Changing dominance of key plant species across a Mediterranean climate region; implications for fuel types and future fire regimes

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ABSTRACT

Herbaceous and woody plants represent different fuel types in flammable ecosystems, due to contrasting patterns of growth and flammability in response to productivity (moisture availability). However, other factors, such as soil type, fire regimes and competitive interactions may also influence the relative composition of herbaceous and woody plants within a community. The Mediterranean climate region of south eastern Australia is transitional between two contrasting fuel systems; herbaceous-dominated in the dry north, versus woody-dominated shrublands in the relatively moist south. Across the rainfall gradient of the region, there are confounded changes in dominant soil types and fire frequency. We used model-subset selection using Akaike's Information Criterion to examine potential driving mechanisms of community compositional change from herbaceous (e.g. *Triodia scariosa, Austrostipa* sp.) to woody plants (e.g. *Beyeria opaca*, *Leptospermum coriaceum, Acacia ligulata*) by measuring relative cover across combinations of rainfall, time since the last fire (TSF) and soil type. We examined the relative influence of environmental versus competitive interactions on determining the cover of perennial hummock grass, *Triodia scariosa*, and co-occurring woody shrubs. Rainfall and soil types, rather than competition, were the over-arching determinants of the relative cover of grasses and shrubs. Given the sensitivity to rainfall, our results indicate there is strong potential for the nature of fuel, flammability and fire regimes to be altered in the future via climate change in this region.

1 INTRODUCTION

Foliage (live or dead) constitutes fuel for fires. Processes controlling the growth and state of foliage will therefore have a major bearing on fire regimes, in addition to weather and ignitions (Pausas and Bradstock 2007; Bradstock 2010). For example, the amount of foliage and its spatial connectivity will tend to increase with moisture, thereby promoting fire, but high moisture also has the potential to inhibit fire by causing foliage to be too moist to burn (Bond and Keeley 2005; Archibald et al. 2009).

Moisture also influences fire by determining the distribution and abundance of species which have the potential to dominate plant cover (Bradstock 2010; Lehmann et al. 2011). Dominance by either grasses and herbs or woody plants (i.e. trees and shrubs) is a key dichotomy in fuel systems. Grasses and shrubs have contrasting patterns of growth and flammability (Murphy et al. 2013; Pausas and Paula 2012). For example, ephemeral grasses respond rapidly to fluxes in resource availability, while woody plants use more stable resources, such as deeply stored water and exhibit more regular growth patterns (Ogle and Reynolds 2004). Therefore fire typically occurs in communities dominated by ephemeral grasses after periods of above average rainfall, due to increased biomass (Bradstock 2010; Pausas and Paula 2012). By contrast, fire in communities dominated by woody plants is influenced by regular patterns of woody litter fuel accumulation and preceding drought conditions, which influence fuel moisture content (Bradstock 2010; Pausas and Paula 2012).

Dominant plant life forms, and therefore alternative fuel systems, are influenced by other factors such as edaphic conditions, fire regime effects and competitive interactions. For instance, the rooting depth of grasses is typically not as deep as shrubs (Schenk and Jackson 2002), hence soils with contrasting infiltration rate and water holding capacity may promote dominance of one life form over the other (Ogle and Reynolds 2004; Wills and Clarke 2008). Fire regimes with different frequency and severity characteristics may also promote dominance of one life form over the other (Sankaran et al. 2005). Relative differences between shrubs and grasses in response to environmental conditions may influence competitive interactions (Throop et al. 2011).

Mediterranean-type ecosystems contain a variable mix of herbaceous and woody plant species. attributable to variations in phylogeny, soils, climate and fire regimes, both within and between different regions of the world (Keeley et al. 2012; Pausas and Bradstock 2007). The Mediterranean climate region of south eastern Australia is a transitional zone positioned between the arid zone to the north and temperate forests and shrublands in the wetter, temperate south (Pausas and Bradstock 2007). In the arid zone, fire is limited by fuel connectivity and mass, except when ephemeral herbs and grasses respond vigorously to periodic heavy rainfall (Bradstock 2010). By contrast in the south, spatially continuous surface litter fuels accumulate in a regular manner and become available to burn under combined antecedent drought and concurrent fire weather conditions (Bradstock 2010). Previous research across this region indicates that fire frequency is positively correlated with rainfall and woody plant cover (i.e. shrub and tree cover, Pausas and Bradstock 2007). However, with an increase in total rainfall, there is also a change in rainfall seasonality and dominant soils across the region; rainfall becomes winter-dominated (Hutchinson et al. 2005) and soils change from solonised brown earths (i.e. red/brown, alkaline and more fertile) to solodised solonetz soils (i.e. pale/yellow, acidic and less fertile) in a southerly direction (Blackburn and Wright 1989). Given the largely confounded nature of potential environmental drivers of changes in fuel systems and fire regimes, the processes that control this transition are not well understood.

We addressed the following questions, through comparative analyses of the cover of key fuel elements along the rainfall gradient within the Mediterranean region of southern Australia:

1. How do rainfall, time since last fire (TSF, an indicator of potential fuel accumulation) and soils influence the relative cover of the key species?
2. Is competition from dominant woody life-forms (i.e. trees and shrubs) a determinant of grass and herb abundance?
3. How are such competitive effects mediated by variations in rainfall, TSF and soils?
4. Do potential interactions of environmental and competitive effects with TSF cause a shift in the relative influence of key species on how fire probability changes with TSF?

The timing of this study (2010-2011) provided an opportunity to examine ephemeral plant cover following one of the strongest La Niña events on record, where significantly higher than average rainfall occurred for approximately eight months from late 2010 to early 2011 (BOM 2013). Extensive rainfall events, particularly those associated with the La Ninã phase of the El Ninõ/Southern Oscillation (ENSO), prompt population booms of ephemeral and annual plants (Letnic et al. 2005). In arid regions, this increase in fuel biomass leads to an increased risk of extensive wildfires in the years immediately after exceptional rainfall events (Letnic and Dickman 2006).

