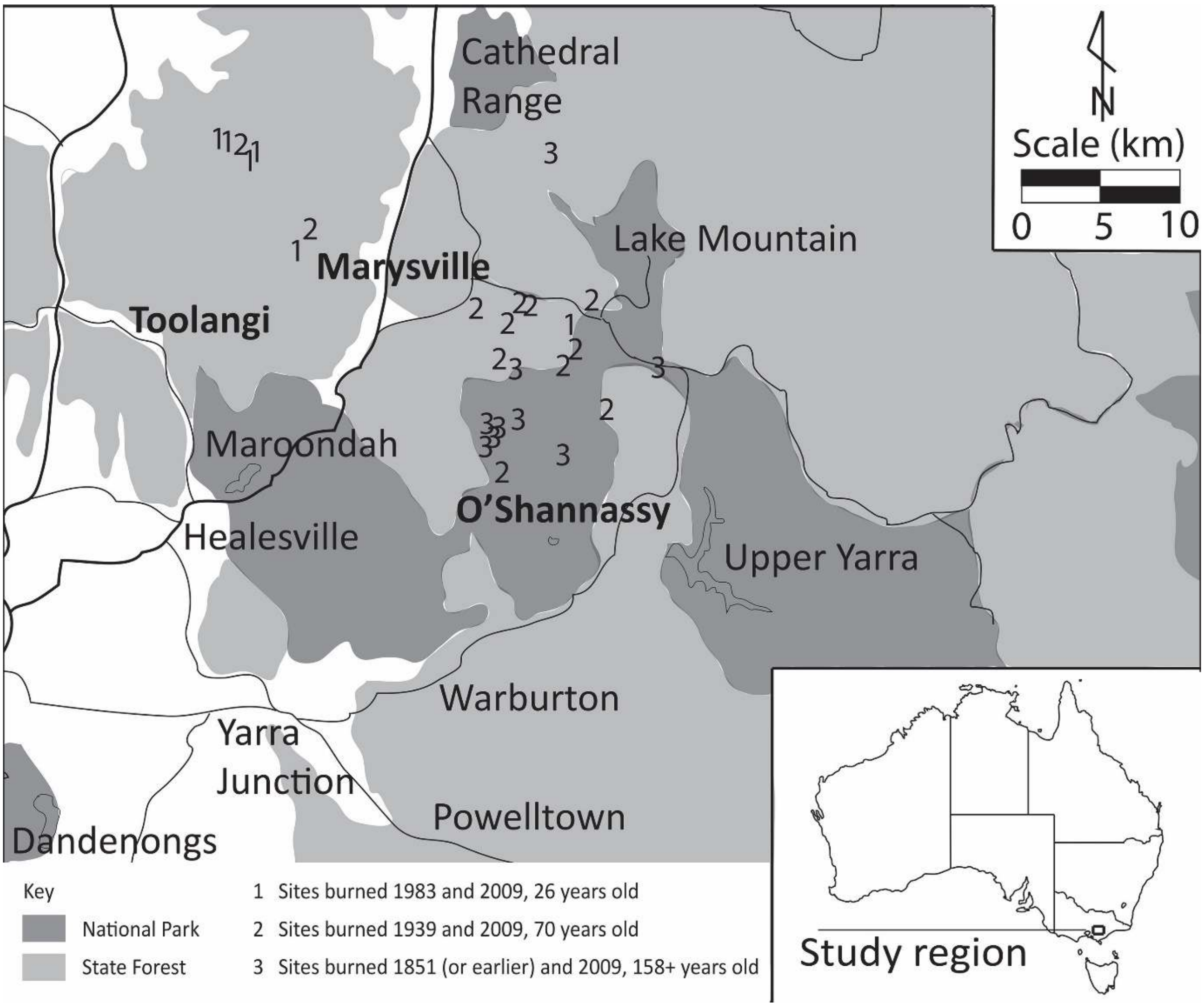

Figure 1: Map of study area showing location of sites.

The Central Highlands region has a history of wildfires, with areas of forest burning in 1851, 1905, 1906, 1926, 1932, 1939, 1948, 1954, 1983 and 2009 (Victorian Government DELWP 2018a). The fires in 1939 were severe and widespread, burning 79% of the Central Highlands region (Noble 1977).

Our study comprised 27 sites assigned three pre-fire age cohorts. The cohorts originated from fires in 1983 (six sites), 1939 (12 sites) and in or prior to 1851 (nine sites). All 27 sites were burned in 2009 at high severity. The overstorey on the sites was 26, 70 and 158+ years old respectively at the time of the 2009 fires. To ensure our results were associated with the age of the forest at the time it was burned, we controlled other variables which can affect forest plant species composition. Covariates of successional changes and climatic differences were constrained through surveying regeneration from a single fire event in 2009, resulting in all regenerating plants being of the same age. We avoided sites that had been logged in the past as this can influence species composition (Blair et al. 2016). We also avoided sites burned by more than two fires in the last century in our study design as frequent fires can affect species composition (Bowd et al. 2018b).

Each of our 27 sites was 100m x 100m in size, with a 10m wide central transect bisecting the site from front to back. Along this transect, we recorded the species richness of all live vascular plants. We did not measure individual plant abundance as many species would number in the thousands at that scale and the young germinants of many species are extremely difficult to distinguish at the early stage of growth. We did not record species for the first 10m of the transect to avoid potential edge effects. We conducted our surveys between March and August, 2017, eight years after the 2009 fire that burned all 27 field sites.

We divided the plants into life forms based on physical traits and on reproductive strategy (see Appendix S1 for species and functional groups). **Life forms** included: 1) Eucalypts (the dominant overstorey species), 2) *Acacia*, 3) Midstorey trees, 4) Shrubs, 5) Ferns, 6) Graminoids, 7) Herbs, and 8) Climbers. The three main *Acacia* species (*Acacia dealbata, A. frigescens,* and *A. obliquinervia*) are midstorey trees. However, due to Acacias being the focus of other research because of their special ecological roles in nutrient cycling (Adams and Attiwill 1984) and provision of habitat for fauna (Lindenmayer et al. 1993), it was decided to separate them from the other midstorey trees. Tree ferns *Dicksonia antarctica* and *Cyathea australis* were categorised as midstorey trees, not ferns, due to their large physical form and importance in midstorey structure (Blair et al. 2017). Plants were assigned categories based on the Victorian State Government Department of Environment, Land, Water and Planning's Highlands Southern Fall Bioregion Ecological Vegetation Class (EVC) (Victorian Government DELWP 2018b).

