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# Environmental factors associated with the abundance of forest wiregrass (*Tetrarrhena juncea*), a flammable understorey grass in productive forests

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**Abstract.** When flammable plant species become dominant they can influence the flammability of the entire vegetation community. Therefore, it is important to understand the environmental factors affecting the abundance of such species. These factors can include disturbances such as fire, which can promote the dominance of flammable grasses causing a positive feedback of flammability (grass–fire cycle). We examined the potential factors influencing the abundance of a flammable grass found in the understoreys of forests in south-east Australia, the forest wiregrass (*Tetrarrhena juncea* R.Br.). When wiregrass is abundant, its structural characteristics can increase the risk of wildfire ignition and causes fire to burn more intensely. We measured the cover of wiregrass in 126 sites in mountain ash forests in Victoria, Australia. Generalised additive models were developed to predict cover using climatic and site factors. The best models were selected using an information theoretic approach. The statistically significant factors associated with wiregrass cover were annual precipitation, canopy cover, disturbance type, net solar radiation, precipitation seasonality and time since disturbance. Canopy cover and net solar radiation were the top contributors in explaining wiregrass cover variability. Wiregrass cover was predicted to be high in recently disturbed areas where canopy cover was sparse, light levels high and precipitation low. Our findings suggest that in areas with wiregrass, disturbances such as fire that reduce canopy cover can promote wiregrass dominance, which may, in turn, increase forest flammability.

**Additional keywords:** canopy cover, disturbance, fire regime, grass–fire cycle, mountain ash.

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## Introduction

The influence of species on the emergent properties of an ecosystem is often proportional to their abundance (Parker *et al*. 1999). In fire-prone landscapes, such as in Australia, species within vegetation communities are fuels for wildfires (Murphy *et al*. 2013; Duff *et al*. 2017), and the traits of each species combine to influence flammability at landscape scales (Schwilk 2003; Schwilk and Caprio 2011; Zylstra *et al*. 2016; Tumino *et al*. 2019). When a flammable species becomes abundant it can increase the flammability of an entire vegetation community (Gill and Zylstra 2005; Schwilk and Caprio 2011; Zylstra 2011) by contributing a disproportionate amount to the total fuel load or by altering structural characteristics of the vegetation community, for example, increasing fuel continuity (Brooks *et al*. 2004; Berry *et al*. 2011). However, an increase in the abundance of a flammable species may not correlate with an increase in the flammability of a vegetation community if the fuel becomes more densely packed with a higher packing ratio or bulk density (van Wilgen and Richardson 1985; Scarff and Westoby 2006; Schwilk 2015; Fraser *et al*. 2016).

An example of an individual species that has become dominant and altered the flammability of a vegetation community is *Lantana camara* L. in the dry rainforest of north-eastern Australia. This species increases the continuity of fuel in the understorey, consequently increasing the potential intensity and extent of fires that occur (Berry *et al*. 2011). Similarly, the dominance of the invasive African gamba grass (*Andropogon gayanus* Kunth) in northern Australia savanna causes higher intensity fires by increasing the fuel load 7-fold in comparison to natural fuels (Rossiter *et al*. 2003; Setterfield *et al.* 2010). In some instances, a positive feedback can be created where fire promotes the abundance of a flammable grass species, which, in turn, facilitates further fires (D'Antonio and Vitousek 1992; Rossiter *et al.* 2003). This process, known as a grass–fire cycle, has been observed in different ecosystems around the world (D'Antonio and Vitousek 1992). A contrasting example is the succulent *Carpobrotus edulis* (L.) N.E. Br. in California (Zedler and Scheid 1988; D'Antonio *et al.* 1993), which has a high water content and low flammability, hence, reduces the flammability of the vegetation community when abundant (Brooks *et al.* 2004).

To better understand the drivers of flammability, it is important to understand the factors influencing the abundance of species that can have an effect on the flammability of plant communities. Many environmental factors are potentially important determinants of plant abundance, including precipitation, temperature, solar radiation, canopy cover and disturbance (Fig. 1). For example, studies have shown that in drier areas, drought-intolerant species are rare whereas drought-tolerant ones are generally abundant (Gaff and Latz 1978; Badano *et al.* 2005). Similarly, in warmer areas, cold-adapted plants are rare whereas thermophilic species are generally abundant (Vesperinas *et al.* 2001; Kullman 2008). Shade-tolerant species are also reported to dominate under deep shade where shade-intolerant ones are generally absent (Chávez and Macdonald 2010).

In multi-strata forest systems, canopy cover plays a role in regulating plant abundance by modifying the factors that directly drive plant abundance (Fig. 1). For example, light and water (from precipitation) are intercepted by the canopy (Valladares *et al.* 2016), resulting in a decrease in the availability of these resources. Canopy shading also decreases diurnal temperature and increases nocturnal temperature (Jacobs *et al.* 1994; Niinemets and Valladares 2004), resulting in narrower daily temperature fluctuations than those in the open. Studies also have shown that air humidity is increased, and evaporation is decreased under the canopy (Chen *et al.* 1995; Holmgren *et al.* 1997). Canopy cover can change in response to other factors including forest disturbance (e.g. fire, logging), drought or disease. Disturbances by themselves can also directly affect plant composition and abundance through their effects on mortality of plant populations or as a cue for regeneration and germination (e.g. fire-induced seed germination) (Gill 1981). The role of past disturbance influencing species abundance directly and indirectly is also emphasised by the grass–fire cycle concept (D'Antonio and Vitousek 1992).