2 METHODS

2. 1 Study Area

The study area encompassed the Murray Lowland province in the semi-arid region of south eastern Australia (Fig. 1), across undulating dune fields of aeolian sands. Eucalypts with the multi-stemmed mallee growth habit are the dominant life form in the region, occurring on the infertile sandy substrates under rainfall from approximately 200-600mm/year (Bradstock and Cohn 2002). As total rainfall increases across this region, there are corresponding changes in temperature and rainfall seasonality. Temperatures become cooler and rainfall becomes winter-dominated (Hutchinson et al. 2005).

Solonised brown earth (hereafter ‘red sands’) soils dominate the study area from 220-370mm/year. These soils are alkaline with poor to moderate fertility and support semi-arid mallee woodlands with and understory comprised of *Triodia scariosa*, shrubs and ephemeral herbs (Blackburn and Wright 1989). Solodised solonetz are pale/yellow in colour (hereafter ‘yellow sands’) and occur where rainfall exceeds 300mm/year. These sands are relatively more acidic, less fertile and more coarse than the red sands and commonly support mallee heath with a diversity of sclerophyllous shrubs (Blackburn and Wright 1989). In the transitional zone from 300-370mm/year, *Triodia scariosa* occurs on both the red and yellow sands, but is largely absent further south where mallee heath vegetation occurs on yellow sands.

Species in fire-prone landscapes, such as the Mediterranean region of south eastern Australia, respond to fire by vegetative regrowth (i.e. resprouters such as *Triodia scariosa, Eucalyptus* sp. and *Melaleuca uncinata*) or by regeneration from a soil or canopy-stored seedbank (i.e. obligate seeders such as *Beyeria opaca, Callitris verrucosa* and *Westringia rigida*; Bradstock and Cohn 2002; Clarke et al. 2013). Previous research in this region indicates that as rainfall increases, the proportion of obligate seeders declines while resprouters increase, corresponding with an increase in fire frequency (Pausas and Bradstock 2007).

2. 2 Site Selection

Sites were selected in each of three categories of rainfall; low (220-240mm/yr), moderate (260-280mm/yr) and high (310-330mm/yr). Each site represented a contiguous area of at least 100 square metres in size, where the vegetation appeared to be of an even age-class (i.e. evenly burnt in the last fire). At each site, a 50 metre transect was set up, with the starting point randomly selected. In order to examine how competitive interactions may change with TSF, we used space-for-time substitution whereby three TSF categories were sampled within each rainfall category; recent (<10 years), medium (20-40 years) and long (>60 years). Fire history mapping from State government agencies (NSW, SA and Victoria) was used for site selection. Sites were selected on each of the sand types at high rainfall only, where both types co-occur. A total of 48 sites were selected for field sampling. This included 4 replicate sites within each combination of rainfall and TSF on red sands, plus 4 sites in each TSF category at high rainfall on yellow sands.

Sites were selected within the perimeters of past wildfires only, due to wider availability. Care was exercised to ensure each transect was situated within an evenly burnt patch of target TSF. Although fire frequency may effect community composition and structure (Watson et al. 2009), differences in mean fire return interval were unavoidable in site selection as fire frequency increases with increasing rainfall in the region (Pausas and Bradstock 2007). At low rainfall, all sites had been burnt only once during the period of fire history records, whereas sites at moderate and high rainfall had either been burnt once or twice. In cases where sites had multiple previous fires, the minimum fire return interval was greater than 30 years. Given that the heavier textured soils of swales support a different mix of herbaceous species and woody shrubs than dunes (Bradstock and Cohn 2002), sites were chosen on crests of east-west trending dunes in order to ensure consistency in comparisons of community composition across rainfall, TSF and sand categories.

Replicate transects were mostly sampled within the perimeter of a single fire for each TSF category due to the limited availability of discrete wildfires of equivalent age. The distance between transects was maximised to improve their spatial independence. In moderate and long TSF, transects were 1-2km apart, as the area available to sample was generally >10,000 hectares. However, in recent TSF sites at low, moderate and high rainfall, transects were 100-500 metres apart, as the size of these fires were relatively small (< 800 hectares).

2. 3 Cover

On each transect, the first 25 individuals of each life form (shrub and *T. scariosa*) within 1 metre either side of the transect line were selected. The size of each individual hummock and shrub (height and two perpendicular measurements of width) was measured. The distance at which the 25th individual occurred along the transect was used to calculate the area sampled and to estimate cover. For each mallee eucalypt intersecting the transect, the length and width of the canopy was measured. Due to the high densities of individual shrub seedlings in the recent TSF classes, shrub cover was estimated in ten evenly spaced plots ($1m^2$) along the transect, rather than selecting the first 25 individuals. Similarly, the cover of ephemeral fuels was estimated in ten even spaced plots ($1m^2$) along the transect in each TSF class. In general, litter fall is confined to the space beneath the canopy of perennial plants, therefore, the cover of bare ground was inferred from the sum of cover of all perennial plants across each transect.

2. 4 Nearest neighbour

Nearest neighbour analysis assumes that a positive correlation between the distance separating the neighbouring plants and the sum of their sizes is evidence of competition (Pielou 1962; Shackleton 2002). This approach was used to test for the presence of interspecific competition among *T. scariosa* and shrub individuals. Given that *T. scariosa* cover was expected to diminish with increasing rainfall due to increased competition with shrubs, the presence and/or strength of intraspecific competition was predicted to diminish accordingly, while interspecific competition was predicted to increase.

