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Resilience of a eucalypt forest woody understorey to long-term (34–55 years) repeated burning in subtropical Australia

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Abstract. We investigated the effects of annual burning since 1952, triennial burning since 1973, fire exclusion since 1946 and infrequent wildfire (one fire in 61 years) on woody understorey vegetation in a dry sclerophyll eucalypt forest, south-eastern Queensland, Australia. We determined the influence of these treatments, and other site variables (rainfall, understorey density, topsoil C : N ratio, tree basal area, distance to watercourse and burn coverage) on plant taxa density, richness and composition. The richness of woody understorey taxa 0–1 m in height was not affected by burning treatments, but richness of woody plants 1–7.5 m in height was lower in the annually burnt treatment than in the triennially burnt treatment from 1989 to 2007. Fire frequency and other site variables explained 34% of the variation in taxa composition (three taxon groups and 10 species), of which 33% of the explained variance was explained by fire treatment and 46% was explained by other site variables. Annual burning between 1974 and 1993 was associated with lower understorey densities mainly due to reduced densities of eucalypts 1–7.5 m in height. Triennial burning during the same period was associated with higher densities of eucalypts 0–7.5 m in height relative to the annually burnt and unburnt treatments. Most woody taxa persisted in the frequently burnt treatments through resprouting mechanisms (e.g. lignotuberous regeneration), and fire patchiness associated with low-intensity burning was also found to be important. Persistence of plants <1 m tall demonstrates the resilience of woody taxa to repeated burning in this ecosystem, although they mainly exist in a suppressed growth state under annual burning.

Additional keywords: fire regimes, plant composition, plant density, regeneration, richness, vegetation structure.

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Introduction

Long-term studies are vital for understanding vegetation changes associated with differing fire regimes. Plant populations are influenced more strongly by a fire regime than individual fire events (Gill 1981; Noble and Slatyer 1981; Whelan *et al.* 2002), such that incorrect conclusions may be drawn from short-term studies (Freckleton 2004). Fire frequency is an important component of a fire regime that can alter vegetation structure, composition and richness (Whelan 1995). Long-term frequent fire often results in a more open understorey in forests, by reducing the shrub layer and tree regeneration (Russell and Roberts 1996; Russell-Smith *et al.* 2003; Fairfax *et al.* 2009). Reductions in shrub and tree densities promote grassy understories, so frequent fire is commonly used by land managers to encourage pasture productivity for livestock grazing (e.g. Lemon 1946; Hodgkinson *et al.* 1990). Frequent fire may also reduce long-term fuel accumulation (Birk and Bridges 1989), minimising the potential wildfire effects to human life, properties and other assets, such as timber resources (Sneeuwjagt 2008; although see Penman *et al.* 2011*a* for a discussion on the effectiveness of prescribed burning programs).

Despite the potential benefits of frequent fire as a management tool, long-term frequent burning has demonstrated negative consequences for some ecosystem components. Decline and elimination of plant populations whose seed production is interrupted by frequent fires have been documented in a wide range of fire-prone habitats (Fox and Fox 1986; Nieuwenhuis 1987; Gill and Bradstock 1995; Hoffmann 1998; Gill 1999). Obligate seeder species that are unable to produce seeds within the interfire period are expected to decline (Keith 1996; Bradstock *et al.* 1997; Watson *et al.* 2009) and other species that rely on seed regeneration may also decrease if fires are too

Table 1. Description of treatments at the Bauple fire experiment

Treatment	Annually burnt	Triennially burnt	Unburnt and infrequent wildfire
Burn history	Since 1952	Since 1973. Burnt pretreatment in 1951, 1965 and 1969	Unburnt 1946–2006. Wildfire in 2006
Number of fires from 1973 to 2007	33	11	1
Area (ha)	314	423	296[A]
Plot logging and thinning history[B]	~1918, 1948–1950, 1972–1974, 1992[C]	~1918, 1948–50, 1969–73	~1918, 1948–50, 1972–74

[A]Approximately 200 ha (five of six monitoring plots) were affected by 2006 wildfire.
[B]Low-intensity selective logging occurred in 1984 in all treatments, but not within monitoring plots.
[C]0–4 trees per 400-m^2 plot of *Corymbia citriodora* subsp. *variegata* trees were selectively removed from monitoring plots.

frequent to allow height development beyond scorch height (Hoffmann 1998; Hoffmann and Solbrig 2003). Species that produce lignotuberous seedlings are more resistant to repeated burning than obligate seeders but may decline over a long period of frequent fire if repeated defoliation depletes starch reserves or if seedlings die before they can develop a lignotuber (Bowen and Pate 1993; Walters *et al.* 2005; Fensham and Fairfax 2006). Seemingly low annual rates of fire-induced mortality may lead to considerable changes in population densities when compounded over many years of frequent burning. Thus, long-term (34–55 years) repeated burning is expected to change the composition and density of non-herbaceous plants in the understorey, resulting in a simplification of vegetation structure (Spencer and Baxter 2006; Fairfax *et al.* 2009). Temporal changes in woody plant communities will also be affected by fluctuations in environmental factors other than fire (Bradstock *et al.* 1997; Sharp and Bowman 2004; Fensham *et al.* 2005), such that it is important to consider the effects of other environmental influences.

We present results from a long-term dataset that provides vital information to address contemporary management controversies regarding 'appropriate' fire frequencies for land managers in subtropical eastern Australia. Debate continues in Australia and internationally regarding the benefits and ecological costs associated with frequent prescribed burning (Fernandes and Botelho 2003; Sneeuwjagt 2008; Penman *et al.* 2011*a*). Published management recommendations for dry sclerophyll eucalypt forests and woodlands with shrubby understories usually suggest interfire intervals greater than 6 years, based on ecological considerations (e.g. Bradstock and Myerscough 1988; Cary and Morrison 1995; Watson and Wardell-Johnson 2004). Such recommendations are often based on short-term studies and knowledge of plant population life-cycles, but are rarely tested using long-term experiments, and may not apply equally to forests that have grassy understories. Historical data from a long-running fire experiment in Queensland, Australia, provide an opportunity to investigate the long-term effects of different fire regimes on the composition and richness of non-herbaceous understorey plants (hereafter referred to as 'woody' plants). In particular, we aim to determine the relative influence of frequent fire regimes and environmental variables on understorey plant composition, plant density and richness. We hypothesised that frequent prescribed burning undertaken during the periods 1952–2007 (annual burning) and 1973–2007 (triennial burning) would reduce the density and richness of woody understorey plants and alter vegetation composition. The effects of frequent burning on the persistence and regeneration of understorey taxa are discussed.

