MR. MATTHEW CHICK (Orcid ID : 0000-0001-7852-8313)

DR. CRAIG R NITSCHKE (Orcid ID : 0000-0003-2514-9744)

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Factors influencing above-ground and soil-seedbank vegetation diversity at different scales in a quasi-Mediterranean ecosystem

Matthew P. Chick, Craig R. Nitschke, Janet S. Cohn, Trent D. Penman, Alan York¹

Chick, M.P. (Corresponding author, mchick@student.unimelb.edu.au)¹

Nitschke, C.R. (craign@unimelb.edu.au)¹

Cohn, J.S. (janet.cohn@unimelb.edu.au)¹

Penman, T.D. (trent.penman@unimelb.edu.au)¹

York, A. (alan.york@unimelb.edu.au)¹

¹ School of Ecosystem and Forest Sciences, University of Melbourne, 500 Yarra Boulevard, Richmond, 3121 Victoria, Australia.

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Abstract

Questions: Are factors influencing plant diversity in a fire-prone Mediterranean ecosystem of southeast Australia scale dependent?

Location: Heathy-woodland in the Otways region of Victoria, southeast Australia

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Methods: We measured patterns of above-ground and soil-seedbank vegetation diversity and associated them with climatic, biotic, edaphic, topographic, spatial, and disturbance factors at multiple scales (macro to micro) using linear mixed effect and generalised dissimilarity modelling.

Results: At the macro-scale we found species richness above-ground best described by climatic factors and in the soil-seedbank by disturbance factors. At the micro-scale we found species richness best described above-ground and in the soil-seedbank by disturbance factors; in particular; time-since-last-fire. We found variance in macro-scale beta-diversity (species turnover) best explained above-ground by climatic and disturbance factors and in the soil-seedbank by climatic and biotic factors.

Conclusions: Regional climatic gradients interact with edaphic factors and fire-disturbance history at small spatial scales to influence species richness and turnover in the studied ecosystem. Current fire management regimes need to incorporate key climatic-disturbance-diversity interactions to maintain floristic diversity in the studied system.

Introduction

Understanding the processes that drive spatial variation in plant species diversity is critical for measuring and understanding vegetation-environment-disturbance relationships (Siefert et al. 2012). Research findings stipulate that hierarchical spatial patterns in factors influence vegetation diversity (Whittaker et al. 2001; Sarr et al. 2005). At macro spatial scales, such as across landscapes, climate mediated productivity is typically found to influence species composition (Benayas et al. 2002; Forey et al. 2008) and richness patterns (O'Brien 1998; Hawkins et al. 2003; Field et al. 2009). At meso-scales, such as within regions of similar climate, soil edaphics and environmental heterogeneity are typically found to influence vegetation diversity (Schimper 1902; Siefert et al. 2012; Myers et al. 2013) by governing nutrient and moisture accessibility (Sarr et al. 2005). At micro-scales, such as within communities and across topographic gradients (Harris et al. 1996), disturbance history (e.g., time since fire (TSF) or fire-frequency) is often found to influence vegetation diversity through governing localised resource and competition processes (Huston 1979; Lavorel 1999; Forey et al. 2008; Keeley 2009). Although the detectability of these factors is often stronger at certain scales, it is considered that all factors are likely interacting across scales to influence diversity (Urban et al. 1987; Whittaker et al. 2001). With little empirical support for this theory of interacting factors (Cohn et al. 2015; Murphy et al. 2015) further testing through observing and analysing vegetation diversity patterns across environmental and disturbance factor variation has been advocated (Siefert et al. 2012).

Disturbance through prescribed fire immediately affects small spatial-scales (i.e. sites) which can cumulatively affect larger spatial-scales (i.e. landscapes) over time. Using prescribed fire to manipulate patterns of vegetation community developmental stages, known synonymously as seral or growth-stage management and based on successional change with TSF, has become a commonly adopted conservation strategy in flammable ecosystems worldwide (Parr & Andersen 2006; van Wilgen et al. 2011; Spies et al. 2012). However, the link between growth-stage patterns and vegetation diversity often remains largely unknown (Driscoll et al. 2010) and difficult to quantify due to strong external climatic factors interacting with post-fire competition processes (Sarr et al. 2005). Understanding these interactions remains an ecological challenge that is fundamental to the management and conservation of biodiversity in fire-prone ecosystems and warrants further research (Driscoll et al. 2010).