In order to scrutinise potential effects of rainfall, TSF and sand type on competitive interactions, nearest neighbour data was collected along each transect sampled for cover. Between five and ten *T. scariosa* individuals were selected at least five metres apart on each transect. Target *T. scariosa* individuals were selected so that no two plants shared any nearest neighbours, thus ensuring independent sampling. For each plant, canopy volume was estimated, rather than canopy area as previous reports have suggested the use of canopy area is too simplistic (Shackleton 2002). We investigated effects of the five nearest neighbours, to avoid the potential case in which another close neighbour may be larger than the first nearest neighbour and thus could have an over-riding influence on the size of the target plant (Pielou 1962; Shackleton 2002).

2. 5 Statistical Analysis

Cover Data

Effects of rainfall, TSF and sand type on the cover of each growth form; eucalypts, *T. scariosa,* shrubs, and ephemerals, were explored using analysis of variance (ANOVA) and

Tukey's Honestly Significant Difference (HSD) tests on the ANOVA models. Rainfall (low/moderate/high), TSF (recent/medium/long) and sand type (red/yellow) were represented as factors, while the cover of each of the alternative perennial life forms (shrubs, *T. scariosa* and/or eucalypts) was included as a covariate. As sand type effects could only be tested for one level of rainfall (i.e. high rainfall, where they co-occur), TSF and sand type were included in a separate analysis for each growth form. All models were tested for normal distribution of errors using the Shapiro-Wilks test on the residuals. Eucalypt and *T. scariosa* cover required a square root transformation, and ephemeral cover required a quartic root transformation to achieve normality. All analyses were done using R, v.2.13.1 (R Development Core Team 2011).

The cover of target perennial species (eucalypts, *T. scariosa* and shrubs) may be influenced by competition from the other perennials. Therefore, each cover analysis included the cover of alternative perennial species along with rainfall, TSF and sand type as potential predictors. Similarly, the cover of perennial plants may competitively influence ephemeral cover. Therefore the influence of rainfall, TSF and sand type on total cover of combined perennial plants was initially examined. Then ephemeral cover was analysed in relation to the combined cover of perennial plants (eucalypts, *T. scariosa* and shrubs) along with rainfall, TSF and sand.

Nearest Neighbour Effects

To test for intraspecific competition, the classic nearest neighbour method (equation 1) was used, along with all combinations of effects and interactions of the environmental variables

(TSF, rainfall and sand type) as explanatory variables to produce the candidate set of GLMs. The equation takes the form:

$$(\sum \mathrm{SizeTN}_{1:x} + \mathrm{T}_{size}) \sim (\sum \mathrm{Dist.SN}_{1:x}) + (\text{environmental variables}) \qquad (1)$$

Where '$\sum$SizeTN$_{1:x}$' represents the summed size of the 'x' number of conspecifics (i.e. *T. scariosa*) plants within the nearest 5 neighbours, 'T$_{size}$' represents the size of the target *T. scariosa* and '$\sum$Dist. TN$_{1:x}$' represents the summed distance to each of the *T. scariosa* neighbours from the target *T. scariosa.* A positive correlation between the response variable (summed size of the target *T. scariosa* and *T. scariosa* neighbours) and the distance explanatory variable (summed distance from the target *T. scariosa* to its *T. scariosa* neighbours) was expected to provide evidence of competition. Any competitive effects will be expressed as an inverse relationship between plant size and distance to conspecific neighbours.

A variation of this formula was used to test for interspecific competition between shrubs and *T. scariosa,* by replacing the summed size and summed distance of intraspecific neighbours with that of shrub neighbours using the formula:

$$(\sum \mathrm{SizeSN}_{1:x} + \mathrm{T}_{size}) \sim (\sum \mathrm{Dist.SN}_{1:x}) + (\text{environmental variables}) \qquad (2)$$

Where '$\sum$SizeSN$_{1:x}$' represents the summed size of the 'x' number of shrubs within the nearest 5 neighbours, 'T$_{size}$' represents the size of the target *T. scariosa* and '$\sum$Dist. SN$_{1:x}$' represents the summed distance to each of the shrub neighbours.

Using the classic nearest neighbour formula may be problematic in testing for interspecific competitive interactions between shrubs and *T. scariosa*. A positive correlation between ($\sum SizeSN_{1:x}$ + T_{size}) and ($\sum$ $Dist.SN_{1:x}$) (see equation 2) had the potential to reflect competitive interactions between the shrub neighbours themselves (irrespective of the presence of *T. scariosa*), given that shrubs were usually much larger than *T. scariosa* in medium and long TSF classes. Therefore, a comparison of the results from equation (2) was made to an alternative equation (3) that excludes the size of the target *T. scariosa* from the response variable, to examine whether the presence of *T. scariosa* made a difference to the relationship between summed size and distance to neighbours, using the formula:

$$(\sum SizeSN_{1:x}) \sim (\sum Dist.SN_{1:x}) + (\text{environmental variables}) \qquad (3)$$

An additional variation on the classic nearest neighbour formula was implemented to test for interspecific competition between shrubs and *T. scariosa* using the formula:

$$T_{size} \sim (\sum SizeSN_{1:x} * \sum Dist.SN_{1:x}) + (\text{environmental variables}) \qquad (4)$$

A negative correlation between the size of the target *T. scariosa* and the summed size and distance to shrub neighbours was expected to provide evidence of a competitive effect of shrubs on *T. scariosa*.

