

Logging and fire regimes alter plant communities

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Abstract. Disturbances are key drivers of plant community composition, structure, and function. Plant functional traits, including life forms and reproductive strategies are critical to the resilience and resistance of plant communities in the event of disturbance. Climate change and increasing anthropogenic disturbance are altering natural disturbance regimes globally. When these regimes shift beyond the adaptive resilience of plant functional traits, local populations and ecosystem functions can become compromised. We tested the influence of multiple disturbances, of varying intensity and frequency, on the composition and abundance of vascular plant communities and their respective functional traits (life forms and reproductive strategies) in the wet sclerophyll, Mountain Ash *Eucalyptus regnans* forests of southeastern Australia. Specifically, we quantified the effect of the type and number of disturbances (including fires, clearcut logging, and salvage logging) on plant community composition. We found that clearcut and salvage logging and the number of fires significantly influenced plant community composition and functional traits. Specifically, multiple fires resulted in lower populations of species that depend on on-site seeding for persistence. This includes the common tree species *Eucalyptus regnans*, *Pomaderris aspera*, and *Acacia dealbata*. In contrast, clearcut and salvage logged sites supported abundant on-site seeder species. However, species that depend on resprouting by surviving individuals, such as common and keystone “tree ferns” *Dicksonia antarctica* and *Cyathea australis*, declined significantly. Our data have important implications for understanding the relationship between altered disturbance regimes and plant communities and the respective effects on ecosystem function. In a period of rapid global environmental change, with disturbances predicted to increase and intensify, it is critical to address the impact of altered disturbance regimes on biodiversity.

Key words: clearcut logging; disturbance regimes; *Eucalyptus regnans*; plant functional traits; post-disturbance environment; species composition; wildfire.

INTRODUCTION

Disturbances are key drivers of the composition and function of ecosystems worldwide (Bowman et al. 2009, Seidl et al. 2014a, Fraver et al. 2017). Fire is a major form of natural disturbance and it can influence many ecological patterns and processes including biogeochemical cycles, climate, plant composition, and functional diversity (Westerling and Bryant 2008, Bowman et al. 2009, 2011, Sitters et al. 2016).

Species are adapted to specific fire and disturbance regimes that occur within ecosystems (Keeley 2009, Seidl et al. 2014a). When these regimes exhibit novel intensities and frequencies of disturbance events, or are altered beyond adaptive mechanisms, several key properties can be compromised including (1) resilience (the ability of an ecosystem to return to its original, pre-disturbance, state post-disturbance) and (2) resistance (the ability of an ecosystem to maintain its original, pre-disturbance, state in the face of disturbance). Changes to these properties can fundamentally modify the environmental conditions required for habitat suitability and species persistence (Diaz and Cabido 2001, Cochrane and Laurance 2008, Bowman et al. 2009, Seidl et al. 2014b, Lindenmayer et al. 2016).

In recent decades, large-scale, high-severity fires and anthropogenic disturbances have increased across terrestrial ecosystems worldwide (Hooper et al. 2005, Cochrane and Laurance 2008, Bowman et al. 2009, Seidl et al. 2014a,

Lindenmayer et al. 2017). Key examples include the impacts of novel fire regimes and logging that now characterize disturbance patterns in the Pacific northwestern forests of the United States (Odion et al. 2004, Thompson et al. 2007), Amazonian rainforests (Cochrane and Laurance 2008), and southeastern Australian wet sclerophyll forests (Lindenmayer et al. 2011, Taylor et al. 2014). Changing climatic conditions are predicted to increase dry and hot conditions in many parts of the world, which would amplify and further alter these disturbance regimes (Seidl et al. 2014a, Thom and Siedl 2016). In a period of rapid global environmental change, it is critical to examine the impact of changing disturbance regimes on biodiversity (Bowman et al. 2011).

Plant populations are influenced by climate (Levine and Rees 2004, Westerling and Bryant 2008), natural disturbance (Lloret and Zedler 2009), human-accelerated environmental change (Likens 1991, Ribeiro-neto et al. 2016), or a combination of these (Lindenmayer et al. 2011). Plant functional traits such as physiological adaptations and reproductive strategies are critical to plant species persistence under the prevailing disturbance regime (McIntyre and Lavorel 1999, Johnstone et al. 2016). These structural and functional traits are an important ecological tool for determining how plant communities respond to disturbance and the respective effect on ecosystem function (Noble and Slatyer 1980, McIntyre and Lavorel 1999, Cornelissen et al. 2003, Sitters et al. 2016). They also can act as surrogates for physiological functional patterns that are often impractical to measure (McIntyre and Lavorel 1999, Diaz and Cabido 2001). Plant communities and natural disturbances such as fire interact and influence the dynamics of one another (Cochrane and

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Laurance 2008). For example, post-disturbance, early seral environments can be more susceptible to high-severity fire, which in turn, increases early-successional fire-prone vegetation and suppresses the return of mature composition and structure (Thompson et al. 2007, Cochrane and Laurance 2008, Taylor et al. 2014). This can drive positive feedback loops leading to increased fire frequency and severity (Thompson et al. 2007, Cochrane and Laurance 2008). It has been proposed that additional disturbances such as clearcut logging (Thompson et al. 2007, Cochrane and Laurance 2008, Lindenmayer et al. 2011) and altered climatic conditions (Westerling and Bryant 2008, Bowman et al. 2009) can intensify these positive feedback loops and shift ecosystems into functionally compromised states (Lindenmayer et al. 2016).

Changes in natural disturbance regimes can alter plant population dynamics and trigger declines in common and key-stone species (Walker 1995, Diaz and Cabido 2001, Brigham and Schwartz 2003, Rodrigo et al. 2004, Hooper et al. 2005, Honnay and Jacquemyn 2006, Ribeiro-neto et al. 2016). The implications of these changes can extend beyond individual species and impact ecological function and resilience (Lawton 1994, Walker 1995, Ough and Murphy 2004, Cochrane and Laurance 2008). Determining the response of plant communities to changing disturbance regimes is therefore fundamental for environmental conservation, planning, and management (Pickett and White 1985, Stevens-Rumann and Morgan 2016). While the effects of altered disturbance regimes are described for some ecosystems (Hessburg et al. 2005, Donato et al. 2009), relatively few studies have examined the synergistic effects of altered disturbance regimes on plant communities and their respective functional traits (Thuiller et al. 2004, Bowman et al. 2009, Osazuwa-Peters et al. 2015).

We quantified the disturbance responses of vascular plant communities in southeastern Australian, wet sclerophyll, Mountain Ash *Eucalyptus regnans* F.Muell. forests. These forests provide an ideal system to address key questions about the response of plant communities to disturbance regimes as they have a well characterized and diverse disturbance history and have been subject to more than 30 years of long-term ecological monitoring (Lindenmayer 2009). To examine plant community responses, we gathered data in forests that had last been burned in 1850, 1939, 1983, and 2009 and also forests that had experienced clearcut logging in 1980–1985 and 2009–2010 and salvage logging in 2009–2010. We quantified plant species richness, abundance, and respective functional traits (life forms and reproductive strategies) in forests subject to these different kinds of disturbance. This enabled us to address two important questions.

What is the effect of the number of fires on plant community composition and functional traits?—Floristic variation within forests can be strongly influenced by fire (Ough and Ross 1992, Rodrigo et al. 2004, Bowman et al. 2009). Fire regimes in *Eucalyptus regnans* forests are characterized by infrequent, high-intensity fires that historically had a return period of 75–150 yr (McCarthy et al. 1999). We hypothesized that following fire within this fire return period, plant communities would follow the pattern of gradual succession described by the Initial Floristic Composition model (Elger 1954, McCarthy et al. 1999). The model describes shifts in

dominant plant communities that are consistent with the initial, natural succession of wet sclerophyll forests (Elger 1954, Noble and Slatyer 1980, Ashton and Attiwill 1994, Pulsford et al. 2016). This can be partially explained by the resilience and availability of dominant plant propagules that persist post-fire (Lindenmayer and Laurance 2016). Additionally, following this model, we predicted species richness would increase with multiple fires (Elger 1954). We made this prediction based on the post-disturbance influx of early successional and ruderal herbaceous species that are largely absent from mature forests (Cochrane and Laurance 2008, Donato et al., 2009, Blair et al. 2016).

