

Prior disturbance legacy effects on plant recovery post-high-severity wildfire

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Abstract. Large, high-severity wildfires are an important component of disturbance regimes around the world and can influence the structure and function of forest ecosystems. Climatic changes and anthropogenic disturbances have altered global disturbance patterns and increased the frequency of high-severity wildfires worldwide. While the recovery of plant communities at different successional stages after fire is well known, the influence of prior disturbances and stand age is poorly understood. Despite this, high-intensity wildfires can produce long-lasting legacy effects, which can influence the resistance and resilience of ecosystems. Here, we quantified the influence of prior stand age and disturbance history on the recovery of plant communities in the Mountain Ash and Alpine Ash forests of south-eastern Australia after high-severity wildfire. Specifically, controlling for stand age, we compared the abundance (percent cover) of different plant life forms and reproductive strategies in forests that were, at the time of high-severity wildfire in 2009, “young” (28–35 yr old and previously logged), “mixed” age (26, 70–83, >150 yr old), “mature” (70–83 yr old), and “old-growth” (>150 yr old). We uncovered evidence that the legacy of prior disturbance and stand age at the time of high-severity wildfire can influence the recovery of plant communities in early successional forests. Specifically, we found that “young” forests burnt in 2009 had a higher abundance of ruderal and graminoid species, but had a lower abundance of persistent, onsite seeders, including *Acacia* and eucalypt species, relative to “old-growth” forests burnt in 2009. “Mature” aged forests burnt in 2009 also had a lower abundance of *Acacia*, eucalypt, and shrub species, relative to “old-growth forests” burnt in 2009. Our findings provide evidence of advanced recovery in forests that were older when burnt by high-severity wildfire, relative to younger forests burnt by the same wildfire. Further, we also demonstrate the influence of different environmental conditions on plant communities. In a period of rapid, global, environmental change, our study provides insights into the recovery of plant communities post-wildfire with implications for forest management. Further, our findings suggest that predicted increases in the frequency of high-severity wildfires may have consequences for forest regeneration.

Key words: disturbance legacies; *Eucalyptus regnans*; fire frequency; functional groups; life forms.

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INTRODUCTION

Large, high-severity wildfires are an important component of disturbance regimes in many forest ecosystems globally (Bond et al. 2005, Bowman et al. 2009), and they can influence spatial

and structural dynamics, biodiversity and biogeochemical processes (Donato et al. 2009, Bače et al. 2015). Historically, high-severity wildfires occur infrequently in temperate and boreal forests and produce long-lasting legacy effects (Foster et al. 1998, Franklin et al. 2002, Bače et al.

2015). However, climate change and anthropogenic disturbances have increased the frequency of wildfires in recent decades across many terrestrial ecosystems, worldwide (Bradstock et al. 2009, Taylor et al. 2014, Jolly et al. 2015, Abatzoglou and Williams 2016, Sommerfeld et al. 2018). Multiple high-severity wildfires within short intervals can produce novel conditions that exceed the adaptive resilience (ability to recover from) and resistance (ability to withstand) of ecological communities (Enright et al. 2015, Nimmo et al. 2015, Turner et al. 2019). While post-fire successional trajectories have been well documented, few studies have considered the legacy effects of prior disturbances on forest recovery after additional disturbance (Connell and Slatyer 1977, Bergeron et al. 1988, Johnson and Miyanishi 2008, Swanson et al. 2011). High-severity wildfires are predicted to increase with future climatic and land-use changes (Bradstock et al. 2009, Jolly et al. 2015, Abatzoglou and Williams 2016, Schoennagel et al. 2017), and understanding how prior disturbances influence forest recovery is critical for forest management and planning (Johnstone et al. 2016, Seidl et al. 2017, Turner et al. 2019).

Legacies of prior disturbances or “disturbance legacies” include large fire-killed trees, logs, woody debris, plant propagules, and organic patterns that persist after disturbance (Foster et al. 1998, Franklin et al. 2000, Johnstone et al. 2016). These legacies can influence the resistance and resilience of ecosystems to future perturbations, but may be lost by compounding disturbances (Enright et al. 2015, Johnstone et al. 2016, Fairman et al. 2019, Turner et al. 2019). The types and numbers of legacies of high-severity disturbances in forests is influenced by several factors. These include (1) disturbance-specific characteristics (Gill 1975) such as the origin (natural or human-induced) (Foster et al. 1998, Barlow et al. 2016) scale (Frelich 2002, Seymour and White 2002), severity (Kennard et al. 2002, Keeley 2009) and frequency (Bowd et al. 2018) of disturbances; and (2) environmental variables like topography, climate, and abiotic conditions (Likens 1991, Hobbs and Huennike 1992, Abatzoglou and Williams 2016, Sommerfeld et al. 2018). The influence of these factors on plant communities can be species-specific or vary between different plant life forms and reproductive strategies

(Duveneck and Scheller 2016, Johnstone et al. 2016).

In fire-prone landscapes, plant species have evolved adaptations and traits that allow them to resist high-severity wildfire (Halpern 1988, Russell and Connell 2014) or be resilient to high-severity wildfire (Walker 1995, Seidl et al. 2014a). For instance, some fire-tolerant species possess epicormic buds protected under thick bark, and subterranean lignotubers and rhizomes that resprout after fire (Lawes and Clarke 2011, Clarke et al. 2013). Other species establish a new regrowth cohort by germinating from persistent soil seed banks (Parrotta 1993, Greene et al. 1999, Clarke et al. 2009) or canopy-stored seed (Ashton 1981, Clarke et al. 2009). However, these adaptations and reproductive strategies can be compromised under altered disturbance regimes (Johnstone et al. 2016). For instance, multiple disturbances within short-return intervals can deplete soil-stored seed banks, or species with canopy-stored seed before maturation (Bowman et al. 2014, Turner et al. 2019), and resprouting species can be at risk of “resprout failure” (Fairman et al. 2019).

Disturbance legacies are an important component of the structural heterogeneity of ecosystems and can interact with environmental changes to influence the recovery of plant communities in the event of future disturbances (Seidl et al. 2014b, Johnstone et al. 2016, Perring et al. 2018). While previous studies have examined the successional trajectories of plant communities after major disturbance (Connell and Slatyer 1977, Bergeron et al. 1988, Swanson et al. 2011), knowledge of how prior disturbance legacies influence forests recovering from additional high-severity wildfire is limited (Swanson et al. 2011, Lindenmayer et al. 2019).

