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EFFECTS OF FIRE REGIME ON PLANT SPECIES RICHNESS AND COMPOSITION DIFFER AMONG FOREST, WOODLAND AND HEATH VEGETATION

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ABSTRACT

Question: Do the effects of fire regimes on plant species richness and composition differ among floristically similar vegetation types?

Location: Booderee National Park, south-eastern Australia.

Methods: We completed floristic surveys of 87 sites in Sydney Coastal dry sclerophyll vegetation, where fire history records have been maintained for over 55 years. We tested for associations between different aspects of the recent fire history and plant species richness and composition, and whether these relationships were consistent among structurally defined forest, woodland and heath vegetation types.

Results: The relationship between fire regime variables and plant species richness and composition differed among vegetation types, despite the three vegetation types having similar species pools. Fire frequency was positively related to species richness in woodland, negatively related to species richness in heath, and unrelated to species richness in forest. These different relationships were explained by differences in the associations between fire history and species traits among vegetation types. The negative relationship between fire frequency and species richness in heath vegetation was underpinned by reduced occurrence of resprouting species at high fire frequency sites (more than four fires in 55 years). However, in forest and woodland vegetation, resprouting species were not negatively associated with fire frequency.

Conclusions: We hypothesise that differing relationships among vegetation types were underpinned by differences in fire behaviour, and/or biotic and abiotic conditions, leading to differences in plant species mortality and post-fire recovery among vegetation types. Our findings suggest that even when there is a high proportion of shared species between vegetation types, fires can have very different effects on vegetation communities, depending on the structural vegetation type. Both research and management of fire regimes may therefore benefit from considering vegetation types as separate management units.

INTRODUCTION

The management of fire regimes is a significant challenge for biodiversity conservation in fire-prone ecosystems (Bowman et al. 2009; Penman et al. 2011; Moritz et al. 2014). The structure, composition and diversity of vegetation communities in these ecosystems reflects the long-term fire regime (Pausas et al. 2004; Pausas & Keeley 2014). Species in these systems are often dependent on some burning for their long-term persistence, and can be highly responsive to changes in the fire regime (Buma et al. 2013). Contemporary fire regimes are often very different from the historical regimes under which ecosystems have developed, but detailed knowledge of historical regimes, including the frequency, variability, intensity, severity, extent, and seasonality of fires, is rarely available (Russell-Smith et al. 2003; Miller et al. 2007; Bowman et al. 2011; O'Donnell et al. 2011). Conservation managers are therefore tasked with conserving fire-prone vegetation communities without sufficient knowledge of the processes necessary to maintain them.

The dry sclerophyll vegetation complexes of south-eastern Australia are one example of a fire-prone ecosystem that is highly responsive to fire regimes (Bradstock & Kenny 2003). Differences in the seasonality, intensity and severity of fire have been associated with differences in the diversity and dominance patterns of dry sclerophyll vegetation by affecting the ability of different species to survive fire and/or re-establish after fire (Morrison & Renwick 2000; Morrison 2002; Ooi et al. 2006). One element of the fire regime that has repeatedly been found to be important for the diversity and composition of dry sclerophyll vegetation is the length of inter-fire intervals (Pausas et al. 2004). Repeated short inter-fire intervals (less than 5-7 years) can cause: declines in species richness; local extinction of species that rely on seed for post-fire regeneration (obligate seeders); and divergence in species composition towards herbaceous, fire-tolerant species (Cary & Morrison 1995; Penman et al. 2008a; Penman et al. 2008b). Similarly, long periods of fire exclusion can lead to low plant richness, diversity and evenness by either allowing mid-storey shrubs to dominate and exclude understorey species (Keith & Bradstock 1994; Tozer & Bradstock 2003; Bargmann & Kirkpatrick 2015; Freestone et al. 2015), or by exhausting the seedbank of short-lived species (Lamont et al. 1991). In contrast, variability in the length of inter-fire intervals has been associated with greater richness and evenness in plant communities (Morrison et al. 1995). Variation in inter-fire intervals can promote diversity by driving differences in propagule supply among species over time, thereby preventing dominance by a single plant functional type (Keith & Bradstock 1994). As the dry sclerophyll vegetation of south-eastern Australia includes some of the most diverse vegetation communities in Australia, identifying appropriate fire management practices to promote and maintain floristic diversity is a conservation priority (Bradstock & Kenny 2003; Keith 2004).

Knowledge of species responses to fire has led to the estimation of fire intervals tolerated by different vegetation types. These are commonly known as tolerable intervals, and describe the minimum and maximum inter-fire intervals that managers should aim to generate to prevent the extinction of key plant functional types (Kenny et al. 2004). For example, based on the reproductive and fire response traits of species occurring in dry sclerophyll vegetation of south-eastern Australia, it has been recommended that managers aim for fire return intervals of between 7 and 30 years for heaths and between 7 and 30-50 years for woodlands and forests (Bradstock & Kenny 2003; Kenny et al. 2004). Fire management recommendations such as these, which are based on the vital attributes (i.e. reproductive and fire-response traits) of individual species, are focused on extremes of fire regimes, and the risk of too much or too little fire causing local extinctions of particular species through death or recruitment failure (Kenny et al. 2004; Tulloch et al. 2016). Therefore, while useful for identifying scenarios to avoid (e.g. return intervals of < 7 years), approaches based on tolerable intervals provide little guidance for managers about the specific fire regimes that will promote diverse vegetation communities (Duff et al. 2013).

Dry sclerophyll vegetation in south-eastern Australia typically occurs as a complex spatial mosaic, comprised of structurally defined forest, woodland and heath vegetation types (Keith 2004). While dry sclerophyll forests, woodlands and heaths differ in structure and dominant species, they often have considerable overlap in the composition of their species pools (Keith 2004). This similarity in species pools means that management guidelines derived from species fire-response traits are often broadly similar among these vegetation types (Kenny et al. 2004). Yet, plant species can respond differently to fire, depending on the environmental and competitive conditions they experience (Tozer & Bradstock 2003; Gosper et al. 2010; Enright et al. 2014; Torres et al. 2017). Therefore, because vegetation types differ in both abiotic (e.g. soil nutrients) and biotic conditions (e.g. canopy shading) (Keith 2004; Keith & Tozer 2012), fire regimes likely to promote biodiversity may differ among vegetation types. Therefore, an important question is whether fire management goals should differ among dry sclerophyll forest, woodlands and heaths to ensure the maintenance of floristic diversity.

In this study, we aimed to determine whether structurally defined vegetation types that have a high level of floristic similarity should be considered as separate units for fire management and research. We used a space-for-time approach, combining 55 years of fire history records with floristic surveys of 87 sites to explore associations between fire history variables and plant community attributes, addressing the question: Do associations between fire regime and plant species richness and composition differ among dry sclerophyll forest, woodland and heath vegetation types?