One understorey species in south-eastern Australia that reportedly increases in abundance after a fire disturbance is the forest wiregrass (*Tetrarrhena juncea* R.Br., hereafter referred to as wiregrass) (Stuwe and Mueck 1990; Penman *et al.* 2009). Wiregrass has been reported to have a strong influence on the overall flammability of the coastal and foothill forests in south-eastern Australia (Buckley 1993; Fogarty 1993) by increasing the continuity of the fuel bed when it is abundant. It can sustain fire within a vegetation community even at high levels of humidity and at much higher surface litter moisture contents than fire would otherwise be sustained (Buckley 1993). Presumably this is because wiregrass has an aerated and elevated structure with a high fraction of suspended dead material (Fogarty 1993), which has a lower moisture content than the fuel on the forest floor as suspended materials have a high degree of exposure to atmospheric drying. Wiregrass is a scrambling grass that can climb over rigid supports even up to 6 m high, and as such, it is likely to become a ladder fuel, increasing the

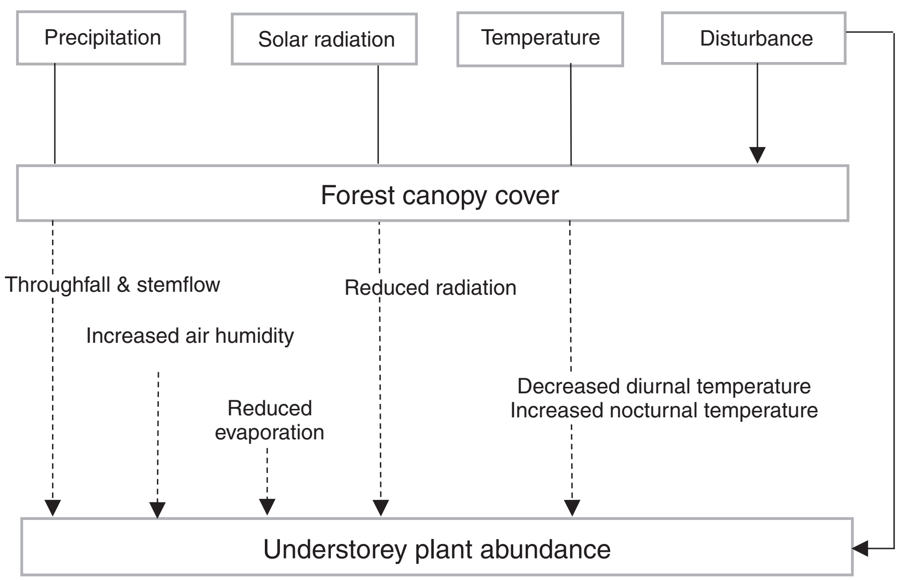


**Fig. 1.** Canopy cover alters the micro-climate in the forest understorey affecting plant abundance. (In this study, canopy cover is the canopy provided by the vegetation from ~1.6 m and above.) Broken lines represent the conditions as affected by canopy cover. Disturbance (e.g. fire, logging) may directly affect both canopy cover and understorey plant abundance.

vertical and horizontal continuity of the fuel bed. Wiregrass is observed to abound under canopy gaps, with higher light levels thought to be the responsible factor stimulating thick growth in gaps (Lamp *et al*. 2001). However, Ashwell (1985), in his study on wiregrass ecology in mountain ash-dominated (*Eucalyptus regnans* F.Muell.) forest, could not confidently conclude which abiotic variable – light or soil moisture – played a greater role in defining wiregrass abundance. Wiregrass is a common species but occurs at vastly different levels of abundance in mountain ash-dominated forest, hence, this forest type provides an ideal environment to study wiregrass abundance.

In the present study, the aim was to identify the key environmental factors influencing wiregrass abundance. We conducted field surveys of wiregrass abundance in mountain ash-dominated forest. We use our results to discuss the conditions under which wiregrass becomes abundant and the potential of wiregrass to initiate a positive flammability feedback loop akin to the grass–fire cycle.

## Methods

### Study species

Wiregrass is a rhizomatous perennial grass that flowers during the warmer part of the year – between November and April (Walsh and Entwisle 1994). It assumes different structural forms when abundant, such as thick swards and stook-like structures climbing up to 6 m high over rigid supports like tree trunks, tree ferns, tree stumps and shrubs. It is often found in low abundances but can exhibit prolific growth and become the dominant understorey species in certain areas. Wiregrass is found in the states of Victoria, Tasmania, New South Wales, Queensland and South Australia. It occurs in a wide range of environmental conditions, from dry to moist habitats, and occurs from sea level to the subalpine regions (Willis 1970; Ashwell 1985; Ough and Ross 1992).