Large, high-severity wildfires in 2009 burnt forests of multiple stand ages and disturbance histories across south-eastern Australia. This provided a rare opportunity to quantify the legacy of prior disturbances on forest recovery. Here, we take advantage of this “natural experiment” to quantify the influence of different prior disturbance histories and subsequent stand age on the abundance (percent cover) of vascular plant life forms and functional groups in early successional (10 yr old) Mountain Ash (*Eucalyptus regnans*) and Alpine Ash (*Eucalyptus delegatensis*)

forests in south-eastern Australia. These included forests that, at the time of high-severity fire in 2009, were (1) “old-growth” (unburnt since 1850s–1900s; aged ~150 yr old), (2) “mature” (aged between 70 and 83 yr old), (3) “young” and previously logged (aged between 28 and 35 yr old), or (4) “mixed” age (aged between 26 and ~150 yr old). To do this, we answered two inter-related questions: Does prior disturbance history and stand age at the time of high-severity wildfire influence the diversity of plant communities post-fire? And, How does prior disturbance history and stand age influence the recovery of plant functional groups (life forms and reproductive strategies) in early successional forests?

At the onset of this investigation, we made three key predictions about the influence of prior disturbances and subsequent stand age on post-fire plant communities, which varied between plant functional groups. Specifically,

1. We predicted that relative to younger successional forests burnt in 2009, persistent, onsite seed species would be most abundant in older forests that were burnt in 2009.
2. We predicted that persistent, sprout species would be more abundant in forests that were older when burnt in 2009, relative to younger successional forests burnt in 2009.
3. We also predicted that forests that were young at the time they were burnt in 2009 would have a higher abundance of plant species that are ruderal, including herb and graminoid life forms.

METHODS

We conducted this study in the Mountain Ash (*E. regnans*) and nearby Alpine Ash forests (*E. delegatensis*) forests of the Central Highlands of Victoria, in south-eastern Australia (Fig. 1). These species are obligate seeders, and *E. regnans* is the tallest flowering plant in the world, typically 55–75 m in height (Costermans 2009). Our study sites were between 569 and 1182 m in elevation, and were located in national parks, closed water catchments, and multi-purpose State Forest.

Disturbance patterns in the Mountain Ash and Alpine Ash forests of Victoria are characterized

by high-severity stand-replacing wildfires, with a historical fire-return interval of between 75 and 150 yr (McCarthy et al. 1999). However, the frequency of these wildfires has increased with wildfires occurring in 1851, 1905, 1906, 1926, 1932, 1939, 1948, 1954, 1983, and 2009 (Victorian Government DELWP 2021). In addition to wildfires, these forests have been subject to ongoing clearcut logging since 1970s and post-fire (salvage) logging since the 1940s (Noble 1977, Florence 1996, Lindenmayer and Ough 2006). Collectively, these natural and anthropogenic disturbances have resulted in forest landscapes supporting a mosaic of stands of different ages (Lindenmayer et al. 2019).

Our study consisted of 28 sites, each of 1 ha, in 10-yr-old Mountain Ash and Alpine Ash forest stands that regenerated after high-severity wildfire in 2009. Our sites were stratified across four different disturbance histories and respective stand age cohorts at the time of high-severity wildfire in 2009: (1) “old-growth” (unburnt since 1850s–1900s; aged ~150 yr old) ($n = 4$), (2) “mature” (burnt in 1926/1939; 70–83 yr old) ($n = 14$), (3) “young” (burnt in 1939, clearcut logged in 1974–1981; aged 28–35 yr old) ($n = 6$), and (4) “mixed” age forest ($n = 4$). Mixed aged forests had experienced wildfires in 1850s–1900s, 1939, and 2009; however, they supported multiple stand ages (>50% old growth; remaining trees were 26–70 yr old). We used a combination of mapped information and stand-level onsite assessment to determine the age of stands (Ash-ton 1976).

We visually estimated the projective (percentage) foliage cover of individual vascular plant species in each of the 28 sites during 2019–2020. To do this, we established six 10 × 10 m quadrats located at 20 m increments along a 110 m transect on each of our sites. In each of the 100 m² plots, we recorded the projective foliage cover of shrubs, midstorey trees, overstorey trees, and tree ferns to the nearest 1%. We also recorded the projective foliage cover of plant species in smaller life forms and sporadic growth-habitats including herbs, ground ferns, and small shrubs (<2 m high) across 20 randomly selected 1 × 1 m sub-plots in each of the three of the 10 × 10 m quadrats situated at the beginning (10 m), middle (50 m), and end (100 m) of the transect to increase detectability.