METHODS

Study area

We conducted this study in Booderee National Park (BNP), a ~ 6500 ha reserve located on a coastal peninsula approximately 200 km south of Sydney in south-eastern Australia (35°10′S, 150°40′E, Appendix S1). Booderee National Park is at the southern extent of the floristically diverse Sydney Coastal Heath and Sydney Coastal Dry Sclerophyll Forest vegetation types, which occur in complex spatial mosaics over sandstone. Woodlands occur in transitional areas between forests and heaths (Taws 1997; Keith 2004), and the distribution of these vegetation types is driven primarily by abiotic factors (Beadle 1954; Keith 2004; Keith & Tozer 2012). In this study, we focused on the three most widespread vegetation formations in BNP ; forests (36.2 % of the park area), woodlands (12.9 %), and heaths (15.3 %) (Taws 1997). For more detailed descriptions of vegetation types see Appendix S1. While we acknowledge that vegetation structure will vary substantially within, as well as among these vegetation types, our study focuses on broad structural vegetation types (i.e. categories), rather than direct measures of vegetation structure for two reasons: (i) broad vegetation type classifications are commonly used in conservation and land management planning, and so differences in fire responses among these types have direct application value, and (ii) vegetation structure is comprised of many different components which would make direct tests of interactions between fire history and vegetation structure overly complex to implement and interpret.

Fire in Booderee National Park

Booderee National Park has a well-documented fire history and records of fire perimeters and cause (wildfire or prescribed fire) have been maintained for fires occurring in the park since 1957 (for details, see Appendix S2). From the 55 years of fire history data, we calculated time since fire and the number of fires (fire frequency) for each of the 87 sites at which we conducted floristic surveys (Table 1, Appendix S2). We were not able to include variables relating to the mean length or variability of fire intervals in this study as many sites had burnt less than three times in the 55 year record period. Instead, we recorded whether each site had experienced an inter-fire interval of less than seven years or greater than 30 years (Table 1); outside the recommended tolerable fire intervals for dry sclerophyll heaths and woodlands (Bradstock & Kenny 2003; Kenny et al. 2004). Among the 87 sites surveyed in this study, most (79%) had burnt between one and three times in the period 1957-2012, few were long-unburnt at the time of survey (12% were > 20 years post-fire), and the length of fire intervals was highly variable (Appendix S2, Fig. S2.3).

Plant surveys

We surveyed the plant community at long-term monitoring sites which were established in 2003 to assess biodiversity responses to fire (Lindenmayer et al. 2008a; Lindenmayer et al. 2008b; Lindenmayer et al. 2016). These sites were selected in 2003 (prior to the 2003 wildfire) using a stratified randomised approach. Polygons were generated to divide the park area into units that were "homogenous" in both vegetation type and known fire history at the time of site selection (2003) (Lindenmayer et al. 2008a). Sites (maximum of one per polygon) were then selected so that they were stratified by vegetation type and time since fire, with the goal of distributing sites widely throughout the park (see Lindenmayer et al. 2008b for details, and Appendix S1 for site locations). The number of sites per vegetation type was selected to be roughly proportional to the area of that type, and for our study we included data from the 87 study sites that were surveyed in 2012-2013, and were located in our three vegetation types (forest = 40, woodland = 22 and heath = 25). Each site comprised a 100 m transect which was located so that the full transect fell within the boundary of the mapped polygon.

We conducted plant surveys once at each site between April 2012 and May 2013. Surveys were conducted within two 20 x 20 m quadrats at each site, located between the 20 and 40 m, and 60 and 80 m marks of the transect (i.e. 20 m apart), one on each side of the transect. We completed a timed 30 minute search in each quadrat (excluding breaks to identify plants), and identified each vascular plant species present according to Harden (1991), then pooled these (presence/absence) data at the site level for analysis. We used a 30 minute search time as earlier (pre-2012) surveys at these sites had indicated that extending searches beyond this time yielded few additional species.

Data analysis: Species richness

We focused our analysis on plant species richness as maintaining plant species diversity has been identified as a conservation priority for the dry sclerophyll vegetation of the Sydney Basin region (Keith 1995; Tozer & Bradstock 2003; Keith 2004). We tested for associations between the recent fire history and plant species richness using generalised linear models in R (version 3.2.3, R Foundation for Statistical Computing, Vienna, Austria). To allow the effects of fire history to vary among vegetation types, fire history variables were included as interactions with vegetation type in the full model. Variation in fire history in space-for-time studies such as ours is unlikely to be independent of underlying environmental variation because the occurrence of fire is influenced by spatially co-varying factors such as site moisture, topography and the type, quantity and dryness of fuels (i.e. living and dead vegetation) (Cheney et al. 2012). To reduce potential confounding of fire effects with other spatially related environmental factors, we therefore included key topographic variables as covariates in the models (aspect and elevation, Table 1). We did not allow any interactions other than the two-way interactions between fire history and vegetation type, as although other interactions are ecologically possible, they were not directly relevant to our study questions, and we were unable to test more complex models with the available sample size.

We fit models using the "glm" function in R, using species richness as the response variable, Poisson error distributions and a log-link function. The linear predictor for the full (maximal) model was = veg + TSF + FF + shortI + longI + veg*TSF + veg*FF + veg*shortI + veg*longI + AspE + AspN + Elev (see Table 1 for variable descriptions). We converted continuous predictor variables to z-scores prior to analysis to allow direct comparison of regression coefficients. We did not include the variable surface geology in the regression model due to a moderately strong association with vegetation type (Generalised Variance Inflation Factor [GVIF] = 7.3, $\mathrm{GVIF}^{(1/(2*\mathrm{df})}$ = 1.4, Fox & Monette 1992). All other pairwise correlations between predictor variables were less than 0.7 (Dormann et al. 2013). After checking the fit of the full models by inspecting residual plots (Zuur et al. 2009), checking for over-dispersion, and testing for spatial autocorrelation in the residuals ("correlog" function in the "ncf" package), we used Akaike's Information Criterion corrected for small sample sizes (AICc), to rank subsets of the full model ("dredge" function in "MuMIn" package) (Burnham & Anderson 2002). To reduce the number of models being compared, we retained the topographic environmental variables (aspect easting, aspect northing, and elevation) in all models and restricted comparisons to among models with different subsets of fire history variables and their interaction with vegetation type. We used the "confint" function to estimate 95% confidence intervals for coefficients in the top-ranked model, and the "predict.glm" function (both in the "R stats" package) for model predictions.