### Study area and site selection

The study was conducted in mountain ash (*Eucalyptus regnans* F.Muell.) forests in the Central Highlands region of Victoria, Australia. Mountain ash forests occur in areas with deep, fertile soils and high rainfall (>1000 mm year$^{-1}$) (Ashton and Attiwill 1994). The overstorey is dominated by mountain ash trees but other eucalypt species including *E. cypellocarpa* L.A.S. Johnson and *E. obliqua* L'Hér. are sometimes present (Ashton and Attiwill 1994). Common species in the understorey aside from wiregrass include *Pomaderris aspera* Sieber ex DC, *Olearia argophylla* F.Muell. ex Benth, *Dicksonia antarctica* Labill., *Cyathea australis* (R.Br.) Domin, *Correa lawrenciana* Hook., *Clematis aristate* R.Br. ex Ker Gawl., *Coprosma quadrifida* (Labill.) B.L.Rob*.*, *Polystichum proliferum* (R.Br.) C.Presl and *Pteridium esculentum* (G.Forst.) Cockayne (Ashton and Attiwill 1994; Department of Sustainability and Environment 2004).

Fires are an important part of the lifecycle of mountain ash forests (Ashton 1981; Ashton and Attiwill 1994), and the subsequent regeneration pathway after high and low severity fires can be different (Ashton and Martin 1996). Where fire severity is high, both the overstorey and understorey are affected, and dense regeneration of eucalypts from seed occurs, resulting in an even-aged stand (Ashton 1976). Where fire severity is low, the understorey and a few trees in the overstorey are affected (Ashton and Martin 1996; Benyon and Lane 2013), and a multi-age forest could result (McCarthy and Lindenmayer 1998; Lindenmayer *et al*. 2000). Major wildfires have affected the study region, including those that occurred in 1939, 1983 and 2009 (Collins 2009). Selective harvesting (Griffiths 2001) and clear-fell logging (Florence 1996) have also been practised.

The study area was stratified based on time (in years) since last disturbance, type of disturbance (fire and logging) and aridity. Time since last disturbance was determined from mapped fire history (Department of Environment, Land, Water and Planning 2009, 2016*a*, 2016*b*) and logging history (Department of Environment, Land, Water and Planning 2016*c*). The type of fire disturbance included a combination of low and high fire severities. Aridity index (Nyman *et al*. 2014) was used as proxy for topographic position and we aimed to locate sites across a range of aridity values (Cawson *et al*. 2018). Additionally, all sites were within 50–150 m of a road for accessibility, with less than 30° slope for safety, and at least 500 m apart when they had the same disturbance history. A total of 200 candidate plot locations within each stratification unit were selected through a spatial randomisation process.

We surveyed 126 sites out of the 200 candidate sites between April and June 2016. Table 1 outlines the different disturbance classes of the surveyed sites and the sample sizes for each disturbance class. The majority of our study sites were in the adolescent growth stage (9–35 years since fire or logging) (Cheal 2010). The sites were a subset of those surveyed by Cawson *et al*. (2018).

### Field data collection

Wiregrass cover and canopy cover were assessed at each site along two 50-m transects orientated parallel and perpendicular to the slope. We used a line-point intercept method to measure cover along each transect (Elzinga *et al*. 1998) as the method provides higher precision than visual estimates (Godínez-Alvarez *et al*. 2009). Hits were recorded at 2-m intervals using a metal pin (1 m tall and 1.6 mm in diameter) oriented vertically; a hit was when the pin touches wiregrass at least once along its length. Wiregrass cover

**Table 1. Disturbance classes, time since disturbance and growth stages (according to Cheal 2010) of the study sites, and their sample sizes**

| Disturbance classes | Time since disturbance (years) | Growth stage | Sample size (total $n$ = 126) |
|---|---|---|---|
| 2009 fire | 7 | Juvenility | 33 |
| 1983 fire | 33 | Adolescence | 20 |
| 1939 fire | 77 | Maturity | 33 |
| 2000–2010 clearfell logging | 6–16 | Adolescence | 20 |
| 1990–1999 clearfell logging | 17–26 | Adolescence | 11 |
| 1980–1989 clearfell logging | 27–36 | Adolescence | 6 |
| Long unburnt | 100+ | Maturity | 3 |

was computed as the total number of hits from the two transects divided by the total number of intervals from the two transects. Canopy cover was recorded at the same 2-m intervals along the transect using a vertical sighting tube (GRS Densitometer, Geographic Resource Solutions, Arcata, CA, USA; Wilson 2011) and using a binary system of 'canopy' or 'sky' for each point. Measurements were taken from a height of ~1.6 m, thus canopy cover as used in this study encompassed any vegetation above that height. Canopy cover was computed as the total number of 'canopy' hits from the two transects divided by the total number of intervals from the two transects.

Aspect and elevation were recorded at each site. Aspect was converted to degrees from north to account for the effect of topography on microclimatic conditions. North-facing slopes in the southern hemisphere have greater light intensity, higher temperatures and lower moisture availability than south-facing slopes (Swanson *et al*. 1988).