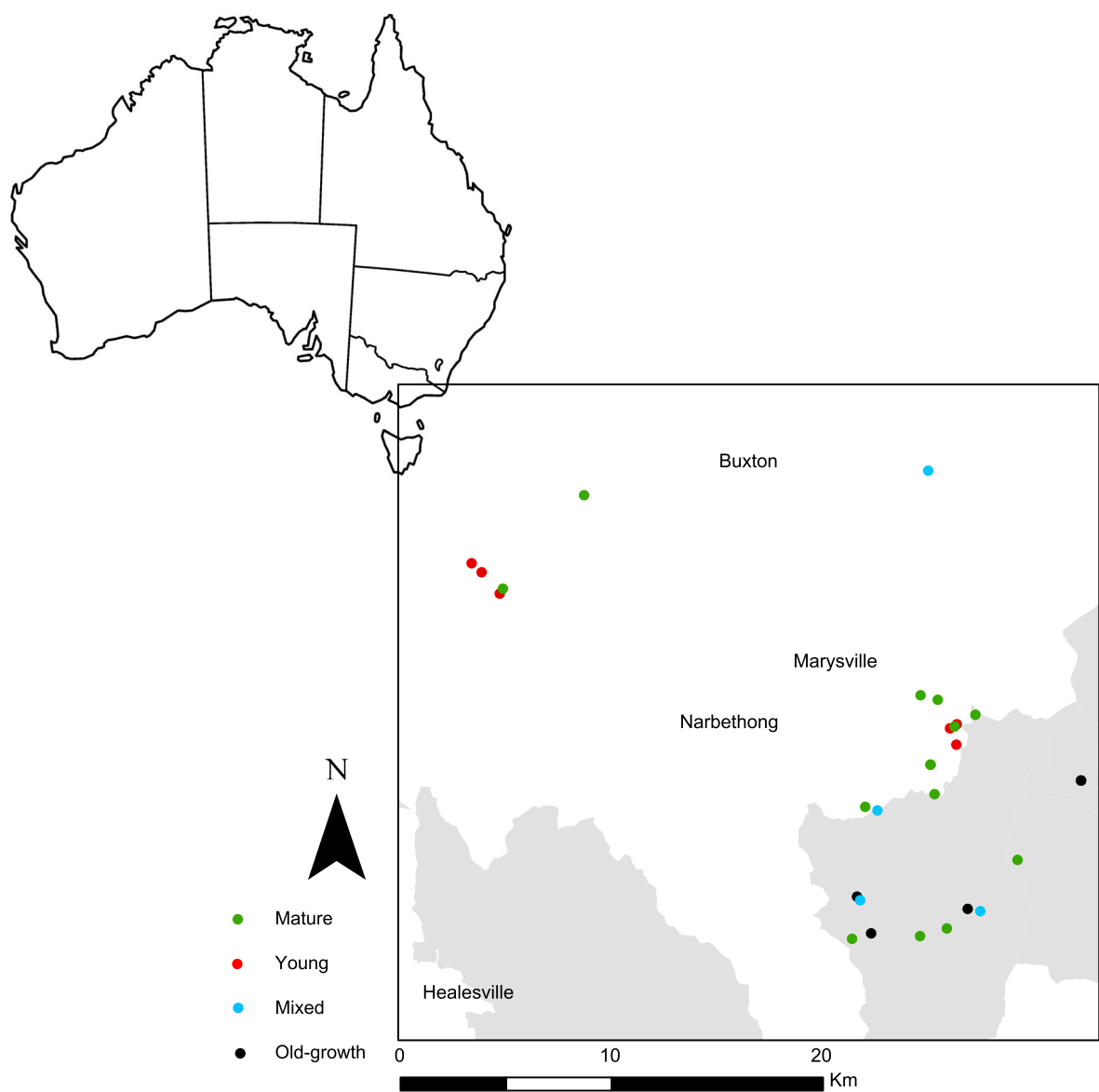


Fig. 1. Map of study area showing location of sites. Gray shading indicates National Park areas.

We assigned plant species to life forms based on physical traits and on reproductive strategies. Life forms included: (1) “eucalypts” (the dominant overstorey species), (2) “*Acacia*,” (3) “(midstorey) trees,” (4) “shrubs,” (5) “ground ferns,” (6) “graminoids,” (7) “herbs,” (8) “climbers,” and (9) “tree ferns.” The three main *Acacia* species (*A. dealbata*, *A. frutescens*, and *A. obliquinervia*) are midstorey trees. However, because *Acacia* species have specialized functions in ecosystems

associated with nitrogen fixation (Adams and Attiwill 1984) and provision of habitat for fauna (Lindenmayer 1996), we separated them from the other midstorey trees in our analysis as per Blair et al. (2016). We also assigned plants to life form categories based on the Victorian State Government Department of Environment, Land, Water and Planning’s Highlands Southern Fall Bioregion Ecological Vegetation Class (EVC) and literature review (Costermans 2009, Bull and

Stolfo 2014, Victorian Government DELWP 2018).

We categorized plant species into reproductive strategy groups: “persistent” species or “ruderal” species. Ruderal species are short-lived early colonizers that are out-competed by other plants, typically in less than 10 yr (Grime 1977). We further divided persistent reproductive strategy groups based on their primary method of regeneration after disturbance: (1) “persistent, onsite seeder” species, (2) “persistent, sprout” species, (3) “persistent (no single defined reproduction strategy)” species, and (4) “persistent, seed and sprout” species. We assigned reproductive strategy groups to individual species based on those described in Blair et al. (2016), various literature reviews (Walsh and Entwistle 1994, 1996, 1997, Clarke et al. 2009, Costermans 2009, Kattge et al. 2011, Bull and Stolfo 2014), field observations, and consultations with botanists at Melbourne Botanical Gardens. Exotic plant species are rare in these forests and were excluded from analyses. We used the total mean projective cover of individual plant life forms and reproductive strategies as a measure for each entire site. Hereafter, the projective foliage cover of plant species is referred to as plant species abundance.

Statistical analysis

We used beta regressions to determine how the mean proportion of each life form and reproductive strategy group was influenced by prior disturbance histories (categorical variable) assuming constant precision using the *betareg* package in R (Cribari-Neto and Zeileis 2012). We included slope (continuous variable), Northerly (N) aspect (categorical variable: non-N aspect and N aspect), topographical wetness index (TWI; continuous variable), and elevation (continuous variable) in each model to account for their potential influence on the abundance of plant functional groups and life forms. We performed model selection with prior disturbance history as a fixed effect and selected the model with the lowest Akaike’s Information Criterion value using the *MuMIn* package in R (Bartoń 2013). We generated Cook’s distance plots to identify and remove significant outliers (Cook 1977). To meet assumptions of beta regressions that data points range from >0 to <1 , we corrected any “0” measures by adding half of the

next lowest measure. We estimated the marginal means of each life form and reproductive strategy across all disturbance histories from beta regressions using the *emmeans* package in R (Lenth 2020). Using the relative differences between these estimates, we made pairwise comparisons between the influence of disturbance histories on individual life forms and reproductive strategies.

RESULTS

We identified 89 vascular plant species across our 28 sites. “Young,” logged forests (28–35 yr old) burnt by wildfire in 2009 had the highest mean species richness of $25.7 (\pm 1.89)$; followed by those that were “old growth” (~150 yr old) (22.25 ± 3.94) and “mature” (70–83 yr old) (20.92 ± 1.61). “Mixed” age (28 to ~150 yr old) forests burnt by the 2009 wildfires had the lowest mean species richness (20 ± 1.29) (Fig. 2; Appendix S1: Table S1).

Functional groups

Reproductive strategies.—We assigned each of the 89 vascular plant species into five reproductive strategy groups: (1) persistent, onsite seeder, (2) persistent (no single defined strategy), (3) persistent, sprout, (4) persistent, seed, and sprout, and (5) ruderal. Persistent, onsite seeder species

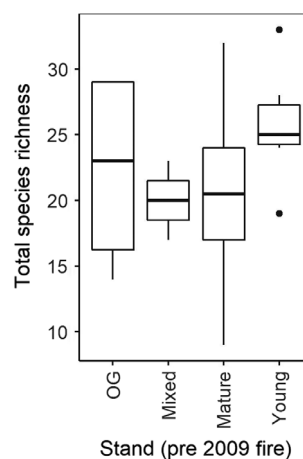


Fig. 2. Box and whisker plot of the total richness of vascular plant life forms with respect to stand age and disturbance history prior to high-severity fire in 2009. OG, old growth.

had the highest richness (31 species total), followed by persistent, sprout species (23 species total), persistent species (20 species total), persistent seed and sprout species (six species total), and ruderal species (six species total) (Appendix S1: Table S1).

Prior disturbance history and respective pre-fire stand age influenced the recovery of plant species with different reproductive strategies post-high-severity fire in 2009. We found that “young,” logged forests burnt in 2009 supported a significantly higher abundance of ruderal species (no single defined strategy) ($P = 0.00$) and a significantly lower abundance of persistent, onsite seeder species ($P = 0.04$), relative to “old-

growth” forests burnt in 2009 (Fig. 3). “Mixed” forests burnt in 2009 also supported a significantly higher abundance of ruderal species ($P = 0.04$), relative to “old-growth” forests burnt in 2009 (Appendix S1: Table S2). Furthermore, “young” forests had a significantly higher abundance of ruderal species than “mature” forests burnt in 2009 as indicated by pairwise contrasts of estimated marginal means. We found no evidence of any other significant pairwise contrasts between disturbance histories for other reproductive strategies (Appendix S1: Table S3).

