

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 yr 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 2 and 3 yr post fire. Mean species richness decreased across the disturbance gradient from 30.1 species/site on low-severity burned sites and 28.9 species/site on high-severity burned sites, to 25.1 species/site on clearcut sites and 21.7 species/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: *clearcut logging; Eucalyptus regnans; plant attributes; post-disturbance environments; regeneration strategies; species richness; wildfire.*

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. 2014). 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 unburned areas, we were also

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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 southeastern Australia. An extensive wildfire in 70 yr-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 to post-fire salvage logging?

We hypothesized 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 initial floristic composition theory (Wilson et al. 1992) more closely, we predicted overall species richness would increase when compared to undisturbed forest due to the influx of early successional species that may be largely absent from long-unburned forest (Martin-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-colonizing 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. 2014). 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, 60–120 km east of Melbourne in southeastern Australia (Fig. 1). These forests receive high rainfall (750–1700 mm/yr) and are found at altitudes ranging from 150 to 1100 m (Boland et al. 2006). Mountain ash forests are characterized 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 yr (McCarthy et al. 1999).

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 yr old. In February 2009, wildfire burned large areas of forest which had previously burned in 1939 (Cruz et al. 2012, Burns et al. 2015).

The usual silvicultural technique applied in mountain ash forests is clearcut logging. This involves the cutting

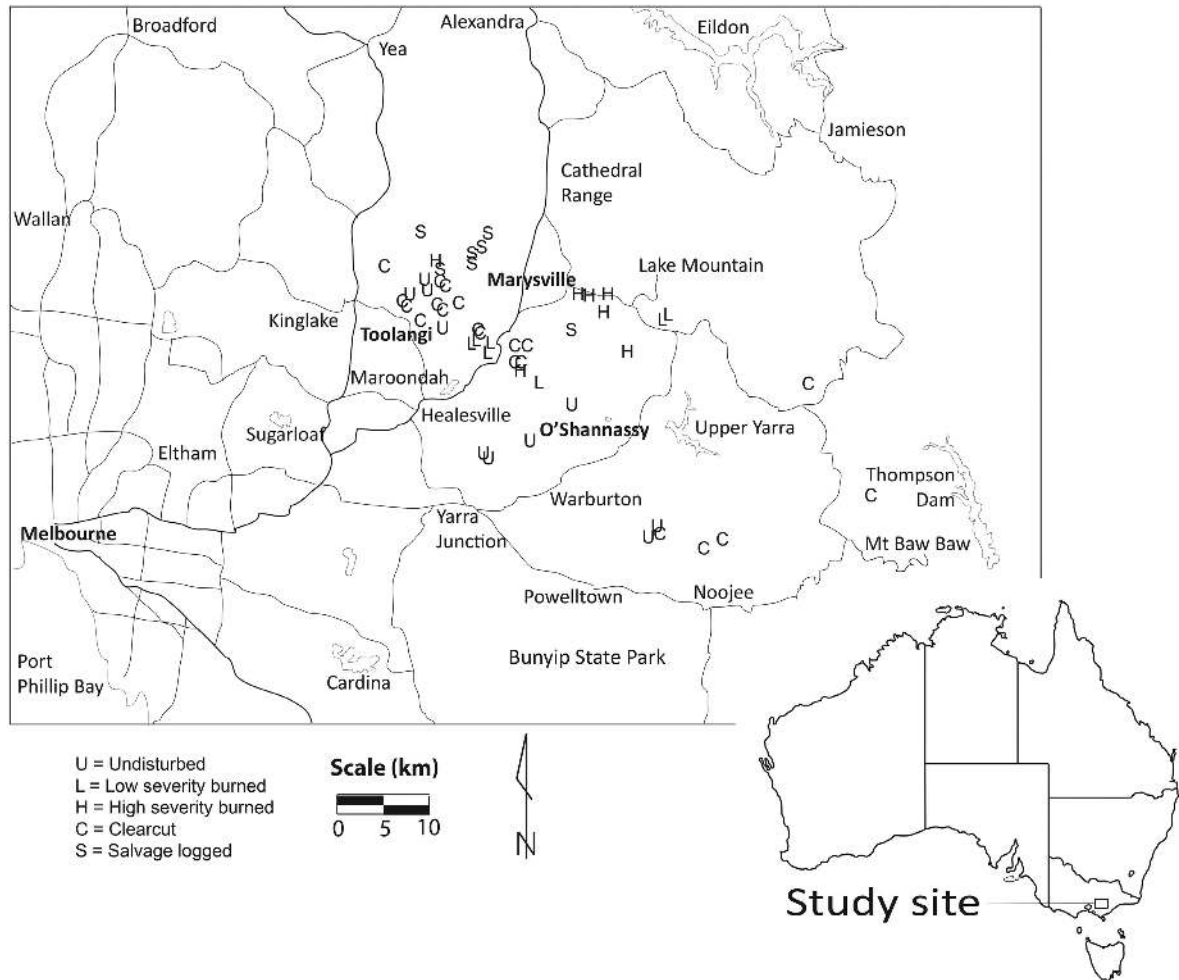


FIG. 1. Maps of study area showing location of sites in Australia.

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 burned 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 burned 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 yr), (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 among 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 2 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.

TABLE 1. Descriptions of disturbance classes and number of sites per class.

| Disturbance class | Number of sites | Burned in 2009 | Logging |
|--------------------------|-----------------|--------------------|-----------------------------|
| Undisturbed/ Unburned | 14 | No, still green | None |
| Low severity | 7 | Yes, low severity | None |
| High severity | 7 | Yes, high severity | None |
| Clearcut | 22 | No | Clearcut in 2009 |
| Salvage | 7 | yes, high severity | Clearcut postfire 2009/2010 |

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

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 ha in size (100 × 100 m) with a central 100 m long transect running perpendicular from the middle of the site's front edge. All sites were buffered around the transect by a minimum of 100 m of uniform forest disturbance to reduce edge effects from adjacent forest with different disturbance history. We established three 10 × 10 m plots straddling this transect between 10–20, 50–60, and 90–100 m. The first plot (10–20 m) 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 5 m of either side of the central transect. We counted only live plants. For logged sites, the 100-m 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 5 m on 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 × 1 transect × 2 yr).

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 characterized 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 (seven 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 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 mid-story 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 three plots (10 × 10 m) 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 modeled 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 generalized 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 2013) 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 2 yr of observations together, resulting in the number of occurrences of the species for each site to be a value out of six (3 plots × 2 yr).