### Environmental spatial data

We obtained precipitation and temperature variables from WorldClim 1 global coverage climate map (resolution = 0.5 min of 1°, ~1 km), which uses long-term average climate data from 1960 to 1990 (Hijmans *et al*. 2005). The spatial resolution of this dataset may be considered coarse for a site-level study; however, the distances between our sites are generally more than 1 km, thus it should be suitable for representing broad macroclimatic patterns. Smaller scale effects were accounted for by the elevation and aspect variables as potential indirect measures of changes in temperature and moisture at finer scales.

We used the net total solar radiation derived from Nyman *et al*. (2014), which accounted for the effect of topography on radiation reaching the ground. Table 2 lists all the candidate predictor variables in this study.

### Data processing and analyses

A variable reduction process was undertaken to reduce the confounding effect of collinear predictor variables. Pearson correlation coefficients between predictor variables were calculated (Appendix 1). When two variables had a correlation greater than 0.7 (Green 1979; Dormann *et al*. 2013), we retained proximal variable over distal, or direct variable over indirect, or resource variable over non-resource. Austin (2002) defines proximal and distal as 'the position of the predictor in the chain of processes that link the predictor to its impact on the plant' – proximal being the more likely to be causal in determining plant responses. Direct variables are those with direct physiological effect on plants such as temperature, as opposed to indirect variables such as elevation (Austin 2002). Variables in bold in Table 2 were the final set of predictor variables after removing correlated variables.

**Table 2. Potential predictors for the generalised additive modelling (GAM) process**
Variables included in building the model after exclusion of highly correlated variables are in bold

| Variables | Units | Source |
|---|---|---|
| Annual mean diurnal range | °C | WorldClim |
| Annual mean temperature | °C | WorldClim |
| **Annual precipitation** | mm $year^{-1}$ | WorldClim |
| Annual temperature range | °C | WorldClim |
| Aspect | Degrees | Field measured |
| **Canopy cover** | % | Field measured |
| **Disturbance type** | None | Department of Environment, Land, Water and Planning (2009, 2016*a*, 2016*b*) |
| Elevation | m | Field measured |
| Isothermality | % | WorldClim |
| Maximum temperature of warmest month | °C | WorldClim |
| Mean temperature of coldest quarter | °C | WorldClim |
| Mean temperature of driest quarter | °C | WorldClim |
| Mean temperature of warmest quarter | °C | WorldClim |
| Mean temperature of wettest quarter | °C | WorldClim |
| Minimum temperature of coldest month | °C | WorldClim |
| **Net solar radiation** | MJ $m^{-2}$ $day^{-1}$ | Nyman *et al*. (2014) |
| Precipitation of coldest quarter | mm | WorldClim |
| Precipitation of driest month | mm | WorldClim |
| Precipitation of driest quarter | mm | WorldClim |
| Precipitation of wettest month | mm | WorldClim |
| Precipitation of warmest quarter | mm | WorldClim |
| Precipitation of wettest quarter | mm | WorldClim |
| **Precipitation seasonality** | % | WorldClim |
| Temperature seasonality | °C | WorldClim |
| **Time since disturbance** | Years (log-transformed) | Cawson *et al*. (2018) |

We fitted a quasi-binomial generalised additive models (GAM) of wiregrass cover against the final set of predictor variables to determine which variables explained the observed variability of wiregrass cover. GAMs were used as they fit data-defined splines and make no assumptions about the form of the relationships before fitting. GAMs were fitted using an information theoretic approach whereby the degrees of freedom available for each model term were set using a shrinkage approach. This reduces complexity of fitted relationships where there is limited statistical support. Where statistical support for inclusion was not significant, terms were excluded from the final model (in effect, a variable selection process). A maximum of four knots were allowed for each variable in fitting the GAMs. Models were fitted in R using the *mgcv* package (ver. 1.8-24, https://CRAN.R-project.org/package=mgcv; Wood 2011). The Shapiro–Wilk's test was performed on the residuals of the model to check for normality of the distribution of residuals. We checked model performance by comparing fitted values against the observed values. We determined the relative importance of predictors by calculating the change in $R^2$ when each variable is added to the model that contains all the other variables.

All analyses were performed using R (ver. 3.5.0, R Foundation for Statistical Computing, Vienna, Austria, see at https://www.R-project.org/).

## Results

Wiregrass was present in most of the study sites (115 sites out of 126), ranging in cover from 2 to 100% (mean = 43.9; s.d. = 30). Almost half (47%) of the study sites had a wiregrass cover of at least 50%, where wiregrass either formed a sward on the forest floor (Fig. 2) or climbed over rigid supports (e.g. shrubs, tree trunks, tree ferns) up to 6 m (Fig. 2). Canopy cover (i.e. the canopy provided by the vegetation from ~1.6 m and above) in the study area ranged from 46 to 96% (mean = 76.9; s.d. = 12.2), where two-thirds of the study sites had a canopy cover of more than 75%. Some sites with a canopy cover in the higher range (≥90%) still supported relatively high wiregrass cover (at most 76% cover).