We divided **reproductive strategy** into 'Persistent' (P) species, and 'Transitory' (T) species. Transitory species are short-lived early colonisers that are out competed by other plants, typically in less than 10 years after disturbance. In later successional stages, transitory species may still be 'present' on site due to below ground seed, but their above ground foliage will no longer be visually present. Many of the transitory species already appeared absent when we conducted our surveys. We further divided the reproductive strategy groups based on their primary method of regeneration after disturbance from fire. This resulted in 1) Transitory Blow-in species (TBi), 2) Persistent Blow-in species (PBi), 3) Persistent On-site Seeders (POS), 4) Persistent Sprouting species (PS) and species that commonly reproduced in a number of ways, 5) Persistent None (no defined strategy) (PNone). The 'blow in' categorisation was a generalised term for all species with highly mobile seed spread by vectors such as wind, mammals or birds, with seed usually entering the site from outside the disturbance boundary. Our determination of species reproductive strategy was based on literature reviews (Walsh and Entwisle 1994, 1996, 1997, Costermans 2009, Kattge et al. 2011, Bull and Stolfo 2014), field observations and consultation with an expert from the Melbourne Botanical Gardens. Exotic plant species are rare on our sites and were excluded from statistical analysis.

Statistical analysis

We modelled overall species richness at the site level as a function of age cohort, elevation and aspect. We used a Bayesian generalized linear model (GLMM) with a Poisson distribution and log link function. We completed our analysis in R (R Core Team 2017) using the brms package (Bürkner 2016). We used the default priors provided in the package and ran four Markov Chains for 2000 iterations discarding the first 1000 as burn-in. Standard MCMC diagnostics were employed to check for convergence of the chains and all were found to show adequate mixing (Gelman and Rubin 1992). Due to our study design, we included age cohort in all models and used LOOIC (Leave One Out cross validation Information Criterion) to choose whether or not elevation and/or aspect was required in addition to age cohort (Vehtari et al. 2017). We report posterior mean estimates and 95% credible intervals. Species richness in each of the 13 functional groups (eight life form groups and five reproductive strategies) was analysed in a similar fashion.

RESULTS

We identified 87 indigenous vascular plant species across our 27 sites. On the sites that were 26 years old when burned in 2009, we recorded an average species richness of 25.7 species/site (21.7 Lower 95% Credible Interval, 30.4 Upper CI), on the 70 year old sites we recorded 22.7 species/site (19.6 LCI, 26.1 UCI) and on the 158+ year old sites, 20.7 species/site (17.7 LCI, 24.2 UCI) (Figure 2). The 26 year old cohort had significantly higher species richness than the 158+ year old cohort.

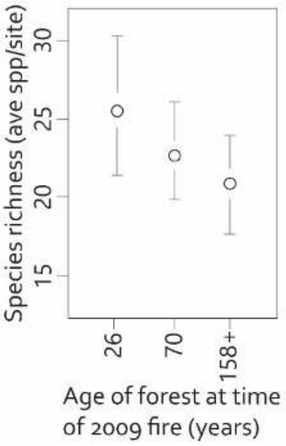

Figure 2: Average species richness per site of vascular plants regenerating from three stand ages all burned in 2009, with 95% Credible Intervals

Of the life forms into which we grouped our species, the most common were herbs (26 species), shrubs (17 species), and midstorey trees (14 species). The remaining life forms were ferns (10 species), graminoids (nine species) and eucalypts (six species). The least diverse groups were *Acacia* (three species) and climbers (two species). Only two life form groups exhibited significant responses to forest age at the time of disturbance (Figure 3); midstorey trees and climbers. The 70 year old cohort of midstorey trees had a species richness of 2.1 species/site, significantly higher than the 26 year old cohort with 1.3 species. Climbers had a significantly greater species richness in the 70 year old cohort (0.6 species/site) than the 158+ year old cohort (0.2 species/site).

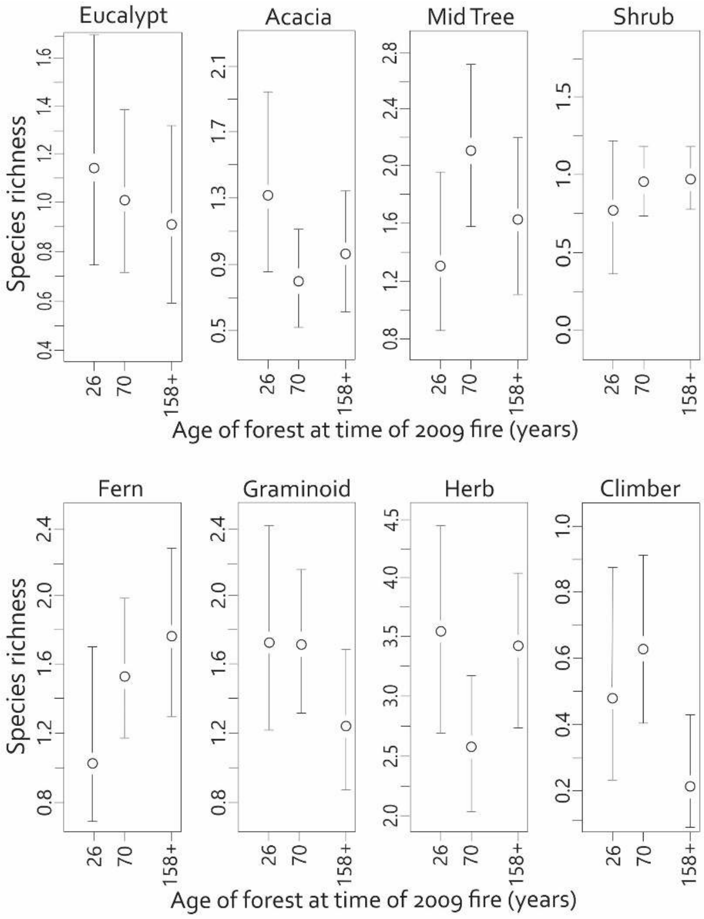

Figure 3: Life form species richness per site, with 95% Credible Intervals for regeneration from three forest age cohorts burned in 2009.