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; Fig. 2). Sites subject to low-severity fire supported the most species (30.1 ± 4.2 species/site; mean

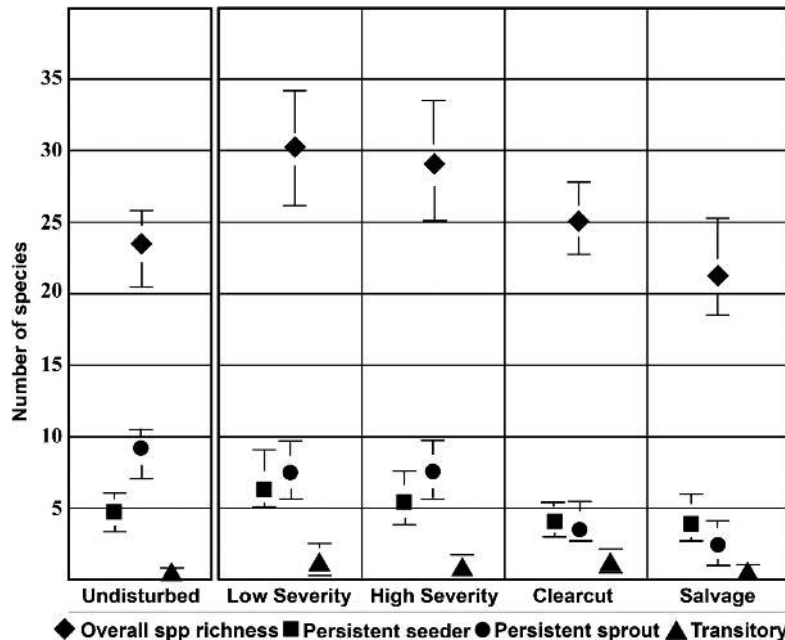


FIG. 2. Mean species richness with error bars showing 95% confidence intervals (CI) of vascular plants per site across a gradient of increasing disturbance intensity showing total species richness and species richness for functional groups including persistent seeder, persistent sprouter, and transitory species.

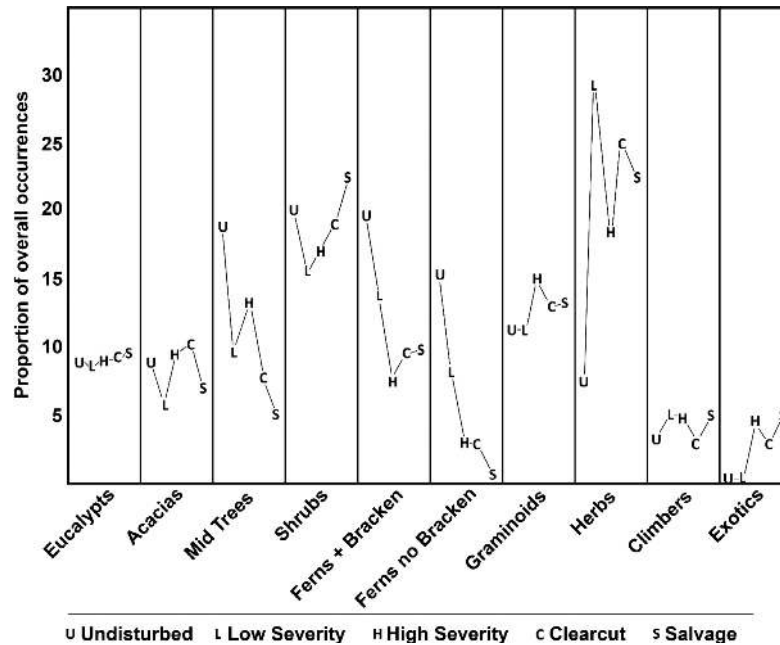


FIG. 3. Frequency of occurrence of each life-form group within each disturbance class as a proportion of the total frequency of occurrence (of all functional groups combined for that disturbance class).

\pm standard deviation, 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).

We identified no significant differences ($P < 0.05$) in species richness between low- 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 $23.5 (\pm 2.6)$ 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 resprouting and seeding groups (Fig. 2). While transitory species were abundant on burned and clearcut logged sites, the group was not diverse. All disturbance categories were represented by relatively few species on average, but the burned and clearcut sites had greater species richness than undisturbed and salvage logged sites (Fig. 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-yr-old (3–6 m tall) saplings (high-severity burned and logged sites) to 75-yr-old, 65 m tall mature trees (undisturbed and low severity, see Figs. 3 and 4 and Appendices 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 Fig. 5. The frequency of occurrence of midstory tree species (which includes tree ferns) exhibited a significant decline across the disturbance gradient (Fig. 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; Fig. 3). Shrubs showed no significant differences in frequency of occurrence across the sites except for those subject to salvage logging (Fig. 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 (Figs. 3 and 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

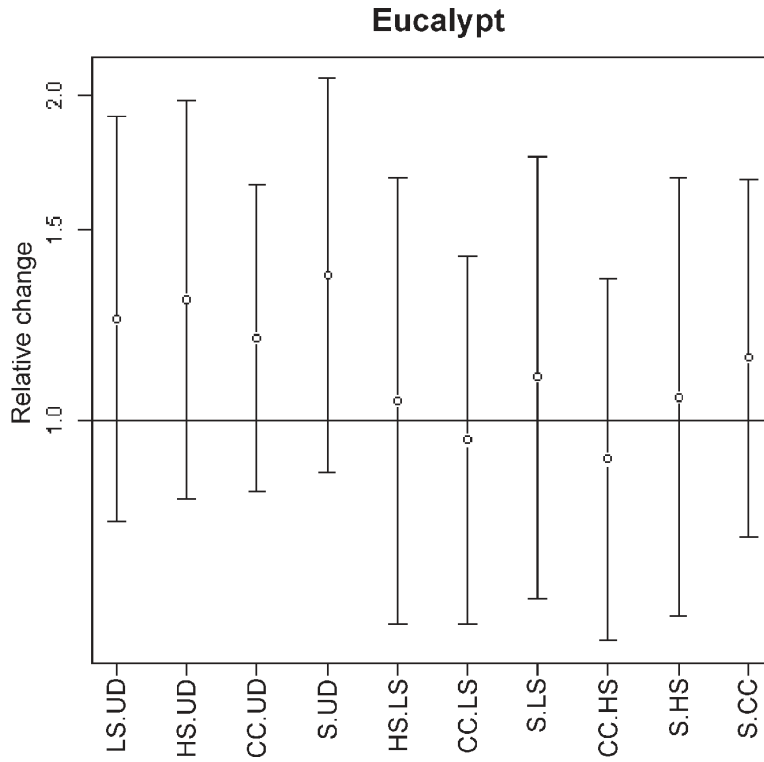


FIG. 4. Relative change for eucalypt life-form group; error bars show 95% CI. UD = Undisturbed, LS = Low Severity burned, HS = High Severity burned, CC = Clear Cut logged and S = Salvage logged.