The model fitting process was able to create a GAM model that explained 37.7% of the variability in wiregrass cover. The parameters of the model are presented in Table 3. The model identified six significant variables that explained the variability in cover: annual precipitation, canopy cover, disturbance type, net solar radiation, precipitation seasonality and time since disturbance. Canopy cover and net solar radiation were the top contributors of the model, with independent contributions of more than 20% of the $R^2$ (22 and 29% respectively), whereas all the other variables contributed less than 10% each. Wiregrass cover is predicted to be high in sites with relatively low canopy cover (Fig. 3*b*), high net solar

**Fig. 2.** Wiregrass in the understorey of wet forests. Top photos: thick wiregrass swards covering the forest floor. Bottom photos: 'stooking' wiregrass, climbing through rigid support like tree trunks.

**Table 3. Model parameters where numbers for each predictor variable are the estimates and *t*-value (for parametric terms) or estimated degrees of freedom (e.d.f.) and *F* (for smooth terms)**

Significant predictor variables based on the fitted generalised additive model (GAM) are indicated: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$

| Variable | Parametric estimates or e.d.f. | *t*-value or *F* |
|---|---|---|
| Annual precipitation | 0.783 | 1.106* |
| Canopy cover | 1.232 | 5.630*** |
| Disturbance type | | |
| Fire (reference) | –0.1132 | –0.915 |
| Logging | –0.5537 | –2.176* |
| Net solar radiation | 1.136 | 6.211*** |
| Precipitation seasonality | 1.25 | 1.221* |
| Time since disturbance | 1.435 | 3.513** |
| Adjusted $R^2$ | 0.392 | |
| Deviance explained (%) | 37.7 | |

radiation (Fig. 3*d*), lower annual precipitation with less variation (Fig. 3*a, c*), and are recently burnt (Fig. 3*c, f*). The model tended to overpredict low wiregrass cover and underpredict high cover (Fig. 4).

## Discussion

### *Environmental factors associated with wiregrass abundance*

Low canopy cover and high net solar radiation are associated with high wiregrass abundance, suggesting that wiregrass can be considered as a gap or pioneer species. Canopy cover has a direct influence on resources (i.e. solar radiation and precipitation) reaching the understorey (Valladares *et al*. 2016), and it is likely that for this reason it was one of the two most important factors influencing wiregrass cover. Although this may be the case, net solar radiation reaching wiregrass in the understorey can differ between sites having the same canopy cover but different aspect (equator-facing *v*. pole-facing slope) (Swanson *et al*. 1988), hence the independent effect of net solar radiation from canopy cover on wiregrass cover. The variability of wiregrass cover in the understorey is likely to be a net response to a combination of factors shaped by the canopy cover. Stands with sparse canopies let more light and precipitation into the understorey than stands with dense canopies (Anderson *et al*. 1969; Chen *et al*. 1999), but the moisture will be reduced because of increased evaporation (Nyman *et al*. 2018). These conditions under sparser canopies correspond to higher wiregrass cover. This pattern is consistent with the results of Ashwell (1985), who found wiregrass was highly abundant in illuminated, drier areas. Further research is needed to decouple the effects of light and water (both influenced by canopy cover) on wiregrass growth and biomass to help us understand the individual role and interactive effects of these resources on wiregrass dominance.

Disturbance in general was associated with high wiregrass cover, suggesting that wiregrass can take advantage of disturbances to become dominant. Wapstra *et al*. (2003) observed that wiregrass occurrence in Tasmania was more pronounced in greatly disturbed sites (disturbances include fire, logging and anthropogenic ones). Disturbance has been associated with native species becoming unusually dominant in their own range (Pivello *et al*. 2018), and also with exotic invasive species that dominate new areas (Sher and Hyatt 1999).

The influence of time since disturbance on wiregrass cover in the understorey is likely mediated by direct effects on competition and indirect effect by changes in canopy cover. During early post-disturbance, competition among species for space and resources is lesser as many species are eliminated (Sousa 1984), which means that species with the ability to reproduce asexually like wiregrass can quickly increase in abundance (Ashton and Martin 1996). Furthermore, resources (e.g. light) can increase where disturbances reduce the canopy cover. Consequently, wiregrass cover can become relatively higher in the recently disturbed sites. Wiregrass cover did not continue to decline significantly as time since disturbance increased, most likely because of declining number of stems per hectare in mountain ash forest as it ages (Ashton 1976). This decline in the number of stems per hectare allows gradual increase in light to the understorey. Wiregrass cover is likely to increase again in very old stands (~200 years) where light may have significantly increased (Ashton 1976).

Fire and logging disturbances differed in their effects on wiregrass cover, most probably because of the differential degree of disturbance fire and logging had on the sites. Logging disturbs both vegetation and soil (Murphy and Ough 1997; Lindenmayer and Ough 2006), whereas fire mainly disturbs the vegetation. Soil disturbance during a logging operation may expose soil-stored seeds and rhizomes, which are then destroyed during the burning employed as part of the clear-fell logging procedure (Lindenmayer and Ough 2006). Consequently, wiregrass regeneration after clear-fell logging is potentially lower than after fire. Fire does not necessarily disturb the soil, and the smoke stimulates wiregrass seeds to germinate (Penman *et al*. 2008). This could explain relatively higher wiregrass cover in burnt than logged sites.