Data analysis: Species traits

To investigate whether differences in fire responses among vegetation types were associated with plant species traits, we implemented a parametric approach to the fourth corner problem, employing multivariate latent variable models (Warton et al. 2015) using the R package Boral (Hui 2016). We fit a separate model for each of two traits of interest: plant growth form when mature (shrubs, trees, herbs [non-graminoid], ferns and graminoids) and dominant fire response (obligate seeder, resprouter, or one of three intermediate levels, see Appendix S3). Trait data for each species were collated from the Australian Fire Ecology Database, available from the TRY plant trait database (Kattge et al. 2011). This model-based approach to ordination employs a hierarchical multilevel approach to fit correlated response models that combine separate species occurrence models with latent variables to account for residual variation. Species traits are incorporated into the correlated response model as random effects. Where traits are associated with responses in the correlated response model, this will be reflected in differences in the estimated model coefficients among trait groups. We fit the model using the top-ranked model from the analysis of species richness (linear predictor = veg + TSF + FF + shortI + veg*FF + veg*shortI + AspE + AspN + Elev), using presence/absence data for all individual species occurring at five or more sites (n = 196), and a probit link function. As we were primarily interested in differences in fire responses associated with species traits, we restricted the inclusion of traits to the interaction of the trait random effects with the fire (TSF, FF, shortI) and fire × vegetation type (veg*FF and veg*shortI) terms in the model. All model parameters were assigned Cauchy priors with a centre of zero and scale parameter 2.5 (Gelman et al. 2008).We also included two latent variables in the model to parsimoniously model residual correlation among species (e.g. resulting from processes such as spatial autocorrelation) (Hui 2016). We ran a single chain with 40,000 iterations with a burn in of 10,000 and a thinning factor of 30 (Robert & Casella 2004; Hui 2016).

Data analysis: Species composition

Tests of relationships between fire and species composition can be prone to confounding effects as both the occurrence of species, and the occurrence of fire are likely to be associated with underlying variation and co-variation in spatial (e.g. site proximity) and environmental factors (e.g. topography). We therefore used redundancy analysis (RDA) to test for associations between variation in fire history variables and multispecies occurrences, as these techniques can account for potentially co-varying effects of space and environment (Legendre & Legendre 2012). We conducted three separate analyses, analysing sites within each of the three vegetation types separately. This approach allowed us to compare the fire history and environmental factors that were important among the three vegetation types. To reduce spurious effects from rare species, we included only those species that occurred at > 5% of sites.

We based all multivariate analyses on three groups of explanatory variables: fire history variables (Table 1), environmental variables (Table 1), and spatial variables. Continuous fire and environmental variables were standardised prior to analysis. Spatial variables were generated using principal coordinates of neighbour matrix analysis (PCNM, “pcnm” function in the package “vegan”) (Legendre & Legendre 2012). PCNM models the spatial structure among sites via eigenvalue decomposition of a truncated matrix of geographic distances (Borcard & Legendre 2002). As this analysis relies on distances between sites, we ran a separate PCNM analysis, generating a separate set of spatial variables for each of the vegetation types. The PCNM method emphasises neighbouring sites, which is achieved by truncating all distances in the input distance matrix above a nominated threshold to an arbitrary “large” value (4 times the threshold). For our analyses, we employed a threshold distance equal to the minimum distance needed to keep all sites connected in a network (3.5 km for forest, 2.7 km for woodland and 2.6 km for heath sites). PCNM uses principal coordinate analysis to generate multiple linear spatial variables (eigenvectors) from the truncated distance matrix, which can then be used to control for spatial autocorrelation. The first PCNM vectors reflect variation at large-scales and later PCNM vectors reflect variation at smaller spatial scales (Borcard & Legendre 2002). We used ½ the number of created PCNM vectors (given they possessed positive eigenvalues) as the spatial variables in our analysis (Borcard & Legendre 2002).

Implementation of the RDA involved three steps: variable selection, redundancy analysis, and variance partitioning. For the variable selection step, we used forward selection with double stopping criteria ($P < 0.05$ and adjusted $R^2 <$ global R^2) (Blanchet et al. 2008) to select variables from each of the three variable groups (fire history, environmental and spatial variables, see Table 1), that were significantly associated with variation in the site by species occurrence matrix. For the redundancy analysis step, we used the selected variables as inputs for a canonical redundancy analysis (function “rda” in package “vegan”), to test for associations between multivariate species occurrence and fire frequency variables, after conditioning for environmental variables, and the spatial structure of sites (Legendre & Legendre 2012). Significance testing of variable groups in the redundancy analysis was performed via 999 permutations of the data, using the “anova” function in the R “stats” package. Finally, for the partitioning step, we used partial RDAs (and adjusted R-squared) to quantify the pure and shared contributions of fire history variables, environmental variables, and spatial variables (PCNM eigenvectors), to variation in multivariate species occurrence (function “varpart” in package “vegan”) (Peres-Neto et al. 2006).

RESULTS

Species richness

The most strongly supported model for species richness included fire frequency, time since fire and the occurrence of short inter-fire intervals (< 7 years), but did not include the occurrence of long fire intervals (>30 years, Appendix S4). The two fire by vegetation type interactions included in the top model indicate that associations between fire variables and species richness intervals differed among vegetation types for both fire frequency and the occurrence of short intervals, but not for time since fire. Species richness was positively associated with fire frequency in woodland, negatively associated with fire frequency in heath, and not associated with fire frequency in forest vegetation (Table 2, Fig. 1a). The occurrence of short fire intervals was associated with plant species richness only in woodland vegetation, where sites which had been subject to short fire intervals supported lower species richness than sites which had no short intervals (Table 2, Fig. 1c). In contrast, the negative association between plant species richness and time since fire was consistent among the three vegetation types, although this effect was not large and confidence intervals were wide (Table 2, Fig. 1b). None of the topographic environmental variables were strongly associated with site level species richness (Table 2).

Species traits

Fourth corner analysis of interactions between species traits and fire history variables revealed that some, but not all fire associations were related to species trait groups. Within heath vegetation, species that resprout after fire were negatively associated with fire frequency, while obligate seeding species were not (Fig. 2a, see Appendix S5 for full model tables). This trend was not apparent for forest or woodland sites. We found that all growth forms in heath were negatively associated with fire frequency, while in forest vegetation, grasses and herbs were positively associated with fire frequency (Fig. 2b). The association between species occurrences and time since fire was also related to species traits groups, with obligate seeding species and shrub species negatively associated, and ferns positively associated, with time since fire (Figs. 2c, d). We found little association between short fire intervals and species traits, except for herbs, which were negatively associated with the occurrence of short fire intervals in forest vegetation (Figs. 2e, f).

Species composition

The spatial, environmental and fire history variables associated with differences in species composition of vegetation differed among vegetation types. For forest sites, the variable selection procedure identified three spatial variables (PCNM 1, 2 and 3– all representing large-scale spatial patterns), two environmental variables (elevation and surface geology), and three fire history variables (fire frequency, time since fire, and the occurrence of long fire intervals) that were significantly associated with differences in plant species composition. However, partial RDA analysis revealed that after conditioning for the effects of spatial and environmental variables, fire history variables were not associated with differences in species composition ($P = 0.512$, Appendix S6). Variation partitioning showed that although 9.2% of variation in species composition was associated with fire history variables, all of this this was shared with the spatial and environmental components of the model (Fig. 3).