Methods

Description of the experiment

The experiment is located at Bauple State Forest (25°48′S, 152°37′E) in south-east Queensland, Australia (Fig. S1 of the Supplementary material, see http://www.publish.csiro.au/?act=view_file&file_id=WF11003_AC.pdf). The ecosystem is an open forest dominated by *Corymbia citriodora* subsp. *variegata* with *Eucalyptus siderophloia*, *E. acmenoides*, *E. fibrosa*, *E. tereticornis*, *E. moluccana* and *C. intermedia* as co-dominants. The understorey is generally grassy; dominant herbaceous taxa include *Themeda triandra*, *Imperata cylindrica*, *Aristida* spp. and *Entolasia* spp. Average annual rainfall is 1007 mm (1950–2007), with rainfall being higher in summer months. The topography consists of undulating hills and rises, and the soils are shallow with loamy surface textures and clay loam to clay textures at 30–40-cm depth (Guinto *et al.* 2001).

The experiment has three treatments: (1) burnt annually since 1952; (2) burnt triennially on average since 1973 and (3) unburnt since 1946 (Table 1). A wildfire burnt through the eastern part of the unburnt treatment in October 2006, effectively splitting the unburnt treatment (Fig. S1). We refer to fire regimes as annually burnt, triennially burnt, unburnt (pre-wildfire) and infrequent wildfire for the purposes of this analysis. Prescribed burning treatments are ongoing and are conducted in winter and spring (June to October) and are generally of a low intensity (<500 kW m^{-1}). There is no true replication of the experimental treatments. However, the treatments have been applied over large areas (Table 1) and there is generally more than 0.5 km between monitoring plots, reducing spatial dependence among plots within the same treatment. Results from this experiment focussing on soil chemistry (Guinto *et al.* 2000, 2001) and tree growth (Guinto *et al.* 1999) have been published previously.

Most logging and thinning operations in the study area occurred before the establishment of treatments, with the exception of operations in 1969–74 and selective logging in 1984 and 1992 (Table 1). All three compartments were subject to periodic cattle grazing (stocking rate of 80 to 110 adult beasts over 1033 ha) before cattle were removed from the experiment between 1999 and 2001.

Vegetation data were collected at six 100×40-m non-randomly positioned permanent plots per treatment through time (Fig. S1). The 2006 wildfire that burnt through the eastern part of the previously unburnt treatment left only one long-unburnt experimental plot. This plot was excluded from our 2007 analysis. During prescribed burning operations, each plot was burnt as completely as possible. However, in many cases it was not possible to achieve 100% burn coverage owing to a lack of flammable fuels across a given plot.

Vegetation sampling

In this study, we focussed on woody plants in the understorey (<7.5-m height) for two main reasons. First, historical measurements at this experiment have focussed on woody taxa because these plants were initially measured to determine potential competition with the commercial trees. Second, populations of woody understorey plants should be responsive to repeated burning because they are susceptible to scorch from low-intensity fires and have life-cycles that are longer than the interburn period in the annual and triennial burn treatments.

The number of understorey woody plants was counted in a 100×1-m belt transect on the northern margin of each plot. Plant taxa were recorded in three height classes: 0–1, 1–3 and 3–7.5 m in height. Taxonomy follows Bostock and Holland (2007). Surveys in all three treatments were carried out in 1973–74 (referred to as 1974 measure), 1976, 1978, 1982, 1988–89 (referred to as 1989 measure), 1993 and 2007. Surveys took place just before the next scheduled burn (9–12 months after burning in the annually burnt treatment and 3–4 years after burning in the triennially burnt treatment) in all years except 1978, when sampling was carried out <2 years after burning. Time since fire in the unburnt treatment increased from 28 years (1974) to 47 years (1993) and sampling was carried out ~1 year after the 2006 wildfire in the infrequent-wildfire treatment. We have focussed on data collected from 1974 onwards because: (1) understorey data collected before 1974 were for a limited range of species and no data were available for the triennial burning treatment, and (2) the logging and thinning treatments that occurred in 1972–74 effectively split the dataset into pre- and post-logging periods. For certain analyses, we focussed on data collected between 1989 and 2007 because detailed plant surveys with identification of woody plants to species level were only conducted during this period.

Environmental variables

We chose five environmental variables in addition to fire-frequency treatment that may influence the density of woody plants: (1) relative rainfall; (2) tree basal area (as a surrogate of canopy cover); (3) soil fertility (C : N ratio); (4) distance to the nearest watercourse, and (5) average plot burn coverage. Rainfall is known to have an important influence on plant dynamics (Fensham *et al.* 2005). Relative rainfall was defined as the average annual rainfall from 2 years before the first measure to 2 years before the next measure divided by the long-term average annual rainfall for the site (1007 mm; 1950–2007). The 2-year lag in relative rainfall was used to account for the delay in woody plant growth in response to rainfall (Fensham *et al.* 2003). Historical rainfall values for the study site were based on spatially interpolated Bureau of Meteorology observational data (Jeffrey *et al.* 2001).

Tree basal area (the cross-sectional area a tree occupies at 1.3 m above ground) is a recognised correlate of canopy cover (McElhinny *et al.* 2006). Basal areas for each permanent plot were derived from diameter at breast height (DBH) measures by summing individual tree basal areas for all trees in a plot. Basal area increased at a similar rate through time across the three treatments (Fig. S2), and hence we used initial basal area (i.e. basal area in 1974) for each treatment in the analysis. Soil C : N was derived from topsoil organic carbon and total nitrogen. The change in C : N through time (data collected in 1976, 1978, 1982 and 1994) was consistent across the different treatments (Fig. S2), and hence we used the first available C : N values in subsequent analysis. In 1976, 1978 and 1982, soil samples were collected before burning to a depth of 7.5 cm. A stratified random sampling technique was used to collect 24 samples across each plot. In 1994, six 10-cm-deep cores were taken from randomly located points within the plot and combined. Samples were air-dried and sieved to a particle size of <2 mm for analysis.