We also hypothesized that the composition of plant communities would differ between sites rarely burned (only once since 1850), and frequently burned within a period substantially less than the historical fire return period (e.g., 70 yr). This was largely because multiple fires within a short period have the potential to alter ecosystem function (Burns et al. 2015). For example, biological legacies such as logs and large dead trees can be lost after multiple fires, subsequently influencing plant spatial dynamics, as forecast from trait-based disturbance models (Noble and Slatyer 1980, Franklin et al. 2000, Siedl et al. 2014b, Mason et al. 2016). Additionally, fire intervals must be sufficient to allow species to develop reproductive propagules. For example, when fire intervals are <25 yr, *Eucalyptus regnans* fails to attain sexual maturity and is displaced by *Acacia* species (Adams and Attiwill 1984, Lindenmayer 2009). Therefore, with successive fires in the last 70 yr, we predicted the decline of species that are dependent on on-site seeding (low seed dispersal ability), especially those without persistent soil seed banks or rapid maturation.

What is the effect of clearcut and salvage logging on plant communities and functional traits and how does it differ from unlogged sites in similarly aged, burned forest?—Some authors have argued that clearcut logging imitates the post-disturbance environment of high-severity fire (Attiwill 1994). However, empirical evidence suggests this is not the case (Cochrane and Laurance 2008, Lindenmayer et al. 2011, Blair et al. 2016). We hypothesized that sites subject to clearcut logging would support different plant communities compared to similarly aged, unlogged/burned sites. Specifically, we predicted a reduced occurrence of species that are sensitive to mechanical disturbance. These include species that possess resprouting functional traits, such as “tree ferns,” midstory “trees,” and “ground ferns” that occur in this ecosystem. This is because logging machinery can uproot and cause physical damage to resprouting structures and subsequently expose them to the high intensity, slash-burn that occurs after clearcutting (McIntyre and Lavorel 1999, Ough and Murphy 2004, Blair et al. 2016).

We also hypothesized that plant communities within salvage logged sites and sites subject to multiples fires and clearcut logging, would be the most different in comparison to similarly aged clearcut and unlogged/burned sites. This is largely because these sites have experienced two successive, different disturbances relative to sites subject only to fire. Moreover, in the event of salvage logging, burned areas are subject to clearcut logging at a time when natural regeneration is just beginning to occur and young plants are vulnerable to disturbance (Lindenmayer and Ough 2006). Such

intense disturbances within a relatively short time interval would likely result in the reduction of plant species with particular functional traits such as those with on-site seed and resprouting propagules (McIntyre and Lavorel 1999, Siedl et al. 2014b).

Our study addresses the ecological outcomes of changes in climate (fire) and anthropogenic (logging) disturbance regimes that are also characterizing many other forest ecosystems worldwide.

METHODS

Site description

We conducted this study in the *Eucalyptus regnans* forests of the Victorian Central Highlands, 80–100 km northeast of Melbourne in southeastern Australia (Fig. 1). These forests occur at altitudes ranging from 150 to 1100 m and experience consistent high rainfall, receiving on average between 600 and 2000 mm annually (Blair et al. 2016, Keenan and Nitschke 2016). The typical climate of the region is defined by cool summers and mild, humid winters, with occasional periods of snow (Mackey et al. 2002, Burns et al. 2015). However, periodic hot and dry summers and infrequent

wildfires also occur and the frequencies of both have increased over time (Commonwealth Scientific and Industrial Research Organisation (CSIRO) 2010, Taylor et al. 2014).

Eucalyptus regnans forests are characterized by tall eucalypt overstory trees, scattered understory trees, broad-leaved shrubs, and a moist ground layer rich in fern species (Ough 2001, Burns et al. 2015). The world's tallest flowering plant, *Eucalyptus regnans*, dominates these forests. *Eucalyptus obliqua* LHer. (Messmate), *Eucalyptus cypellocarpa* LAS. Johnson (Mountain Grey Gum), *Eucalyptus viminalis* Labill. (Manna Gum), *Eucalyptus nitens* Deane & Maiden (Shining Gum), and *Eucalyptus delegatensis* RT. Baker. (Alpine Ash) may also be present (Flint and Fagg 2007, Victorian State Government, 2014, Burns et al. 2015). *Acacia* species such as *Acacia dealbata* Link., *Acacia frigescens* J. H. Willis, and *Acacia obliquinervia* Tindale, Contr. dominate the midstory (Adams and Attiwill 1984, Lindenmayer 2009). Common understory species include *Correa lawrenceana* Hook., *Prostanthera lasianthos* Labill., *Olearia argophylla* Labill., *Pomaderris aspera* Sieber., *Coprosma quadrifida* Labill., *Pimelea axiflora* F Muell., *Bedfordia arborescens* Hochr., and tree ferns *Dicksonia antarctica* Labill. and *Cyathea australis* R.Br. (Ough and Murphy 2004, Flint and Fagg 2007, Blair et al. 2016).

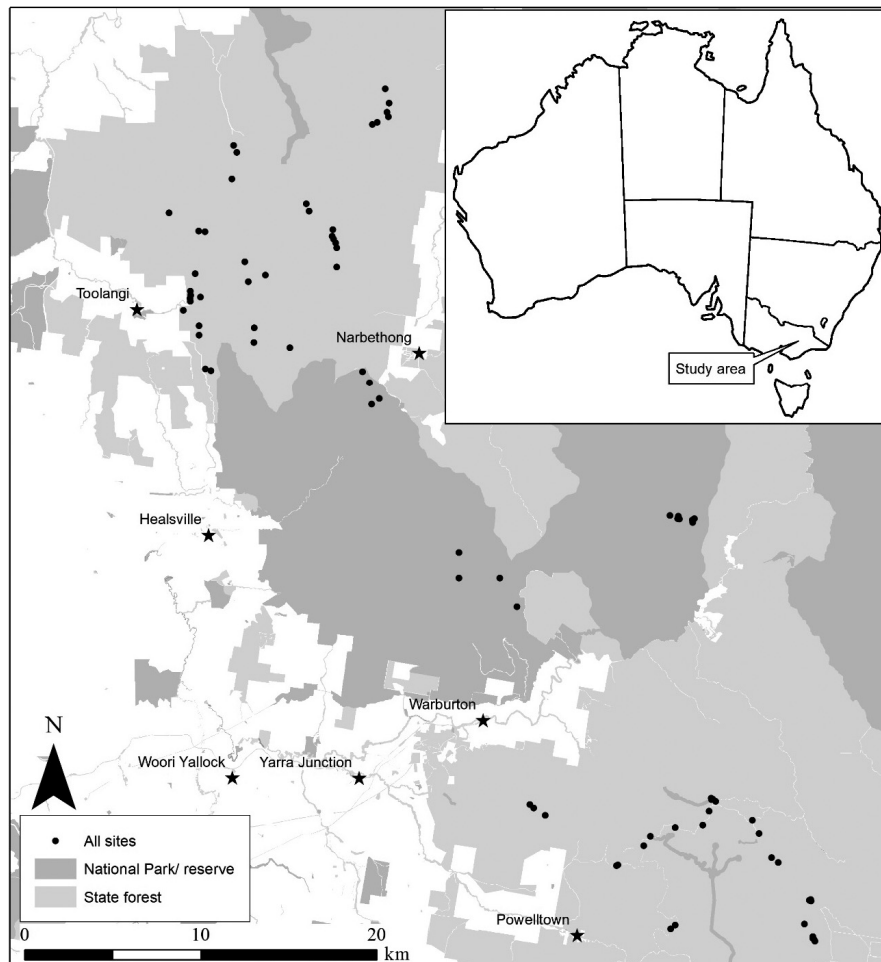


FIG. 1. Location of study sites within the southeastern Victorian Central Highlands in Australia with respect to National Parks and reserves and State forest.

The edaphic environment of *Eucalyptus regnans* forests is characterized by well-drained, deep, and nutrient-rich soils that primarily consist of dermosols derived from Ordovician and Devonian sediments, extrusives, granitic rocks, and alluvium (McKenzie et al. 2004, Burns et al. 2015).