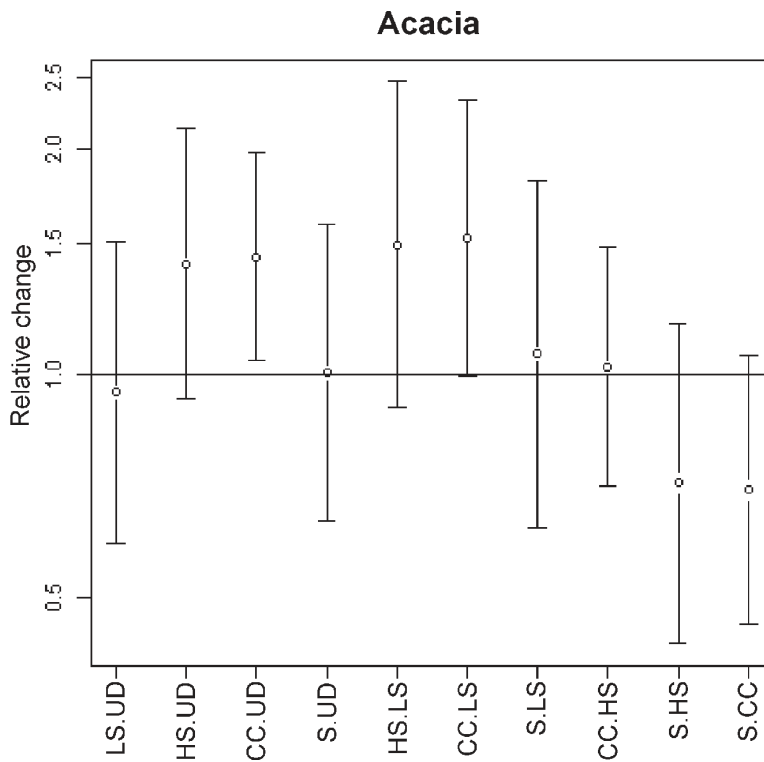


FIG. 5. Relative change for acacia life-form group; error bars show 95% CI.

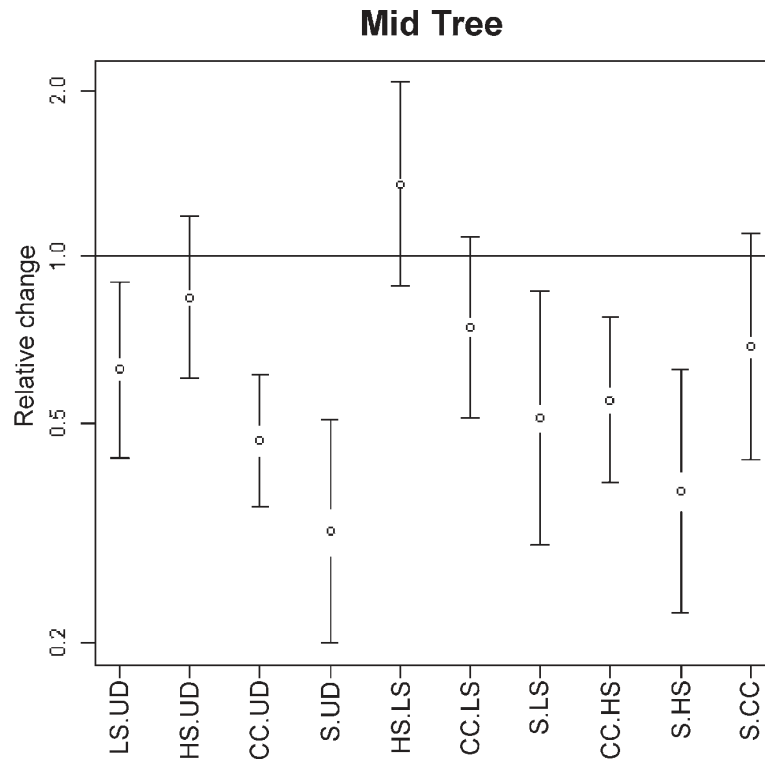


FIG. 6. Relative change for midstory tree life-form group; error bars show 95% CI.

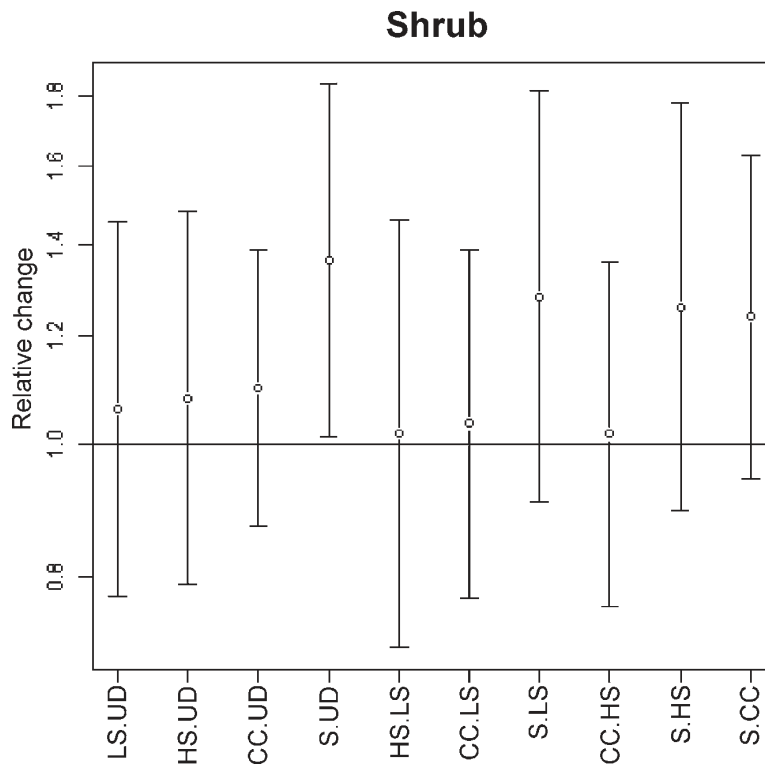


FIG. 7. Relative change for shrub life-form group; error bars show 95% CI.