The effects of rainfall and TSF on intra- and interspecific competition were examined in separate analyses to the effects of TSF and sand type because yellow sand was sampled at high rainfall only. Model-subset selection using Akaike's Information Criterion corrected for small sample size (AIC_c) was done to identify the best model from the full set of candidate generalised linear models (GLMs) (Burnham and Anderson 2002). Any model within 2 AIC_c points of the top model (i.e. the model with the smallest AIC_c) was considered to have strong support (Burnham and Anderson 2002). All effects or interactions represented in the best set of models (i.e. all models within 2 AIC_c points of the top model) were analysed for their relative importance in explaining total deviance using hierarchical partitioning (MacNally 2000). In all cases, the response variable was transformed to meet the assumptions of normality, determined by the Shapiro-Wilks test on the residuals of the model.

3 RESULTS

3. 1 Factors controlling the cover of contrasting plant growth forms

Eucalypt cover was significantly influenced by TSF and rainfall, whereby cover increased with TSF ($p < 0.0001$, Table 1, Figure 2a) and rainfall ($p=0.016$, Table 1, Figure 2b). There was no effect of sand type or shrub and *T. scariosa* cover on eucalypt cover.

A significant interaction between rainfall and TSF influenced *T. scariosa* cover, whereby cover increased with TSF at low and moderate rainfall, but not at high rainfall, where it remained low ($p < 0.0001$, Table 1, Figure 2c.). There was no effect of sand type, shrub or eucalypt cover on *T. scariosa* cover.

Shrub cover was significantly influenced by rainfall, sand type and eucalypt cover. Shrub cover was lower at low rainfall compared to moderate and high rainfall ($p = 0.045$, Table 1,

Figure 2d), higher on yellow sand than red sand (p = 0.003, Table 1, Figure 2e) and there was a significant negative correlation of shrub cover with eucalypt cover (p = 0.04, Table 1 and Figure 2f). There was no effect of *T. scariosa* cover on shrub cover.

Total perennial plant cover was significantly influenced by rainfall and TSF, where cover was higher at moderate, compared to low and high rainfall (p = 0.043, Table 1 and Figure 2g) and increased with TSF (p<0.0001, Table 1 and Figure 2h).

Ephemeral cover was significantly influenced by interactions between TSF and rainfall and between TSF and sand. Ephemeral cover increased with TSF at low rainfall, but decreased with TSF at moderate and high rainfall (p = 0.0007, Table 1 and Figure 2i). At high rainfall, ephemeral cover significantly decreased with TSF on yellow sand, but not red sand (p = 0.006, Table 1 and Figure 2j). Perennial cover did not have a significant influence on ephemeral cover.

3. 2 Competitive interactions within and between key species

The preferred model testing for the effects of TSF and rainfall on intraspecific competition between *T. scariosa* plants (i.e. lowest AICc) contained a significant positive relationship between target *T. scariosa* plants and their *T. scariosa* neighbours (p = 0.007, equation 1; Table 2), which did not interact with rainfall or TSF classes. The preferred model testing for the effects of TSF and sand on intraspecific competition between *T. scariosa* plants contained a significant interaction between distance to neighbours and sand type. There was a positive correlation between the summed size of the target *T. scariosa* plants and their *T. scariosa* neighbours and the summed distance to the neighbours that occurred on red sand but not yellow sand (p=0.003, equation 1, Table 3 and Fig**.** 3a).

There was a significant positive relationship between the 'summed size of the target *T. scariosa* and size of shrub neighbours' with the 'summed distance to shrub neighbours', consistent across TSF and rainfall/sand categories (equation 2, Table 2 and Table 3, Fig**.** 3a). However, there was no difference between the results using equation (2) and equation (3) which removed the target *T. scariosa* size from the response variable. This suggests that intraspecific competition between shrubs was having an over-riding influence on the result. The best model of *T. scariosa* size (i.e. equation 4) contained a significant interaction of rainfall and TSF (equation 4, Table 2 and Fig**.** 3b) but did not contain the explanatory variable of 'summed size and distance to shrub neighbours'. Therefore, any competitive effects of shrubs on *T. scariosa* were not detected in this study.

3. 3 Dominance of key species across the landscape

At low rainfall, cover of grasses was strongly dominant in medium and long TSF classes (approximately 30-50%), with shrubs and grasses approximately equal at recent TSF (Fig. 4). At moderate rainfall, cover of grasses was strongly dominant at long TSF (approximately 30%), while the cover of shrubs and grasses was approximately equal at recent and medium TSF. At high rainfall on red sand, shrub cover was dominant over grass cover by approximately 25% at medium TSF, while the cover of shrubs and grasses was approximately equal at recent and long TSF. At high rainfall on yellow sand, shrub cover was strongly dominant irrespective of TSF (approximately 25%).

4 DISCUSSION

The cover of species that constitute different fuel types varied strongly across Mediterranean climate mallee woodlands, in accordance with predictions. A transition occurred from predominantly grass and herb cover to woody shrub cover as rainfall increases and sand types change across the study area (Fig. 4). Our results suggest that rainfall and sand types, rather than competition, were the over-arching determinants of the relative cover of grasses and shrubs (Table 2 and 3). Eucalypt cover was an exception to this pattern, as there was no significant linear response to increasing rainfall, or an effect of sand type (Table 1). Unexpectedly, perennial cover did not significantly influence ephemeral cover, indicating that ephemeral cover was not driven simply by the available space between perennial plants. Sampling took place during the wettest 24-month period on record for Australia (703mm in 2010 and 708mm in 2011, both well above the long-term average of 465mm/yr; BOM 2013). As ephemeral cover is responsive to recent rainfall, our measurement of ephemeral cover is likely to be particularly high. Given the sensitivity to rainfall of understory fuel elements, the results suggest there is strong potential for the nature of fire regimes to be altered in the future via climate change mediated shifts in fuel types and flammability in these mallee woodlands.