For woodland sites, the variable selection procedure identified one spatial variable (PCNM 1), two environmental variables (aspect northing and surface geology), and three fire history variables (time since fire, fire frequency and the occurrence of short fire intervals) that were significantly associated with differences in plant species composition. Partial RDA showed that after conditioning for the effects of environmental and spatial variables, fire history variables were still significantly associated with differences in species composition ($P = 0.003$, Appendix S6). Of the 20.5% variation in species composition that could be explained through variance partitioning, 12.5% was associated with fire history variables, and 7.6 % was explained by fire history variables alone (Fig. 3).

For heath sites, three spatial variables (PCNM 2 and 3 – large-scale variables, and PCNM 11 – a small-scale variable), and one fire history variable (time since fire) were selected as being associated with plant species composition. No environmental variables were selected in the variable selection component of the analysis. Partial RDA showed that time since fire was still associated with differences in plant species composition after conditioning for spatial variables ($P = 0.028$, Appendix S6). Variation in species composition that could be explained through variance partitioning was attributed to spatial variables (10.2%), with only a small amount (2.5%) attributed to fire history variables (Fig. 3).

DISCUSSION

Our study investigated whether associations between fire regime and plant species richness and composition differed among dry sclerophyll forest, woodland and heath vegetation types. Despite substantial overlap in the species pools of these vegetation types (see Appendix S2), we found that relationships between fire regime variables and plant community measures differed markedly among forest, woodland and heath vegetation. Our study suggests that fire management decisions, even those within identified tolerable ranges (Bradstock & Kenny 2003; Kenny et al. 2004), could have substantially different effects on plant communities, depending on the structural vegetation type in question. We hypothesise that these differences in fire history associations occur due to differences in abiotic and biotic conditions among vegetation types, and suggest that dry sclerophyll forests, woodlands and heaths be considered as distinct units in future fire research and management programs.

Species richness and traits

Total species richness was positively correlated with fire frequency in woodland sites, but negatively correlated with fire frequency in heath sites and showed no association with fire frequency in forest sites. Opposing relationships in heath and woodland vegetation are particularly interesting given these vegetation types share a high proportion of species (72% of the 192 species recorded in heath vegetation were also recorded at woodland sites and Jaccard similarity between heath and woodland vegetation types was 0.7, Appendix S1). Therefore, the opposing effect of fire frequency was unlikely to be due to differences in species composition (with different fire responses) between heath and woodland vegetation, but rather species responding differently to the occurrence of fire in different vegetation types. This idea was supported by the analysis of associations between fire responses and trait groups, which revealed that in heath vegetation, species that resprout after fire were negatively associated with fire frequency, while obligate seeding species were not, a pattern that was not evident in forest or woodland vegetation types. Differences among vegetation types were evident also for species growth form, where grasses and herbs (many of which resprout after fire) were positively associated with fire frequency in forest sites, but negatively associated with fire frequency in heath sites. We hypothesise that the different fire frequency associations we observed in forest, woodland and heath vegetation occurred through a combination of three interacting factors: (1) the fire regimes recorded in our study are predominantly within tolerable ranges, and so direct extirpation of plant populations due to inappropriate fire intervals was unlikely, (2) differences in vegetation structure can lead to differences in fire properties (e.g. fire intensity) between vegetation types, leading to variation in direct fire impacts on plants, and (3) vegetation responses to fire are mediated by biotic and abiotic conditions in the post-fire environment, which differ among vegetation types.

Fire frequencies for 85 of our 87 study sites ranged from one to five fires in a 55-year period (Fig. 1). This meant that both low fire frequency sites (one to two fires in 55 years, or fire return intervals of approximately 25 – 30 years) and high fire frequency sites (four or five fires, or fire return intervals of approximately 10-13 years) were, on average, within tolerable fire intervals for dry sclerophyll vegetation types (Bradstock & Kenny 2003; Kenny et al. 2004). In contrast, many other studies of the effects of fire frequency on dry sclerophyll vegetation have been in areas which have experienced average fire intervals of less than five years (e.g. Morrison et al. 1995; Watson & Wardell-Johnson 2004; Penman et al. 2008b), with some experiencing as many as three fires in three years (Bradstock et al. 1997). Such fire frequencies are outside the biological limits of persistence for many dry sclerophyll species (Bradstock & Kenny 2003), and under such conditions, the same types of species would be expected to be lost from forest, woodland and heath communities. In contrast, the fire frequencies (and corresponding intervals) recorded in our study are unlikely to have led to the direct extirpation of species, and so the responses of the vegetation community to fire frequency are likely to be mediated by both the properties of fires, as well as post-fire conditions (Keith 1995), which will differ among vegetation types.

Differences in vegetation structure and biomass mean that the three vegetation types studied will vary substantially in the quantity and spatial arrangement of fine fuels. Fine fuel is an important driver of fire behaviour (Cheney et al. 2012). Therefore, variation in fire properties among vegetation types (driven by differences in fuels) is one explanation for the different fire-history-species richness associations we observed in different vegetation types. For example, we observed that fire frequency was negatively associated with species richness in heath vegetation, particularly for resprouting species. Heath vegetation has a high density of fine fuels compared with woodlands and forests (Ingwersen 1977; Bradstock et al. 2012), meaning that fires in heath are likely to be, on average, more intense than fires in woodlands and forests (Cheney et al. 2012). Resprouting species rely on surviving fire for persistence, and in intense fires, fewer individuals are likely survive (Noble 1984; Bradstock & Myerscough 1988). This means that fire-induced mortality rates of resprouting species may have been higher in heath than other vegetation types, leading to the negative association we observed between fire frequency and species richness for heath sites, but not for sites in forest or woodland vegetation.

Differences in environmental and competitive conditions can also lead to differences in plant responses to fire (Tozer & Bradstock 2003; Gosper et al. 2010; Torres et al. 2017). While sharing many species, dry sclerophyll heaths, woodland and forests differ in both abiotic (e.g. soil depth and nutrients), and biotic conditions (e.g. canopy shading) (Keith 2004; Keith & Tozer 2012), and these differences could have led to the contrasting associations between fire frequency and species richness that we observed. For example, species richness in heath was negatively associated with fire frequency, and this negative association was related to reduced occurrences of resprouting species, grasses and herbs under high fire frequencies. This relationship was not evident in woodland and forest sites. Compared with woodlands and forests, heath vegetation is found in areas of shallow soils and low productivity (Beadle 1954; Keith 2004). Under low productivity conditions, regular fires can deplete the stored resources of resprouting species, leading to higher rates of mortality, and a consequent dominance of obligate seeding species (Clarke & Knox 2002; Clarke et al. 2005). The low productivity of heath sites may therefore have led to the negative association between fire frequency and species richness that we observed in heath but not in forest or woodland vegetation.