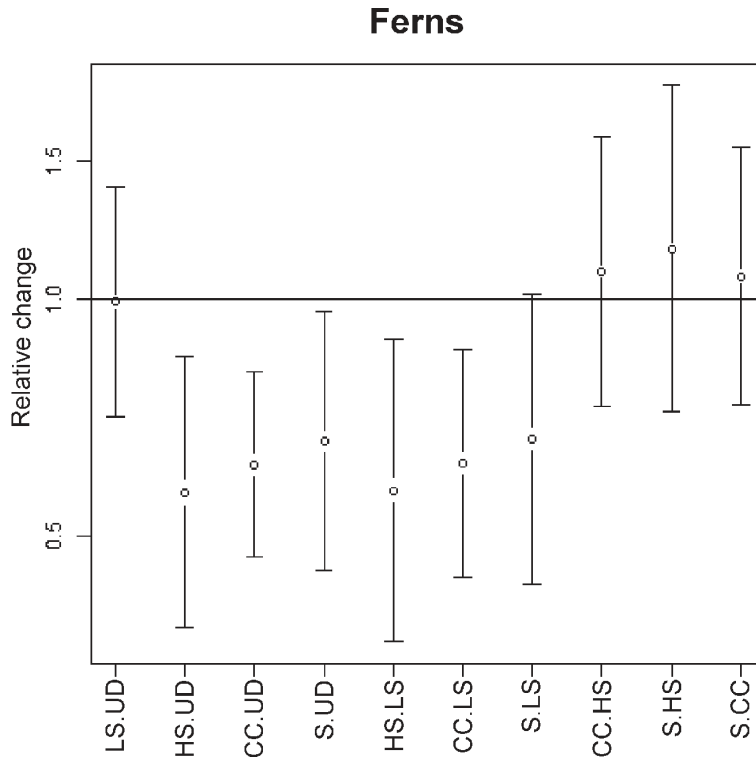


FIG. 8. Relative change for fern life-form group; error bars show 95% CI.

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 from 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 Fig. 9) compared to all other disturbance categories ($P < 0.0001$). Low-severity burn sites were characterized 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 Fig. 10). Graminoids were more abundant on high-severity burned sites than undisturbed sites ($P = 0.007$, see Fig. 11). Exotic species are discussed in the following section.

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 (Figs. 12

and 13; Appendix S5). Sites in non-logged disturbance classes (undisturbed, low-, and high-severity burned) were characterized 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 unburned 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, Fig. 12). The frequency of occurrence of persistent on-site seeding species varied little between sites in different disturbance classes (Fig. 14), with the only significant result being on sites subject to high-severity fire that were characterized by supporting a greater frequency of occurrence of this group than undisturbed sites ($P < 0.05$). Persistent “other” species were favored 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 Fig. 15). Persistent blow-in species showed no variation across disturbance classes for frequency of occurrence

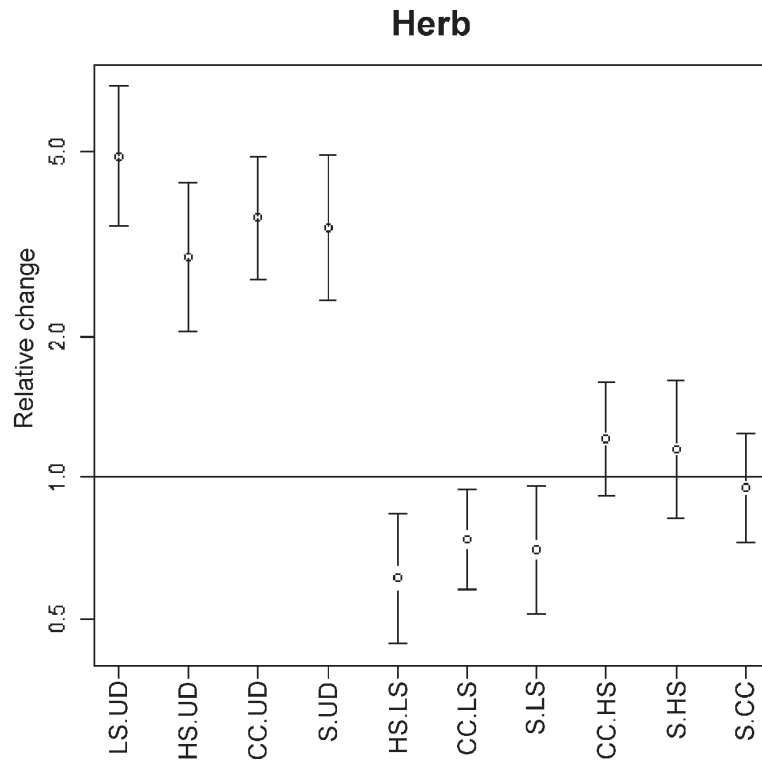


FIG. 9. Relative change for herb life-form group; error bars show 95% CI.

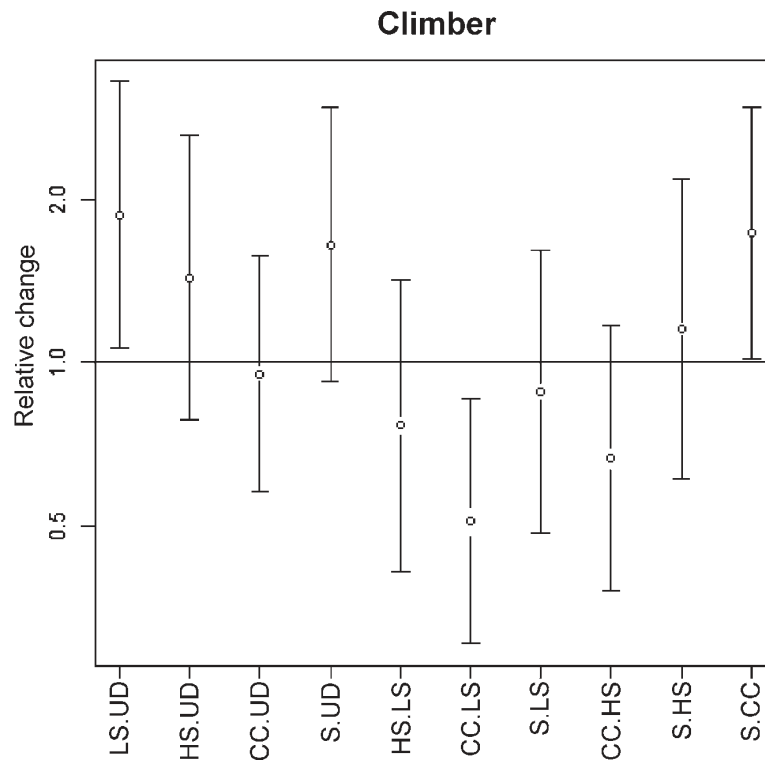


FIG. 10. Relative change for climber life-form group; error bars show 95% CI.