Vegetation diversity can be expressed as the count of species at a site, known as richness (Whittaker 1960; Gotelli & Colwell 2001), the turnover in species compositions between sites, known as beta-diversity (Anderson et al. 2011), and the total species pool across a landscape, known as gamma diversity (Whittaker 1960). Beta-diversity comprises two metrics, (1) directional turnover in species composition along environmental gradients; and, (2) non-directional composition variation between sample units within a defined spatial and temporal extent (Anderson et al. 2011). Therefore, the analysis of beta-diversity provides a quantitative means of linking the processes that influence richness at a site scale and gamma diversity at a landscape scale (Murphy et al. 2015). Most studies of beta-diversity have typically ignored the impacts of past and current management and disturbance (Murphy et al. 2015). Historical disturbance can impart a spatial signature on vegetation communities and influence beta-diversity in a manner that is uncorrelated with dominant environmental gradients (Murphy et al. 2015). Accounting for stochastic processes can increase the amount of variance explained in beta-diversity in landscapes with high environmental heterogeneity (Myers et al. 2013).

Plant fire-persistence traits include re-sprouting from lignotubers or epicormic buds (termed obligate re-sprouting), germinating solely from seeds banked in the soil or canopy (termed obligate seeding), or both in combination (termed facultative) (Noble & Slatyer 1980; Pausas et al. 2004). Within quasi-Mediterranean ecosystems, such as heathy-woodland, obligate re-sprouting is almost absent, with species predominantly being facultative or obligate seeding (Pausas et al. 2004). Diversity conservation in these ecosystems is achieved through the standing species (termed above-ground diversity) persisting at an individual level through re-sprouting or at a population level through the soil-seedbank (Noble & Slatyer 1980). Frequent fire, wild or prescribed, may favour re-sprouting as species may not have time to mature and produce seed, thereby limiting population recruitment (Gill & Bradstock 1995; Pausas & Bradstock 2007; Tucker & Cadotte 2013). When fires occur too infrequently, the soil-seedbank of species that require fire-related cues for germination may be lost (Pausas 2001). Further, whilst negative successional relationships are often reported between above-ground diversity and TSF in these ecosystems (Morrison & Cary 1995; Myerscough et al. 1995; Freestone et al. 2015), the limited soil-seedbank research has found variable (Wills & Read 2007) or weak positive relationships (Chick et al. 2016). Therefore, in these fire-managed ecosystems the soil-seedbank plays an important role in plant community conservation (Amiaud & Touzard 2004) through post-fire regeneration and recruitment, which shapes community composition for years (Tucker & Cadotte 2013). Despite this importance, diversity measures and research into diversity-environment-disturbance relationships in these ecosystems have historically only focused above-ground, which is relatively easy to measure, meaning the soil-seedbank dynamics remain much less understood (Parker & Kelly 1989; Auld et al. 2000). The incorporation of soil-seedbank responses into plant diversity research provides a holistic approach to understanding how environmental drivers (Plue et al. 2017) and disturbance interact (Whittaker et al. 2001) to shape plant communities.

We associated patterns of vegetation richness and beta-diversity above-ground and in the soil-seedbank with climatic, biotic, edaphic, topographic, spatial and disturbance factors (Siefert et al. 2012) at three scales (termed macro, meso, and micro) across three discrete geographic regions of a fire-prone heathy-woodland. Aligning with empirical research in the region of this study (Cohn et al. 2015) and internationally (Field et al. 2009), we

tested the hypothesis that climate would have the strongest detectable influence on above-ground diversity at the macro-scale, edaphic, biotic, and topographic factors at the meso-scale, and fire-disturbance at the micro-scale. Secondly, and also aligning with empirical research in the region (Chick et al. 2016), we hypothesised that climatic, edaphic, and disturbance factors would influence soil-seedbank diversity at larger scales. Lastly, and aligning with current theory (Whittaker et al. 2001), we hypothesised that larger scale climate factors are interacting with smaller scale edaphic and disturbance factors to influence total diversity pattern.