Our results suggest that climatic factors affect wiregrass abundance. Wiregrass cover was significantly correlated with both annual precipitation and precipitation seasonality, even though the data resolution was coarse. However, the precipitation variables were highly correlated with temperature variables, so it is unclear whether precipitation or temperature is more important to wiregrass cover. Whichever is the case, it is clear that climate variables can be important determinants of wiregrass abundance.

An important biotic factor that may contribute to the remaining unexplained variance (>50%) in wiregrass cover is herbivory, which we did not include in our study. Herbivores like the wombat (*Vombatus ursinus* Shaw, 1800) (Ashwell 1985; Ashton and Chappill 1989), sambar deer (*Cervus unicolor* Kerr, 1972) (Forsyth and Davis 2011), eastern grey kangaroo (*Macropus giganteus* Shaw, 1790) and black wallaby (*Wallabia bicolor* Desmarest, 1804) (de Munk 1999) reportedly graze on wiregrass. It has been suggested that wombat abundance could have a considerable effect on wiregrass cover (Ashwell 1985; Ashton and Chappill 1989). Further research could consider the influence of herbivory on wiregrass abundance and structure.

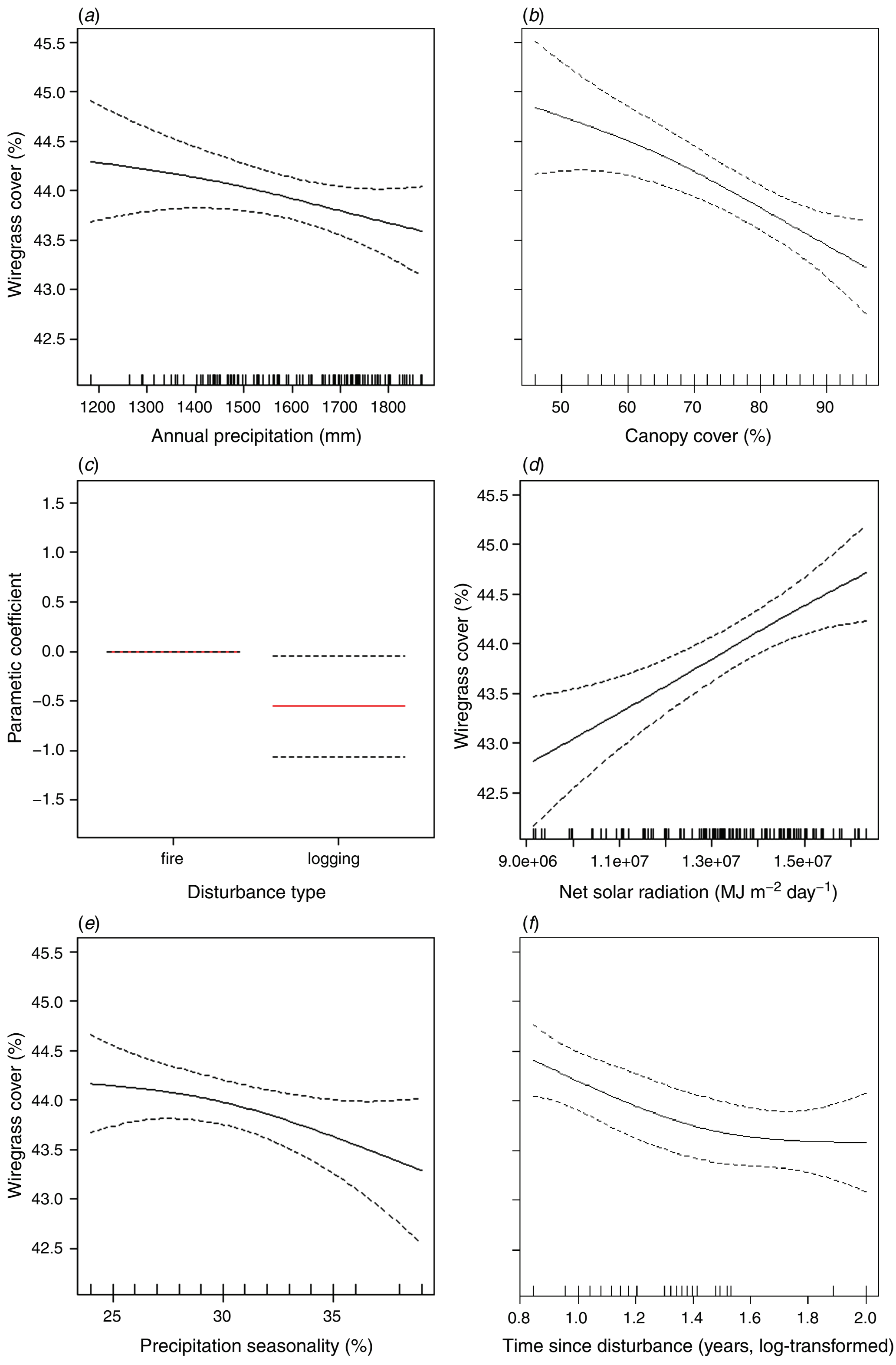


**Fig. 3.** Partial plots of generalised additive model (GAM) fits for wiregrass cover against (*a*) annual precipitation (mm), (*b*) canopy cover (%), (*c*) disturbance type, (*d*) net solar radiation (MJ $m^{-2}$ $day^{-1}$), (*e*) precipitation seasonality (%), and (*f*) time since disturbance (years, log-transformed).