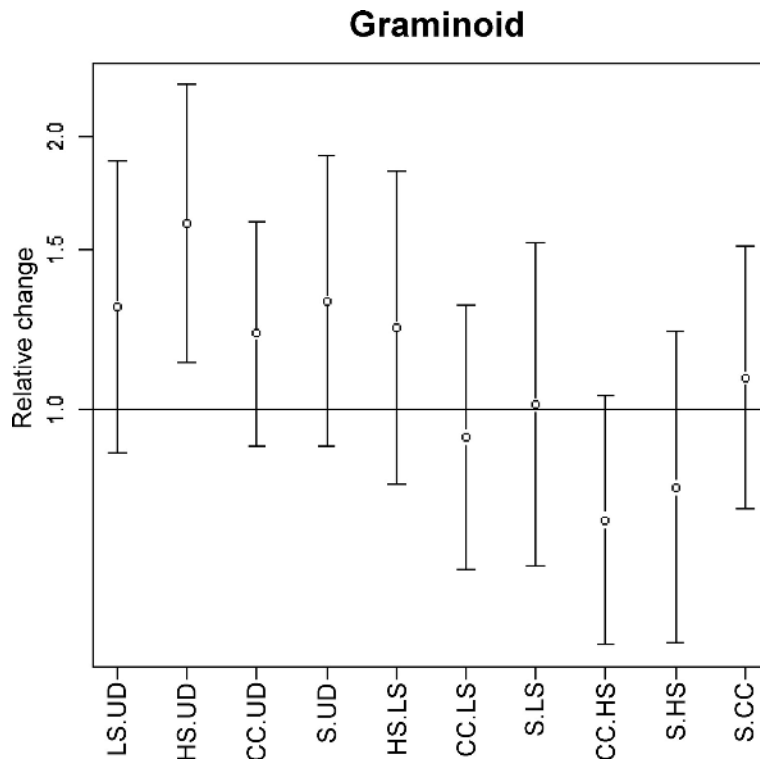


FIG. 11. Relative change for graminoid life-form group; error bars show 95% CI.

(Figs. 12 and 16). Exotic species were significantly ($P < 0.05$) more abundant on the logged and high-severity burned sites than undisturbed sites and sites subject to low-severity fire (Fig. 17).

Results were very similar for the two groups of transitory species, onsite seeders (Fig. 18) and blow-in seeders (Fig. 19; see also Fig. 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.

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 multifaceted, and diversity–disturbance relationships (DDRs) have been found to encompass a range of different relationship curves (Miller et al. 2011). The most recognized 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- to high-severity fire to clearcut logging of unburned 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 40–70 m above the ground) and the shrub layer (which is generally 5 m 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 (Figs. 3–11) and functional groups based on regeneration strategy (Figs. 12–19).

Acacia, herbs, graminoids, and climbers.—Acacia occurred least frequently on sites where disturbance was insufficient to trigger a new cohort (Fig. 5). Undisturbed sites and low-severity burned sites had fewer acacia than the other three disturbance classes, and the acacia 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 the 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 recolonize or recover. High disturbance classes of clearcut,

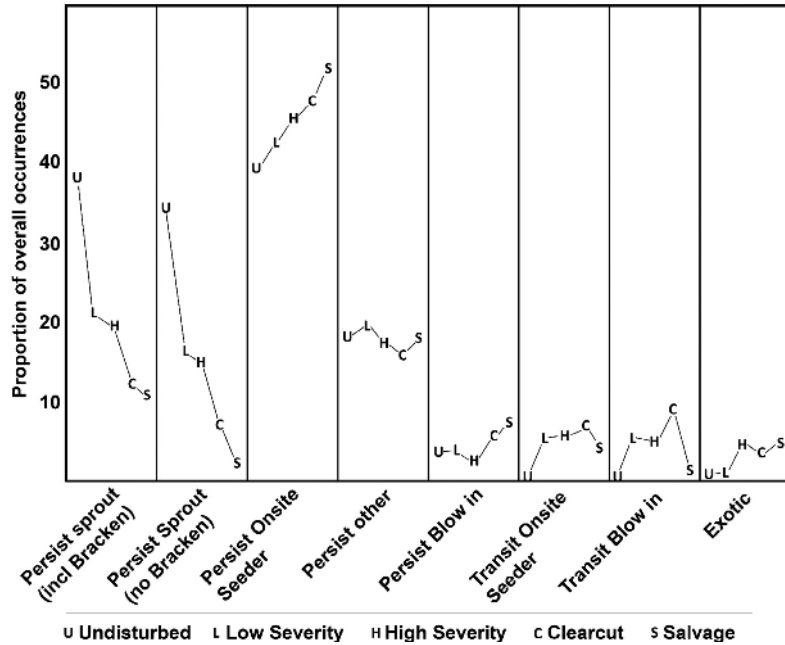


FIG. 12. Frequency of occurrence of each regeneration strategy functional group within each disturbance class as a proportion of the overall frequency of occurrence (of all functional groups combined for that disturbance class).