Distance to the nearest watercourse (typically with ephemeral flows) was calculated from a map of the site, because distance from watercourses is known to affect vegetation through changes in microhabitat conditions and resource availability (e.g. Lyon and Gross 2005). Plot burn coverage was also included in our analysis given the likely importance of burn patchiness on plant assemblages (Penman *et al.* 2007). The percentage area of each plot burnt was accurately mapped from 1952 to 1994 in the annually burnt treatment and from 1973 to 1994 in the triennially burnt treatment. We calculated an average percentage area burnt across all years for each plot to account for the variability in burn coverage.

Analysis

Multivariate analysis was carried out using *CANOCO* (ter Braak and Šmilauer 2002). Partial redundancy analysis (RDA) was used to explain variation in plant density with the environmental variables. RDA, which assumes that plant taxa respond linearly to environmental variables, was used because a preliminary detrended correspondence analysis confirmed that plant responses to environmental predictors were more linear than Gaussian (<3 s.d., ter Braak and Šmilauer 2002). Principal components analysis (PCA) is the unconstrained linear equivalent to RDA and was used to investigate the relationships between plant taxa and plots without environmental variables. Only taxa or taxon groups that were recorded through time were retained for the multivariate analysis because more detailed plant surveys were conducted from 1989 to 2007 and identification to species level was not consistently carried out before 1989. Taxon groups comprised 'eucalypts' (*Eucalyptus* and *Corymbia*), 'acacia' (all *Acacia* species) and 'pultenaea' (all *Pultenaea* species). We report taxa composition rather than species composition given the whole suite of species was not analysed. A total of 13 plant taxa (10 species and 3 taxon groups) and 126 samples (18 plots $\times$ 7 sampling times) were included in this analysis. Plant data were transformed by taking logarithms, using the transformation $\ln(10X + 1)$, where X = taxa density (ter Braak and Šmilauer 2002).

We tested for spatial autocorrelation (Legendre 1993) among plots using a Mantel test, which compared matrices of: (1) the geographic distance between pairs of plots, and (2) Bray–Curtis similarities of taxa density data averaged across all times. No significant spatial autocorrelation was detected ($r = -0.15$, $P > 0.05$). We determined whether environmental variables were collinear using a Spearman rank test and Student's t-statistic (to determine whether correlations differed significantly from zero). Sampling time was significantly correlated with relative rainfall ($t = -36.3$, d.f. = 124, $P < 0.001$), so we dropped sampling time from the explanatory variables. Automatic forward selection was used to determine the relative importance of each variable in determining taxa composition (ter Braak and Šmilauer 2002) and Monte Carlo permutation tests (499 permutations) were used to test the significance of each variable. Partitioning of variance was used to determine the variance described by fire treatment effects versus other variables. The method involved the use of partial ordination by accounting for confounding of effects from fire treatments and other environmental variables through the use of covariates (Borcard *et al.* 1992). Three RDA runs were carried out to determine the: (1) sole effect of treatments (with other variables selected as covariables); (2) sole effect of other environmental variables (with treatment effects selected as covariables), and (3) combined variation due to confounding effects of burn treatment and other environmental variables. The remaining variation was unexplained.

Repeated-measures ANOVA was carried out in *GENSTAT* (11th edition, VSN International Ltd, United Kingdom) to determine the effects of fire treatments and environmental variables on the richness of woody taxa and the density of acacias, eucalypts and other woody taxa in each of the three height classes (number of taxa or plants per 100 m^2). Analysis of woody taxa richness was only possible for the 1989–2007 period (Table 2). We divided this dataset into obligate-seed-regenerating and resprouting taxa, but obligate seed regenerators occurred too infrequently across this period to include in the analysis: 3.3% of 8656 plant occurrences in this period, and 2.8% of these occurrences were attributed to two obligate seeders in a single plot. The results from the resprouting taxa analyses did not differ greatly from those for woody taxa richness, and hence are not reported here.

Competitive effects were also investigated by assigning the woody understorey density of all individuals in the plot (minus the density for the particular response variable being analysed) at the start of each data period as a covariate. Environmental variables that varied spatially among plots but did not vary temporally were assigned to the plot stratum, with fire frequency as our main predictor and understorey density, tree basal area, topsoil C : N, distance to the nearest watercourse and plot burn coverage assigned as covariates. Understorey density varied both spatially and temporally and was included in both the plot and plot × time strata. Given that time was correlated with relative rainfall, we could not include both terms in the model as variation in relative rainfall was explained by variation in time.

Separate ANOVAs investigated the effect of the 2006 wildfire on richness or density in 2007, by using the last pre-wildfire measure of richness or density (1993) as a covariate along with the other covariates (Table 2).

A Spearman rank test and Student's t-statistic were used to determine correlation between total understorey density and the number of times a plot was burnt between 1974 and 2007.

Results

PCA of taxa densities from 1974 to 2007 showed groupings of sites according to the different treatments (Fig. 1): *Alphitonia excelsa*, *Lantana camara*, *Cyclophyllum coprosmoides* and *Psydrax odorata* were associated with the infrequent-wildfire treatment, whereas *Acacia* species, *Pultenaea* species, *Eucalyptus* species, *Jacksonia scoparia* and *Lophostemon confertus* were associated with the triennially burnt treatment and *Lophostemon suaveolens* with the annually burnt treatment. RDA showed that there were significant treatment effects on species composition, and all variables had a significant or marginally significant (i.e. tree basal area) influence on taxa composition (Table 3). All variables together explained 34% of the variation in taxa composition. Of this, fire treatments accounted for 33% of the explained variance and other variables

Table 2. Summary of the different analyses conducted and their respective time periods

Analyses of the 2007 data excluded the one plot in the infrequent-wildfire treatment that was not burnt by the 2006 wildfire

Variable	Time period analysed	Analysis used and treatments investigated
Woody plant richness (0–1, 1–3, 3–7.5 and 0–7.5 m)	(1) 1989–93	(1) Repeated-measures ANOVA with treatments: annual burning, triennial burning and no burning since 1946, and covariates
	(2) 2007	(2) ANOVA with treatments: annual burning, triennial burning and infrequent wildfire, and covariates
Plant taxa composition (for taxa recorded through time)	1974–2007	(1) Redundancy analysis with treatments: annual burning, triennial burning and infrequent wildfire, and covariates
		(2) Principal components analysis with species and plots only
Acacia density, eucalypt density and other woody plant density (0–1-, 1–3-, 3–7.5-m height classes)	(1) 1974–93	(1) Repeated-measures ANOVA with treatments: annual burning, triennial burning and no burning since 1946, and covariates
	(2) 2007	(2) ANOVA with treatments: annual burning, triennial burning and infrequent wildfire, and covariates

accounted for 46% of the explained variance in taxa composition. The combined variation due to the confounding effects of fire treatment and other environmental variables accounted for 21% of the explained variance.