Although not statistically significant, the mean abundance of persistent, sprout species declined with decreasing forest stand age at the time of

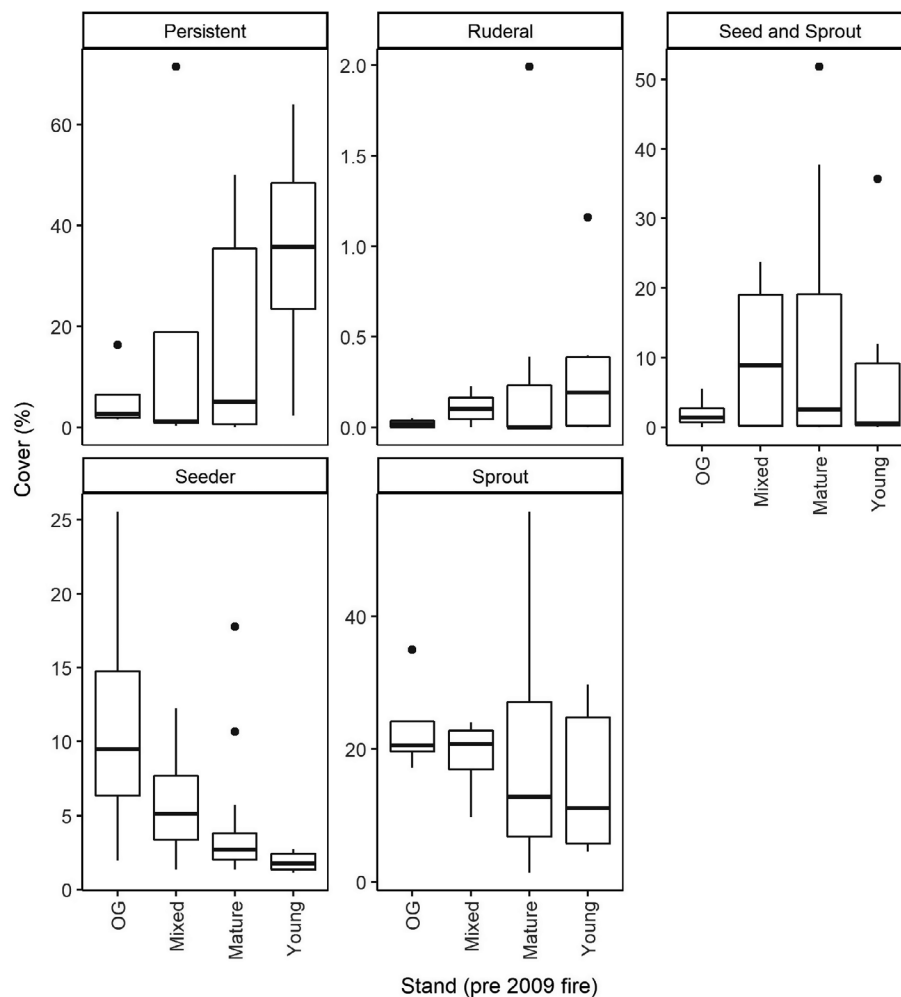


Fig. 3. Box and whisker plot of plant reproductive groups with respect to stand age and prior disturbance history at the time of high-severity wildfire in 2009 in early successional forests. OG, old growth.

the 2009 wildfires (Fig. 3; Appendix S1: Table S2). For instance, common persistent, sprout species including the ground ferns, *Blechnum wattsi* and *Polystichum proliferum*, and tree species, *Olearia argophylla* were most abundant in “old-growth” and “mature” forests, burnt in 2009 and least abundant in “young” forests, burnt in 2009. Other common, persistent, sprout species including *Bedfordia arborescens* and *Hedycarya angustifolia* were found only in forests that were “old growth” and “mature” when burnt in 2009. In contrast, “old-growth” forests burnt in 2009 had a much lower abundance of the persistent, sprouting fern *Pteridium esculentum*, relative to younger forests, and the tree species *Tasmannia lanceolata* was absent (Appendix S1: Table S1).

Environmental influence.—Environmental variables were significant drivers of the abundance of plant species with different reproductive strategies post-wildfire in 2009. Elevation was significantly associated with an increase in the abundance of ruderal species ($P = 0.00$) and a decrease in the abundance of persistent species ($P = 0.00$). Slope and TWI also were negatively associated with the abundance of persistent species ($P = 0.03$ – 0.04). The abundance of persistent, seed and sprout and persistent, sprout species were associated with non-northerly aspects (Appendix S1: Table S2; Fig. 4).

Life forms

We assigned each of the 89 vascular plant species into eight life form groups: (1) herb, (2) tree, (3) *Acacia*, (4) eucalypt, (5) shrub, (6) ground fern, (7) graminoid, and (8) tree fern. Herb life forms were the most species rich (29 species total), followed by shrub (18 species total), tree (11 species total), fern (nine species total), and graminoid life forms (seven species total) (Appendix S1: Table S1).

The legacy of prior disturbance and stand age significantly influenced the abundance of different plant life forms post-high-severity wildfire in 2009. “Young,” “mature,” and “mixed” forests that burnt in 2009 supported a significantly higher abundance of graminoid species ($P = 0.00$ – 0.03), and a significantly lower abundance of eucalypts ($P = 0.00$ – 0.03), relative to “old-growth” forests burnt in 2009. “Mature” and “young” forests that burnt in 2009 also had a significantly lower abundance of *Acacia*

($P = 0.01$ – 0.03), relative to “old-growth” forests burnt in 2009. Further, “mature” aged forests burnt in 2009 had a significantly lower abundance of shrub species ($P = 0.00$), relative to “old-growth” forests burnt in 2009 (Fig. 5; Appendix S1: Tables S2, S3).

Pairwise contrasts also indicated that “young” forests had a significantly higher abundance of graminoid species than “mature” forests burnt in 2009. We found no evidence of any other significant pairwise contrasts between disturbance histories for other reproductive strategies (Appendix S1: Table S3).

Environmental influence.—Environmental variables significantly influenced the abundance of life forms in early successional forests ($P < 0.05$). Sites with a non-northerly aspect had a significantly higher abundance of ground ferns ($P = 0.00$), but lower abundance of *Acacia* ($P = 0.02$) and climber ($P = 0.02$) life forms (Appendix S1: Table S2). Elevation was associated with significantly lower abundances of eucalypt species ($P = 0.02$) and higher abundances of shrub life forms ($P = 0.00$). Slope was associated with a significant increase in the abundance of shrub life forms ($P = 0.00$) and a decrease in graminoid species ($P = 0.00$). Topographical wetness index was associated with a significant increase in the abundance of ground ferns, and a decrease in *Acacia* ($P = 0.01$) and graminoid species ($P = 0.00$) (Appendix S1: Table S2; Fig. 6).