Of the five reproductive strategy categories, persistent on-site seeders had the greatest species richness (36 species), followed by sprouters (26 species), persistent 'none' (19 species). The least diverse were the blow-in seed groups with persistent blow-in species (four species) and transitory blow-in species (two species).

Statistical analysis of species richness by reproductive strategy identified two significant results for species richness at site level (Figure 4). Both were for the 'persistent none' (no defined reproductive strategy) category. Stands regenerating after the 70 year old and 26 year old forests had been burned, supported an average of 2.2 and 2.9 species/site respectively, both significantly higher than stands regenerating after the 158+year old forest had been burned (1.4 species/site).

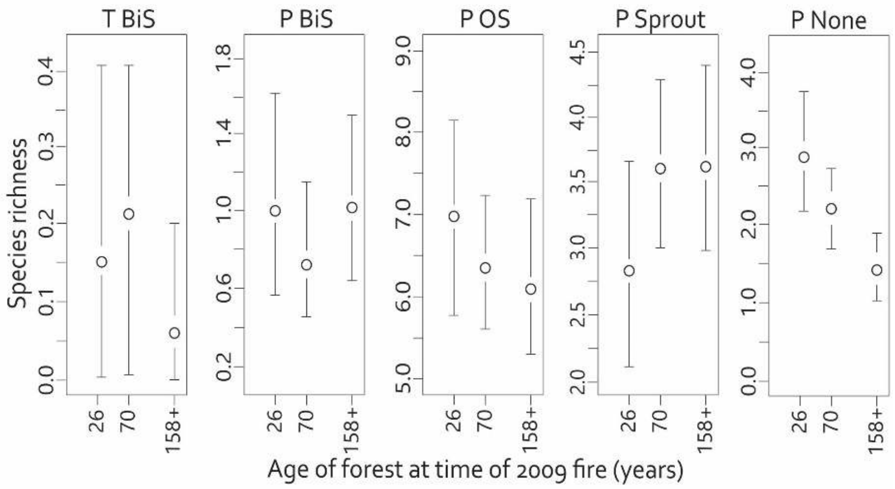

Figure 4: Reproductive strategy species richness per site, with 95% Credible Intervals for regeneration from three forest age cohorts burned in 2009.

DISCUSSION

We found forest age at the time of disturbance influenced the species richness and composition of the post-fire forest, but the effects were generally limited.

Prediction 1: Patterns of overall species richness.

Consistent with our predictions, species richness declined with increasing stand age prior to disturbance (Figure 2). We suggest these differences were likely attributable to diminished seed bank viability or greater competition from ground ferns in old forest cohorts (George and Bazzaz 1999, Coomes et al. 2005). Given there is less diversity in ground ferns than the range of seeding species (which includes most of the herbs and graminoids), this would lead to lower overall species richness on sites that were old when burnt by the 2009 fire. Forests of the Northern Hemisphere also have a significant component of their overall species diversity found in the richness of the herb layer. However, in contrast with our study, the diversity of this ground layer generally increases with time since disturbance (Gilliam 2007).

Prediction 2: Effects on on-site seeding species.

On-site seeder species richness decreased, as predicted, with increasing forest age prior to disturbance (Figure 4). Species within the on-site seeding functional groups of ‘Persistent on-site seed’ and ‘Persistent none’ have a highly diverse range of characteristics. Forest age is likely to have influenced regeneration success due to some of these traits. For example, seed longevity or viability may decline with time (Bossuyt et al. 2002), so we would expect reduced numbers of germinants when old forest is burned. In contrast, the quantity of seed in a seed bank may increase if long lived plants continue to produce seed over many years (Wang 1997) or if they continue to grow larger, producing increased seed crop volumes (Smith et al. 2014).

In the Mountain Ash forests of the Central Highlands, the return interval for high severity (tree killing) fire has historically been 75-150 years (McCarthy et al. 1999). For this reason, species that recover from fire with seed within the disturbed area either constantly produce short-lived seed (requiring the plant to remain extant to continue production), or produce very long-lived seed that is able to persist in the soil for decades. The overstorey eucalypts are an example of a long-lived genus that produces seed crops annually, with seed stored in the canopy (Judd and Ashton 1991). In contrast, species of *Acacia* and *Poa*, and the species *Dryopoa dives* store seed within the soil that may not germinate for well over a century (Lindenmayer et al. 2015). This indicates reductions in seed viability over time (Bossuyt et al. 2002), at least for some species, may have a limited effect. It also is likely for some species that the quantities of seed produced are so great, losses over time from seed longevity or ant predation (Ashton 1979) were insignificant. Interestingly, Wang (1997) found seed densities and species richness of seed within the seed bank increased with forest age from 0.6 years to 54 years, further supporting the proposition that seed in Mountain Ash forests is long lived and/or seedbanks have additional seed laid down over time beyond the initial successional stage. Woody species within the Mountain Ash forests were found not to produce seed until around 10 years after fire (Wang 1997) and *Eucalyptus regnans* takes 20 years to mature and produce viable seed (McCarthy et al. 1999). Consequently, frequent repeat fire could result in loss of these species (Bassett et al. 2015). As our sites were 26, 70 and 158+ years old prior to disturbance, this should not have limited these species.

A key determinant of successful seedling establishment is not how much viable seed was present at the time of the fire, but subsequent competition with other functional groups. Reduced seedling establishment due to competition with ground ferns has been demonstrated in the deciduous forests of the New England region of the US (George and Bazzaz 1999), New Zealand (Coomes et al. 2005) and Puerto Rico (Walker et al. 2010a) although in contrast, in the tropical rainforests of Queensland, Australia, ground ferns were found to be positively correlated to the successful establishment of seedlings (Song et al. 2012). Given a high abundance of ground ferns in the older forest cohorts of Mountain Ash forest which then resprouted after the 2009 fire, it seems likely that competition from ground ferns may be an important predictor of seedling establishment that is influenced by forest age prior to disturbance. Given *POS* and *Pnone* had the highest and third highest total number of species (36 and 19 respectively), these two groups have a large influence on overall species richness. In contrast to our findings, studies by Bowd et al. (2018b) in the same forests, showed 1983 cohorts that subsequently burned in 2009, but importantly, had also burned a third time in 1939 (= three high severity fires in 70 years) were characterized by a low abundance of onsite seed regeneration, indicating a limited ability of the seedbank to replenish with repeated short return intervals of fire.