4. 1 The role of competition

Intraspecific competition between *T. scariosa* plants and among individual shrubs may affect plant dimensions (Fig. 3). Furthermore, we found evidence that eucalypt cover had possible negative, competitive effects on shrub cover, but not on *T. scariosa* cover (Fig. 2f). We found no evidence, however, of competitive suppression of *T. scariosa* by woody shrubs. Resource use between contrasting life-forms can be separated in space and/or time (February et al.

2011; Fowler 1986). For example, the extensive, fine root morphology of grasses generally occurs at shallower depths compared to the root systems of shrubs (Schenk and Jackson 2002; Throop et al. 2011). The presence of intraspecific competition in both *T. scariosa* and shrubs, along with the lack of competition between perennial grasses and shrubs suggests that resource partitioning may occur between the contrasting life-forms in this region. Therefore, dominance of one fuel type over the other across the mallee landscape is most likely controlled by relative suitability to environmental conditions, and not by competitive interactions.

4. 2 Mechanisms underlying rainfall and soil effects

Rainfall had opposite effects on the contrasting understory fuel types. *Triodia scariosa* cover declined with increasing rainfall, while shrub cover increased. Grasses with C_4 photosynthesis, such as *T. scariosa,*,are more likely to occur in Australia where rainfall is summer-dominant rather than winter-dominant (Murphy and Bowman 2007). The change in seasonality of rainfall across the rainfall gradient of the study area may therefore be a key mechanism driving the change in *T. scariosa* cover, relative to shrubs. However, further research would be required to separate the effects of increases in total rainfall compared to changes in seasonality of rainfall on the relative cover of *T. scariosa* compared to shrub species from this region.

Shrub cover was higher on yellow compared to red sand (Fig. 2e), though soil effects were examined only at high rainfall sites, possibly reflecting selective effects of acidic, nutrient-poor soils for plants with small, hard sclerophyllous leaves (Keeley et al. 2011). Furthermore, in arid and semi-arid systems, nitrogen is often co-limiting with water and many shrubs species occurring in these regions are from families in which symbiotic N_2-fixation occurs (e.g., Fabaceae and other leguminous species (Throop et al. 2011). In addition, shrubs generally have lower nitrogen requirements compared to perennial grasses (Carrera et al. 2000). This may give shrubs an advantage over grasses on the acidic, less fertile yellow sands.

Eucalypt cover was not influenced by different sand types and did not increase linearly with rainfall. This is consistent with previous research in this region, reporting no significant change in eucalypt cover from 240-320mm/year (Pausas and Bradstock 2007). While rainfall is expected to influence net primary production (Specht and Specht 1999; Sankaran et al. 2005), the scale examined in this study may be too fine for any significant changes in eucalypt cover to occur. For example, tree cover in African savannas increased by only 5 to 10 % in response to a change in average rainfall from 240 to 320mm/year (Sankaran et al. 2005). As eucalypt cover did not significantly increase with increasing rainfall, the results indicate that changes in fuel types across the study area may be primarily a function of variations in relative cover of understory shrubs and grasses, rather than variations in eucalypt cover.

An unexpected result was the significant interaction of TSF and rainfall on ephemeral cover. The largest proportion comprised of ephemerals (approximately 50% of the grassy fuel total) occurred at long TSF (> 60 years) and low rainfall. The factors controlling this effect are uncertain, however, several explanations are plausible. Ephemerals may have higher variance in their local population dynamics than other life forms or may be influenced by factors not captured in this study, such as dune height and fine scale soil moisture patterns. In these cases, larger sample sizes may be needed to characterise the patterns in variation. An alternative or additional factor may be higher grazing pressure in recently burnt patches (< 10 years) at low rainfall sites. For example, kangaroos and feral goats may be attracted to burnt sites, thereby reducing the cover of tussock grasses (the largest contributor to ephemeral cover) in recent TSF compared to the longer TSF sites where grazing may be more diffuse (Noble 1989). Further research would be needed to understand the processes controlling the interaction of TSF and rainfall on ephemeral cover across the study region.

4. 3 Implications for fire regimes

Ephemerals contributed approximately 50% of the total grassy fuel cover in long TSF at low rainfall (Fig**.** 4). Given that, he majority of the landscape at low rainfall is contained within the long TSF class (authors' unpublished data) flammability in the northern part of the study region is likely to be greatly enhanced by flushes of ephemeral fuels following heavy rainfall. By contrast, shrubs dominated all TSF classes in the wetter south of the region on yellow sands, suggesting that flammability is more likely to be a function of the accumulation of leaf litter and the drying out of woody fuels (e.g. following drought). Further research is required to quantify predicted changes in fire probabilities with fuel age in association with the environmental determinants (i.e. rainfall and soil types) of the cover of grass and shrub fuels.

Across the Mediterranean region in Australia, there has been an average increase in temperature of 1.24°C from 1920 to 2000 (Collins 2000), which is equivalent to a displacement of about 1° latitude, or 110 km towards the north (Pausas and Bradstock 2007). Changes in the relative mix of key fuel components are related to their position within the rainfall gradient and therefore may be expected to change in the future. However, the future response of plant communities to changes in environmental factors is difficult to predict, as different species may exhibit independent responses to changing environmental variables

(Pucko et al. 2011). Further research is required to determine the relative influence of temperature, moisture, soil type and CO_2 on the relative growth patterns of grass and shrub species in the Mediterranean region of south eastern Australia to provide insight into potential consequences of global change for fuels and fire regimes in the future.

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7 TABLES

Table 1 Summary of statistics for the two ANOVA models for each fuel element; eucalypts, *T. scariosa* shrubs, combined perennials and ephemerals. Significant p-values are in bold.