Differences among vegetation types in the post-fire competitive environment could also have contributed to the differences in fire-history-species richness associations we observed. In Sydney coastal heaths, fire return intervals of 10-15 years (equivalent to high fire frequency in our study) would be expected to lead to the dominance of a few tall, obligate seeding shrubs, such as *Banksia ericifolia*, which can form dense thickets, out-competing, and reducing the diversity of understorey species (Keith 1995; Keith & Tozer 2012), particularly slow-growing resprouting species (Fig. 2a, Bond & Midgley 2001). In contrast to heaths, woodlands support an open canopy of *Eucalyptus spp.* (Taws 1997) that survives, and resprouts after fire. Competition from overstorey species could slow the growth of tall, obligate seeding shrubs in woodlands, and may even prevent closed shrub thickets from forming altogether. In the absence of closed thickets, fire return intervals of 10-15 years in woodlands could promote high plant diversity by maintaining midstorey and canopy gaps (and hence ground-layer light) (Menges & Hawkes 1998), while also facilitating the establishment and persistence of a diversity of obligate seeding shrubs, which tend to decline with increasing time since fire (Fig. 2c ,d, Morrison et al. 1995; Tozer & Bradstock 2003; Freestone et al. 2015). In forest vegetation, fires often do not reach the canopy, and even if a fire is crowning, canopy species in our study area can regrow rapidly from above-ground epicormic growth (Ingwersen 1977). Fires will therefore often have limited effects on the growing conditions experienced by understorey species in our forest study system, which may explain the limited associations we found between fire history and the plant community in forest vegetation compared with heaths and woodlands.

Although these different explanations would need more targeted, and ideally longitudinal, studies to be verified (see examples from heaths: Keith & Bradstock 1994; Tozer & Bradstock 2003; Keith et al. 2007; Keith & Tozer 2012; Freestone et al. 2015), our results suggest that different processes are driving fire responses of heath, woodland and forest vegetation. Fire management regimes may therefore need to differ among vegetation types if the goal is to maintain high levels floristic of diversity in dry sclerophyll vegetation.

Species composition

Vegetation composition was associated with fire history variables in woodland and heath vegetation, but not in forests (Fig. 3). As for species richness, it is possible that the different strength of fire associations among vegetation types occurred due to differences in fire intensity and/or in the competitive environment post-fire. Fires that consume understorey and midstorey strata but not the canopy will substantially modify the conditions experienced by understory plants in woodland and heath environments, which do not have a continuous canopy, but may have a lesser effect on the understorey conditions in forests (Peterson & Reich 2008). Growing conditions may therefore undergo more change following fire in heath and woodland than in forest environments, leading to stronger associations with fire history variables (*sensu* Barton et al. 2014). Alternatively, it is possible that the weak associations between fire variables and forest species composition occurred because such effects were masked by high levels of spatial turnover in species composition within this vegetation type (variance partitioning showed that much of the explained variation in forest vegetation was shared between spatial and fire variables, Fig. 3). Because spatial and temporal turnover in species composition is often driven by similar processes (Soininen 2010), high levels of spatial turnover in species composition (as we observed here), have the potential to mask relationships between species composition and spatially aggregated processes (e.g. fire) in space-for time studies. Quantifying the level of spatial turnover in species composition should therefore be an important step in studies using a space-for-time approach to study community responses to disturbance.

Conclusions

Studies of fire regimes in dry sclerophyll vegetation are often focused on plant responses to extreme regimes, and rarely compare plant community responses among different vegetation types. This is a problem because the consequences of different management decisions within established tolerable ranges remain poorly understood (Duff et al. 2013). Our findings indicate that fire regimes within tolerable ranges may have quite variable effects among vegetation types due to differences in fire behaviour, and biotic and abiotic conditions, even when these vegetation types are comprised of highly overlapping species pools. Specifically, we found that the association between fire history variables and plant species richness and composition differed among dry sclerophyll heath, woodland and forest vegetation types, which differ in the density of fine fuels, abiotic conditions and the cover of fire-tolerant canopy species. These different associations were underpinned by differences in trait-fire history relationships among vegetation types. Our results suggest that future studies of fire-prone ecosystems should acknowledge the probability of differences in fire responses among vegetation types, even if they are floristically similar, and account for these in study design. Further, the distinct differences in fire response that we found among vegetation types indicate that consideration of different dry sclerophyll vegetation types as separate management units may be needed to effectively conserve plant diversity in these fire-prone ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Descriptions of the vegetation types of Booderee National Park.

Appendix S2. Description of the fire history of Booderee National Park.

Appendix S3. Plant species and traits

Appendix S4. Model selection table for the species richness GLM.

Appendix S5. Results of BORAL analysis.

Appendix S6. Ordination plots for the canonical redundancy analysis.

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TABLES

Table 1. Explanatory variables used in analysis of associations between fire history variables and plant species richness and composition.

Variable	Code	Description	Range	Type	Source
Vegetation type					
Vegetation type	veg	Broad vegetation type. Classification based on height and cover of tallest strata.	Forest, Woodland, Heath	Factor (3 levels)	Taws (1997)
Fire history variables					
Fire frequency	FF	The number of fires recorded as occurring at a site between 1957 and 2012.	0 to 6 (Fig. S1)	Integer	BNP fire perimeter maps
Time since fire	TSF	Time in years since the most recent fire (as of 1.7.2012). If no fire recorded the maximum of 55 years was used. Natural log transformed.	3.5 to 55 (Fig. S1)	Continuous	BNP fire perimeter maps
Intervals < 7 years	shortI	0= no interval < 7 years 1= one or more intervals < 7 years	0 or 1 (Fig. S1)	Factor (2 levels)	BNP fire perimeter maps
Intervals >30 years	longI	0= no interval >30 years 1= one or more intervals >30 years	0 or 1 (Fig. S1)	Factor (2 levels)	BNP fire perimeter maps
Environmental variables					
Aspect Easting	AspE	Aspect was split into two linear components for inclusion in analysis. Easting component = sine of the prevailing aspect of the site.	-0.99 to 0.99	Continuous	BNP digital elevation model
Aspect Northing	AspN	Aspect was split into two linear components for inclusion in analysis. Easting component = cosine of the prevailing aspect of the site.	-0.99 to 0.99	Continuous	BNP digital elevation model
Elevation	Elev	Height above sea level (m)	3.2 to 127.7	Continuous	BNP digital elevation model
Surface Geology	Geol	Dominant lithology of parent material: Young sands: grey-brown sand over Permian bedrock Old Sands: leached quartz sand veneering feldspathic sand with podzolic soil profiles Clay-sands: Clay, peat and clayey sands Gravel/rocky: quartz gravel and/or quartz-pebbly sandstone	Young sand, Old sand, Clay, Gravel	Factor (4 levels)	Abell (1992)
Spatial Variables					
Site Location	LatLong	Site latitude and longitude		Decimal degrees	Measured with handheld GPS

Table 2. Results of the generalised linear model testing the association between fire regime variables and site species richness (i.e. the total number of species detected within the two 400 m^2 quadrats at each site) across the 87 survey sites. Standardised regression coefficients and estimated 95% confidence intervals are shown for the top-ranked model (by AICc, see Appendix S4 for model selection table). Note that the reference level for vegetation type, and vegetation type × fire interactions (against which other types are compared) is Forest.