Materials and Methods

Study area

The study area is located within the heathy-woodlands (Department of Sustainability and Environment 2012) of the Otway Ranges region 130 km west of Melbourne, in southeast Australia (Fig. 1). The climate is a quasi-Mediterranean-type (Dodson 2001), with warm summers, mild winters, and winter dominant rainfall. Vegetation is dry sclerophyll and dominated by a short overstorey of *Eucalyptus baxteri* (Benth.) Maiden & Blakely ex J.M. Black (Brown Stringybark) and a heathy understorey comprising shrubs from the families: Fabaceae, Ericaceae, Myrtaceae, Proteaceae, Thymelaeaceae, Xanthorrhoeaceae and Dilleniaceae. Three discrete heathy-woodland distributions exist around the townships of Anglesea, Forrest, and Carlisle River (Fig. 1A). Across these three regions climate and edaphic attributes vary (Table 1). Wildfire last burned the Anglesea region in 1983 and the Forrest and Carlisle River regions in 1967. Since 1983, all regions have been the subject of small-scale prescribed burning (individual burn blocks range in size < 400 to ~1000 ha) to satisfy fuel reduction and ecological goals (Department of Primary Industries 2013). Because of its proximity to urban areas the Anglesea region has been subject to more prescribed burning; meaning, combined with the 1983 wildfire, the average inter-fire interval is lower in this region (Table 1). These gradients in climate, topography, edaphics, and fire history make this area useful for research regarding the influence of scale-dependent factors on vegetation diversity.

Sampling design

We used digitised fire history layers accessed from the local land managers to stratify the landscape into a continuous scale of TSF (wildfire or prescribed). For meso-scale analysis, the landscape was further stratified according to four post-fire growth stages (Cheal 2010): 0-3 yrs (juvenile); 4-10 yrs (young); 11-34 yrs (mature); and >34 yrs (old). We selected seventy-one sites that achieved a good representation of each growth stage within each region (Table 1) and stratified each by topography to sample at a micro-scale (discussed below). Criteria for site selection: (1) heathy-woodland of a minimum patch size of 1 ha; and, (2) having a slope of ~5% or over with a ridge 50 m or more from the road and that ran >100 m into a gully. To validate the mapped TSF of each site, we aged at least 30 individual *Banksia marginata* Cav. shrubs using growth whorls (Jenkins et al. 2005; Chick et al. 2016). Ten individuals were sampled within a 20-meter radius of the three sampling points established along transects (discussed below).

Vegetation sampling and seed germination

Because topographic position is expected to influence plant community composition, we established sampling transects extending from ridge to gully. At each site, we counted all above-ground shrub, sub-shrub, and

herbaceous species in six 3m × 3m quadrats, two each at ridge, mid-slope and gully topographic locations (Fig. 1c). This was achieved by randomly selected a ridge point using ArcMap 10 (ESRI 2011) and establishing two quadrats, calculating the mid-slope using a GPS as half way between the ridge and gully and established two more, and moving to the gully to established the final two. At each topographic location, the two quadrats were established 10 metres apart and parallel to the dominant aspect of each slope. The soil seedbank was sampled by extracting soil cores (6 cm diameter, 5 cm depth) systematically at 13 positions within each quadrat (Fig. 1c), and then combining soil from the two ridge, mid-slope and gully quadrates resulting in three composite samples per site. Cores sampled the top 5 cm soil layer, as this is where most soil stored seed occurs (Carroll & Ashton 1965). Surface litter was included in the soil core as it can represent a source of fresh seed (Enright & Kintrup 2001). Above-ground sampling and core collection occurred in autumn of 2014/15 to capture seeds released in spring and summer (Enright & Kintrup 2001). Soil-seed bank germination and species identification followed the methods of Chick et al. (2016).

Statistical analyses

Predictor factors

We derived predictor factors from digital data layers and measurements in the field at the time of sampling. Topographic factors were obtained from CSIRO soil and landscape grids (CSIRO, <http://www.clw.csiro.au/aclep/soilandlandscapegrid>, accessed March 2015). Climatic factors were represented by bioclimatic temperature factors at a spatial resolution of 250 m and obtained from Stewart and Nitschke (2017), annual precipitation obtained from WorldClim grids (Hijmans et al. 2005), and climate-scaled water-energy dynamics and dryness represented by the Aridity Index (considered a proxy for site productivity) (Nyman et al. 2014). Disturbance was represented by TSF and fire frequency measures generated from fire history mapping and validated in the field. Field measured topographic and biotic factors were slope, aspect, and basal area. Edaphic factors were obtained by collecting 18 soil samples (three per quadrat) using bulk density rings (6.5 cm diameter, 5 cm depth) (Fig. 1C) to measure site-scale soil bulk density, organic matter content, particle size, pH, and electrical conductivity using the methods of Carter (1993). Spatial factors included latitude and longitude (Anderson et al. 2011) collected at each site using a Garmin GPS unit.