Fuel Element	*Model 1: Cover ~ TSF*Sand + Covariate*				*Model 2: Cover ~ TSF*Rainfall + Covariate*			
	Coefficient	*Df*	*F-value*	*P-value*	*Coefficient*	*Df*	*F-value*	*P-value*
Eucalypts	TSF	2	10.45	**0.001**	TSF	2	14.81	**<0.0001**
	Sand	1	2.89	0.11	Rainfall	2	4.88	**0.016**
	Shrubs	1	0.06	0.81	Shrubs	1	3.81	0.06
	T. scariosa	1	2.33	0.15	*T. scariosa*	1	2.40	0.13
	TSF*Sand	2	0.42	0.66	TSF*Rainfall	4	2.62	0.06
T. scariosa	TSF	2	0.64	0.53	TSF	2	13.22	**<0.0001**
	Sand	1	1.20	0.29	Rainfall	2	13.42	**<0.0001**
	Eucalypts	1	2.62	0.13	Eucalypts	1	0.24	0.63
	Shrubs	1	1.75	0.21	Shrubs	1	2.52	0.12
	TSF*Sand	2	2.44	0.14	TSF*Rainfall	4	4.67	**0.002**
Shrubs	TSF	2	1.81	0.20	TSF	2	3.14	0.06
	Sand	1	11.75	**0.003**	Rainfall	2	3.53	**0.045**
	Eucalypts	1	0.23	0.64	Eucalypts	1	4.68	**0.040**
	T. scariosa	1	1.57	0.23	*T. scariosa*	1	0.90	0.35
	TSF*Sand	2	1.17	0.34	TSF*Rainfall	4	2.37	0.08
Perennials	TSF	2	7.82	**0.004**	TSF	2	13.64	**<0.0001**
	Sand	1	0.09	0.77	Rainfall	2	3.56	**0.043**
	TSF*Sand	2	0.53	0.60	TSF*Rainfall	4	0.42	0.79
Ephemerals	TSF	2	51.04	**<0.0001**	TSF	2	8.43	**0.001**
	Sand	1	15.45	**0.001**	Rainfall	2	23.99	**<0.0001**
	All Perennials	1	0.07	0.80	All Perennials	1	0.90	0.35
	TSF*Sand	2	7.22	**0.006**	TSF*Rainfall	4	6.80	**0.0007**

Table 2 Hierarchical partitioning for nearest neighbour results on red sand (TSF and rainfall effects). Statistical significance level: *<0.05, **<0.01, ***<0.001, n.s = non-significant.

Competitor	*Best Models*	*dAICc*	*Deviance Explained*	*Relative percentage of total explained deviance*			
				Dist.	*Rainfall*	*TSF*	*Rainfall*TSF Int.*
T. scariosa equation (1)	**$(\sum \mathrm{SizeTN}_{1:x} + \mathrm{T}_{size}) \sim (\sum \mathrm{Dist.TN}_{1:x}) + \mathrm{rainfall} * \mathrm{TSF}$**	0.00	53.11	8.60**	5.97***	25.09***	60.33***
Shrubs equation (2)	**$(\sum \mathrm{SizeSN}_{1:x} + \mathrm{T}_{size}) \sim (\sum \mathrm{Dist.SN}_{1:x}) + \mathrm{rainfall} * \mathrm{TSF}$**	0.00	53.51	24.92***	1.23(n.s)	24.71***	49.11*
Shrubs equation (3)	**$(\sum \mathrm{SizeSN}_{1:x}) \sim (\sum \mathrm{Dist.SN}_{1:x}) + \mathrm{rainfall} * \mathrm{TSF}$**	0.00	53.51	34.52***	2.92(n.s)	18.69***	43.84*
Shrubs equation (4)	**$\mathrm{T}_{size} \sim \mathrm{TSF} * \mathrm{rainfall}$**	0.00	35.17	-	6.76***	23.99**	69.23**

Table 3 Hierarchical partitioning for nearest neighbour results, at high rainfall (TSF and sand effects). Statistical significance level: *<0.05, **<0.01, ***<0.001, n.s = non-significant.

Competitor	*Model Formula (TSF and sand)*	*dAICc*	*Deviance Explained*	*Relative percentage of total explained deviance*				
				Dist.	*Dist*Sand Int.*	*Sand*	*TSF*	*Sand *TSF Int*
T. scariosa equation (1)	**$(\sum \mathrm{SizeTN}_{1:x} + T_{size}) \sim (\sum \mathrm{Dist.TN}_{1:x}) * \mathrm{sand}$**	0.00	27.47	77.61***	11.19**	11.19(n.s)	-	-
	$(\sum \mathrm{SizeTN}_{1:x} + T_{size}) \sim (\sum \mathrm{Dist.TN}_{1:x}) + \mathrm{TSF}$	1.55	26.32	51.72**	-	-	48.27**	-
Shrubs equation (2)	**$(\sum \mathrm{SizeSN}_{1:x} + T_{size}) \sim (\sum \mathrm{Dist.SN}_{1:x}) + \mathrm{sand} * \mathrm{TSF}$**	0.00	49.45	24.05***	-	0.14***	32.39***	43.40***
Shrubs equation (3)	**$(\sum \mathrm{SizeSN}_{1:x}) \sim (\sum \mathrm{Dist.SN}_{1:x}) + \mathrm{sand} * \mathrm{TSF}$**	0.00	46.23	24.05***	-	0.14***	32.39***	43.40***
Shrubs equation (4)	**$T_{size} \sim \mathrm{TSF} + \mathrm{sand}$**	0.00	9.4	-	-	40.24*	49.75**	-

8 LIST OF FIGURES

Figure 1: Location of the Mediterranean climate region of south eastern Australia, with the national parks and nature reserves where the study was conducted.