Variable		**Coefficient**	**(95% CI)**
Intercept		3.72	(3.65, 3.79)
Time since fire (ln transformed)		-0.043	(-0.082, -0.003)
Fire Frequency (FF)		-0.056	(-0.122, 0.010)
Short interval (ShortI)		0.08	(-0.056, 0.216)
Vegetation type (veg)	– woodland	0.282	(0.181, 0.383)
	– heath	-0.122	(-0.224, -0.019)
FF x veg	– woodland	0.198	(0.105, 0.292)
	– heath	-0.197	(-0.316, -0.078)
ShortI x veg	– woodland	-0.248	(-0.472, -0.026)
	– heath	0.236	(-0.055, 0.518)
Aspect easting		-0.007	(-0.042, 0.028)
Aspect northing		-0.014	(-0.049, 0.022)
Elevation		0.019	(-0.021, 0.058)

FIGURES

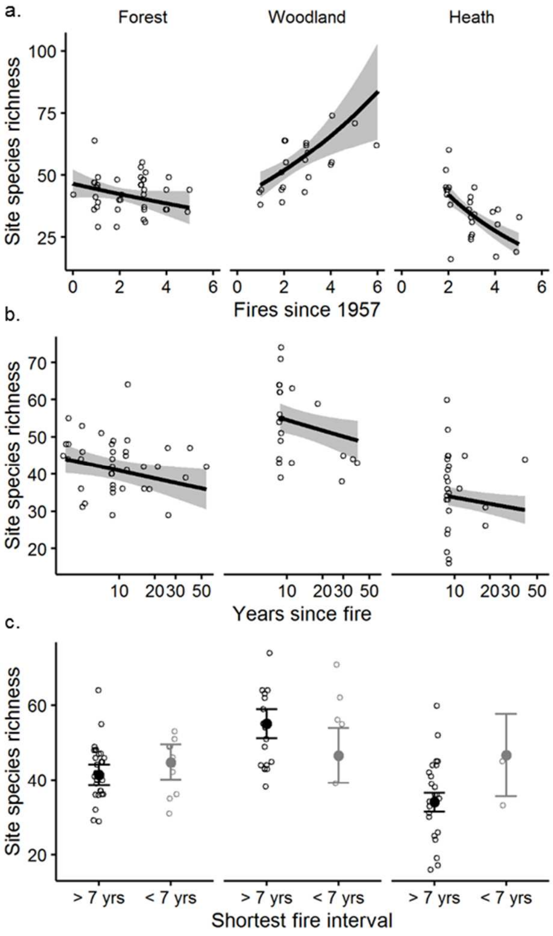


Figure 1. Relationship between (a) fire frequency, (b) time since fire, and (c) the length of the shortest fire interval and site species richness (total number of species detected within the two 400 m^2 quadrats at each site) within different vegetation types in Booderee National Park. Predicted values from the top-ranked GLM and 95% confidence intervals, as well as raw values (open circles, n = 87) are shown. Variables not depicted in the plot that were included in the top-ranked model (see Table 2, Appendix S4) were held at the median for that vegetation type for predictions (mode for categorical variables).