Disturbance history

Approximately 157,000 ha of the Central Highlands support *Eucalyptus regnans* forests. Of this, 20% is in closed water catchments and National Parks and 80% in State forests, which consist of large areas designated for timber and pulp production (Langford 1976, Burns et al. 2015). Large stand-replacing fires in *Eucalyptus regnans* forests have historically had an average return interval of 75–100 yr (McCarthy et al. 1999). However, over the past century, these forests have experienced major fires in 1926, 1932, 1939, 1983, and most recently in 2009 (Lindenmayer et al. 2011, Turner et al. 2011). In 1939, more than 70% of these forests were burned and many were subsequently salvage logged until the 1960s (Lindenmayer and Franklin 1997, Lindenmayer and Ough 2006). Because *Eucalyptus regnans* is an obligate seeder, forests regenerating after large fires, such as those in 1939, have resulted in landscapes with relatively homogenous-aged regrowth (Fig. 2). This dominant age cohort is now the primary resource for the logging industry (Florence 1996, Lutze et al. 1999). The 2009 fires burned 78,300 ha of *Eucalyptus regnans* forest, with a large proportion of the burned area being the 70-yr-old forest that regenerated after the 1939 fires. The 70-yr-old dead trees resulting from this fire were generally too small to form hollows and the majority of older hollow-bearing trees that pre-dated the fires, were lost (Lindenmayer et al. 2012, Burns et al. 2015). The result has been young, dense, fire-prone regrowth with limited structural diversity (Fig. 3; Lindenmayer et al. 2009, Taylor et al. 2014). Less common, low-intensity fires are not severe enough to kill overstory trees, but trigger a new cohort

of regeneration-producing, mixed-age, heterogenous forests (Lindenmayer et al. 1999, Burns et al. 2015).

In the early 1960s, clearcut logging replaced the less intensive, selection logging as the primary silvicultural system in Victorian wet sclerophyll forests (Florence 1996, Lindenmayer et al. 2011, Turner et al. 2011). Clearcutting is a practice where all trees are cut within a block of between 15 and 40 ha (Lutze et al. 1999, Flint and Fagg 2007, Lindenmayer et al. 2011). The remaining debris or slash within a “cut-block” is then burned at high intensity and the cut over area is then aerially seeded with the dominant eucalypt species (Lutze et al. 1999, Flint and Fagg 2007, Lindenmayer et al. 2011). Salvage logging is a form of clearcut logging that occurs usually within three years following high-severity fire (Lindenmayer and Ough 2006, Blair et al. 2016). This practice emulates standard clearcut logging methods, with the exception that there is no slash burn if the regeneration from the initial wildfire is adequate (Blair et al. 2016). In addition, in salvage logging, harvesting occurs after fire, whereas in conventional clearcutting the sequence is reversed. That is, the forest is logged and then subsequently burned.

Study design

The design of our study was based on the diversity of disturbance histories and the respective availability of replicate sites. We selected nine disturbance types in total: five types experienced fire only and the remaining four types were clearcut or salvage logged. Fire-only sites consisted of forests, long-undisturbed (unburned since 1850), burned once (1939 fire), twice (1939/1983 and 1939/2009), and three times (1939/1983/2009). Logged sites were those burned in 1939 and clearcut in 1980–1985 or 2009–2010 and salvage logged in 2009–2010 after a second fire in 2009. In addition, sites that experienced multiple fires and clearcut logging were those burned in 1939/1983 and clearcut in 2009–2010. All sites were replicated 10 times with the exception of



FIG. 2. *Eucalyptus regnans* forest: 1939 fire regrowth (photographer: David Blair).



FIG. 3. *Eucalyptus regnans* forest: 2009 fire and salvage logging regrowth.

forests long-undisturbed (1850), burned twice (1939/2009), and three times (1939/1983/2009; Table 1). All fires were of high severity. However, given the “patchy” nature of fire events, all sites were inspected prior to sampling to ensure consistent age structure, accounting for the potential variability in disturbance severity within each site type. In this study we define “twice-burned” sites as those that had experienced two fires relative to our long-undisturbed sites. This differs from the North American use of “twice burned” that refers to a repeat fire early in succession, which can produce dramatic ecological effects (Fontaine et al. 2009).

Sites were characterized by a southerly aspect and were positioned away from ridges and gullies, which can provide a lot of the variation in disturbance regimes and recovery (Keeton and Franklin 2004).

We sampled all 81 sites during the Australian summer of December 2016–March 2017. Using 1-ha long-term monitoring and newly established plots, we measured quadrats of 25 × 25 m at least 20 m away from the roadside to account for edge effects (Dupuch and Fortin 2013). In each 625-m² quadrat we estimated the projective foliage cover (percent)

of each vascular plant species using the survey protocol and sample configurations developed by the Australian Department of the Environment, Land, Water, and Planning (Victorian State Government, 2004). Projective foliage cover was used as a measure of species abundance, and is hereafter referred to as “abundance.”

Defining functional traits

We assigned all species into one of 11 life forms and one of nine reproductive categories (Appendix S1: Table S1). These categorizations allowed us to examine potential trends in the occurrence and abundance of functional traits as per trait-based disturbance models (Noble and Slatyer 1980, Blair et al. 2016, Sitters et al. 2016). We assigned these categorizations based on field observation and literature reviews (Walsh and Entwisle 1994, 1996, 1997, Costermans 2009, Wood et al. 2010, Bull and Stolfo 2014). Life forms were (1) eucalypts (overstory), (2) *Acacia*, (3) trees (mid-story), (4) shrubs, (5) tree ferns, (6) ground ferns, (7) climbers, (8) graminoids, (9) epiphytes, (10) herbs, and (11)

TABLE 1. The disturbance history and number of replicate sites of each of the nine disturbance types.

Disturbance type	1850 fire	1939 fire	1983 fire	2009 fire	1980–1985 clearcut	2009–2010 clearcut	2009–2010 salvage	Number of sites
1850F	X							4
39F		X						10
39/83F		X	X					10
39/09F		X		X				11
39/83/09F		X	X	X				6
80CC		X			X			10
09CC		X				X		10
09SL		X		X			X	10
83F/09CC		X	X			X		10

Note: F, fire; CC, clearcut; SL, salvage logged. X in a cell indicates ???.

exotic (Blair et al. 2016). Tree ferns and ground ferns were categorized into separate groups as tree ferns are structurally a midstory tree, differing in size and function from other fern species and midstory trees (Blair et al. 2016). Additionally, we separated eucalypts and *Acacia* species from other lifeform groups. This was because eucalypts (trees belonging to the *Eucalyptus* genus) are the dominant overstory species within these forests, whereas *Acacia* species dominate the midstory and have different ecological roles, such as nitrogen fixation (Blair et al. 2016). In determining reproductive strategy groups, each species was characterized by their respective temporal dynamics (persistent [long-lived] or transitory [species that thrive in post-disturbance environments but do not usually persist beyond several years, otherwise known as ruderal species]) and reproductive mechanisms (wind-dispersed seed, sprout, on-site seed, on-site seed and sprout). These groups were (1) transitory, wind-dispersed seed, (2) transitory, on-site seed, (3) transitory, sprout, (4) persistent, wind-dispersed seed, (5) persistent, on-site seed, (6) persistent, (7) persistent, seed and sprout, (8) persistent, sprout, and (9) exotic. Persistent species were separated from other groups because they are not limited to one reproductive strategy (May and Attiwill 2003, Blair et al. 2016). Exotic species are not specifically a lifeform or reproductive strategy. However, as they are relatively uncommon, and primarily are transitory, herbaceous species such as *Cirsium vulgare* (Savi.), we grouped them into a separate category.

Statistical analysis

We evaluated the influence of the number of fires and the effect of clearcut and salvage logging on the composition and abundance of plant communities and respective functional traits (reproductive strategies and life forms) using multivariate permutational analysis of variance (PERMANOVA) based on the Bray-Curtis resemblance matrix of square-root-transformed abundance data (Bray and Curtis 1957, Anderson 2001, Anderson and Walsh 2013). PERMANOVA is routine testing of the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) based on resemblances between measures using permutation methods (Anderson 2001). All data for each analysis were square-root transformed to minimize the contributions of common taxa with consistently high abundance values (within each group) in relation to those rarer species with consistently lower abundance values (Clarke and Warwick 2001). Significant terms were investigated using a posteriori pair-wise comparisons with the PERMANOVA t statistic (Anderson and Walsh 2013). A maximum of 999 permutations were used to obtain P values in each data set.

Analysis of similarity percentages (SIMPER) allowed us to identify species and functional groups that were responsible for 70% of the dissimilarity between the number of fires and similarly aged logged and unlogged/burned sites, respectively, as confirmed by the PERMANOVA (Clarke and Warwick 2001).