Figure 2: a. Effect of TSF on eucalypt cover, b. Effect of rainfall on eucalypt cover, c. Interaction of TSF and rainfall on *T. scariosa* cover, d. Effect of rainfall on shrub cover, e. Effect of sand eucalypt cover on shrub cover, f. Effect of sand type on shrub cover (dotted lines represent 95% confidence interval, C.I.), g. Effect of rainfall on total perennial cover, h. Effect of TSF on total perennial cover, i. Interaction of rainfall and TSF on ephemeral cover, j. Interaction of sand and TSF on ephemeral cover. 'Recent' TSF is <10 yrs, 'medium' TSF is 20-40 yrs and 'long' TSF is >60 yrs. 'Low' rainfall is 220-240mm/yr, 'moderate' rainfall is 260-280mm/yr and 'high' rainfall is 310-330mm/yr. Bars represent 95% confidence limits.

Figure 3: a. Effect of sand type on intra-specific competition between T. scariosa plants, b. Intra-specific competition between shrubs

Figure 4 Relative cover of grasses and herbs compared to shrubs across rainfall, sand types and TSF. Rainfall and sand types are ordered from left to right as they appear in the landscape from north to south (i.e. increasing rainfall from north to south with yellow and red sand at high rainfall only). 'Recent' TSF is <10 yrs, 'medium' TSF is 20-40 yrs and 'long' TSF is >60 yrs. 'Low' rainfall is 220-240mm/yr, 'moderate' rainfall is 260-280mm/yr and 'high' rainfall is 310-330mm/yr.

Fig. 1


N
W
E
S
Dangalli CP
Tarawi NR
NSW
SA
Murray Sunset NP
Annuello FFR
VIC
Wyperfeld NP
Wathe FFR
0
25
50
100 Kms

Fig. 2 a-j

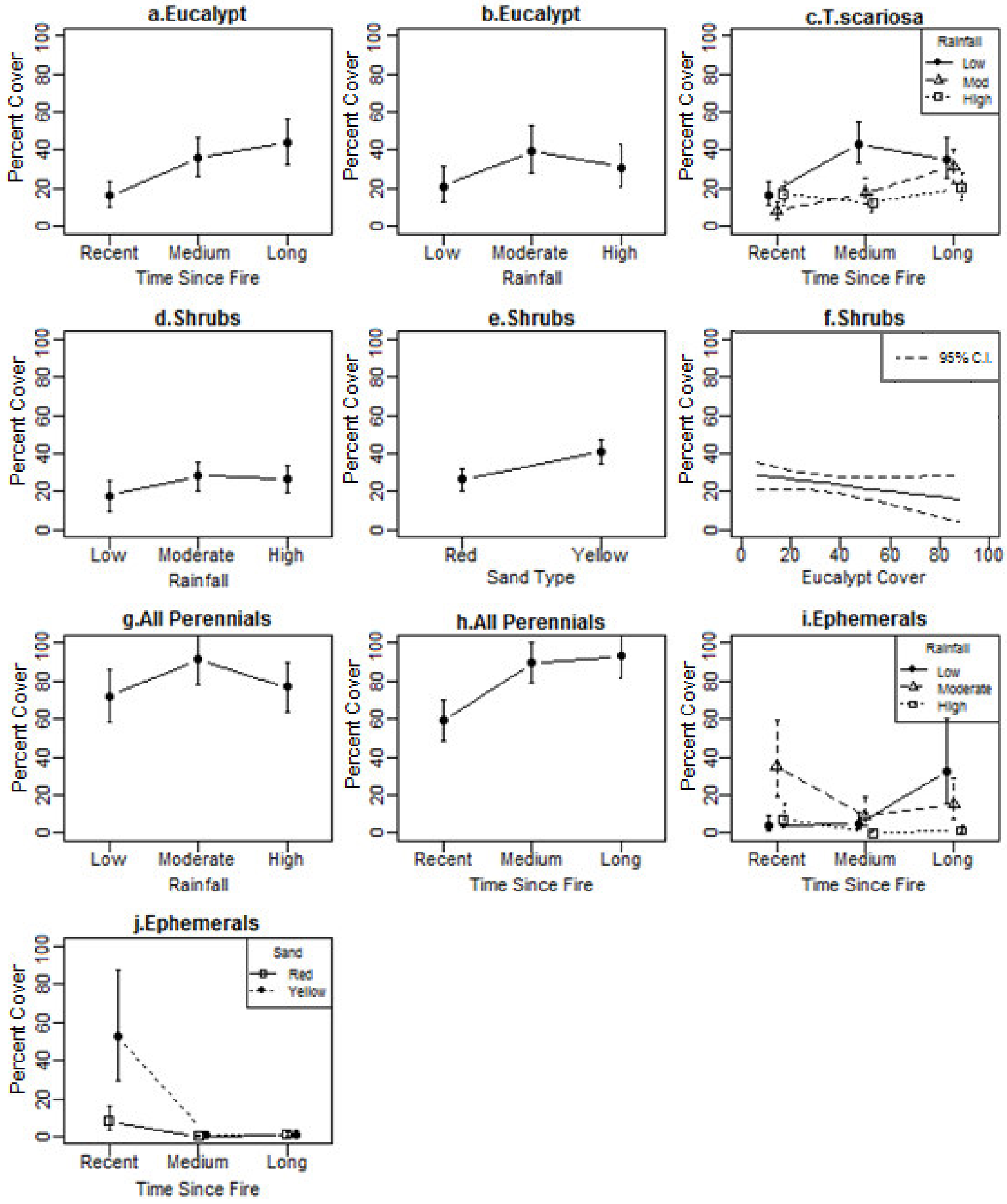

a.Eucalypt
Percent Cover
0
20
40
60
80
100
Recent
Medium
Long
Time Since Fire
b.Eucalypt
Percent Cover
Low
Moderate
High
Rainfall
c.T.scariosa
Percent Cover
Rainfall
Low
Mod
High
Recent
Medium
Long
Time Since Fire
d.Shrubs
Percent Cover
Low
Moderate
High
Rainfall
e.Shrubs
Percent Cover
Red
Yellow
Sand Type
f.Shrubs
Percent Cover
95% C.I.
0
20
40
60
80
100
Eucalypt Cover
g.All Perennials
Percent Cover
Low
Moderate
High
Rainfall
h.All Perennials
Percent Cover
Recent
Medium
Long
Time Since Fire
i.Ephemerals
Percent Cover
Rainfall
Low
Moderate
High
Recent
Medium
Long
Time Since Fire
j.Ephemerals
Percent Cover
Sand
Red
Yellow
Recent
Medium
Long
Time Since Fire