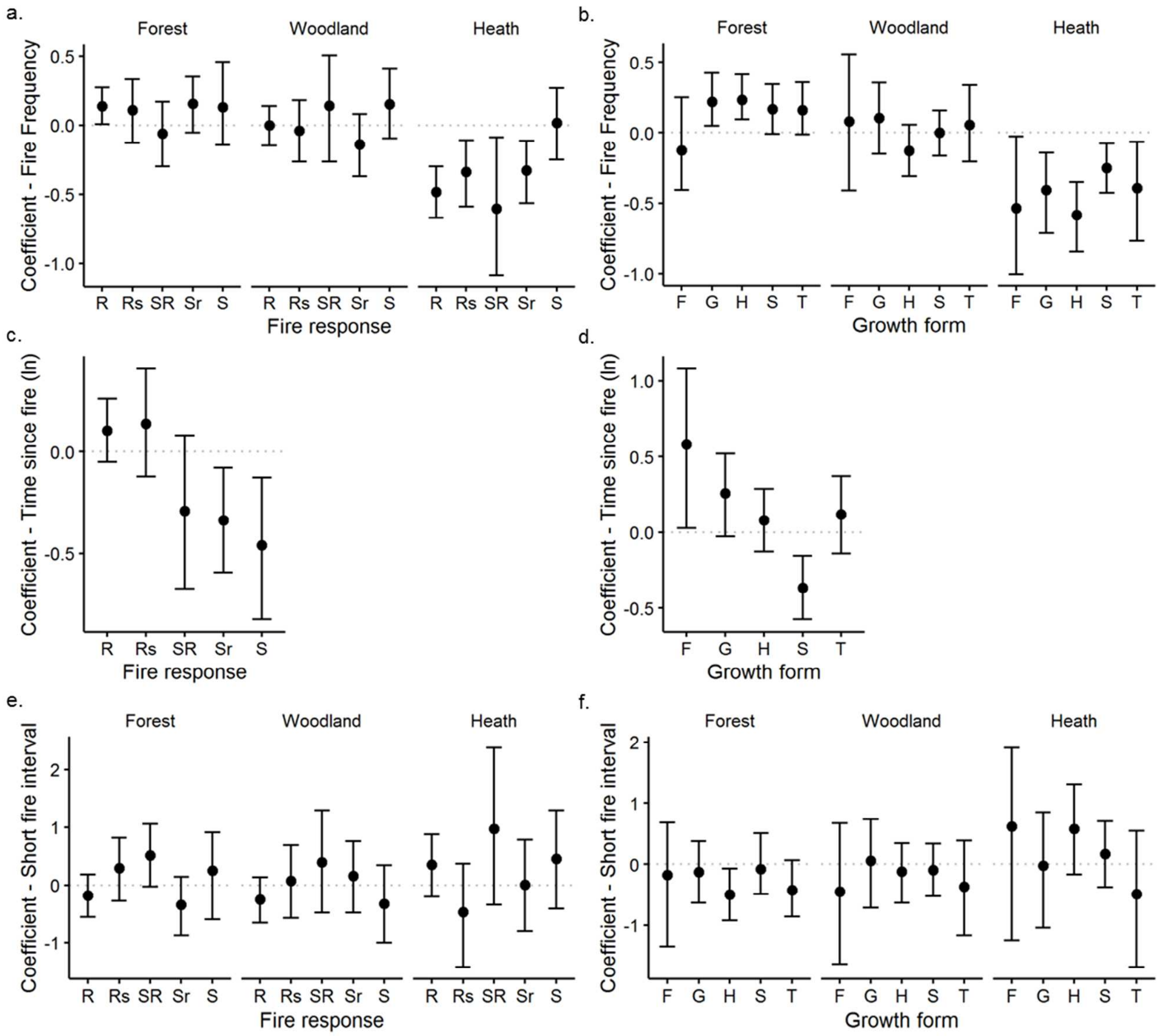


Figure 2. Results of BORAL analysis testing association between fire regime and the occurrence of plant species belonging to different trait groups. Panels a,c and e represent estimated trait group coefficients (and 95% credible intervals) for species fire response (R = resprouter, Rs = resprouter with some seeding capacity, SR = both reseeds and resprouts, Sr = seeder with some capacity for resprouting, S = obligate seeder). Panels b, d and f represent estimated trait group coefficients (and 95% credible intervals) for species growth form (F = ferns, G = graminoids, H = herbs [excluding graminoids], S = shrubs, T = trees). Where the 95% credible intervals of estimated model coefficients do not overlap zero, this indicates that there is an association between that trait group and species' relationships with fire history variables.

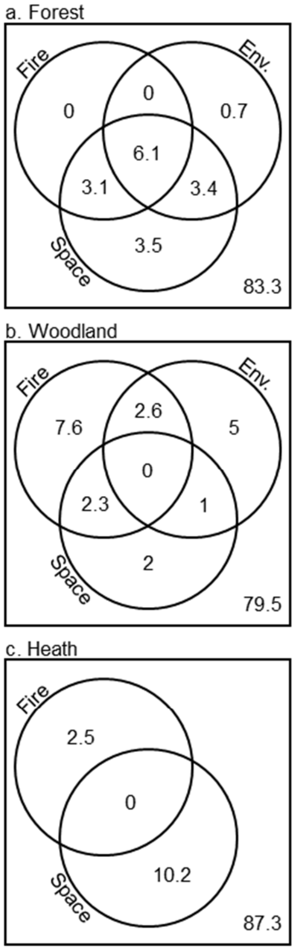
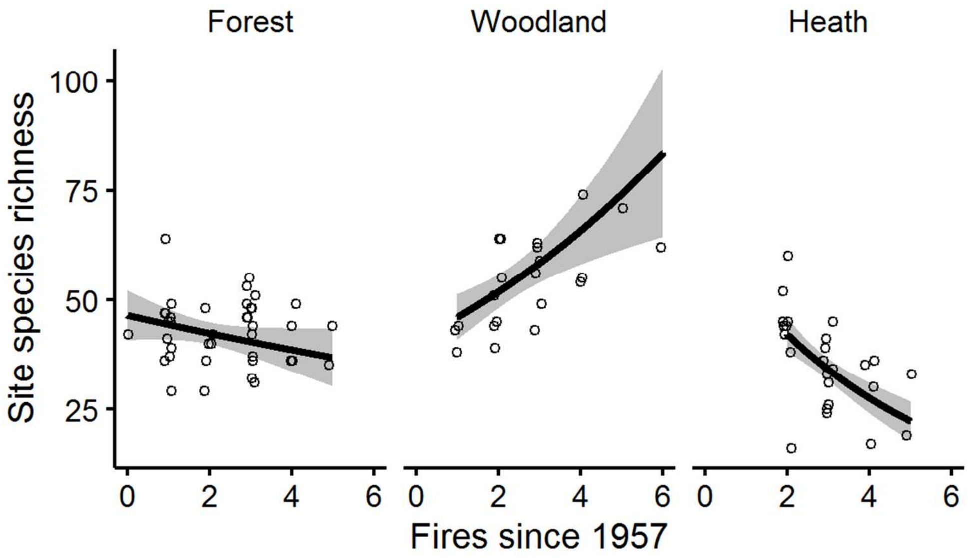


Figure. 3. Results of variance partitioning based on the RDA adjusted R^2, for (a) forest (n=40), (b) woodland (n=22) and (c) heath (n=25) vegetation, showing the percentage of variation in species composition explained by fire history, environmental (Env.), spatial and shared components.

60 word summary

We investigated associations between fire history and plant species richness and composition in three structurally defined vegetation types. Fire frequency was positively associated with species richness in woodland, negatively associated in heath, and unrelated to species richness in forest. These different associations are likely unpinned by variation in fire behaviour, abiotic conditions and biotic interactions among forests, woodlands and heaths.