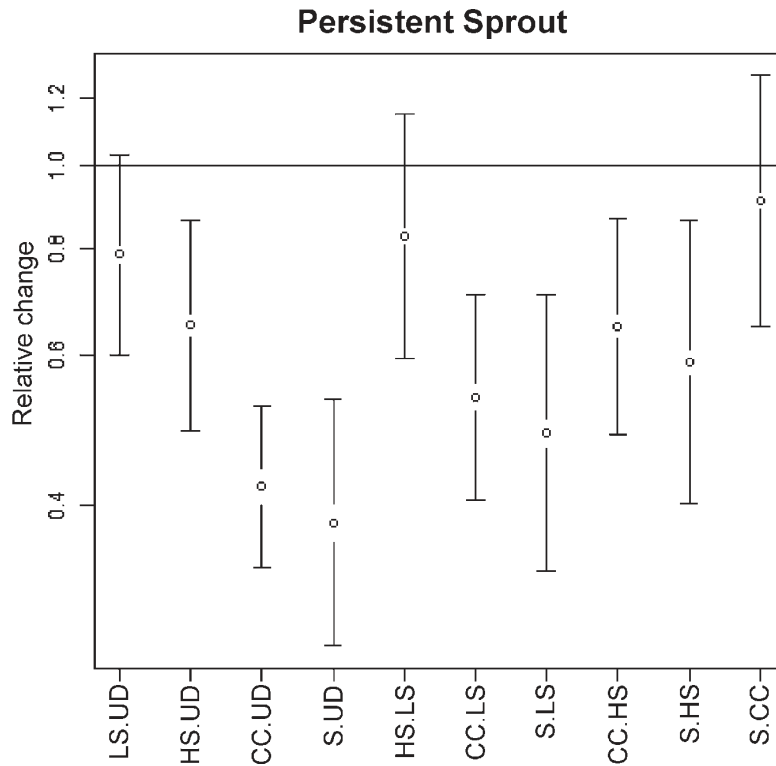


FIG. 13. Relative change for persistent sprout reproductive strategy group; error bars show 95% CI.

high-severity burned, and salvage logged sites fell between these two extremes (see Fig. 9). Graminoids were little affected by the different disturbance classes

(Fig. 11), with flushes of common post-disturbance grasses such as *Dryopoa* occurring across the majority of disturbed sites. Climbers were represented by only

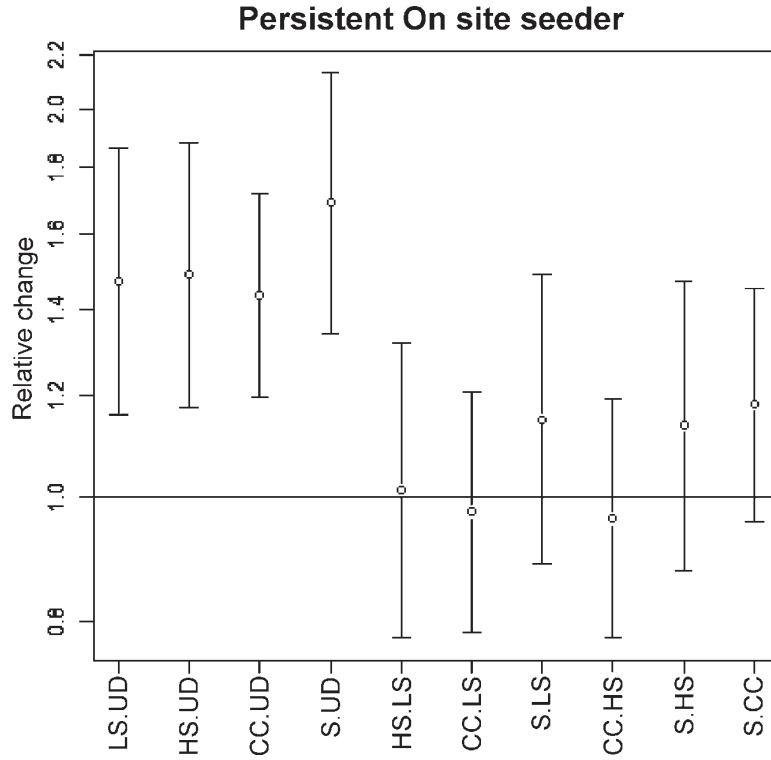


FIG. 14. Relative change for persistent on-site seed reproductive strategy group; error bars show 95% CI.

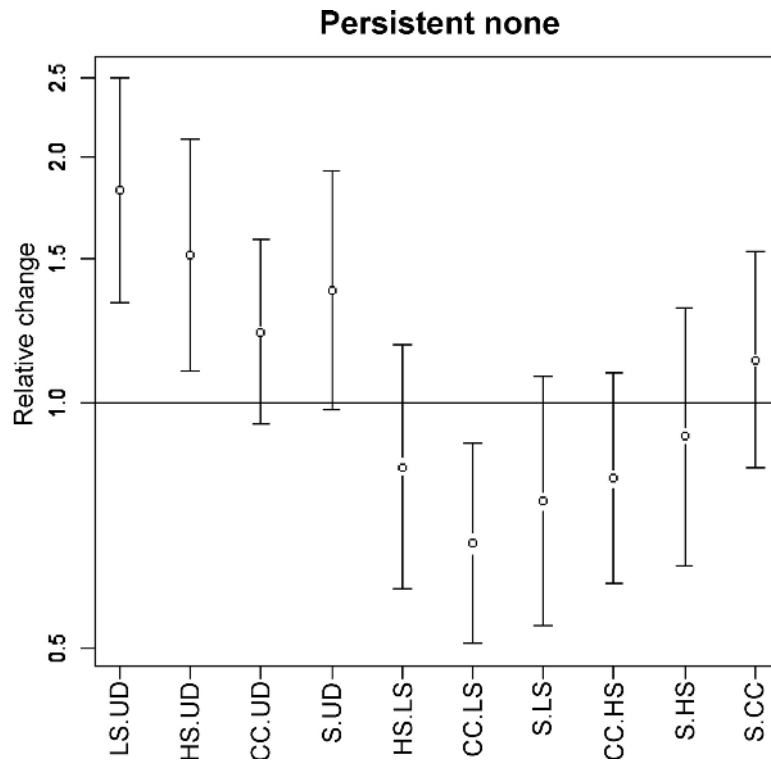


FIG. 15. Relative change for persistent "none" (no defined strategy) reproductive strategy group; error bars show 95% CI.