Prediction 3: **Effects on functional groups with highly mobile seed.**

We predicted blow-in seeders (including the ‘climbers’ life form group) would be unaffected by the age of the forest prior to disturbance. For transitory and persistent blow-in seed species (*TBiS* and *PBiS*) this was the case (Figure 4). For ‘climbers’ this was not the case with the regeneration of burned 70 year old forest supporting significantly greater species richness than the regeneration from burned 158+ year old forest (Figure 3). Forest age before the 2009 fire should have had no effect (due to seed entering from unburned forest outside the fire boundary), additionally, the broad-scale ash bed of the immediate post-fire landscape should have been uniformly receptive for all sites regardless of pre-fire age (Chambers and Attiwill 1994). It is likely the differences were due to the distance to seed sources in unburnt forest in the surrounding landscape (Nathan and Muller-Landau 2000), a variable we did not measure.

Prediction 4: Effects on sprouting species, including midstorey trees and ferns.

The sprouting species group includes one shrub (*Olearia argophylla*), nine of the fourteen midstorey tree species, and eight of the nine ground ferns. We correctly predicted the regeneration following fire in an old forest would have greater sprouting species richness compared to young forest. Most ground ferns are shade tolerant for reproduction (Ashton 2000), or increase in number asexually through rhizome growth or proliferous buds/bulbils on their frond tips (Walsh and Entwisle 1994, Ough 2001). It is common in ecosystems around the world that as time since disturbance increases (such as in old forest compared to young), that diversity usually decreases as the most competitive species persist and proliferate (Mackey and Currie 2001). Importantly for our study, the increase in biological legacies from the competitive sprouting species that become more abundant as forests age, are likely to re-establish in the new stand of regenerating forest. Although sprouting species are well adapted to wildfire, they are the group most detrimentally impacted by clearcutting and salvage logging (Blair et al. 2016, Bowd et al. 2018b).

Prediction 5: Effects on eucalypts and *Acacia*.

Our site selection of *Eucalyptus regnans* dominated forest ensured species richness for this group was uniform across the age cohorts, which it was (Figure 3). Despite recording six species of eucalypt across our 27 sites, occurrences of species other than *E.regnans* were evenly spread and not common enough to produce significant differences between age cohorts. *Acacia* also exhibited limited variation in species richness as predicted. Unlike other species, suppression from ground ferns is unlikely to be a factor in establishment success of the eucalypts and *Acacia*, as both genera grow rapidly in the post fire environment, quickly overtopping ground storey species, including ferns.

Prediction 6: Effect on shrubs, graminoids and herbs.

Despite our prediction that the regeneration from young (26 year old) forest burned in 2009 would have greater species richness for shrubs, our results showed the most even distribution across the regeneration of the three age cohorts of any functional group (Figure 3). This is likely to be a result of shrubs being a variable but robust group that is able to regenerate successfully under a wide range of disturbance scenarios (Blair et al. 2016). As we predicted at the outset of our study, graminoids and herbs were most species rich in the regeneration cohort of the youngest forest (26 years old) when it burned in 2009 (Figure 3), although the contrasts between the ages of forest at the time they were burned were not significant. The majority of herbs are seeding species (17 of 19 species), while half the graminoids are seeders. As discussed in Prediction 2 above (on-site seeders), it is difficult to predict the responses of this group due to its variability in seeding characteristics. Our prediction was premised on the seed bank viability declining with time since disturbance in the older forest stands, as well as increased competition during establishment of these ground level plants from ferns.

Summary of influences on regeneration

We found that once the Mountain Ash forests of Victoria's Central Highlands reach 26 years of age, in the event of a major wildfire, the effect of the forest age prior to that disturbance had only moderate effects on the resulting post fire regeneration. A fire return interval of less than 20 years may compromise eucalypt regeneration due to reproductive immaturity (McCarthy et al. 1999) and similarly for other woody species with fire intervals less than 10 years (Wang 1997). *Eucalyptus regnans* is an obligate seeder and has little or no seed stored in the soil (Ashton 1979), and hence repeated fires in rapid succession (in the absence of artificial seeding) may lead to an *Acacia*-dominated landscape (McCarthy et al. 1999, Bassett et al. 2015). This occurred following consecutive large wildfires in 1926 and 1939 in the Central Highlands, and more recently further north along the Great Dividing Range in areas where the Alpine Fires of 2003, 2006 and 2009 overlapped (Bowman et al. 2014a, Bassett et al. 2015). It also occurs where wildfire burns areas that have been logged and regenerated within the last 20 years (Lindenmayer et al. 2015). The regeneration cohort that developed when the 2009 fire burned old growth forest from 1851 or earlier produced lower species richness than the regeneration from when the same fire burned young forest from 1983 (Figure 2). This is likely to be due to a combination of depletion or deterioration of the seed bank over time which allowed fewer seedlings to germinate, or increased competition from abundant ground ferns found in the older forests which prevented germinating seedlings establishing, or both.

CONCLUSIONS

In our study of how forest age before severe wildfire can influence the subsequent post-fire regeneration cohorts, we found that forest age had a moderate influence on the species composition in Mountain Ash forests.

As forests age, vegetation structure and plant species composition changes (McCarthy et al. 1999, Franklin et al. 2002, Seidl et al. 2014a) and the biological legacies found within a forest also change over time (Foster et al. 1998). Some biological legacies, such as large old trees and logs are visually apparent yet may have only minor influence on a new cohort regenerating after disturbance, while other legacies, including seeds, rhizomes and nutrients (Johnstone et al. 2016) are far less visually obvious, yet may have considerable implications for subsequent regeneration once disturbed.

The implications of our results for forest managers are encouraging. This ecosystem will regenerate well after fire, with a wide range of species present provided the overstorey is sufficiently mature to produce seed and the regeneration cohort is not subsequently disturbed through salvage logging operations.

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SUPPLEMENTARY INFORMATION S1

Plant species classification

Reproductive strategies: POS = Persistent On-site Seeder, Pnone = Persistent None (no defined reproductive strategy, or commonly uses several different strategies), Sprout = Persistent Sprouting species, PBiS = Persistent Blow-in Seeder, TBiS = Transitory Blow-in Seeder.