DISCUSSION

We provide empirical evidence that the legacy of prior disturbances and stand age at the time of high-severity wildfire can significantly influence the recovery of plant communities in early successional forests. Plant recovery was more advanced in forests that were older at the time of high-severity wildfire than forests that were younger. Specifically, the recovery of “old-growth” forests burnt in 2009 was characterized by a higher abundance of dominant midstorey *Acacia* trees and overstorey eucalypt trees and shrubs, than younger forests burnt by the same wildfire. In contrast, the recovery of younger forests burnt in 2009 had a higher abundance of ruderal species, including graminoids, than older forests burnt by the same wildfire. We also

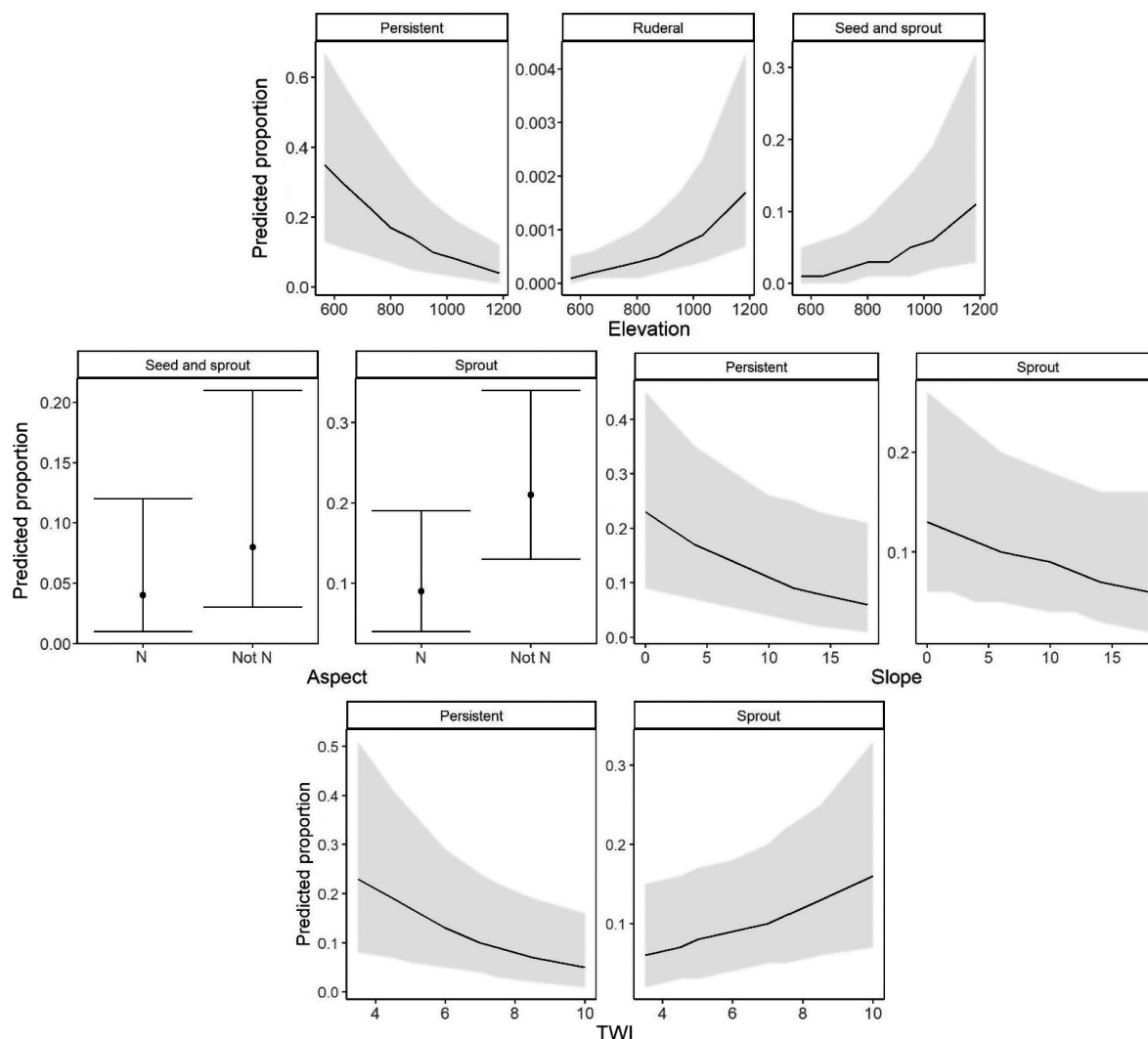


Fig. 4. Predicted proportion of plant species with different reproductive strategies with respect to aspect (northerly or non-northerly), slope, elevation, and topographical wetness index (TWI) (with 95% confidence intervals). Predictions are adjusted for a mature stand age, northerly aspect, and the mean slope and elevation. Predictions are only displayed for variables included in the corresponding final model.

demonstrate differences in the influence of environmental variables (slope, elevation, TWI, aspect) on plant life forms and reproductive strategies. Our study provides important and timely insights into how the legacy of prior disturbance and stand age influence the recovery of forests from high-severity wildfire. Our findings also assist in predicting how forest plant communities may recover from future wildfires with shorter-fire-return intervals, which are projected to increase worldwide (Bradstock et al. 2009,

Taylor et al. 2014, Jolly et al. 2015, Abatzoglou and Williams 2016, Schoennagel et al. 2017).

Legacy effects of “young,” logged forests on the recovery of early successional forests

Consistent with our predictions at the onset of this investigation, we found “young” forests, burnt in 2009 (with the shortest-fire-return interval) had the highest plant species richness. These included a number of ruderal species and graminoids that were more abundant in these forests,