Richness across spatial scales

We used linear mixed modelling (LMM) (Zuur et al. 2007; Bolker et al. 2009; Zuur et al. 2009) to examine relationships between species richness and predictor factors at two of the scales: meso (growth-stage) and micro (topographic). To examine these relationships at the macro-scale (across all regions) we used general linear modelling (LM) with no random effect and with topographic wetness index (TWI), which increases as the site gets wetter, as a surrogate for topographic position. Response data in the macro-scale analysis consisted of species richness pooled across each transect by summing species abundance from ridge, mid-slope, and gully positions, which resulted in each site (transect) being a data point. Response data in the meso-scale analysis consisted of species richness pooled across each transect in each region separately. Response data in the micro-scale analysis consisted of the un-pooled species richness data collected at different topographic positions, resulting in each position (ridge, mid, gully) being a data point. Further scale was then introduced into the meso- and micro-scale LMM analysis by way of random effects (see supplementary material). We checked normality in above-ground and soil-seedbank richness data and modelled each separately (Quinn & Keough 2002). For

micro-scale statistical analysis, we used values for each predictor variable at each topographic position. We averaged these values across each transect for meso- and macro-scale analysis. Predictor variable collinearity was reduced using Principal Components Analysis (PCA), resulting in an independent subset (Appendix 1), and normality of those remaining was checked (IBM 2011). We initially divided this independent subset into climatic, edaphic, spatial, biotic, topographic, and disturbance components and modelled species richness as a response to each - termed factor group models. To avoid bias towards certain predictors, we also modelled richness as a response to model iterations of all independent factors (not in groups), termed full models, at each scale.

Model construction methods (the selection of random and fixed factors) are detailed in the supplementary material and followed Zuur et al. (2009). We compared factor group and full models at each scale using AICc scores and weights estimated with Restricted maximum likelihood (REML), allowing us to estimate the most parsimonious (Zuur et al. 2009). To further evaluate factor group and full model fit we used three metrics: (1) R : the correlation (Pearson's) between the raw observed and model predicted data; (2) marginal R^2 : the variance explained by fixed factors; and, (3) conditional R^2 : the variance explained by both fixed and random factors (Nakagawa et al. 2013). Post-modelling examination of residual errors satisfied assumptions of normality and homogeneity (Zuur et al. 2009). Modelling and analysis was undertaken in R (R Core Team 2015). Pairwise correlations and normality analysis was undertaken using the packages 'highstat' and 'nortest'. LM and LMM was undertaken using the packages 'lm', 'lme4' and 'AICcmodavg' (Mazerolle 2011) and following the methods of Zuur et al. (2009).

Beta-diversity

We used generalised dissimilarity modelling (GDM) (Ferrier et al. 2002; Ferrier & Guisan 2006; Ferrier et al. 2007) to analyse spatial patterns of turnover in community composition (beta-diversity) along macro-scale gradients and to further test the hypothesis that climate would have the strongest detectable influence at this scale. We modelled beta-diversity at the macro-scale as GDM is only appropriate at this scale (Ferrier et al. 2007). Above-ground and soil-seedbank beta-diversity was modelled separately; however, above-ground dissimilarity measures were used as predictor factors in soil-seedbank beta-diversity models, allowing for an indirect comparison. We used non-metric multidimensional scaling (nMDS) (Clarke 1993) to simplify the above-ground composition data into three vegetation factors for subsequent use as a biotic factor in soil-seedbank modelling (nMDS1, nMDS2, nMDS3) (Ferrier et al. 2007; Penman et al. 2011). Three dimensions were required to ensure acceptable nMDS stress; less than 0.20 (Clarke 1993). To facilitate model interpretation, we extracted I-spline values for each predictor and plotted each beta-diversity function in graphical form. Only factors increasing the proportion of variance explained by 4 % illustrated a meaningful function and were included in final models. Modelling was undertaken in R (R Core Team 2015), nMDS using the package 'vegan' (Oksanen et al. 2015) and GDM with the package 'gdm' (Manion et al. 2015).