Fig. 3

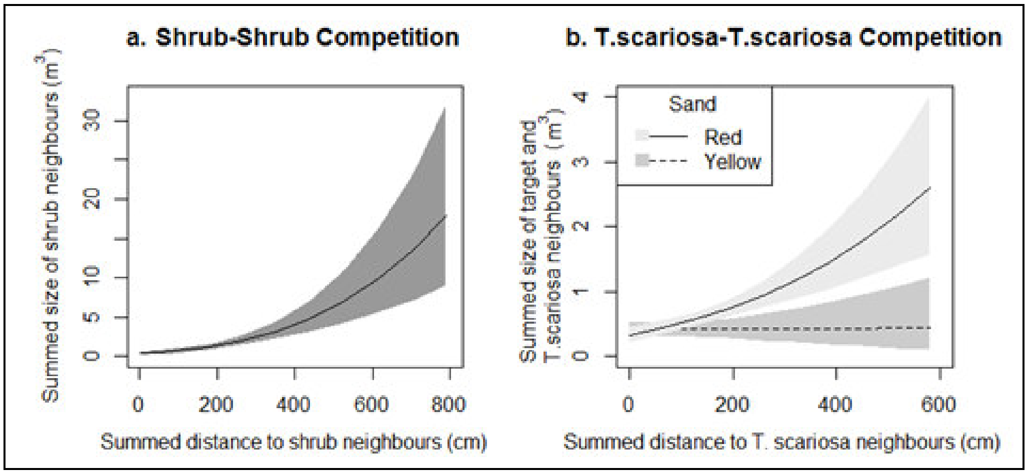
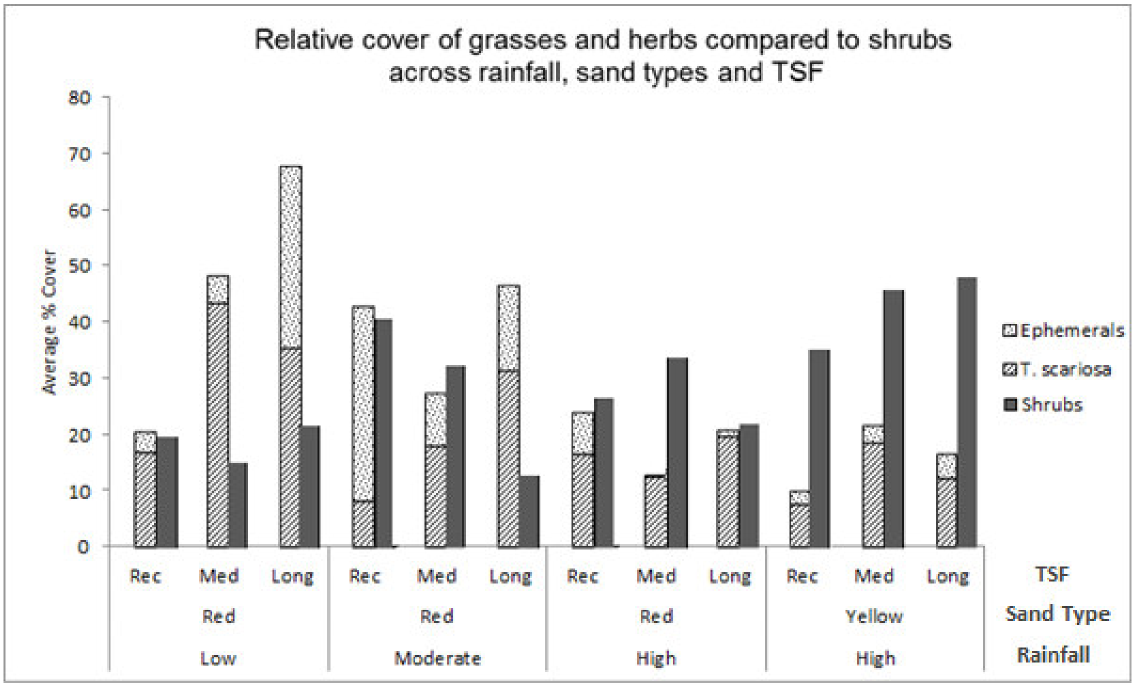

a. Shrub-Shrub Competition
Summed size of shrub neighbours (m^3)
0
5
10
20
30
0
200
400
600
800
Summed distance to shrub neighbours (cm)
b. T.scariosa-T.scariosa Competition
Summed size of target and T.scariosa neighbours (m^3)
0
1
2
3
4
Sand
Red
Yellow
0
200
400
600
Summed distance to T. scariosa neighbours (cm)

Fig. 4


Relative cover of grasses and herbs compared to shrubs across rainfall, sand types and TSF
Average % Cover
0
10
20
30
40
50
60
70
80
Rec
Med
Long
Rec
Med
Long
Rec
Med
Long
Rec
Med
Long
TSF
Red
Red
Red
Yellow
Sand Type
Low
Moderate
High
High
Rainfall
Ephemerals
T. scariosa
Shrubs