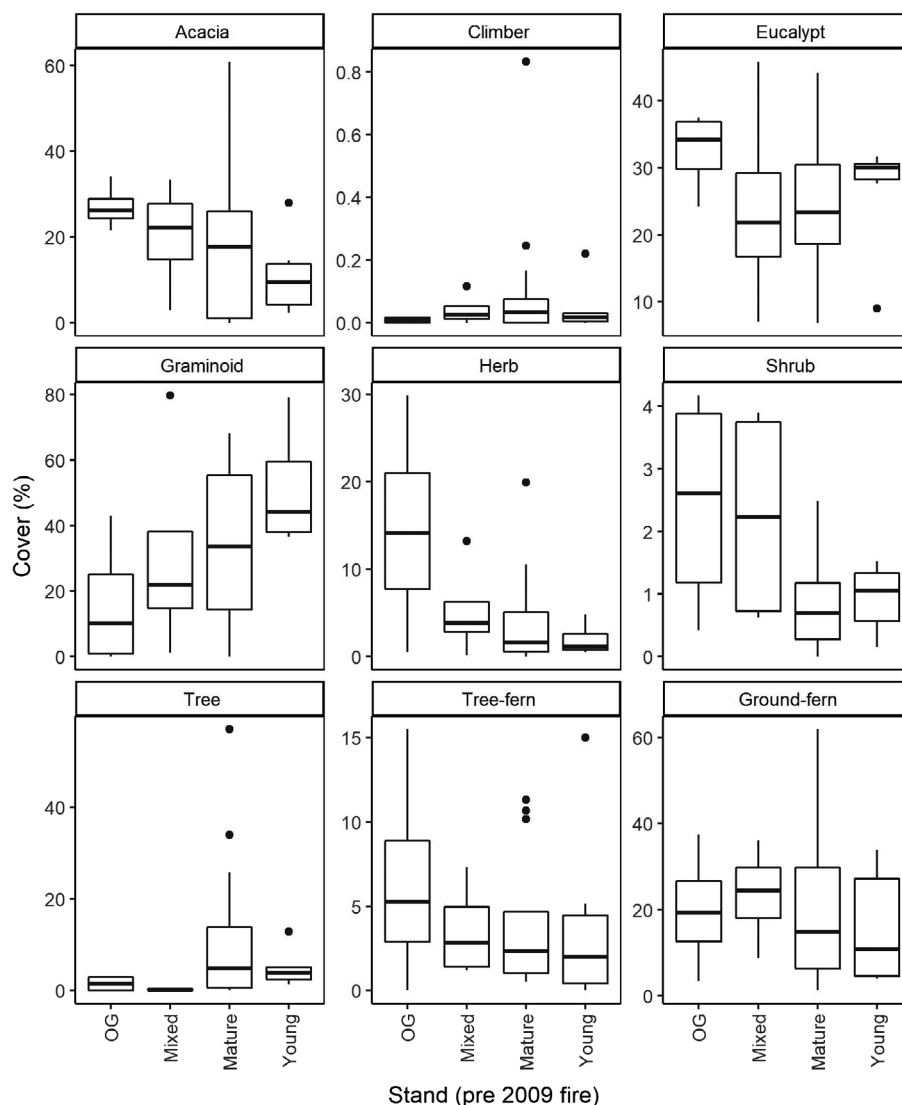


Fig. 5. Box and whisker plot of plant life forms with respect to stand age and prior disturbance history at the time of high-severity wildfire in 2009 in early successional forests. OG, old growth.

relative to older forests that had been burnt in 2009. This result is likely explained by an increase in the availability of resources, such as light and nutrients, which promote the rapid colonization of these species (Connell and Slatyer 1977). Ruderal species can have high dispersal and colonization rates, but typically decline with successional stage as reproductive propagules are depleted and competition increases (Noble and Slatyer 1980, Blair et al. 2016). Similar findings for an increase in species richness with

short-return-intervals have been documented in boreal forests (Donato et al. 2009).

We found the mean abundance of persistent, sprout species and persistent, onsite seed species was lowest in “young” forests, burnt in 2009, and highest in “old-growth” forests, burnt in 2009. Further, common resprouting species including *H. angustifolia* and *B. arborescens* were absent in “young” forests, burnt in 2009. This result may be explained by differences in the availability of reproductive propagules that can

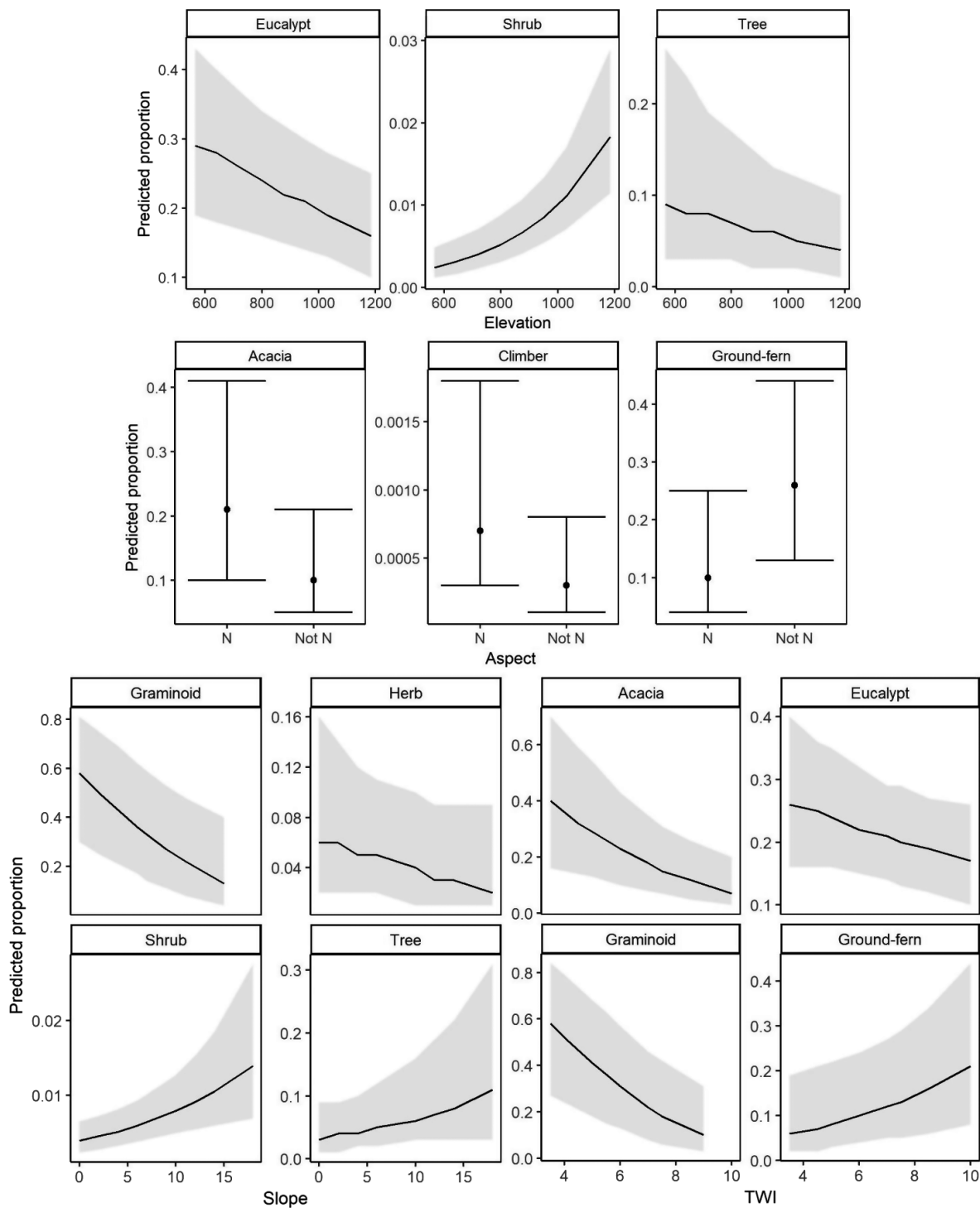


Fig. 6. Predicted proportion of different life forms with respect to aspect (northerly or non-northerly), elevation, topographical wetness index (TWI), and slope (with 95% confidence intervals). Predictions are adjusted for a mature stand age, northerly aspect, and the mean slope and elevation. Predictions are only displayed for variables included in the corresponding final model.

accumulate over time or may reflect short-fire-return intervals. For instance, short-fire-return intervals can result in plant “resprout failure” (Fairman et al. 2019) or depletion of seed stores prior to species maturation in obligate seeder species (Bowman et al. 2014, Turner et al. 2019). However, given all forests in our study had reached plant reproductive maturation (>28 yr) at the time of the 2009 fire, our findings also may be explained by unmeasured extrinsic factors including spatial patterns of reproductive propagules (Seidl et al. 2014a) and differences in disturbance origin.