Species	**Life form**	**Reproductive strategy**	**Occurrence on sites**		
			1983	**1939**	**1851**
Acacia dealbata	Acacia	POS	5	8	6
Acacia frigescens	Acacia	POS	0	2	4
Acacia nanodealbata	Midstorey Tree	POS	0	1	1
Acacia obliquinervia	Acacia	POS	4	4	3
Acacia verniciflua	Shrub	POS	0	1	0
Acaena novae-zelandiae	Herb	Pnone	2	1	0
Asperula euryphylla	Herb	Pnone	0	5	1
Asperula gunnii	Herb	POS	1	0	0
Atherosperma moschatum	Midstorey Tree	Sprout	0	1	0
Australina pusilla	Herb	POS	2	3	4
Bedfordia arborescens	Midstorey Tree	Sprout	2	2	1
Billardiera mutabilis	Climber	Pnone	1	3	0
Blechnum cartilagineum	Fern	Sprout	1	0	0
Blechnum nudum	Fern	Sprout	1	0	1
Blechnum wattsii	Fern	Sprout	1	4	3
Carex appressa	Graminoid	Sprout	0	1	1
Cassinia aculeata	Shrub	PBiS	4	7	5
Cassinia longifolia	Shrub	PBiS	1	2	2
Clematis aristata	Climber	Pnone	5	10	4
Coprosma hirtella	Shrub	POS	1	6	2
Coprosma quadrifida	Shrub	POS	4	4	1
Correa lawrenceana	Shrub	POS	3	4	0
Cyathea australis	Midstorey Tree	Sprout	1	5	1
Daviesia mimosoides	Shrub	POS	0	0	1
Dianella tasmanica	Graminoid	Sprout	1	5	2
Dicksonia antarctica	Midstorey Tree	Sprout	2	8	8
Dryopoa dives	Graminoid	POS	2	6	4
Epilobium billardierianum	Herb	POS	1	0	0
Eucalyptus cypellocarpa	Eucalypt	POS	0	1	0
Eucalyptus delegatensis	Eucalypt	POS	0	3	2
Eucalyptus nitens	Eucalypt	POS	1	1	1
Eucalyptus radiata	Eucalypt	POS	1	0	0
Eucalyptus regnans	Eucalypt	POS	6	10	7
Eucalyptus viminalis	Eucalypt	POS	3	1	0
Gahnia radula	Graminoid	Sprout	1	0	0
Galium propinquum	Herb	POS	4	4	1
Geranium potentilloides	Herb	POS	6	4	3
Gleichenia dicarpa	Fern	Sprout	0	1	0
Gonocarpus humilis	Herb	Pnone	3	2	0
Goodenia ovata	Shrub	Pnone	1	1	0
Goodia lotifolia	Shrub	POS	0	4	0
Hedycarya angustifolia	Midstorey Trees	Sprout	1	4	1
Histiopteris incisa	Fern	Sprout	1	3	4
Hydrocotyle hirta	Herb	POS	5	9	8

Hypolepis rugosula	Fern	Sprout	0	0	3
Isolepis subtilissima	Graminoid	Pnone	0	0	1
Leionema bilobum	Midstorey Tree	POS	0	0	1
Lepidosperma elatius	Graminoid	Sprout	4	2	1
Leptinella filicula	Herb	Pnone	4	0	2
Leptostigma reptans	Herb	Pnone	4	0	0
Lomatia fraseri	Midstorey Tree	Sprout	3	7	2
Mentha laxiflora	Herb	Pnone	2	2	1
Microlaena stipoides	Graminoid	POS	0	0	1
Microsorum pustulatum	Fern	Pnone	0	0	1
Notelaea ligustrina	Midstorey Tree	Sprout	1	1	1
Nothofagus cunninghamii	Midstorey Tree	POS	0	3	3
Olearia argophylla	Shrub	Sprout	1	4	5
Olearia lirata	Shrub	PBiS	1	1	0
Olearia phlogopappa	Shrub	PBiS	5	6	6
Oreomyrrhis eriopoda	Herb	Pnone	0	0	1
Oxalis exilis	Herb	Pnone	3	2	3
Persoonia arborea	Herb	POS	0	1	0
Pimelea axiflora	Shrub	Pnone	1	1	1
Poa ensiformis	Graminoid	POS	0	1	0
Polyscias sambucifolia	Shrub	POS	1	7	7
Polystichum proliferum	Fern	Sprout	4	10	9
Pomaderris aspera	Midstorey Tree	POS	5	7	2
Poranthera microphylla	Herb	POS	0	2	1
Prostanthera lasianthos	Midstorey Tree	Pnone	2	5	1
Prostanthera melissifolia	Shrub	Pnone	2	0	1
Pteridium esculentum	Fern	Sprout	6	10	6
Ranunculus scapiger	Herb	POS	1	0	0
Rubus parvifolius	Herb	Sprout	2	2	0
Sambucus gaudichaudiana	Herb	Sprout	3	2	6
Senecio gunnii	Herb	Sprout	0	1	0
Senecio velleioides	Herb	TBiS	1	3	1
Stellaria flaccida	Herb	POS	1	7	7
Tasmannia lanceolata	Midstorey Tree	Sprout	0	2	1
Tetrarrhena juncea	Graminoid	Pnone	6	9	3
Todea barbara	Midstorey Tree	Sprout	1	1	0
Urtica incisa	Herb	Pnone	0	1	5
Veronica notabilis	Herb	Sprout	0	1	0
Viola eminens	Herb	POS	0	0	2
Viola hederacea	Herb	POS	6	6	4
Zieria arborescens	Shrub	POS	0	3	1

CONCLUSIONS

The Mountain Ash forests of Victoria's Central Highlands have evolved traits allowing them to survive some of the most high severity wildfires in the world. Disturbance has been a key driver of ecological composition and adaption in this ecosystem for millennia with species developing a variety of regenerative mechanisms to deal with the disturbance. The introduction of logging over a century ago, and intensive clearfell logging of these forests over the last 40 years, has introduced the novel disturbance type of wide scale mechanical disturbance. From my research, it has become apparent that certain functional groups are not well adapted to this form of disturbance, especially when it comes directly after a large wildfire in the form of salvage logging.