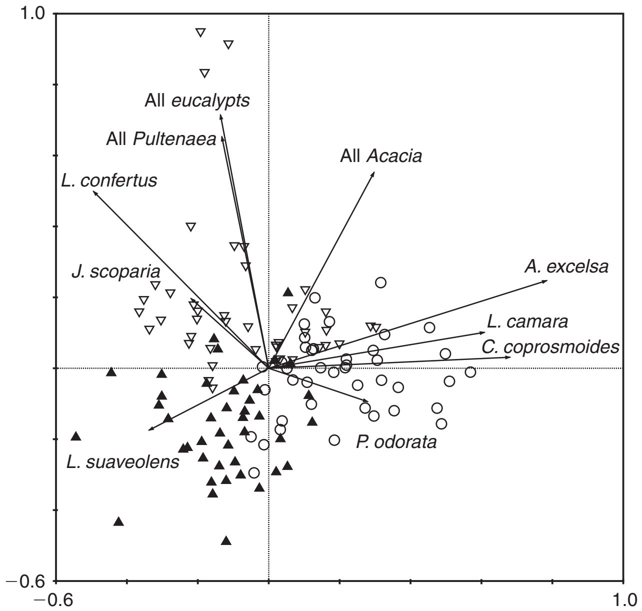

Fig. 1. Principal components analysis (PCA) ordination for taxa (arrows) and plot data collected between 1974 and 2007 (1974, 1976, 1978, 1982, 1989, 1993 and 2007). Plot symbols are: ▲ annually burnt treatment; ▽ triennially burnt treatment; and ○ infrequent-wildfire treatment. Taxa are: all eucalypts (includes *Eucalyptus* and *Corymbia* species), all *Acacia* species, all *Pultenaea* species, *Alphitonia excelsa*, *Lantana camara*, *Cyclophyllum coprosmoides*, *Psydrax odorata*, *Lophostemon suaveolens*, *Jacksonia scoparia* and *Lophostemon confertus.*

In the period from 1989 to 1993, woody taxa richness did not vary through time and there were no treatment by time interactions (Table 4). Treatment effects were significant in both the >1 m in height classes (Table 4). Richness of woody taxa 1–3 m in height was lower in the annually burnt treatment than in the triennially burnt or unburnt treatments. Richness for taxa 3–7.5 m in height was again lower in the annually burnt treatment than in the triennially burnt treatment but richness in the unburnt treatment did not differ from that in the other treatments (Table 4). In 2007, woody taxa richness again varied significantly among treatments in the two tallest height classes (Table 5). The triennially burnt treatment had greater richness than either the annually burnt or infrequent-wildfire treatments, which did not differ significantly in both cases (Table 5). Tree basal area was negatively associated with richness of taxa in the 3–7.5-m height class and with total richness (all height classes) in the 1989–93 data. Burn coverage also had a negative relationship with richness in the 3–7.5-m height class (Table 4). Mean burn coverage of the annually burnt plots was $61 \pm 2.2\%$ (mean ± s.e.) including 2 years where none of the plots were burnt, and was $78 \pm 4.4\%$ for the triennially burnt plots.

Total understorey density was negatively correlated with the number of times a plot had been burnt ($t = -7.05$, d.f. = 124, $P < 0.001$). Across all times, mean understorey density (all plants <7.5 m in height ± s.e.) was 60.7 ± 4.9 plants per plot in the annually burnt treatment, 161.9 ± 12.6 plants per plot in the triennially burnt treatment and 141.0 ± 13.6 plants per plot in the infrequent-wildfire treatment. Higher plant densities were recorded in the 0–1-m height class than in the larger height classes for acacias, eucalypts and other woody taxa (Figs 2, S3).

Relationships through time for all acacia height classes were not consistent across treatments (Table 6, Fig. 2). Densities of acacias <1 m in height fluctuated greatly in the annually burnt treatment over time but less so in the triennially burnt and unburnt treatments (Fig. 2*a*). The treatment by time interaction for acacias 1–3 m in height was due to a reduction in density in

Table 3. Variables used in multivariate analyses for data collected between 1974 and 2007 and Monte Carlo results after forward selection, showing conditional effects and marginal effects on taxa composition for significant ($P < 0.05$) variables

Conditional variance explained is that when all other variables are included in the model, and marginal variance is the amount of variability explained by individual variables (when only that variable is treated as the explanatory variable). NA, no variance calculated as this variable was treated as a dummy variable. Note: a probability of $P = 0.002$ is the lowest achievable given the number of permutations

Variable	Description	Marginal explained variance (%)	Conditional explained variance (%)	*P*
Fire treatments				
(1) Infrequent wildfire	(1) Unburnt from 1946 to 2006, wildfire in 2006	29.5	29.5	0.002
(2) Triennial	(2) Burnt every 3 years (on average) since 1972	23.6	NA	NA
(3) Annual	(3) Burnt annually since 1952	26.5	23.6	0.002
Other variables				
Distance to water	Distance to nearest watercourse (m)	5.9	5.9	0.002
Rainfall	Average annual rainfall over the 2 years before sampling divided by long-term average annual rainfall (1950–2007)	5.9	8.8	0.002
C : N	Ratio of topsoil % organic carbon to % total nitrogen in the topsoil	14.7	11.8	0.002
Tree basal area	Tree basal area (calculated for each plot as a surrogate of canopy cover)	8.8	2.9	0.056
Burn coverage	Average % area of plot burnt between 1952 and 1994 (annual treatment) and between 1973 and 1994 (triennial treatment)	23.6	17.7	0.002