In determining the effect of the number of fires on the abundance and composition of plant communities and respective functional traits, pairwise tests within each analysis

were between fire-only sites: 1850F (no fires), 39F (one fire), 39/83F (two fires), 39/09F (two fires), and 39/83/09F (three fires). When determining the effect of similarly aged logged and unlogged/burned sites within each analysis, pairwise comparisons were made between sites last burned in 2009 (39/09F, 39/83/09F) and those clearcut/salvage logged in 2009–2010 (09CC, 09SL, 83F/09CC) and between sites last burned in 1983 (39/83F) and clearcut in 1980–1985 (80CC).

Additionally, a nonparametric Kruskal-Wallis H test was used to determine differences in species richness between different number of fires, and between similarly aged clearcut and unlogged/burned sites, respectively.

Application of PERMANOVA and SIMPER were conducted in the PRIMER program version 5 and 7 (Primer-E, Plymouth, UK; Clarke 1993, Clarke and Gorley 2015). The Kruskal-Wallis H test was employed using IBM SPSS Statistical software (IBM, SPSS, Armonk, New York, USA).

RESULTS

Species richness

We identified 121 species across 81 sites within nine disturbance types (Appendix S1: Table S1). The most species-rich reproductive functional groups were persistent (31 species total) and persistent, sprout (28 species total) and the most species-rich life forms were herb (31 species total) and shrub (28 species total; Appendix S1: Table S2). Mean species richness differed between the nine disturbance types ($P < 0.05$). Sites burned twice (39/09F) had the highest mean species richness (28 ± 3.6 species/site [mean \pm SD]), followed by clearcut (09CC) sites (27 ± 8.0). Long-undisturbed (1850F) sites supported the lowest number of species (15 ± 5.2 ; Fig. 4).

What is the effect of the number of fires on the abundance and composition of plant communities?

The number of fires that occurred at each site influenced plant composition and abundance (pseudo $F = 4.57$, $P = 0.001$). With the exception of pairwise tests between sites burned once (39F) and twice (39/83F; Average dissimilarity [Av.dis.] = 58.02; $t = 1.20$; $P = 0.189$), the composition and abundance of plant species within all fire-only sites were significantly different from one another ($P < 0.05$). Similarly aged sites burned twice (39/09F) and three times (39/83/09F), respectively, were significantly different from one another ($P < 0.05$). In addition, sites that were both burned twice, (39/09F) and (39/83F), also were significantly different from one another ($P < 0.05$; Table 2).

Twenty-two species explained 70% of the dissimilarity in plant composition and abundance between fire-only sites (Appendix S1: Table S3). Of these species, *Olearia argophylla*, *Pomaderris aspera*, *Dicksonia antarctica*, *Eucalyptus regnans*, *Bedfordia arborescens*, *Polystichum proliferum* R. Br., *Cyathea australis*, *Tetrarrhena juncea* R. Br., *Blechnum watsii* Tindale, and *Correa lawrenceana* consistently contributed the most to these differences. The mean abundance of common species *Eucalyptus regnans*, *Dicksonia antarctica*, and *Blechnum watsii* decreased in sites burned twice (39/83F, 39/09F), and three times (39/83/09F), relative to sites burned once (39F). In

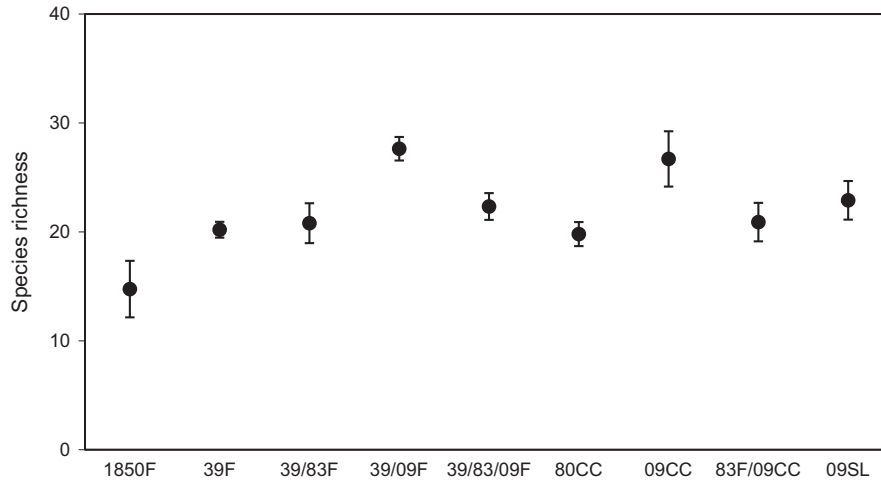


FIG. 4. Species richness across nine disturbance types (mean \pm SE). Disturbance types are described in Table 2.

TABLE 2. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of plant composition and abundance between fire-only sites.

Comparison	Dissimilarity (%)	<i>T</i>	<i>P</i>
1850F (0) vs. 39/83/09F (3)	66.09	2.10	0.009
1850F (0) vs. 39/09 F (2)	76.45	2.12	0.002
1850F (0) vs. 39F (1)	65.08	1.43	0.035
1850F (0) vs. 39/83F (2)	67.17	1.65	0.006
39F (1) vs. 39/83/09F (3)	65.94	2.49	0.002
39/83F (2) vs. 39/83/09F (3)	68.12	2.74	0.001
39/83F (2) vs. 39/09F (2)	70.4	2.45	0.001
39/83F (2) vs. 39F (1)	58.02	1.20	0.189
39/09F (2) vs. 39F (1)	71.82	2.51	0.001
39/09F (2) vs. 39/83/09F (3)	62.69	2.18	0.001

Notes: Numbers in brackets in the first column specify the number of fires. Mean dissimilarity is presented. PERMANOVA: pseudo $F = 4.57$; $P = 0.001$.

contrast, *Olearia argophylla*, *Polystichum proliferum*, and *Bedfordia arborescens* primarily increased across this comparison. Furthermore, in sites burned three times (39/83/09F), the mean abundance of persistent, on-site-seed species such as *Pomaderris aspera* and *Acacia dealbata* decreased, whereas persistent, resprout species such as *Olearia argophylla* and

Bedfordia arborescens increased in comparison to those burned once (39F; Table 3).

How does the number of fires influence plant functional traits?

Reproductive strategies.—The composition and abundance of reproductive functional groups differed with the number of fires that occurred at each site (pseudo $F = 4.25$; $P = 0.001$). However, pairwise tests between sites burned once (39F) and twice (39/83F) and between long-undisturbed (1850F) sites and sites burned once (39F) and twice (39/83F and 39/09F) indicated the composition and abundance of these functional groups were not significantly different from one another ($P > 0.05$; Table 4). Persistent, on-site seed; persistent, on-site seed and sprout; persistent; persistent, sprout; and persistent, wind-dispersed functional groups explained 70% of the differences between sites (Appendix S1: Table S4). The 1850F sites supported the highest mean abundance of persistent, sprout and a low mean abundance of persistent, on-site seed species. Sites burned three times (39/83/09F) had the lowest mean abundance of persistent, on-site seed species; persistent; and persistent, on-site seed and sprout species. In contrast, sites burned twice (39/83F) had the highest mean abundance of persistent, on-site seed and persistent on-site seed and sprout species (Fig. 5).

TABLE 3. Mean abundance of species that consistently contributed to dissimilarity between fire-only sites.

Species	1850(0)	39F(1)	39/83F(2)	39/09F(2)	39/83/09F(3)
<i>Eucalyptus regnans</i>	13.4	20.13	14.63	9.07	5.88
<i>Olearia argophylla</i>	5.31	2.35	1.93	9.66	11.04
<i>Pomaderris aspera</i>	0.00	2.68	12.6	13.78	0.97
<i>Dicksonia antarctica</i>	10.94	11.23	10.14	2.66	5.8
<i>Blechnum wattsii</i>	16.06	6.63	6.28	0.02	0.00
<i>Tettrarrhena juncea</i>	7.82	8.33	3.91	8.92	0.1
<i>Cyathea australis</i>	0.19	6.32	12.58	1.63	2.74
<i>Polystichum proliferum</i>	0.00	1.03	1.25	0.02	0.00
<i>Bedfordia arborescens</i>	0.00	0.3	1.08	4.65	9.83
<i>Correa lawrenceana</i>	1.56	5.65	14.38	0.44	0.00

Note: Numbers in brackets in the top row specify the number of fires.

TABLE 4. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of the composition and abundance of reproductive strategies between fire-only sites.