In **Chapter 1** *Disturbance gradient shows logging affects plant functional groups more than fire*, my findings of a 'disturbance gradient' across low severity fire, high severity fire, (green) clearfell logging and (post-fire) salvage logging showed reductions in species richness and overall implication of forest biota. Specifically, it was the sprouting species including ferns and midstorey trees where losses were greatest. My conclusions were that the mechanical disturbance of logging caused the reductions in these functional groups. This work highlighted the importance of retaining places where the ground remains undisturbed within the area being logged.

Chapter 2 *Non-linear growth in tree ferns, Dicksonia antarctica and Cyathea australis,* found that *C.australis* grows at approximately twice the rate of *D.antarctica*. However, an unexpected finding was that growth rates were greater the taller either species of tree fern was before the 2009 fire. I concluded that growth rate most likely increased with increased light as the taller ferns were above the densely regenerating fire regrowth for longer. The variable growth rates also suggest the common practice of determining a tree fern's age by dividing its total height by an annual average growth rate may have limited application.

Chapter 3 *Testing succession theory using a chronosequence study of Australian Mountain Ash forest following wildfire* showed young (3 year old) Mountain Ash in the early stages of succession after wildfire to be the most species rich, with on-site seeding species such as herbs and graminoids making up a high proportion of the overall species make up. In older forest stands, overall species richness is lower, but the functional groups contributing the greatest numbers to overall species richness also shifts as the forests age, from the seeding species to sprouting species such as ferns and midstorey trees. These findings indicate the ecosystem is not easily described using a single succession theory, but rather while Initial Floristic Composition may describe the seeding species well, the sprouting species follow a Relay Floristics and Inhibition pathway. By selecting sites that have had little human disturbance, this study describes important baseline information on successional change in Mountain Ash forests under conditions that are as close to the long term natural state of these forests. It is hoped this will allow early detection of signs that climate change is altering forest recovery in the future and allow comparisons with areas that have seen human disturbance to know if recovery trajectories have altered.

Chapter 4 *Does forest age influence recovery after fire?* concludes that the Mountain Ash forests are well adapted to fire with age prior to wildfire having only a moderate influence on post-fire recovery. As Chapter 3 had shown, sprouting species were more prominent in older forest stands and through biological legacies that persisted after fire, this resulted in greater species richness of this functional group in the post-fire regrowth when older stands were burned. The reduced species richness when older stands were burned as most likely due to a combination of depletion or deterioration of the seed bank and increased suppression from ground ferns.

In conclusion, my research ties together many different facets of vascular plant recovery after disturbance within the Mountain Ash forests. The findings are important for forest managers as they demonstrate important differences between fire and logging and indicate that while some functional groups recovery well after disturbance, others may not. Through my investigations, I found sprouting species, including tree ferns, ground ferns and many mid storey trees require particular care with management as they are susceptible to loss through the ground-disturbing mechanical damage of logging. In addition, their recovery is slower than many other functional groups. Sprouting species are important structural elements in Mountain Ash forests and are favoured by longer intervals between disturbance. Management of this group of species may be further complicated by the future fire projections in a warming climate and the disturbance history of these forests which has resulted in them being dominated by a greater extent of younger forest than in recent history.

APPENDIX A

Additional publications published in the PhD period (2014-2018)

The Leadbeater's Possum Review

Authors: Blair, D. P., D. B. Lindenmayer, L. McBurney, S. C. Banks, and W. Blanchard.

Contributions: Study concept DB (65%), DL, LM; Research DB (80%), DL, LM; Authorship of original manuscript DB (95%), DL; Statistical analysis N/A; Edits and revision DB (60%), DL, SB, WB, LM.

Current status of paper: Published, including online PDF: https://fennerschool-associated.anu.edu.au/documents/Leadbeater_Pos_Rev_Aug_2017.pdf

Publisher: The Australian National University, 68 pages, technical report

Citation: Blair, D. P., D. B. Lindenmayer, L. McBurney, S. C. Banks, and W. Blanchard (2017). The Leadbeater's Possum Review. The Australian National University, Canberra.

Failing to conserve Leadbeater's Possum and its Mountain Ash forest habitat

Authors: Blair, D. P., D. B. Lindenmayer, L. McBurney.

Contributions: Study concept DB (50%), DL, LM; Research DB (75%), DL, LM; Authorship of original manuscript DB (50%), DL; Statistical analysis N/A; Edits and revision DB (50%), DL, LM.

Current status of paper: Published

Publisher: Australian Zoologist

Citation: Blair, D. P., D. B. Lindenmayer and L. McBurney (2018). Failing to conserve Leadbeater's Possum and its Mountain Ash forest habitat. *Australian Zoologist*, 39(3). pp443-338.

Mountain Ash: fire, logging and the future of Victoria's giant forests

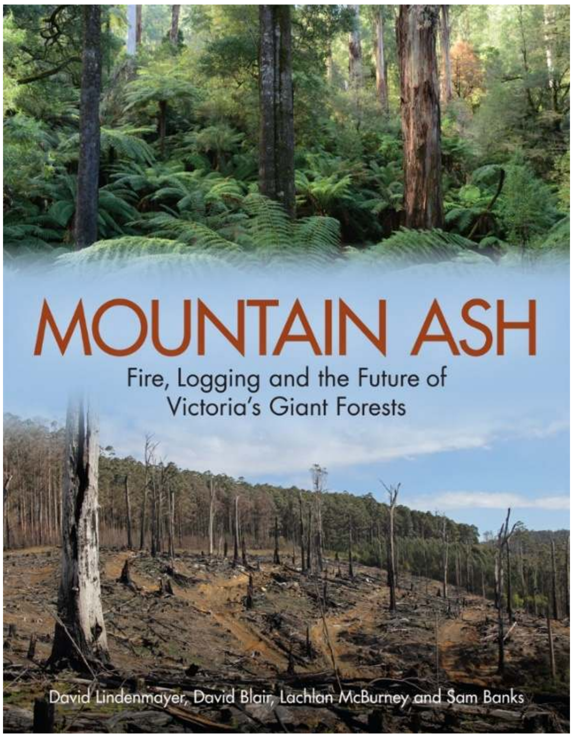
Authors: D. B. Lindenmayer, **D. P. Blair**, L. McBurney and S. C. Banks.