Table 4. Repeated-measures ANOVA results for the effects of fire frequency treatment (annual burning, A; triennial burning, T; and long-unburnt, UB) and covariates on woody taxa richness (number of taxa per 100 m^2) between 1989 and 1993 in three height classes and across all height classes
Time (relative rainfall), the treatment by time interaction and understorey density in the plot × time strata were not significant. Treatment means and least significant differences (l.s.d., at the 95% probability level) and standardised coefficients (β) for covariates are reported where effects were significant. ns, not significant

Source of variation	<1 m	1–3 m	3–7.5 m	Total (0–7.5 m)
Plot stratum				
Treatment	ns	$F_{2,15} = 61.67$, $P < 0.001$, means: A = 0.58, T = 6.83, UB = 7.67 (l.s.d. = 1.49)	$F_{2,13} = 9.56$, $P = 0.003$, means: A = 3.19, T = 6.36, UB = 3.95 (l.s.d. = 2.68)	ns
Covariates				
Understorey density	$F_{1,14} = 8.83$, $P = 0.010$, β = 2.97	ns	ns	$F_{1,13} = 6.66$, $P = 0.023$, β = 2.45
C : N	ns	ns	ns	ns
Tree basal area	ns	ns	$F_{1,13} = 6.05$, $P = 0.029$, β = −2.52	$F_{1,13} = 4.69$, $P = 0.050$, β = −2.16
Distance to water	ns	ns	ns	ns
Burn coverage	ns	ns	$F_{1,13} = 5.51$, $P = 0.035$, β = −2.37	ns

Table 5. ANOVA results for the effects fire frequency treatment (annual burning, A; triennial burning, T; and infrequent wildfire, IW) and covariates in 2007
Only covariates that had a significant or marginally significant influence are reported. 1993 density or richness data (pre-wildfire) were treated as a covariate in this analysis. Treatment means and least significant differences (l.s.d., at the 95% probability level) and standardised coefficients (β) for covariates are reported where effects were significant or marginally significant. ns, not significant

Variable	Treatment effects	Total understorey density	1993 density or richness
Total richness 0–7.5 m	ns	$F_{1,12} = 5.36$, $P = 0.039$, β = −0.53	$F_{1,12} = 10.32$, $P = 0.007$, β = 3.23
Richness 0–1 m	ns	ns	$F_{1,13} = 5.51$, $P = 0.035$, β = 2.33
Richness 1–3 m	$F_{2,13} = 17.71$, $P < 0.001$ Means: A = 1.34, T = 5.35, IW = 2.14 (l.s.d. = 1.41)	ns	$F_{1,13} = 18.11$, $P < 0.001$, β = 4.25
Richness 3–7.5 m	$F_{2,13} = 14.67$, $P < 0.001$ Means: A = 1.39, T = 3.88, IW = 0.26 (l.s.d. = 1.49)	ns	$F_{1,13} = 3.43$, $P = 0.087$, β = 1.85
Acacia density 0–1 m	$F_{2,14} = 10.88$, $P = 0.001$ Means: A = 22.0, T = 48.0, IW = 144.0 (l.s.d. = 59.3)	ns	ns
Acacia density 1–3 m	$F_{2,13} = 12.78$, $P < 0.001$ Means: A = 4.2, T = 14.3, IW = −1.5 (l.s.d. = 8.73)	ns	$F_{1,13} = 3.98$, $P = 0.067$, β = 1.99
Acacia density 3–7.5 m	$F_{2,14} = 4.86$, $P = 0.025$ Means: A = 0.17, T = 2.83, IW = 0.00 (l.s.d. = 2.19)	ns	ns
Eucalypt density 0–1 m	ns	ns	$F_{1,13} = 3.84$, $P = 0.072$, β = 1.96
Eucalypt density 1–3 m	$F_{2,13} = 5.65$, $P = 0.017$ Means: A = 3.38, T = 6.08, IW = 2.21 (l.s.d. = 2.99)	ns	$F_{1,13} = 19.44$, $P < 0.001$, β = 4.38
Eucalypt density 3–7.5 m	$F_{2,14} = 18.58$, $P < 0.001$ Means: A = 0.50, T = 5.17, IW = 0.40 (l.s.d. = 1.92)	ns	ns
Other woody density 0–1 m	$F_{2,14} = 3.62$, $P = 0.054$ Means: A = 4.0, T = 6.0, IW = 78.0 (l.s.d. = 67.7)	ns	ns
Other woody density 1–3 m	ns	$F_{1,13} = 9.03$, $P = 0.010$, β = 3.01	ns
Other woody density 3–7.5 m	$F_{2,12} = 3.86$, $P = 0.051$ Means: A = 0.98, T = 0.67, IW = −0.15 (l.s.d. = 1.05)	$F_{1,12} = 17.96$, $P = 0.001$, β = 0.73	$F_{1,12} = 16.38$, $P = 0.002$, β = 4.05

the triennially burnt treatment between 1974 and 1978 and a subsequent increase between 1978 and 1982, which was not present or as pronounced in the other treatments (Fig. 2*b*). Density of acacias 3–7.5 m in height declined in the unburnt treatment through time, but this decline was not apparent in the other treatments (Fig. 2*c*). Across all times (1974–93), treatment effects had a significant influence on acacias 3–7.5 m in height (Table 6), with higher densities in the unburnt treatment than in the triennially or annually burnt treatments (Fig. 2*c*). Post wildfire (2007 data), treatment effects were significant for all