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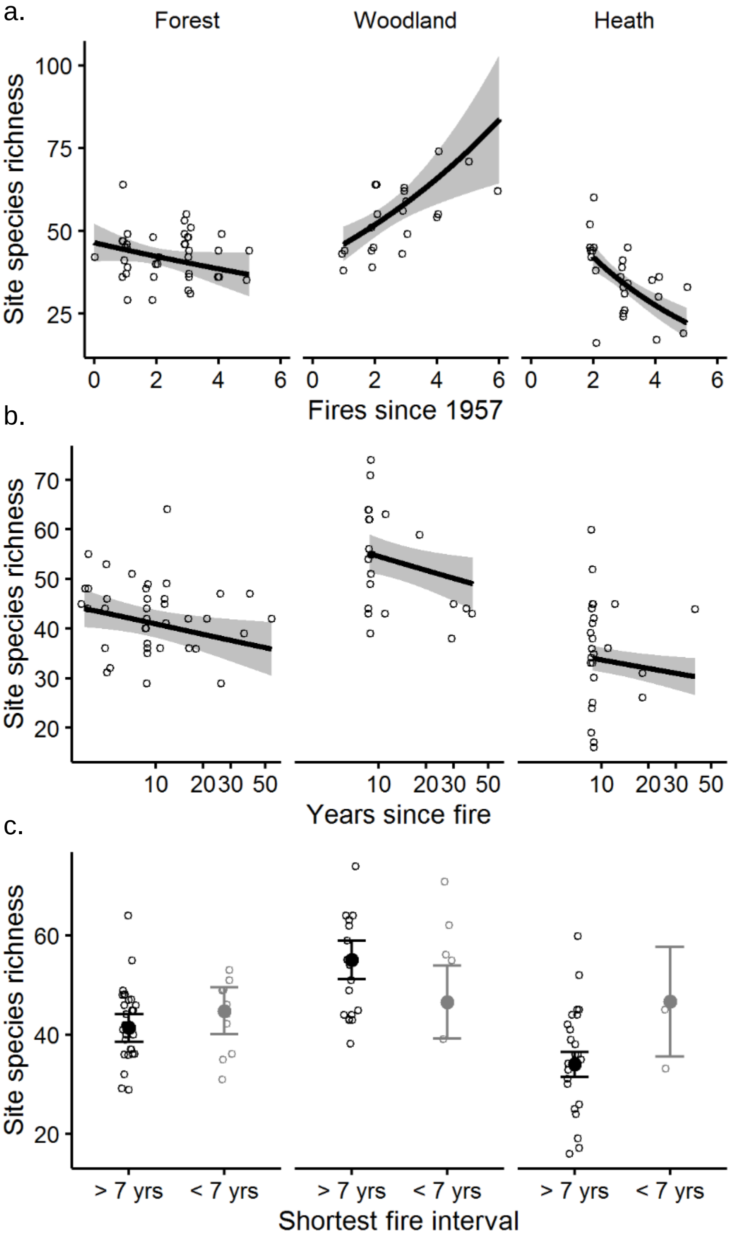
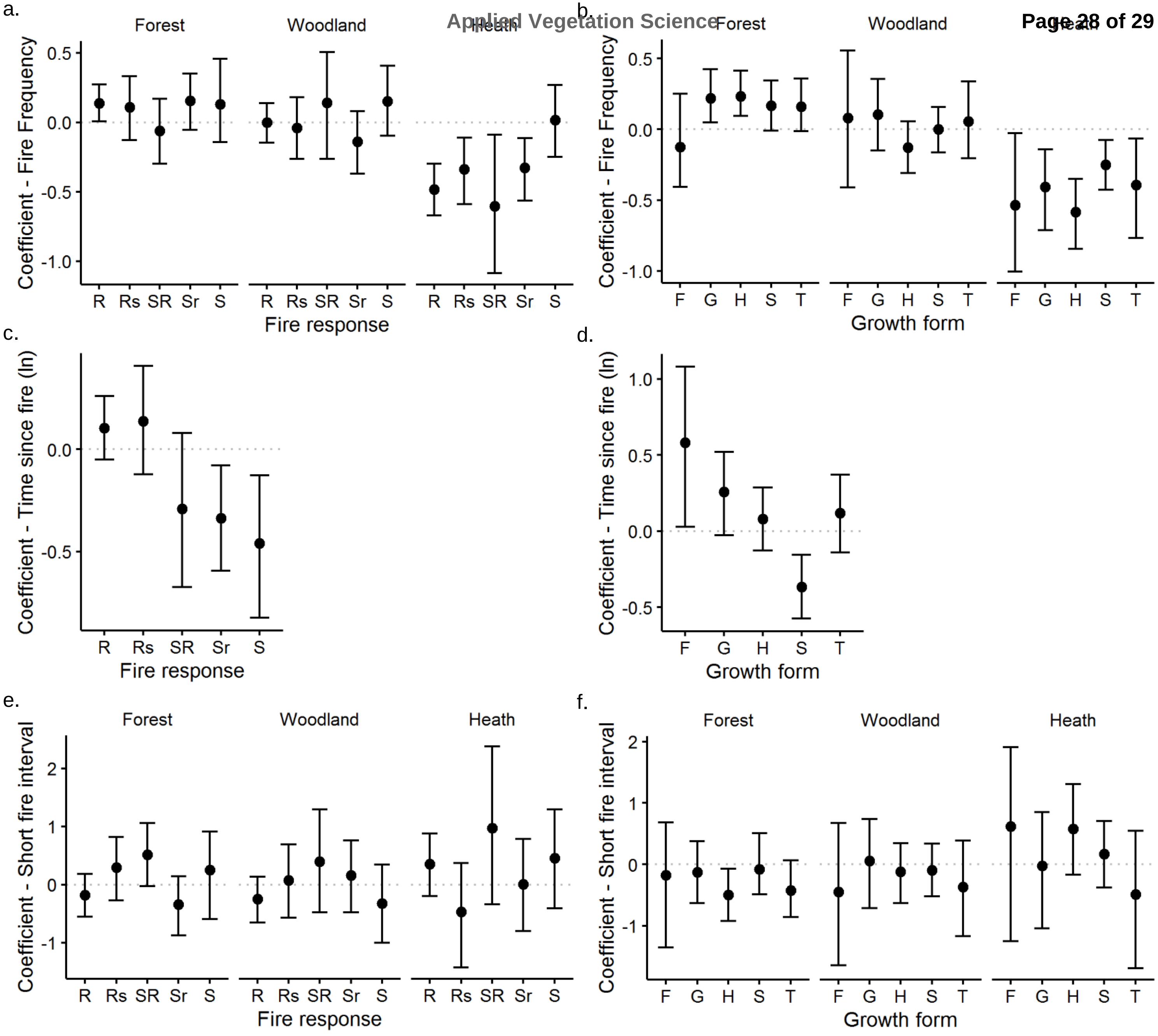
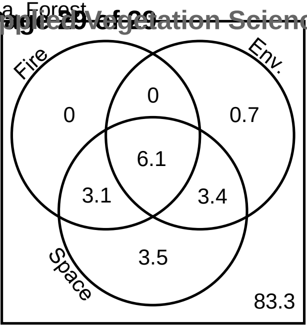
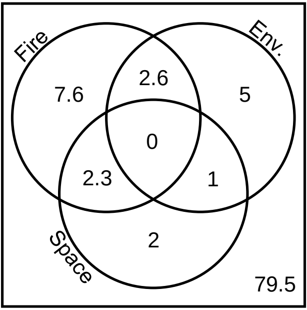

a.
Forest
Woodland
Heath
Site species richness
100
75
50
25
0
2
4
6
Fires since 1957
b.
Site species richness
70
60
50
40
30
20
10
20
30
50
Years since fire
c.
Site species richness
60
40
20
> 7 yrs
< 7 yrs
Shortest fire interval


a.
Forest
Woodland
Heath
Coefficient - Fire Frequency
0.5
0.0
-0.5
-1.0
R Rs SR Sr S
Fire response
b.
Forest
Woodland
Heath
Coefficient - Fire Frequency
F G H S T
Growth form
c.
Coefficient - Time since fire (ln)
R Rs SR Sr S
Fire response
d.
Coefficient - Time since fire (ln)
1.0
0.5
0.0
-0.5
F G H S T
Growth form
e.
Forest
Woodland
Heath
Coefficient - Short fire interval
2
1
0
-1
R Rs SR Sr S
Fire response
f.
Forest
Woodland
Heath
Coefficient - Short fire interval
F G H S T
Growth form

a. Forest



b. Woodland



c. Heath