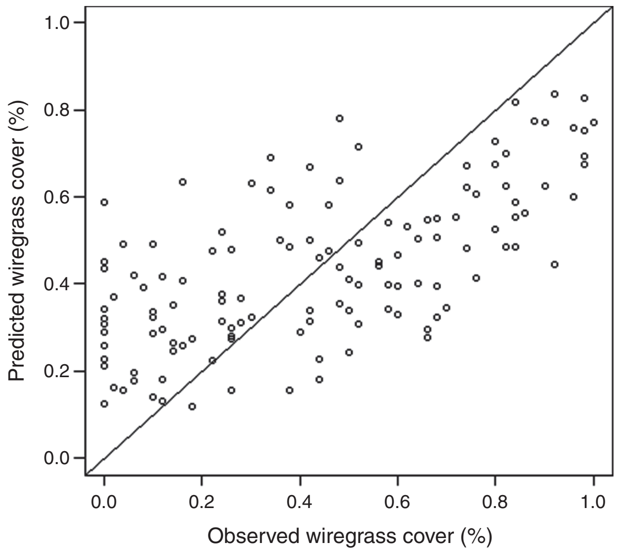


**Fig. 4.** Plot of generalised additive model (GAM)-fitted values of wiregrass cover against the observed values. The model tends to overpredict low wiregrass cover and underpredict high ones.

### *Role of wiregrass in a positive fire–flammability feedback*

Our results suggest that wiregrass has the potential to create a positive fire–flammability feedback in mountain ash forests, akin to the grass–fire cycle in other systems. The grass–fire cycle is based on several premises (D'Antonio and Vitousek 1992; Rossiter *et al*. 2003). First, that grass dominance alters fuel characteristics leading to increased fire frequency, extent or intensity. Field studies by Buckley (1993) suggest that this is the case with wiregrass. When wiregrass is abundant, fires are more likely to ignite and spread at high surface fuel moisture contents, i.e. greater than 20% (Buckley 1993) when fires would otherwise self-extinguish (Cheney 1981). Another premise underpinning the grass–fire cycle is that altered fire regimes resulting from the abundance of particular grasses can create changes in tree cover. Altered fire regimes (i.e. increased fire frequency) in mountain ash forests can eliminate mountain ash from a site (Fairman *et al.* 2016). The extent that wiregrass abundance drives fire frequency in these forests is unclear. The final premise of the grass–fire cycle is that grass cover increases in the post-fire community. Our results show that wiregrass cover is higher in recently burnt sites than long-unburnt ones, with fire disturbance likely acting as a stimulus for wiregrass growth. This evidence suggests that the grass–fire cycle may be applicable to wiregrass in mountain ash forests, but further research is needed to determine the importance of wiregrass abundance to fire frequency or extent in these forests.

### *Potential effect of climate change on wiregrass abundance*

Fire frequency is hypothesised to increase under future climate change scenarios (Pitman *et al*. 2007; Bradstock *et al*. 2014; Seidl *et al*. 2017), and precipitation is predicted to decrease in south-eastern Australia (Whetton 2011). Both these conditions could increase the abundance of wiregrass, although that would also depend on the lower limit of moisture tolerance of wiregrass. Increased aridity may also reduce wiregrass abundance if moisture becomes a factor limiting wiregrass growth. Further study is needed to determine how wiregrass responds to drought, and how reduced canopy cover caused by disturbance interacts with effects of low moisture on wiregrass.

## Conclusion

Dominant species can strongly influence the flammability of vegetation communities, hence understanding the factors affecting the abundance of such species are important. Wiregrass, a species that increases the flammability of forest understoreys when it occurs abundantly, was found to increase in abundance in recently disturbed sites with reduced canopy cover, more light and lower precipitation. This suggests that disturbances such as fire that reduce canopy cover in sites where wiregrass is present can promote wiregrass dominance, which in turn increases flammability. This may create a positive flammability feedback.


## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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## Appendix 1. Pairwise correlations of continuous predictor variables