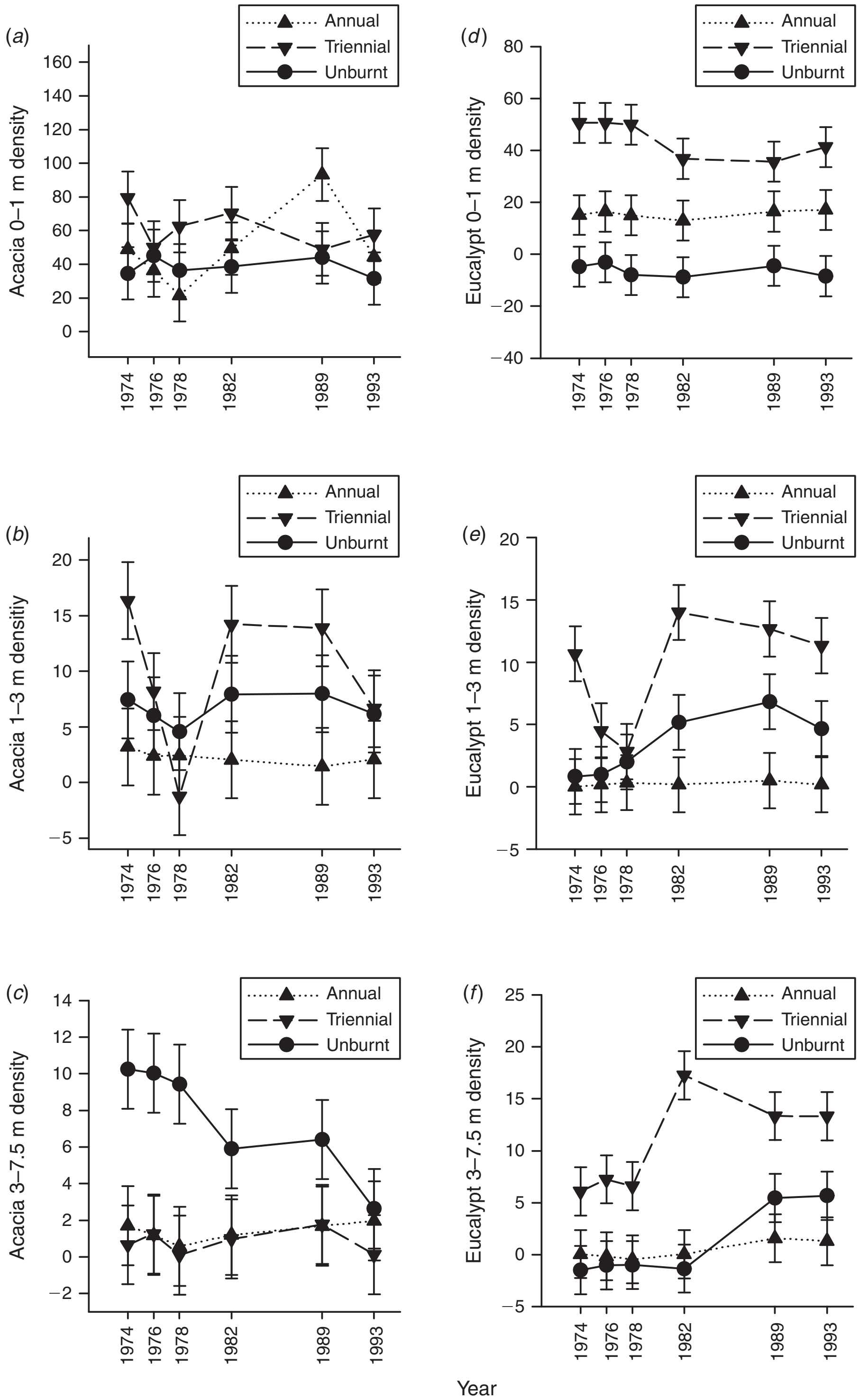

Fig. 2. Changes in density (plants per $100\,m^2$, mean adjusted for covariates ± standard error) of all understorey acacia (*a–c*) and eucalypts (*d–f*) in different height classes (0–1, 1–3 and 3–7.5 m) through time (1974 to 1993) within annually burnt, triennially burnt and unburnt treatments.

height classes (Table 5). Densities of acacias <1 m in height were significantly higher in the infrequent-wildfire treatment than in either of the frequently burnt treatments, whereas densities of acacias >1 m in height were greater in the triennially burnt treatment than in the annually burnt and infrequent-wildfire treatments (Table 5).

There were significant treatment by time interactions for all three eucalypt height classes (Table 7, Fig. 2). Eucalypts 1–3 m

Table 6. Repeated-measures ANOVA results for the effects of fire frequency treatment (annual, triennial and unburnt), time (relative rainfall) and covariates on *Acacia* species between 1974 and 1993 in three height classes

Covariates that were not significant ($P < 0.1$) are not reported. Standardised coefficients (β) for covariates are reported for marginally significant effects. ns, not significant

Source of variation	<1 m	1–3 m	3–7.5 m
Plot stratum			
Treatment	ns	$F_{2,14} = 3.41$, $P = 0.062$	$F_{2,14} = 12.12$, $P < 0.001$
Covariate			
Understorey density	ns	$F_{1,14} = 3.69$, $P = 0.076$, $\beta = 1.90$	ns
Plot × time stratum			
Time	$F_{5,75} = 2.43$, $P = 0.043$	$F_{5,74} = 4.89$, $P < 0.001$	$F_{5,74} = 2.35$, $P = 0.049$
Time × treatment	$F_{10,75} = 3.31$, $P = 0.001$	$F_{10,74} = 3.21$, $P = 0.002$	$F_{10,74} = 2.72$, $P = 0.007$
Covariate			
Understorey density	ns	ns	$F_{1,74} = 3.89$, $P = 0.052$, $\beta = -1.21$

Table 7. Repeated-measures ANOVA results for the effects of treatment (annual, triennial and unburnt), time (relative rainfall) and covariates on eucalypts between 1974 and 1993 in three height classes

Covariates that were not significant ($P < 0.1$) are not reported. Standardised coefficients (β) for covariates are reported where effects were significant or marginally significant. ns, not significant