Aside from time-since-disturbance and fire frequency, disturbance origin (human or natural) can influence the post-disturbance recovery of forest plant communities with different reproductive mechanisms (Ough and Murphy 2004, Blair et al. 2016, Bowd et al. 2018). For instance, while obligate seeder species may be sensitive to multiple repeated wildfire (Bowman et al. 2014, Bowd et al. 2018, Turner et al. 2019), resprouting species can be vulnerable to mechanical disturbance associated with clearcut logging, that can destroy resprouting organs (Ough and Murphy 2004, Blair et al. 2016, Bowd et al. 2018). In our study, “young” forests burnt in 2009 had experienced prior clearcut logging in 1970s–1980s. Previous studies have demonstrated an increase in the abundance of obligate seeder species such as *Acacia* post-clearcut logging (Bowd et al. 2018, Trouvé et al. 2019). However, in contrast, we recorded the lowest abundance of *Acacia* species in “young, logged” forests burnt in 2009, relative to older forests, burnt in 2009. This may be explained by a decline in the *Acacia* seed bank with successive disturbances, which can rapidly germinate after large disturbances (Passos et al. 2017, Strydom et al. 2017).

Given that “young” forests in our study were previously logged, we are unable to differentiate the influence of disturbance origin and stand age. This is a limitation of our study as there can be marked differences in plant species composition between early successional forests regenerating from clearcut logging and those regenerating following wildfire (Blair et al. 2016, Bowd et al. 2018). For instance, clearcut logging can compact soils that may displace seed banks (Lindenmayer and Noss 2006, Cambi et al. 2015), remove biological legacies (Lindenmayer and McCarthy

2002), reduce the availability of soil nutrients (Kishchuk et al. 2015, Bowd et al. 2019), and kill resprouting structures (Ough and Murphy 2004, Blair et al. 2017, Bowd et al. 2018). Future research is required to quantify the recovery of plant communities with short-fire-return intervals, with histories of wildfire only.

Another limitation of our study is that we have identified patterns of forest recovery using post-fire data. While we have found marked differences in the abundance of regenerating forests with different prior disturbance histories, we acknowledge the need for pre-fire data to further quantify these differences. This is because post-fire plant community composition may reflect pre-fire composition and stores of available propagules.

Legacy effects of “old-growth” forests on the recovery of early successional forests

We correctly predicted an increase in the abundance of some persistent, onsite seed species, including *Acacia*, eucalypt, and shrub species in “old-growth” forests, burnt in 2009, relative to younger forests burnt in 2009. Some persistent obligate seeder species including dominant, mid-storey *Acacia* tree species, have long-lived seed banks which increase with standing stem diameter, and remain viable for multiple decades (Passos et al. 2017, Strydom et al. 2017, Burrows et al. 2018). Further, other obligate seeder species including dominant overstorey eucalypts can accumulate large canopy-seed stores in older successional forests (Leck et al. 1989, Wang 1997), which (when triggered by wildfire) can produce high densities of seedling germination that increase with increasing fire-return intervals (Smith et al. 2014).

We also found that “old-growth” forests that were burnt in 2009 had the highest abundances of common, resprouting species, including *O. argophylla*, which were least abundant in “young” forests, burnt in 2009. These findings are likely explained by the increased resistance of older successional “old-growth” forests to high-severity wildfires within natural fire-return intervals (Gill 1997, Clarke et al. 2013). These forests can support high abundances of resprouting plant propagules and soil-stored seed that can persist for multiple decades, and increase with stand age (Wenk and Falster 2015, Strydom et al. 2017, Burrows et al. 2018). Post-wildfire, these forests also produce significant biological legacies

(Franklin et al. 2002), which increase structural heterogeneity, substrate availability, and provide critical habitat for animal species post-wildfire (Lindenmayer 2009).

Legacy effects of “mixed” and “mature” aged forests on the recovery of early successional forests

Our analyses contained evidence that “mixed” and “mature” aged forests that were burnt in 2009 had lower abundances of eucalypts, relative to “old-growth” forests. “Mature” aged forests, burnt in 2009 also had a lower abundance of shrub and *Acacia* species, relative to “old-growth” forests burnt in 2009. These lower abundances may be explained by declines in reproductive propagules with successive disturbances that trigger the germination of a new cohort of species. However, these significant declines also may be explained by other extrinsic factors that can influence the availability of reproductive propagules. For instance, soil seed banks can be depleted by declines in seed viability, seed loss through abiotic means (crush, abrasion, water logging etc.), biotic seed predation by ants (Ash-ton 1979), and competition for resources with other plant species (George and Bazzaz 1999, Coomes et al. 2005). However, seed longevity can vary between forest ecosystems (Chambers and MacMahon 1994). For instance, in tropical rainforests, seed is in constant production, but generally short-lived (Vázquez-Yanes and Orozco-Segovia 1993), whereas in temperate deciduous forests, seed banks typically receive large early deposits, which decline over time (Pickett 1989).

Environmental influence on regenerating forests

Environmental factors including aspect, topography, elevation, and slope influence abiotic conditions which, in turn, influence the structure and diversity of plant communities (Gallardo-Cruz et al. 2009, Petter et al. 2015, Dearborn and Danby 2017, Muscarella et al. 2020). Our study provides evidence of differences in the influence of environmental factors on plant life forms and reproductive strategies. Specifically, we found sites on non-northerly aspects and with high values for the TWI had an increased abundance of species that resprout after fire including ground ferns. This is likely explained by the well-known

relationship between topography and soil moisture (Huggett and Cheeseman 2002, Petter et al. 2015), which can influence plant communities (Dearborn and Danby 2017, Muscarella et al. 2020). Further, resprouting ferns are typically shade-tolerant and occupy mesic environments with high soil moisture due to their poor control of water conduction and loss (Woodhouse and Nobel 1982, Hunt et al. 2002, Page 2002). Therefore, these species can be sensitive to water stress (Hunt et al. 2002, Volkova et al. 2010, Riaño and Briones 2013) and the harsh solar radiation associated with north-facing slopes (Petter et al. 2015). In contrast, we found a higher abundance of *Acacia* and climber species on northerly aspects, and a higher abundance of *Acacia* and graminoid species with lower topographical indices. This is likely explained by the ecophysiology of these species that may be less sensitive to drier conditions, with increased solar radiation (Petter et al. 2015). For instance, previous research has shown that *Acacia* species can grow rapidly and are more abundant when light availability is high (Hunt et al. 2006, Aguilera et al. 2015).