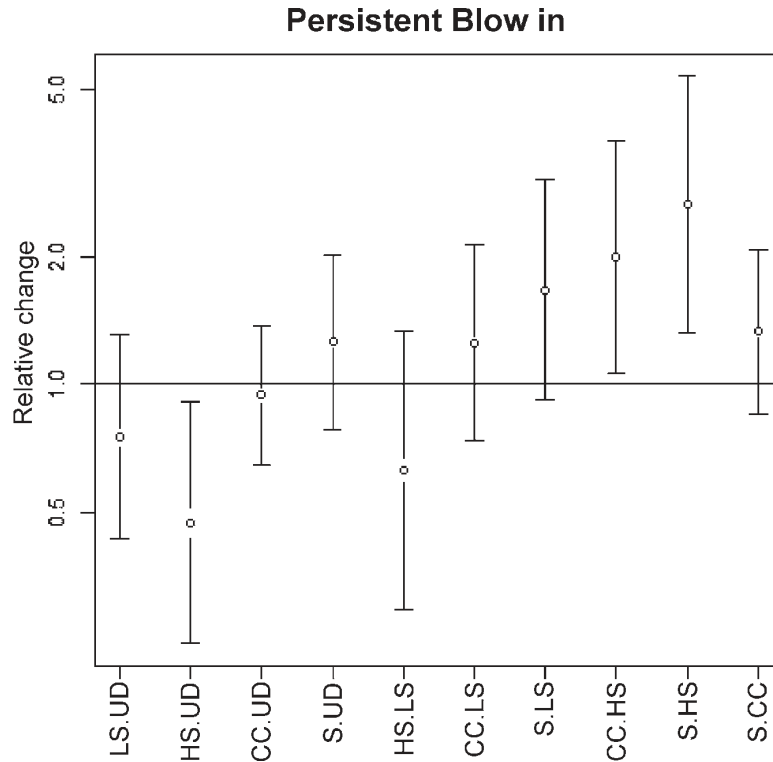


FIG. 16. Relative change for persistent blow-in seed reproductive strategy group; error bars show 95% CI.

four species in these forests and showed limited trends in response to the different disturbance levels (Fig. 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 (Fig. 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 (Fig. 19). All species within this group were *Senecio* (fireweeds) and are usually strong colonizers 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 (Fig. 14), while those that blew in (Fig. 16) tended to be favored in 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 following section). The persistent none group (Fig. 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 favored 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 (Fig. 13), ferns (Fig. 8), and midstory trees (Fig. 6) were significantly negatively affected across the disturbance gradient, with several species such as *Nothofagus cunninghamii* and

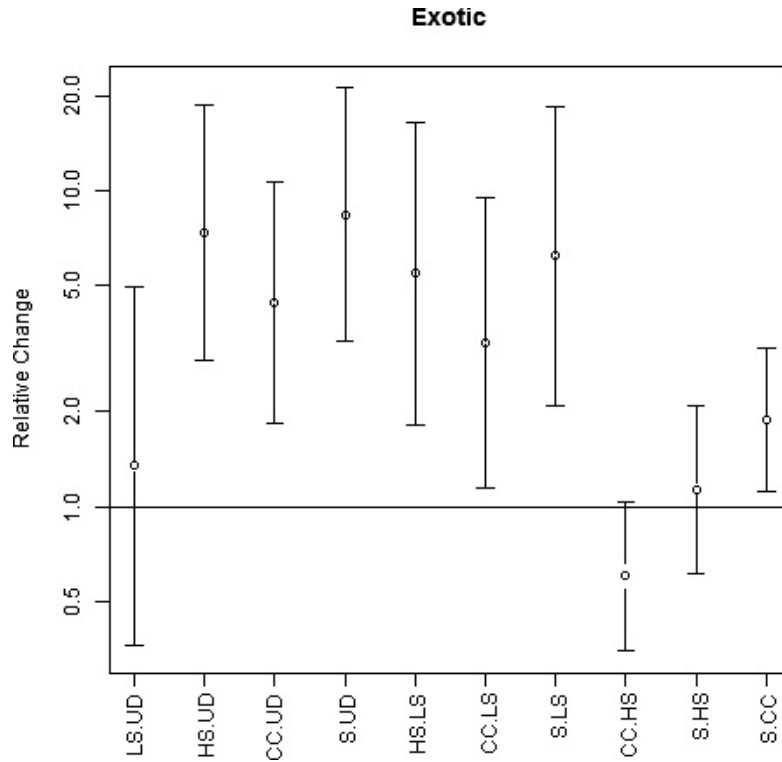


FIG. 17. Relative change for exotic reproductive strategy group; error bars show 95% CI.

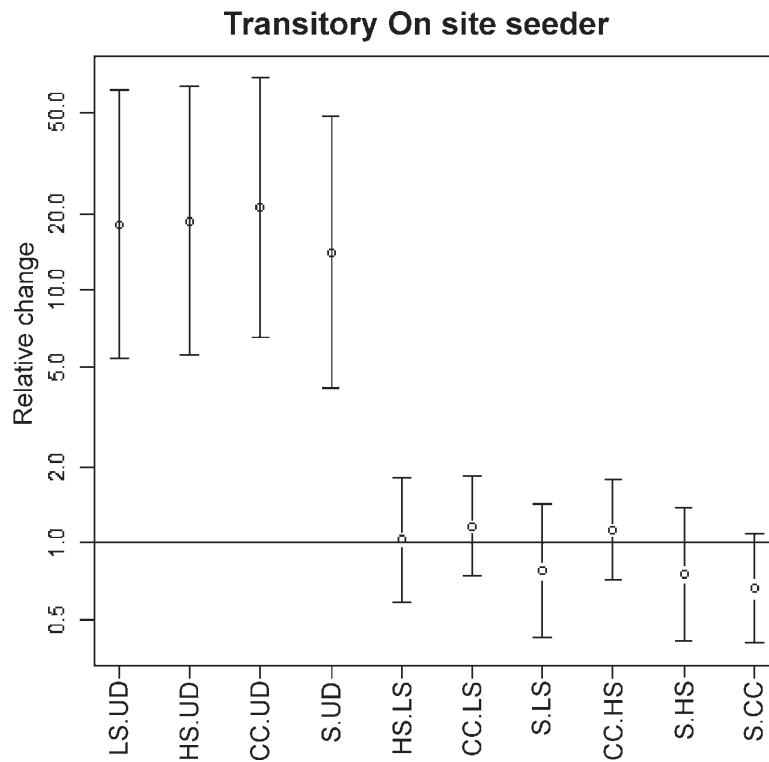


FIG. 18. Relative change for transient on-site seed reproductive strategy group; error bars show 95% CI.