Source of variation	<1 m	1–3 m	3–7.5 m
Plot stratum			
Treatment	$F_{2,14} = 14.01$, $P < 0.001$	$F_{2,15} = 24.51$, $P < 0.001$	$F_{2,13} = 27.21$, $P < 0.001$
Covariates			
Understorey density	ns	ns	$F_{1,13} = 3.81$, $P = 0.073$, $\beta = -2.51$
Burn coverage	$F_{1,14} = 5.56$, $P = 0.033$, $\beta = -2.34$	ns	$F_{1,13} = 3.48$, $P = 0.085$, $\beta = -1.86$
Plot × time stratum			
Time	$F_{5,75} = 2.75$, $P = 0.025$	$F_{5,75} = 7.65$, $P < 0.001$	$F_{5,74} = 13.92$, $P < 0.001$
Time × treatment	$F_{10,75} = 1.80$, $P = 0.075$	$F_{10,75} = 3.34$, $P = 0.001$	$F_{10,74} = 5.62$, $P < 0.001$
Covariate			
Understorey density	ns	ns	$F_{1,74} = 4.30$, $P = 0.042$, $\beta = -2.07$

in height followed a similar trend to acacias in this height class; there was a decline in density between 1974 and 1978 and an increase in density between 1978 and 1982 in the triennially burnt treatment that was not apparent or as pronounced in the other treatments (Fig. 2*e*). Response to treatments varied within eucalypts depending on height class (Fig. 2). Across all times (1974–93), treatment effects were significant for all height classes (Fig. 2). Densities of eucalypts <1 m in height were higher in the triennially burnt treatment than in the unburnt treatment, and the annually burnt treatment exhibited intermediate densities (Fig. 2*d*). Densities of eucalypts >1 m in height were consistently lower in the annually burnt treatment relative to the unburnt and triennially burnt treatments (Fig. 2*e*, *f*). In 2007, treatment effects were significant in the >1-m height classes (Table 5). The infrequent-wildfire treatment carried a lower density of eucalypts 1–3 m in height than either of the frequently burnt treatments, whereas the triennially burnt treatment had a greater density of eucalypts 3–7.5-m height than either the annually burnt or infrequent-wildfire treatments (Table 5). There was a significant negative relationship between percentage burn coverage and eucalypt densities <1 m in height during the 1974–93 period (Table 7). Across all treatments, there was a significant negative relationship between total understorey density and the density of eucalypts 3–7.5 m in height (Table 7).

There were no significant treatment by time interactions for other woody taxa in any height class. Densities of other woody taxa 3–7.5 m in height did vary over time and among treatments (Table 8; Fig. S3). After incorporating covariate effects, the unburnt treatment carried a lower density of other woody taxa relative to the frequently burnt treatments (Table 8). Burn coverage had a significant negative influence on other woody taxa densities >1-m height, whereas understorey density had a significant positive influence on these height classes, across all times (Table 8). Post wildfire (2007 data), treatment effects were only marginally significant in the <1- and 3–7.5-m height classes (Table 5).

Discussion

Effects of fire regimes on richness and composition of woody understorey plants

The hypothesis that long-term frequent burning would result in changes in the composition of woody taxa in the understorey,

Table 8. Repeated-measures ANOVA results for the effects of treatment (treatment: annual, A; triennial, T; and unburnt, UB), time (relative rainfall) and covariates on woody plant taxa other than acacias and eucalypts between 1974 and 1993 in three height classes

Covariates that were not significant ($P < 0.1$) are not reported. Treatment means and least significant differences (l.s.d., at the 95% probability level) and standardised coefficients (β) for covariates are reported where effects were significant or marginally significant. ns, not significant

Source of variation	<1 m	1–3 m	3–7.5 m
Plot stratum			
Treatment	ns	ns	$F_{2,13} = 8.31$, $P = 0.005$, Means: A = 2.82, T = 4.67, UB = −4.02 (l.s.d. = 3.77)
Covariates			
Understorey density	$F_{1,14} = 3.73$, $P = 0.074$, $\beta = 1.92$	$F_{1,13} = 19.44$, $P < 0.001$, $\beta = 3.40$	$F_{1,13} = 11.20$, $P = 0.005$, $\beta = 1.52$
Burn coverage	ns	$F_{1,13} = 6.30$, $P = 0.026$, $\beta = -2.50$	$F_{1,13} = 18.5$, $P < 0.001$, $\beta = -4.30$
Plot × time stratum			
Time	ns	ns	$F_{5,74} = 2.56$, $P = 0.034$
Time × treatment	ns	ns	ns

a reduction in richness and simplification of vegetation structure was somewhat supported by our results. The density and richness of woody understorey plants >1 m in height was generally lower in the annually burnt treatment than in either the triennially burnt or unburnt treatments. However, treatments had no effect on total richness of woody plants and little effect on the density of woody plant groups <1 m in height (only eucalypts responded significantly).

Persistence of most plant taxa in the frequently burnt areas may be partly attributed to the patchiness of the fire treatments (Ooi *et al.* 2006; Penman *et al.* 2008). Fires in the annually burnt treatment were patchier in nature than those in the triennially burnt treatment owing to low fuel loads. Plot burn coverage had a significant negative influence on the richness of taxa 3–7.5 m in height, densities of other woody taxa 1–7.5 m in height and densities of eucalypts <1 m in height. This supports the idea that patchiness allows individuals to escape the effects of repeated fire, as individuals that would normally be killed or suppressed by fire are able to survive and grow in unburnt patches (Penman *et al.* 2008). If understorey plants are able to avoid the effects of fire for 1 or more years, they may be more likely to survive the next fire, because fire resistance increases with age and height in many woody plant species (Fensham and Fairfax 2006; Gignoux *et al.* 2009). Development of fire resistance is likely to be important for allowing plants to produce a seed crop, as most woody understorey plants in the study are unlikely to be able to grow from a seedling and reach reproductive maturity in the period between prescribed fires.

Henry (1961) suggested that mature acacia plants will eventually become rare, or be eliminated through frequent burning in this experiment. He reported high numbers of small acacia in the annually burnt area (from resprouting and seed regeneration) but a low proportion of these surviving to larger height classes relative to the unburnt area. Our analysis through time supports this trend. It is unlikely that the existing acacias 3–7.5 m in height in the annually burnt treatment will be replaced when they die as there are very few plants in the 1–3-m height class to replace them and acacias <1 m in height are suppressed by annual burning (Fig. 2). Some period of fire exclusion in the annual burning treatment would be necessary to allow acacias <1 m in height to grow to a height where they can resist the effects of repeated burning (i.e. escape the 'fire trap', Bond and Keeley 2005; Werner and Franklin 2010).