Correlation values $\geq$0.70 are in bold

| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Canopy cover | 1 | | | | | | | | | | | | | | | | | | | | | | | |
| 2. Aspect | 0.04 | 1 | | | | | | | | | | | | | | | | | | | | | | |
| 3. Elevation | 0.05 | -0.06 | 1 | | | | | | | | | | | | | | | | | | | | | |
| 4. Net solar radiation | -0.03 | **-0.79** | 0.17 | 1 | | | | | | | | | | | | | | | | | | | | |
| 5. Time since disturbance | 0.35 | -0.03 | 0.18 | -0.06 | 1 | | | | | | | | | | | | | | | | | | | |
| 6. Annual mean temperature | -0.08 | 0.05 | **-0.92** | -0.16 | -0.14 | 1 | | | | | | | | | | | | | | | | | | |
| 7. Annual mean diurnal range | -0.06 | 0.08 | **-0.83** | -0.1 | -0.21 | **0.85** | 1 | | | | | | | | | | | | | | | | | |
| 8. Isothermality | 0.07 | 0.12 | **-0.81** | -0.12 | -0.08 | **0.73** | **0.89** | 1 | | | | | | | | | | | | | | | | |
| 9. Temperature seasonality | -0.22 | -0.16 | 0.52 | 0.12 | -0.19 | -0.34 | -0.4 | **-0.73** | 1 | | | | | | | | | | | | | | | |
| 10. Maximum temperature of warmest month | -0.15 | 0.02 | **-0.82** | -0.13 | -0.22 | **0.96** | **0.83** | 0.6 | -0.06 | 1 | | | | | | | | | | | | | | |
| 11. Minimum temperature of coldest month | -0.05 | 0.07 | **-0.9** | -0.19 | -0.07 | **0.98** | **0.74** | 0.67 | -0.36 | **0.91** | 1 | | | | | | | | | | | | | |
| 12. Temperature annual range | -0.24 | -0.06 | -0.45 | -0.01 | -0.37 | 0.61 | 0.69 | 0.31 | 0.38 | **0.81** | 0.49 | 1 | | | | | | | | | | | | |
| 13. Mean temperature of wettest quarter | -0.03 | 0.09 | **-0.93** | -0.16 | -0.07 | **0.96** | **0.85** | **0.81** | -0.5 | **0.87** | **0.95** | 0.47 | 1 | | | | | | | | | | | |
| 14. Mean temperature of driest quarter | -0.13 | 0.02 | **-0.84** | -0.14 | -0.19 | **0.97** | **0.79** | 0.59 | -0.1 | **0.99** | **0.95** | **0.74** | **0.89** | 1 | | | | | | | | | | |
| 15. Mean temperature of warmest quarter | -0.13 | 0.02 | **-0.84** | -0.14 | -0.19 | **0.97** | **0.79** | 0.59 | -0.1 | **0.99** | **0.95** | **0.74** | **0.89** | **1** | 1 | | | | | | | | | |
| 16. Mean temperature of coldest quarter | -0.04 | 0.08 | **-0.94** | -0.17 | -0.1 | **0.98** | **0.86** | **0.81** | -0.49 | **0.9** | **0.97** | 0.5 | **0.98** | **0.92** | **0.92** | 1 | | | | | | | | |
| 17. Annual precipitation | 0.08 | -0.01 | **0.9** | 0.12 | 0.15 | **-0.98** | **-0.81** | -0.67 | 0.27 | **-0.95** | **-0.97** | -0.63 | **-0.93** | **-0.97** | **-0.97** | **-0.96** | 1 | | | | | | | |
| 18. Precipitation of wettest month | -0.02 | -0.07 | **0.94** | 0.15 | 0.05 | **-0.95** | **-0.8** | **-0.8** | 0.56 | **-0.83** | **-0.95** | -0.39 | **-0.96** | **-0.86** | **-0.86** | **-0.98** | **0.9** | 1 | | | | | | |
| 19. Precipitation of driest month | 0.17 | 0.09 | 0.63 | 0.04 | 0.29 | **-0.78** | -0.69 | -0.4 | -0.15 | **-0.88** | **-0.7** | **-0.85** | -0.62 | **-0.85** | **-0.85** | -0.69 | **0.8** | 0.6 | 1 | | | | | |
| 20. Precipitation seasonality | -0.16 | -0.16 | **0.73** | 0.15 | -0.13 | -0.6 | -0.55 | **-0.79** | **0.9** | -0.36 | -0.64 | 0.15 | **-0.74** | -0.41 | -0.41 | **-0.72** | 0.6 | **0.8** | 0 | 1 | | | | |
| 21. Precipitation of wettest quarter | 0.01 | -0.06 | **0.93** | 0.14 | 0.07 | **-0.97** | **-0.8** | **-0.76** | 0.48 | **-0.87** | **-0.97** | -0.46 | **-0.97** | **-0.9** | **-0.9** | **-0.98** | **1** | **1** | 0.7 | **0.74** | 1 | | | |
| 22. Precipitation of driest quarter | 0.23 | 0.09 | 0.54 | 0.04 | 0.28 | **-0.74** | -0.55 | -0.21 | -0.35 | **-0.88** | -0.69 | **-0.87** | -0.57 | **-0.87** | **-0.87** | -0.62 | **0.8** | 0.5 | **0.9** | -0.06 | 0.6 | 1 | | |
| 23. Precipitation of warmest quarter | 0.23 | 0.09 | 0.54 | 0.04 | 0.28 | **-0.74** | -0.55 | -0.21 | -0.35 | **-0.88** | -0.69 | **-0.87** | -0.57 | **-0.87** | **-0.87** | -0.62 | **0.8** | 0.5 | **0.9** | -0.06 | 0.6 | 1 | 1 | |
| 24. Precipitation of coldest quarter | -0.01 | -0.07 | **0.94** | 0.14 | 0.06 | **-0.96** | **-0.81** | **-0.79** | 0.54 | **-0.84** | **-0.95** | -0.41 | **-0.97** | **-0.87** | **-0.87** | **-0.98** | **1** | **1** | 0.6 | **0.79** | 1 | 0.6 | 0.6 | 1 |