Management implications

In a period of rapid, global environmental change, identifying the key drivers of forest recovery post-disturbance is becoming increasingly important for predicting the impacts of future disturbances on ecosystems (Bačec et al. 2015, Sass et al. 2018). Our results demonstrate the importance of incorporating past disturbance legacies in making these predictions. Specifically, our findings indicate that when occurring at natural historical fire-return periods of between 75 and 150 yr, forest recovery post-high-severity wildfire can be more advanced and support a high abundance of plant species across all functional groups, relative to younger or mixed aged forests, with shorter-fire-return intervals. Therefore, predicted increases in high-severity wildfires may have consequences for the recovery of plant functional groups in forests with different prior disturbance legacies (Stevens-Rumann and Morgan 2016, Carlson et al. 2017, Tepley et al. 2018). For instance, forests that are subject to multiple disturbances within shorter return intervals may be vulnerable to declines in the abundance of obligate seeder eucalypts and *Acacia*

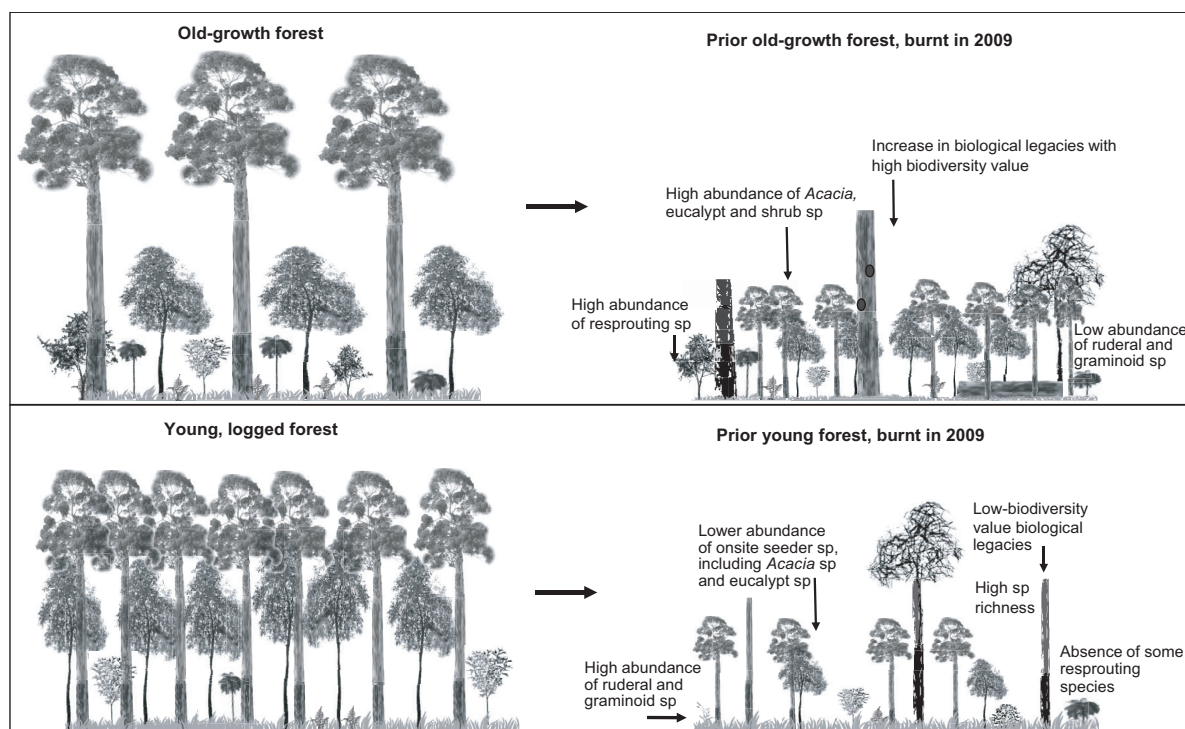


Fig. 7. Conceptual diagram detailing the differences in early successional forests regenerating from high-severity wildfire in 2009 from forests that were previously young, and logged and old-growth forests.

species, relative to those with longer disturbance intervals.

The resilience of old-growth forests to high-severity wildfire can reflect age-related attributes including increases in bark thickness (Clarke et al. 2013), canopy height (Gill 1997), and the maturation and availability of some reproductive propagules (Wenk and Falster 2015), as well as varying species composition (Egler 1954, Franklin et al. 2002, Pulsford et al. 2014). These forests also contain large numbers of biological legacies that remain after disturbance and can influence the regeneration of forests, including plant propagules, standing trees, logs, and nutrients (Barker and Kirkpatrick 1994, Franklin et al. 2002, Pharo et al. 2013, Johnstone et al. 2016). These legacies also provide key structural elements that serve as critical habitat in early successional forests (Franklin et al. 2000, Swanson et al. 2011, Donato et al. 2012, Lindenmayer et al. 2019). In contrast, marked differences exist between the structure of early successional forests regenerating from prior old-growth forests

and those that were previously younger, logged forests at the time of high-severity wildfire (Franklin et al. 2000, Donato et al. 2012, Lindenmayer et al. 2019). For instance, in contrast to later-successional stands, young, logged forests burnt by high-severity wildfire can produce early successional forests with little structural heterogeneity and fewer biological structural legacies, which are typically of low-biodiversity value (Franklin et al. 2000, Donato et al. 2012, Lindenmayer et al. 2019; Fig. 7). This highlights the importance of limiting anthropogenic perturbations that may erode the resilience of forests to additional high-severity wildfire at younger successional stages, and conserving resilient later-successional forests to maintain structural heterogeneity and intact plant communities in the event of future high-severity wildfires.

CONCLUSION

Globally, forests face a myriad of compound-ing threats (Cohen et al. 2016, Barnes et al. 2017)

that have resulted in the rapid decline of intact patches of undisturbed forest (Watson et al. 2018). Predicted increases in high-severity wildfires as a result of climatic changes will likely exacerbate this decline and influence the recovery of plant functional groups (Bradstock et al. 2009, Jolly et al. 2015, Abatzoglou and Williams 2016, Schoennagel et al. 2017). Our findings provide new insights into the temporal influence of prior disturbance histories on early successional forests regenerating from high-severity wildfire and provide for forest management and planning.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3480/full>