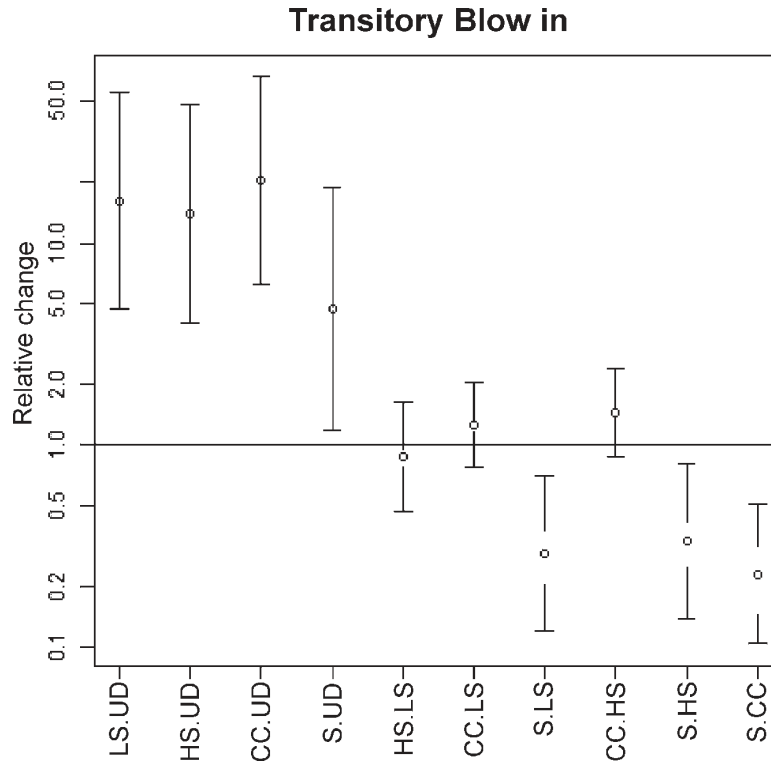


FIG. 19. Relative change for transient blow-in seed reproductive strategy group; error bars show 95% CI.

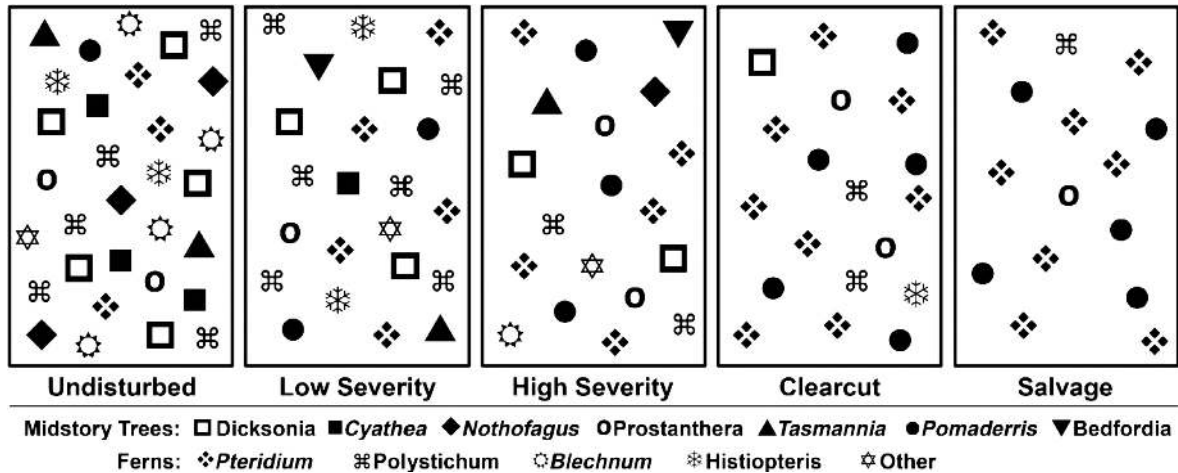


FIG. 20. Fern and midstory tree proportional frequency of occurrence and species richness comparison for each disturbance class (conceptual diagram based on our data). The diagram shows the simplification of the fern and midstory strata through the loss of species such as *Blechnum*, *Tasmannia*, *Cyathea*, and *Nothofagus* when the forest is clearcut or salvage logged compared to burned 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 burned and undisturbed sites.

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 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- and high-severity fire) midstory trees were represented by 18 different species with a maximum frequency of occurrence of any one species being one-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 three 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 characterized 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.

We suggest that the simplification of plant biota observed in this investigation is likely to be repeated in

TABLE 2. Percent frequency of individual midstory tree species, by disturbance classes.

| Midstory tree species | Frequency (%) |
|--------------------------------|---------------|
| Undisturbed | |
| <i>Dicksonia antarctica</i> | 27 |
| <i>Nothofagus cunninghamii</i> | 15 |
| <i>Cyathea australis</i> | 14 |
| <i>Prostanthera lasianthos</i> | 7 |
| <i>Tasmannia lanceolata</i> | 7 |
| <i>Pomaderris aspera</i> | 4 |
| Low severity | |
| <i>Dicksonia antarctica</i> | 25 |
| <i>Pomaderris aspera</i> | 21 |
| <i>Bedfordia arborescens</i> | 11 |
| <i>Cyathea australis</i> | 11 |
| <i>Prostanthera lasianthos</i> | 11 |
| <i>Tasmannia lanceolata</i> | 11 |
| High severity | |
| <i>Pomaderris aspera</i> | 26 |
| <i>Prostanthera lasianthos</i> | 17 |
| <i>Dicksonia antarctica</i> | 17 |
| <i>Lomatia fraseri</i> | 9 |
| <i>Hedycarya angustifolia</i> | 6 |
| <i>Nothofagus cunninghamii</i> | 6 |
| Clearcut | |
| <i>Pomaderris aspera</i> | 56 |
| <i>Prostanthera lasianthos</i> | 20 |
| <i>Dicksonia antarctica</i> | 10 |
| <i>Cyathea australis</i> | 5 |
| Salvage | |
| <i>Pomaderris aspera</i> | 79 |
| <i>Prostanthera lasianthos</i> | 16 |

other forest ecosystems globally, where resprouting species comprise an important part of the plant assemblage. This includes wet tropical forests such as the Brazilian Amazonia (Balch et al. 2013) and 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 decline (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 (Fig. 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. 2014) 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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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1369/supinfo>

DATA AVAILABILITY

Data associated with this paper have been deposited in the Long Term Ecological Research Network Data Portal: <http://www.ltern.org.au/knb/metacat/ltern2.1071/html>.