Comparison	Dissimilarity (%)	<i>T</i>	<i>P</i>
39/09F (2) vs. 39/83/09F (3)	33.59	2.28	0.004
39/09F (2) vs. 39/83F (2)	33.28	2.20	0.001
39/09F (2) vs. 1850F (0)	34.34	1.52	0.065
39/09F (2) vs. 39F (1)	33.46	2.10	0.002
39/83/09F (3) vs. 39/83F (2)	38.43	3.26	0.001
39/83/09F (3) vs. 1850F (0)	32.50	1.69	0.03
39/83/09F (3) vs. 39F (1)	35.46	2.75	0.001
39/83F (2) vs. 1850F (0)	32.10	1.47	0.07
39/83F (2) vs. 39F (1)	27.32	1.24	0.178
1850F (0) vs. 39F (1)	32.71	1.44	0.086

Notes: Numbers in brackets specify the number of fires. Mean dissimilarity is presented. PERMANOVA: pseudo $F = 4.25$; $P = 0.001$.

TABLE 5. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of the composition and abundance of life forms between fire-only sites.

Comparison	Dissimilarity (%)	<i>t</i>	<i>P</i>
39/09F (2) vs. 39/83/09F (3)	34.74	1.89	0.004
39/09F (2) vs. 39/83F (2)	37.61	2.07	0.001
39/09F (2) vs. 1850F (0)	41.73	1.46	0.063
39/09F (2) vs. 39F (1)	38.35	2.0	0.001
39/83/09F (3) vs. 39/83F (2)	36	2.55	0.001
39/83/09F (3) vs. 1850F (0)	35.81	1.35	0.106
39/83/09F (3) vs. 39F (1)	33.16	1.95	0.001
39/83F (2) vs. 1850F (0)	36.42	1.08	0.32
39/83F (2) vs. 39F (1)	31.45	1.02	0.377
1850F (0) vs. 39F (1)	37.24	1.03	0.372

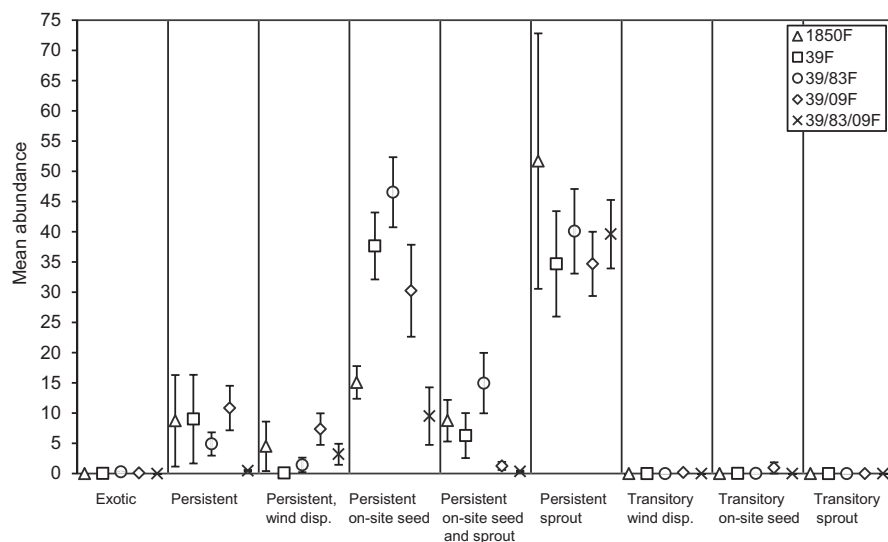
Notes: Numbers in brackets specify the number of fires. Mean dissimilarity is presented. PERMANOVA: pseudo $F = 2.91$; $P = 0.001$.

Life forms.—The composition and abundance of life forms differed with the number of fires that occurred at each site (pseudo $F = 2.91$; $P = 0.001$). However, the composition and abundance of life forms in long-undisturbed (1850F) sites did not significantly differ from other fire-only sites ($P > 0.05$). Furthermore, sites burned once (39F) and twice (39/83F) were also not significantly different from one another (Table 5). Tree, *Acacia*, ground fern, eucalypt, graminoid, shrub, and tree fern species explained 70% of the dissimilarity between sites (Appendix S1: Table S5). Long-undisturbed (1850F) sites had the lowest mean abundance of life forms, *Acacia* and shrub species, but had a high mean abundance of ground ferns and trees. Sites burned once (39F) and twice (39/83F) had the greatest mean abundance of tree ferns, *Acacia* and eucalypt life forms. In contrast, sites burned three times (39/83/09F) had a low mean abundance of eucalypt, *Acacia*, and graminoid species. Herb and graminoid species were the most abundant in sites burned twice (39/09F; Fig. 6). Epiphytes were the most abundant in long-undisturbed (1850F) sites.

What is the effect of clearcut logging in comparison to similarly aged unlogged/burned forest?

Plant species composition and abundance differed between similarly aged unlogged/burned and logged sites (pseudo $F = 6.59$, $P = 0.001$; Table 6). Salvage logged (09SL) and sites burned three times (39/83/09F) were the most different from one another (Av. dis. = 82.03; $t = 3.93$; $P = 0.002$). This trend was followed in pairwise tests between clearcut sites (09CC) and sites burned three times (39/83/09F; Av. dis. = 86.57; $t = 3.50$; $P = 0.001$); and sites burned twice and clearcut (83F/09CC) and sites burned three times (39/83/09F; Av. dis. = 83.70; $t = 3.35$; $P = 0.001$). Similarly aged sites burned twice (39/83F) and clearcut (80CC) had the lowest dissimilarity and t value of all pairwise tests but also differed significantly in species composition and abundance (Av. dis. = 61.57; $t = 1.68$; $P = 0.003$).

Twenty-nine species explained 70% of the dissimilarity in plant composition and abundance between similarly aged logged and unlogged/burned sites (Appendix S1: Table S6).

FIG. 5. Abundance of reproductive functional groups across fire-only sites (mean \pm SE).

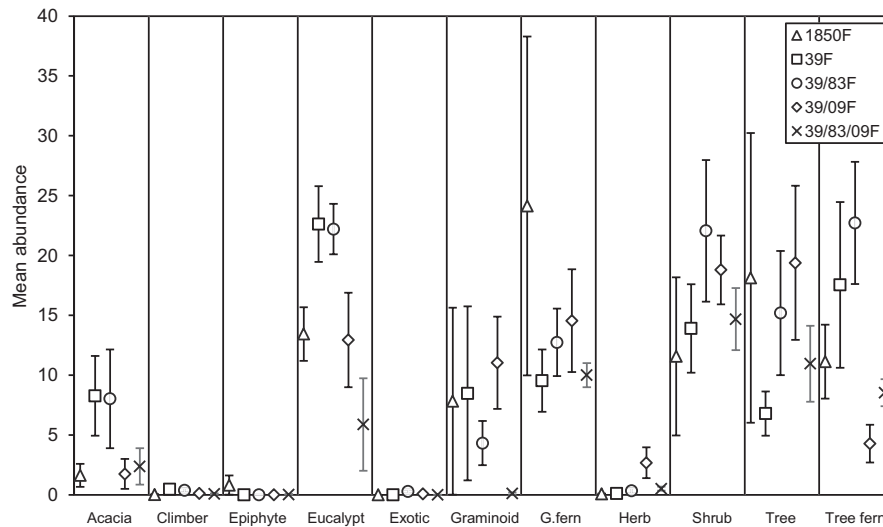


FIG. 6. Abundance of life forms across fire-only sites (mean \pm SE). G. fern, ground fern

TABLE 6. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of vascular plant composition and abundance between similarly aged logged and unlogged/burned sites.

Comparison	Dissimilarity (%)	<i>t</i>	<i>P</i>
39/83F vs. 80CC	61.57	1.68	0.003
39/09F vs. 09CC	73.677	2.39	0.001
39/09F vs. 39/83/09F	62.70	2.18	0.003
83F/09CC vs. 39/09F	74.45	2.49	0.001
83F/09CC vs. 39/83/09F	83.70	3.35	0.001
83F/09CC vs. 09CC	70.16	1.94	0.001
83F/09CC vs. 09SL	68.28	2.26	0.001
09CC vs. 39/83/09F	86.57	3.5	0.001
09SL vs. 39/83/09F	82.03	3.93	0.002
09SL vs. 39/09F	69.44	2.55	0.001
09SL vs. 09CC	65.77	2.03	0.001

Notes: Mean dissimilarity is presented. PERMANOVA: pseudo $F = 6.59$; $P = 0.001$.