A significant trend through time was the decreasing density of acacias 3–7 m in height in the unburnt treatment. This suggests that the presence of fire is important for long-term persistence of *Acacia* species in the 3–7-m height class, a finding that is supported by literature for a range of *Acacia* species (Keith 1996). The 2006 wildfire did encouraged acacia regeneration, as shown by significantly higher <1-m acacia densities in the infrequent-wildfire treatment in 2007, but a lack of significant difference among treatments in the pre-wildfire data. This regeneration should replace the plants that have disappeared from the infrequent-wildfire treatment over time and we expect a transfer of these plants into the larger height classes over time. The triennial burning treatment was more beneficial than the other two treatments for long-term persistence of acacias in this forest type. However, managers should consider less frequent fire regimes to encourage smaller obligate seed regenerators that may be completely scorched by fire and may require >3 years to germinate from seed and produce fruit before the next fire (Keith 1996; Bradstock *et al.* 1997; Bradstock and Kenny 2003).

Time since fire is clearly important when studying movement of plants between different height classes. We suggest that the density decline of 1–3-m acacias and eucalypts between 1974 and 1978 in the triennially burnt treatment reflects the shorter interval between the previous burn and sampling in 1978 (<2 years), which did not allow sufficient time for the cohort to grow into the next height class. Similarly, an insufficient growth period between the 2006 wildfire and post-fire sampling in 2007 may explain the lower woody taxa richness >1 m in height in the infrequent-wildfire treatment relative to the triennially burnt treatment in 2007. The variation in time since fire among the different treatments was an unavoidable confounding effect in this study. Sampling 9–12 months after fire in the triennially burnt treatment would not allow assessment of the vegetation development at the maximum period of time between fires. Nevertheless, some future comparisons between the annually and triennially burnt treatments at the same time since fire (i.e. 9–12 months post fire) are warranted.

The measured environmental variables accounted for more of the variance in taxa composition than fire treatments alone

(46% compared with 33%). The remaining variation (21%) represented confounding effects of the environmental predictors and fire treatments, which were largely due to burn coverage variation among treatments. Our findings support those from similar forests elsewhere, that both site factors, irrespective of fire history (Bradstock *et al.* 1997; Henderson and Keith 2002; Lewis *et al.* 2012) and fire frequency have an important influence on plant composition (Henderson and Keith 2002; Spencer and Baxter 2006; Watson *et al.* 2009; Penman *et al.* 2011*b*; Wittkuhn *et al.* 2011). Our results suggest that species such as *Alphitonia excelsa*, *Lantana camara*, *Cyclophyllum coprosmoides* and *Psydrax odorata* are more likely to proliferate in long-unburnt areas than in frequently burnt forests. The finding that frequent fire reduced the density of the problem weed *L. camara* is significant and is being investigated further by the authors. The three native species associated with the infrequent-wildfire treatment are considered rainforest-associated plants (*A. excelsa*, *C. coprosmoides*, *P. odorata*) and are therefore likely to be sensitive to repeated fire (Unwin 1989; Fensham *et al.* 2003). However, all three species were able to resprout (basally or from root-stock) following the 2006 wildfire, and other woody taxa had marginally higher <1-m-height densities in the infrequent-wildfire treatment in 2007 (Table 5). Hence, occasional wildfires are unlikely to decrease the populations of these species in infrequently burnt parts of the landscape. As such, richness of woody taxa <1 m in height did not decline following the wildfire in 2006, but there was also no evidence of an increase in richness 1 year after this wildfire.

Competitive interactions are known to influence plant densities and growth (Hunt *et al.* 1999; Fensham *et al.* 2005; Debuse *et al.* 2009) and there was some evidence of competitive effects of total understorey density and basal area on the richness and densities of different height classes for the plant groups investigated here (Tables 4, 5, 7). In the 1974–93 period, tree basal area had a negative influence on total richness and richness in the 3–7.5-m height class. Across all treatments, eucalypts 3–7.5 m in height were negatively associated with total understorey density, suggesting that eucalypts may have difficulty obtaining heights >3 m where there is more intense competition from woody understorey plants. This is not unexpected, as competition among woody plants may lead to density-dependent mortality (Fensham and Bowman 1992; Hoffmann 2002; Fensham *et al.* 2005).

Effects of frequent burning on eucalypt regeneration and understorey structure

We expected that frequent burning would decrease the density of tree regeneration as juvenile trees are likely to be scorched by the repeated fires. However, our results suggest that eucalypt regeneration <1 m in height has persisted across all three treatments and was encouraged by triennial burning (Fig. 2*d*). Eucalypt regeneration in this forest type occurs mostly from lignotubers, although seedling regeneration does also occur. Results from this experiment for the first 8 years of annual burning suggested that small lignotubers may become exhausted by repeated burning (Henry 1961). However, our results show that a large regeneration pool has persisted even in the annually burnt area (e.g. 1000 plants ha^{-1} in 2007) and a large proportion of this regeneration is likely to be lignotuberous (Henry 1961). A proportion of seedlings are likely to develop a lignotuber in the period between fires in this study, a hypothesis that is supported by other studies (e.g. Walters *et al.* 2005; Fensham and Fairfax 2006; Werner and Franklin 2010). Nevertheless, the transfer of lignotuberous regeneration into the next height cohort remains suppressed by the annual burning treatment. The low densities of eucalypt regeneration 1–7.5 m in height in the annually burnt treatment (Fig. 2*e–f*) suggest that replacement of overstorey eucalypts through regeneration may require some period of fire exclusion from this treatment.

Our findings suggest that annual burning reduced the total density of woody understorey plants, resulting in a simplification of understorey forest structure. However, densities of understorey eucalypts were generally higher in the triennially burnt area than in the unburnt area. Hence, very frequent burning (i.e. annual burning) is necessary to maintain a low density of understorey plants >1 m in height (but with persistence of woody plants <1 m in height) in this ecosystem.

Conclusions

Long-term annual burning resulted in lower densities of eucalypts >1 m in height and a lower richness of woody taxa >1 m in height relative to triennial burning. However, woody plant densities and richness <1 m in height were not negatively influenced by the frequent fire regimes studied relative to the unburnt treatment. The presence of most woody plant taxa, although often suppressed, in the understorey of the frequently burnt treatments suggests that removal of frequent fire would allow at least some of these plants to mature and sustain their populations. In this respect, this component of the ecosystem is considered resilient to frequent burning over the time frame of this experiment. Thus, from a management perspective, frequent burning for a period of <55 years is unlikely to prevent woody understorey regeneration in this forest type, but does alter species composition. Further studies are needed to determine the effects of frequent fire on other components of the ecosystem.

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