Contributions: Study concept DL, DB (30%), LM, SB; Research DL, DB (20%), LM; Authorship of original manuscript DL, DB (10%), SB, LM; Published photographs DB (170 of 215), various other photographers, Edits and revision DL, DB (40%), SB, LM.

Current status of paper: Published

Publisher: CSIRO Publishing, 176 pages, book.

Citation: D. B. Lindenmayer, **D. P. Blair,** L. McBurney, and S. C. Banks (2015). Mountain Ash: Fire, logging and the future of Victoria's giant forests. CSIRO Publishing, Melbourne, Australia



From unburnt to salvage logged: quantifying bird responses to different levels of disturbance severity

Authors: D. B. Lindenmayer, L. McBurney, **D. P. Blair**, J. Wood, S. C. Banks.

Contributions: Study concept DL; Research DB (20%), DL, LM; Authorship of original manuscript DL; Statistical analysis JW; Edits and revision DB (30%), DL, SB, JW, LM.

Current status of paper: Published

Publisher: Journal of Applied Ecology

Citation: Lindenmayer, D. B., L. McBurney, **D. P.Blair,** J. Wood, and S. C. Banks (2018). From unburnt to salvage logged: quantifying bird responses to different levels of disturbance severity. *Journal of Applied Ecology*, 55(4), 1626-1636.

Empirical relationships between tree fall and landscape-level amounts of logging and fire

Authors: D. B. Lindenmayer, W. Blanchard, **D. P. Blair**, L. McBurney, J. Stein, S. C. Banks.

Contributions: Study concept DL, DB (10%), LM, SB; Research DB (50%), LM; Authorship of original manuscript DL; Statistical analysis WB; GIS analysis JS; Edits and revision DB (20%), DL, SB, LM.

Current status of paper: Published

Publisher: PLoS One

Citation: Lindenmayer, D. B., W. Blanchard, **D. P. Blair**, L. McBurney, J. Stein, S. C. Banks (2018). Empirical relationships between tree fall and landscape-level amounts of logging and fire. *PLoS One*, 13(2).

Logging and fire regimes alter plant communities

Authors: E. J. Bowd, D. B. Lindenmayer, S. C. Banks, **D. P. Blair**.

Contributions: Study concept EB, DL, DB (10%); Research EB; Authorship of original manuscript EB; Statistical analysis EB; Edits and revision DB (20%), DL, SB.

Current status of paper: Published

Publisher: Ecological Applications

Citation: Bowd, E. J., D. B. Lindenmayer, S. C. Banks, **D. P. Blair**. (2018). Logging and fire regimes alter plant communities. *Ecological Applications,* 28(3), 826-841.

Inter-den tree movements by Leadbeater's Possum

Authors: D. B. Lindenmayer, L. McBurney, **D. P. Blair**, S. C. Banks.

Contributions: Study concept DL; Research DL; Authorship of original manuscript DL; Edits and revision DB (30%), SB, LM.

Current status of paper: Published

Publisher: Australian Zoologist

Citation: Lindenmayer, D. B., L. McBurney, **D. P. Blair**, S. C. Banks (2018). Inter-den tree movements by Leadbeater's Possum. *Australian Zoologist*, 39(3), 464-468.

Relationships between tree size and occupancy by cavity-dependent arboreal marsupials

Authors: D. B. Lindenmayer, W. Blanchard, **D. P. Blair**, L. McBurney, S. C. Banks.

Contributions: Study concept DL, DB (10%), LM, SB; Research DB (50%), LM; Authorship of original manuscript DL; Statistical analysis WB; Edits and revision DB (30%), DL, SB, LM.

Current status of paper: Published

Publisher: Forest Ecology and Management

Citation: Lindenmayer, D. B., W. Blanchard, **D. P. Blair**, L. McBurney, S. C. Banks (2017). Relationships between tree size and occupancy by cavity-dependent arboreal marsupials. *Forest Ecology and Management*, 391, 221-229.

Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes

Authors: Banks, S. C., L. McBurney, **D. P. Blair**, I. D. Davies, D. B. Lindenmayer.

Contributions: Study concept DL; Research DL; Authorship of original manuscript DL; Edits and revision DB (30%), SB, LM.

Current status of paper: Published

Publisher: Ecoography

Citation: Banks, S. C., L. McBurney, **D. P. Blair**, I. D. Davies, D. B. Lindenmayer (2017). Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes. *Ecography*, 40(11), 1325-1338.

The dynamic regeneration niche of a forest following a rare disturbance event

Authors: A. L. Smith, W. Blanchard, **D. P. Blair,** L. McBurney, S. C. Banks, D. A. Driscoll, D. B. Lindenmayer.

Contributions: Study concept AS, DL, DD, DB(10%); Research DB(70%), LM; Authorship of original manuscript AS; Statistics AS, WB; Edits and revision DB (10%), AS, DL, DD, SB, LM.

Current status of paper: Published

Publisher: Diversity and Distributions

Citation: Lindenmayer, D. B., L. McBurney, **D. P. Blair**, S. C. Banks (2016). The dynamic regeneration niche of a forest following a rare disturbance event. *Diversity and Distributions*, 22(4), 457-467.

Environmental and human drivers influencing large old tree abundance in Australian wet forests

Authors: D. B. Lindenmayer, W. Blanchard, **D. P. Blair**, L. McBurney, S. C. Banks.

Contributions: Study concept DL, DB (10%), LM, SB; Research DB (70%), LM; Authorship of original manuscript DL; Statistical analysis WB; Edits and revision DB (30%), DL, SB, LM.

Current status of paper: Published

Publisher: Forest Ecology and Management

Citation: Lindenmayer, D. B., W. Blanchard, **D. P. Blair**, L. McBurney, S. C. Banks (2016). Environmental and human drivers influencing large old tree abundance in Australian wet forests. *Forest Ecology and Management*, 372, 226-235.

The need for a comprehensive reassessment of the Regional Forest Agreements in Australia

Authors: D. B. Lindenmayer, **D. P. Blair**, L. McBurney, S. C. Banks.

Contributions: Study concept DL, DB (50%), LM, SB; Research DB (70%), DL; Authorship of original manuscript DL; Edits and revision DB (50%), DL, SB, LM.