Of these species, *Pomaderris aspera*, *Eucalyptus regnans*, *Acacia dealbata*, *Olearia argophylla*, *Tetrarrhena juncea*, *Acacia obliquinervia*, *Polystichum proliferum*, *Bedfordia arborescens*, *Pteridium esculatum*, and *Dicksonia antarctica* contributed

the most to dissimilarity between site types. *Acacia dealbata* and *Acacia obliquinervia* were more abundant in logged sites, whereas persistent, resprout species such as *Cyathea australis*, *Dicksonia antarctica*, *Olearia argophylla*, and *Bedfordia arborescens* declined in comparison to similarly aged unlogged/burned sites. Furthermore, salvage logged (09SL) sites supported no common persistent, resprout species: *Dicksonia antarctica*, *Polystichum proliferum*, and *Olearia argophylla*, (Table 7).

How does clearcut logging influence plant functional traits?

Reproductive strategies.—The mean abundance of reproductive functional groups differed between similarly aged unlogged/burned and logged sites (pseudo $F = 8.48$; $P = 0.001$). However, similarly aged logged sites (83F/09CC, 09CC, 09SL) and, logged and unlogged/burned sites (80CC, 39/83F) were not significantly different from one another ($P > 0.05$; Table 8). Persistent, sprout and persistent, on-site seed species were the highest contributors of dissimilarity across pairwise tests between similarly aged logged and unlogged/burned sites (Appendix S1: Table S7). Persistent, resprout species declined and persistent, on-site seed species increased in sites logged in 2009 (83F/09CC, 09SL, 09CC),

TABLE 7. Mean abundance of species that consistently contributed to dissimilarity between similarly aged unlogged/burned and logged sites.

Species	39/83F	80CC	39/09F	39/83/09F	09CC	83F/09CC	09SL
<i>Eucalyptus regnans</i>	14.6	12.4	9.1	5.9	3.3	16.9	32.0
<i>Pomaderris aspera</i>	12.6	1.9	13.8	1.0	8.6	22.8	2.5
<i>Acacia dealbata</i>	3.6	12.7	1.5	0.0	25.0	8.8	10.3
<i>Tetrarrhena juncea</i>	3.9	2.0	8.9	0.1	17.1	10.2	7.7
<i>Polystichum proliferum</i>	5.5	13.5	2.4	9.1	0.3	0.0	0.0
<i>Dicksonia antarctica</i>	10.1	7.7	2.7	5.8	0.2	0.7	0.0
<i>Olearia argophylla</i>	1.9	1.4	9.7	11.0	0.1	0.1	0.0
<i>Bedfordia arborescens</i>	1.08	0.0	4.6	9.83	0.0	0.0	0.13
<i>Acacia obliquinervia</i>	0.15	1.73	0.00	0.00	17.34	0.00	11.98
<i>Pteridium esculatum</i>	0.21	0.27	11.2	0.3	0.8	0.08	6.53

TABLE 8. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of the composition and abundance of reproductive functional groups between similarly aged logged and unlogged/burned sites.

Comparison	Dissimilarity (%)	<i>t</i>	<i>P</i>
39/09F vs. 09CC	41.63	2.74	0.001
39/09F vs. 39/83/09F	33.58	2.28	0.004
39/09F vs. 83F/09CC	40.43	3.5	0.001
39/09F vs. 09SL	35.5	3.05	0.001
09CC vs. 39/83/09F	58.94	4.33	0.001
09CC vs. 83F/09CC	29.0	1.00	0.424
09CC vs. 09SL	29.44	1.25	0.155
39/83/09 vs. 83F/09CC	57.05	5.53	0.001
83F/09CC vs. 09SL	49.03	1.27	0.199
80CC vs. 39/83F	29.03	1.04	0.338
39/83/09F vs. 09SL	25.20	5.05	0.001

Notes: Mean dissimilarity is presented. PERMANOVA: pseudo $F = 8.48$; $P = 0.001$.

relative to unlogged sites burned in 2009 (39/09F, 39/83/09F; Figs 7 and 8).

Life forms.—The composition and abundance of life forms differed significantly between similarly aged logged and unlogged/burned sites (pseudo $F = 7.88$; $P = 0.001$). However, similarly aged logged sites (83F/09CC, 09CC) were not significantly different from one another ($P > 0.05$). *Acacia*, ground fern, tree fern, tree, eucalypt, shrub, and graminoid life forms contributed to 70% of the dissimilarity between sites (Appendix S1: Table S8). *Acacia* species were more abundant in clearcut and salvage logged sites in comparison to similarly aged unlogged/burned sites. With the exception of sites clearcut in 1980–1985 (80CC), sites clearcut in 2009 (09CC, 09SL, 83F/09CC) supported a lower mean abundance of tree ferns and ground ferns than similarly aged unlogged/burned forest. Salvage logged sites had the highest abundance of herb and eucalypt life forms. Sites logged in 2009–2010 (09CC) had the greatest abundance of *Acacia* species and the least of eucalypt species in comparison to other sites (Fig. 9).

TABLE 9. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of lifeform composition and abundance between similarly aged logged and unlogged/burned sites.

Comparison	Dissimilarity (%)	<i>t</i>	<i>P</i>
39/83F vs. 80CC	39	2.42	0.002
39/09F vs. 09CC	51.35	3.18	0.001
39/09F vs. 39/83/09F	34.74	1.89	0.002
09CC vs. 39/83/09F	57.21	3.82	0.001
83F/09CC vs. 39/83/09F	55.99	3.59	0.001
83F/09CC vs. 09SL	41.80	1.78	0.015
83F/09CC vs. 09CC	42.55	1.60	0.051
83F/09CC vs. 39/09F	47.48	2.60	0.001
09SL vs. 39/09F	47.88	3.15	0.001
09SL vs. 39/83/09F	54.91	4.14	0.001
09SL vs. 09CC	45.50	2.37	0.001

Notes: Mean dissimilarity is presented. PERMANOVA: pseudo $F = 7.88$; $P = 0.001$.

DISCUSSION

The relationship between disturbance and the composition of plant communities is often dynamic and complex (McIntyre and Lavorel 1999, Pulsford et al. 2016). Many plant species are highly tolerant of disturbance and are adapted to specific disturbance intensities and frequencies owing their resilience to functional traits such as physiological adaptations and reproductive strategies (McIntyre and Lavorel 1999, Diaz and Cabido 2001, Johnstone et al. 2016). However, when the frequency, type, or severity of disturbance shifts outside the capacity of the functional traits of local species, plant community composition and structure can be altered (Thompson et al. 2007, Cochrane and Laurance 2008, Blair et al. 2016, Stevens-Rumann and Morgan 2016). We found that clearcut and salvage logging and the respective number of fires influenced plant community composition, abundance, and functional traits in the southeastern Australian, *Eucalyptus regnans* forests. Specifically, species that produce and regenerate from on-site seed decreased with multiple fires and increased with clearcut and salvage logging (in 2009–2010). Whereas species that resprout declined significantly in sites subject to clearcut and salvage logging (in 2009–2010). Our research has important implications for understanding the relationship between altered disturbance regimes and plant communities and the associated effects on ecosystem function.

All sites, apart from those long-undisturbed, were burned in 1939. Therefore, 1939 regrowth acted as a comparative control in our analysis, whereas long-undisturbed forest acted as a reference and contributed to our understanding of succession in *Eucalyptus regnans* forests. Furthermore, in the analysis of clearcut and salvaged logged sites, similarly aged sites were compared to one another to account for successional effects (Kaye et al. 2010). One constraint of this study is it did not examine the difference between low and high fire severities, which could potentially explain some of the variation in plant community composition within sites (Blair et al. 2016).

The number of fires and plant community composition

We have demonstrated that the number of fires influenced the composition and abundance of plant communities and their respective functional traits. Consistent with our predictions, plant community composition and abundance in long-undisturbed sites was the most similar to sites burned once in 1939 and followed the pattern of gradual succession described by the Initial Floristic Composition Model (Elger 1954). Furthermore, following the model, species richness was the lowest in long-undisturbed sites and highest in sites burned twice, in 1939 and 2009. This can be explained by an increase in disturbance-adapted graminoid and herbaceous species, and the ground fern *Pteridium esculatum* post-disturbance in response to an influx in available resources and reduced competition (Kaye et al. 2010, Blair et al. 2016).

In contrast, the composition and abundance of plant communities in eight-year-old forests burned twice and three times differed from other sites and from one another. This indicates that, while succession (time since the most recent fire) is a major factor in determining plant community composition, the number of fires is also a key contributor,

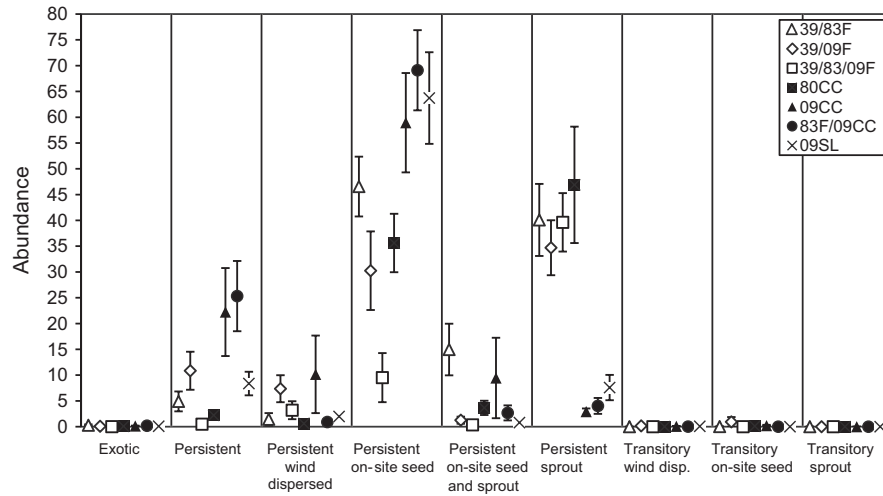


FIG. 7. Abundance of the most common functional groups across logged and unlogged/burned sites (mean \pm SE). Open shapes indicate unlogged/burned sites and solid shapes indicate logged sites.

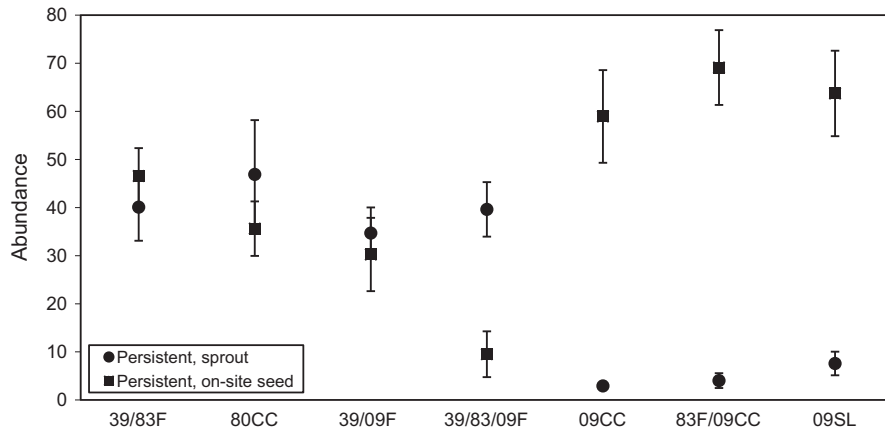


FIG. 8. Abundance of persistent on-site seed and persistent sprout functional groups across similarly aged logged and unlogged/burned sites (mean \pm SE).

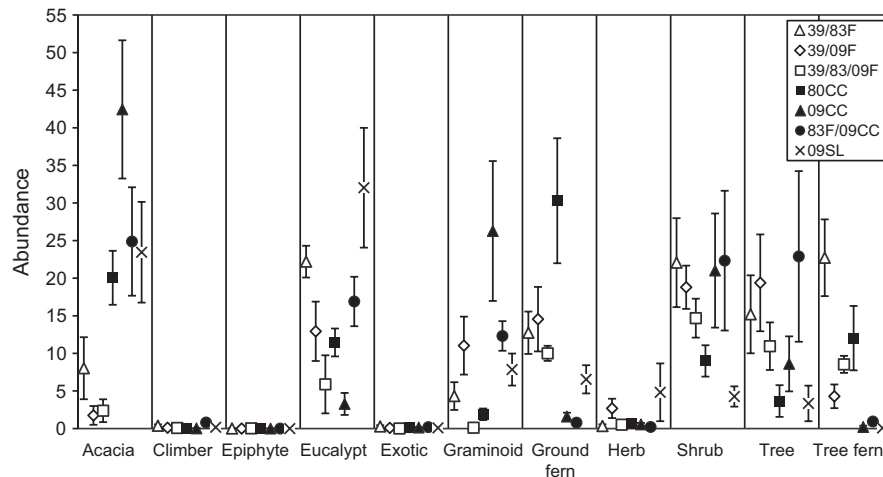


FIG. 9. Abundance of life forms across similarly aged logged and unlogged/burned sites (mean \pm SE). Open shapes indicate unlogged/burned sites, solid shapes indicate logged sites, \times is salvage logged sites.

especially in the event of multiple fires. Similarly, North American forests (Thompson et al. 2007, Stevens-Rumann and Morgan 2016) and Amazonian forests (Cochrane and Laurance 2008) have experienced changes in vegetation community structure and abundance after successive fires. These changes in vegetation communities can alter fire regimes and the risk of high-severity fire in a variety of ways (Thompson et al. 2007, Cochrane and Laurance 2008, Stevens-Rumann and Morgan 2016).

Consistent with our prediction at the outset of this investigation, the composition and abundance of plant functional traits, particularly reproductive strategies, were influenced by the number of fires. The most obvious trends were in eight-year-old forests burned twice and three times, respectively, where we observed declines in dominant on-site seeder species, *Eucalyptus regnans*, and resprouting tree ferns *Cyathea australis* and *Dicksonia antarctica*. However, sites burned three times had a higher abundance of other resprouting species, including *Olearia argophylla*, *Bedfordia arborescens*, and *Polyschitum proliferum*, relative to other sites. This reflects the resilience of resprouting reproductive propagules to fire, as found in North American forests (Donato et al. 2009, Lindenmayer and Laurance 2016). In contrast, sites burned three times had the lowest mean abundance of on-site seeder species, which translated to a decline in common species, *Eucalyptus regnans*, *Pomaderris aspera*, and *Acacia dealbata*, and an absence in *Correa lawrenceana*. On-site seeder species are particularly sensitive to fire return intervals shorter than their maturation ages and this can result in local extinction (Adams and Attiwill 1984, Bowman et al. 2014, Smith et al. 2014). Furthermore, this group of species is vulnerable to recruitment failure and loss of pollinators and dispersers after disturbance (Smith et al. 2014). It is therefore possible that these species declined and were absent as a result of fire return intervals or dispersal failure. However, as this study did not examine the temporal dynamics within each site, or pre-disturbance conditions, it is possible that these species did not previously occupy these sites. It is also possible that nearby populations of these species could re-colonize these sites if conditions are appropriate. Furthermore, in the short-term, it is unlikely that declines in these species would pose serious ecological threats in isolated sites, and may enhance landscape-scale diversity. However, in the long term, the decline of these species lends concern for ecological function, especially in the event of future fire and disturbance.

Plant functional traits, particularly in dominant and common species, confer ecosystem resilience and resistance (Walker 1995, Diaz and Cabido 2001, Johnstone et al. 2016). Declines in these species can have flow on consequences if their functional roles are lost or reduced (Lawton 1994, Walker 1995, Ough and Murphy 2004, Cochrane and Laurance 2008). As an example, the decline and absence of species such as *Acacia* species can have impacts on ecosystem function. *Acacia* species are known for their ability to fix nitrogen, which is particularly important post disturbance (May and Attiwill 2003, Ma et al. 2015). Furthermore, declines in common tree species, *Eucalyptus regnans*, *Pomaderris aspera*, and *Acacia* species, can result in a shift in forest structure and dominance, leading to potentially devastating effects on ecosystem function (Elger 1954, Cochrane and Laurance

2008, Lindenmayer et al. 2011). These effects include changes to the availability of food and complex habitat for biodiversity. For example, mature *Eucalyptus* species develop hollows from ~120+ years of age that provide for hollow-dependent mammals such as the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) and the vulnerable Greater glider (*Petauroides volans*) in *Eucalyptus regnans* forests (Lindenmayer et al. 2013).