Current status of paper: Published

Publisher: Pacific Conservation Biology

Citation: Lindenmayer, D. B., **D. P. Blair**, L. McBurney, S. C. Banks (2016). The need for a comprehensive reassessment of the Regional Forest Agreements in Australia. *Pacific Conservation Biology*, 21(4), 266-270.

Single large versus several small: The SLOSS debate in the context of bird responses to a variable retention logging experiment

Authors: D. B. Lindenmayer, J. Wood, L. McBurney, **D. P. Blair**, S. C. Banks.

Contributions: Study concept DL; Research DB(30%), LM, others; Authorship of original manuscript DL; Statistical analysis JW; Edits and revision DB (20%), SB, LM.

Current status of paper: Published

Publisher: Forest Ecology and Management

Citation: Lindenmayer, D. B., J. Wood, L. McBurney, **D. P. Blair**, S. C. Banks (2015). Single large versus several small: The SLOSS debate in the context of bird responses to a variable retention logging experiment. *Forest Ecology and Management*, 339, 1-10.

Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia

Authors: E. L. Burns, D. B. Lindenmayer, J. Stein, W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks.

Contributions: Study concept DL, EB, DB(10%); Research EB; Authorship of original manuscript EB, DL; Statistical analysis WB; Edits and revision DL, EB, DB (10%), SB, LM.

Current status of paper: Published

Publisher: Austral Ecology

Citation: Burns E. L., D. B. Lindenmayer, J. Stein, W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks. (2015). Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. *Austral Ecology*, 40(4), 386-399.

Dominant drivers of seedling establishment in a fire-dependent obligate seeder: Climate or fire regimes?

Authors: A. L. Smith, **D. P. Blair,** L. McBurney, S. C. Banks, P. S. Barton, W. Blanchard, D. A. Driscoll, M. A. Gill, D. B. Lindenmayer.

Contributions: Study concept AS, DL, DD, DB(30%); Research DB(80%), LM; Authorship of original manuscript AS; Statistics WB, AS; Edits and revision DB (10%), AS, DL, PB, DD, SB, LM.

Current status of paper: Published

Publisher: Ecosystems

Citation: Lindenmayer, D. B., L. McBurney, **D. P. Blair**, S. C. Banks (2014). Dominant drivers of seedling establishment in a fire-dependent obligate seeder: Climate or fire regimes? *Ecosystems*, 17(2), 258-270.

New policies for old trees averting a global crisis in a keystone ecological structure

Authors: D. B. Lindenmayer, W.F. Laurance, J. F. Franklin, G. E. Likens, S. C. Banks, W. Blanchard, P. Gibbons, K. Ikin, **D. P. Blair**, L. McBurney.

Contributions: Study concept DL, WL, JF, GL, DB(5%) SB; Research DB (20%), LM, JF; Statistica analysis, WB; Authorship of original manuscript DL; Edits and revision DB (5%), DL, SB, LM, JF, GL, WL, PG, KI.

Current status of paper: Published

Publisher: Conservation Letters

Citation: Lindenmayer, D. B., W.F. Laurance, J. F. Franklin, G. E. Likens, S. C. Banks, W. Blanchard, P. Gibbons, K. Ikin, **D. P. Blair**, L. McBurney. (2014). New policies for old trees averting a global crisis in a keystone ecological structure. *Conservation Letters*, 7(1), 61-69.

Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers

Authors: D. B. Lindenmayer, W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks, D. A. Driscoll, A. L. Smith, M. A. Gill.

Contributions: Study concept DL, DD, WB; Research DB (20%), LM, others; Authorship of original manuscript DL; Statistics WB; Edits and revision DB (10%), AS, DL, DD, SB, LM, MG.

Current status of paper: Published

Publisher: Diversity and Distributions

Citation: Lindenmayer, D. B., W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks, D. A. Driscoll, A. L. Smith, M. A. Gill (2014). Dominant drivers of seedling establishment in a fire-dependent obligate seeder: Climate or fire regimes? *Diversity and Distributions*, 20(4), 467-477.

An empirical assessment and comparison of species-based and habitat-based surrogates: a case study of forest vertebrates and large old trees

Authors: D. B. Lindenmayer, P. Barton, P. W. Lane, M, J. Westgate, L. McBurney, **D. P. Blair**, P. Gibbons, G. E. Likens.

Contributions: Study concept DL, PB, PL, MW; Research DB (50%), LM; Authorship of original manuscript DL; Edits and revision DB (10%), DL, LM, MW, PB, PL, GL, PG.

Current status of paper: Published

Publisher: PLoS One

Citation: Lindenmayer, D. B., W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks, D. A. Driscoll, A. L. Smith, M. A. Gill (2014). An empirical assessment and comparison of species-based and habitat-based surrogates: a case study of forest vertebrates and large old trees**.** *PLoS One*, 9(2), e89807.

Accounting for biomass carbon stock change due to wildfire in temperate forest landscapes in Australia

Authors: H. Keith, D. B. Lindenmayer, B. G. Mackey, **D. P. Blair**, L. Carter, L. McBurney, S. Okada, T. Konishi-Nagano.

Contributions: Study concept DL, HK, DB (20%); Research DB (80%), HK; Authorship of original manuscript HK; Statistics HK; Edits and revision DB (20%), DL, HK, BM, LC, LM, OS, TK-N.

Current status of paper: Published

Publisher: PLoS One

Citation: Lindenmayer, D. B., W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks, D. A. Driscoll, A. L. Smith, M. A. Gill (2014). Accounting for biomass carbon stock change due to wildfire in temperate forest landscapes in Australia**.** *PLoS One*, 9(9), e107126.

Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks

Authors: H. Keith, D. B. Lindenmayer, B. G. Mackey, **D. P. Blair**, L. Carter, L. McBurney, S. Okada, T. Konishi-Nagano.

Contributions: Study concept DL, HK, DB (20%); Research DB (80%), HK; Authorship of original manuscript HK; Statistics HK; Edits and revision DB (20%), DL, HK, BM, LC, LM, OS, TK-N.

Current status of paper: Published

Publisher: Ecosphere

Citation: Lindenmayer, D. B., W. Blanchard, L. McBurney, **D. P. Blair**, S. C. Banks, D. A. Driscoll, A. L. Smith, M. A. Gill (2014). Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks**.** *Ecosphere*, 5(6), art75.