Clearcut logging and plant community composition

Our study provides evidence that clearcut logging does not mimic the post-disturbance environment of high-severity fire. Forest clearcut, salvage logged in 2009–2010, and similarly aged, unlogged sites burned twice and three times consistently differed from one another. In sites clearcut and salvaged logged in 2009–2010, common and keystone resprouting species including *Cyathea australis*, *Dicksonia antarctica*, *Olearia argophylla*, and *Bedfordia arborescens* declined significantly, whereas on-site seeder species such as *Acacia dealbata* increased (Fig. 8). Resprouting species possess resprouting organs (lignotubers, rhizomes, non-woody tubers, etc.) that, while being resilient to fire, are sensitive to the mechanical disturbances associated with clearcut logging (Ough and Murphy 2004, Keith et al. 2007, Blair et al. 2016). Furthermore, earth-moving machinery used in clearcutting operations can compact soil, displace soil seed banks, and kill, damage, and expose resprouting organs (Rab 1996, Ough and Murphy 2004, Wienk and McPherson 2004, Parro et al. 2015). Our findings are consistent with previous research that has identified declines in resprouting species such as tree ferns following logging (Mueck and Peacock 1992, Hickey 1994, Ough 2001, Ough and Murphy 2004, Blair et al. 2016). Ough and Murphy (2004) found only 16% of 2,391 tree ferns remained alive one year after clearcutting in Australian wet sclerophyll forests with only 5% remaining upright. Resprouting species, such as tree ferns and broad-leaf shrubs, cast shadows on the forest floor, which influence the microclimate (Wood et al. 2010, Taylor et al. 2014). Furthermore, tree ferns, including *Dicksonia antarctica* and *Cyathea australis*, provide substrates for epiphytic species, including rare and vulnerable plant taxa (Ough and Murphy 2004). Changes in the abundance of these species will increase light and the temperatures experienced by the understory, favoring some species over others (Wienk and McPherson 2004, Penman et al. 2008).

The high mean abundance of *Eucalyptus regnans* in most clearcut and salvage logged sites (in 2009) is most likely to be a result of post-logging aerial seeding (VicForests 2016). However, inconsistent with predictions we made at the outset of this investigation, the relative mean abundance of *Eucalyptus regnans* was much lower than expected in some recently clearcut sites that were dominated by *Acacia* species. We suspect re-seeding attempts have failed in some of these sites. If eucalypt stocking rates are not achieved after the initial slash-burn post-logging, “cut-blocks” can be mechanically re-disturbed and re-sewn to ensure a homogeneous stand for future timber harvesting (VicForests 2014).

The impacts of clearcut and salvage logging on biological legacies can explain the patterns we observed in plant communities (Lindenmayer et al. 2008). All natural disturbances

leave behind biological legacies. In the case of plant species, these biological legacies can include live and dead trees, and seeds that facilitate regeneration post-disturbance (Franklin et al. 2000, Lindenmayer et al. 2017). These enhance the recovery and resilience of forest ecosystems (Siedl et al. 2014b). For example, biological legacies provide structural complexity that generates regeneration niches for shade-tolerant species (Keith et al. 2007, Siedl et al. 2014b). However, in the event of clearcut and salvage logging, few of these legacies remain (Lindenmayer et al. 2008, Fraver et al. 2017). Despite a long history of use in forested ecosystems, there is much debate surrounding clearcut and salvage logging practices (Lindenmayer and Ough 2006, Thompson et al. 2007, Lindenmayer et al. 2008, Parro et al. 2015, Blair et al. 2016, Thorn et al. 2017). Salvage logging in some ecosystems has had positive (Boucher et al. 2014) or negative effects (Lindenmayer and Ough 2006, Lindenmayer et al. 2008, Thorn et al. 2017) on long-term forest recovery. In our study, plant composition and abundance differed the most in sites salvage logged and those burned twice and clearcut in comparison to similarly aged unlogged/burned sites. These similarly aged logged sites were characterized by a low mean abundance of resprouting species relative to all other disturbance types. Furthermore, salvage logged sites contained no records of the common species *Polystichum proliferum*, *Olearia argophylla*, and *Dicksonia antarctica*. The lack of biological legacies and subsequent exposure and physical damage caused by logging machinery are thought to have played a major role in the absence of these integral species (Ough and Murphy 2004, Wienk and McPherson 2004). The intensity and lasting impact of these disturbances on microclimatic conditions suggests that it is unlikely that these species will re-occupy these sites in the near future (Ough and Murphy 2004). Similarly, in North American forests, salvage logging has altered plant species composition (Thompson et al. 2007, Parro et al. 2015). Such shifts, especially in common and keystone species, may reduce ecosystem resistance and resilience and can trigger ecosystem collapse and positive feedback loops (Ough and Murphy 2004, Lindenmayer et al. 2011, 2016, Belote et al. 2012).

Previous research in *Eucalyptus regnans* forests predicted species composition to rapidly return to that of pre-disturbance conditions after logging and fire (Attiwill 1994, Ashton and Martin 1996). However, we found that after eight years, some common and keystone species had still not returned post-clearcut logging. We assume that these plant communities will take many years to recover. Sites clearcut and salvage logged in 2009–2010 were dominated by *Acacia* and *Eucalyptus* species and had an understory consisting of species life forms that are more characteristic of drier environments including graminoids, herbs, and shrubs such as *Cassinia aculeata* Labill. Species and life forms that are more characteristic of wet forest, including tree ferns and broad leaved shrubs and trees, were consistently absent or had low populations following these disturbances, indicating a shift favoring drier and disturbance-tolerant species (Mueck and Peacock 1992, Ough and Murphy 2004, Blair et al. 2016). These changes in plant community composition could potentially influence the flammability and likelihood of high-severity fire during a fire. Therefore, our findings provide evidence of the “landscape trap” theory, whereby successive fires,

anthropogenic disturbance, and climate change drive positive feedback loops between vegetation composition, structure, and ecosystem function (Lindenmayer et al. 2011, Hughes et al. 2013). The already changing and intensifying disturbance regimes in North American forests and Amazonian forests could eventually produce similar positive feedback loops (Thompson et al. 2007, Cochrane and Laurance 2008, Bowman et al. 2011, Lindenmayer et al. 2011).

Implications for forest management and conservation

Our findings have important implications for forest management globally. We have found that plant community composition and abundance and their respective functional traits can be altered by clearcut and salvage logging and multiple fires within a 26–70 yr interval. Similar changes in plant communities have occurred in other ecosystems around the world that have been affected by fire and clearcut logging (Thompson et al. 2007, Cochrane and Laurance 2008, Lindenmayer et al. 2009). However, disturbance may sometimes enhance diversity in other landscapes that are subject to multiple disturbances if one disturbance type is not dominant, and historic landscape dynamics are considered (Hessburg et al. 2005, Donato et al. 2009, Fontaine et al. 2009).

Anthropogenic disturbances and climate change are driving large-scale changes to fire and disturbance regimes, globally (Brotons et al. 2013, Hughes et al. 2013, Siedl et al. 2014b). As such, many ecosystems are thought to be at risk of substantial change or collapse (Sato and Lindenmayer 2017). The greatest challenge in addressing altered disturbance regimes is incorporating them into global governance and management (Hughes et al. 2013). Given the changes in plant community composition as a result of altered disturbance regimes in southeastern Australian *Eucalyptus regnans* forests, our results suggest land managers take a precautionary approach to ecological management and conservation. Furthermore, in a period of rapid, global, environmental change, with disturbances predicted to increase and intensify, it is critical we mitigate the negative impacts of altered disturbance regimes on biodiversity (Hughes et al. 2013). Our data indicates major interventions are needed in policy and land management practices to manage the threats associated with altered disturbance regimes (Bowman et al. 2011, Siedl et al. 2014b). These include conserving large areas of intact forest (>1,000 ha) and reducing the rates of clearcut logging, particularly in sensitive locations and areas already subjected to prior disturbance (Lindenmayer et al. 2011, Blair et al. 2016). These patches provide invaluable refugia for biodiversity and are fundamental in providing source populations for the recolonization of disturbed sites (Lindenmayer et al. 2011). Furthermore, we urge land managers to reconsider salvage logging operations to retain crucial biological legacies and plant functional traits, which will allow for the natural recovery of post-fire environments. Moreover, there is a need to incorporate the abundance and diversity of plant functional traits into ecosystem assessments and future empirical studies.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1693/full>

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.18913>