Results

Species richness at different scales

Above-ground gamma diversity equalled 102 species, with site richness ranging from 11 to 34 (mean = 21.5 ± 0.6 (SE)). Soil-seedbank gamma diversity equalled 92 species, with a further 6 taxa identified to genus level. Soil-seedbank site richness ranged from 6 to 27 (mean = 16.1 ± 0.6 (SE)). The majority of these species regenerate through re-sprouting and seeding (facultative) or obligate seeding (Appendix 2). Site specific banksia whorl counts were significantly correlated with site specific GIS fire history (TSF) mapping accessed from the local land managers ($r = 0.85$, $P > 0.001$), indicating this method was a useful validation tool. However, this correlation was stronger within the range of 2–20 years, after which the Banksia whorls underestimated the TSF reported on the fire mapping.

We found a marked difference between the strongest factor group models for above-ground versus soil-seedbank species richness at the three spatial scales (Appendix 3). The climatic factor group model was the strongest for above-ground richness at the macro- and meso-scale, whilst the disturbance factor group model was the strongest at the micro-scale (Table 2). A combination of climatic, disturbance, and edaphic factors constituted the strongest full model (all factors considered ungrouped) of above-ground richness at the macro-scale. This included a weak positive relationship with longitude (spatial), a weak negative relationship with rainfall (climate) and soil clay content (edaphic), and a stronger positive relationship with temperature (climate), indicating above-ground richness higher in the less productive region of the landscape. The Disturbance factor group model was the strongest for soil-seedbank richness across all scales (Table 2). At the macro-scale, climate and disturbance factors constituted the strongest full model of soil-seedbank richness. This included a weak negative relationship with longitude (spatial), aridity index (climate), and clay content (edaphic), and a stronger positive relationship with TSF (disturbance), indicating soil-seedbank richness higher in the more productive region with a larger average-inter-fire interval.

Beta-diversity

The strongest above-ground GDM comprised five factors that explained 34.2 % of beta-diversity. Of the five factors, climate (aridity index) explained the most above-ground variance as a single factor followed by the disturbance (average inter-fire-interval and time since fire), topographic (TWI), and edaphic (bulk density) factors (Table 3). Geographic site location only explained 1 % of the variance. The strongest soil-seedbank GDM comprised five factors that explained 31.4% of beta-diversity. Climatic factors (average annual temperature and precipitation) explained the most soil-seedbank variance followed by biotic (above-ground vegetation dissimilarity), disturbance (fire frequency) and edaphic (Total P) factors (Table 3). Spatial factors explained less than 1 % of the variance. Of the five factors, above-ground vegetation dissimilarity explained the most soil-seedbank variance as a single factor.

Discussion

Above-ground diversity

Consistent with the findings of Murphy et al. (2015) and Paudel et al. (2016) internationally, and Cohn et al. (2015) locally, our above-ground richness and beta-diversity results suggest multiple factors interacting to shape

plant diversity. At larger scales, the best full models (all factors ungrouped) explaining above-ground richness contained a combination of climatic and edaphic factors. Within these full models, temperature and precipitation were strong influences at the macro-scale, whilst aridity was more influential at the meso-scale. Temperature and precipitation were highly correlated with aridity and so were not modelled together (i.e. the macro-scale model included temperature and precipitation and the meso-scale included aridity). Temperature and precipitation were calculated at a 250m scale, whilst the aridity index was calculated at a 20m scale (see Appendix 1) and includes topographic effects on net radiation (Nyman et al. 2014). We found that topography, as measured by the topographic wetness index, contributed a small but significant amount to above-ground beta-diversity, aligning with De Caceres et al. (2012) in tropical, subtropical and temperate forests distributed world-wide, Myers et al. (2013) in temperate and tropical forests in Bolivia and Missouri, and Murphy et al. (2015) in a temperate deciduous forest in Pennsylvania. This suggest that the role of topography in our study may reflect the role of topography on environmental heterogeneity, specifically edaphics, within the study area. Clay content was a significant edaphic factor influencing richness, and bulk density a significant factor influencing beta-diversity. All these above-ground results suggest broad climate patterns interacting with topography and soil-mediated water availability and finer-scales (Murphy et al. 2015) to improve the amount of variance explained by habitat filtering, as was found by Baldeck et al. (2013).

Soil-seedbank diversity

In line with our hypothesis, soil-seedbank diversity was sensitive to climate and disturbance across all scales. This is contradictory to the broad understanding that climate and productivity decline in importance as spatial grain is reduced (Siefert et al. 2012) and that the influence of non-climatic factors average out as spatial grain increases (Field et al. 2009). However, aridity also acted across all scales, suggesting that soil-seedbank richness, as above-ground, may be responding to a productivity gradient. It is possible that the impact of historical prescribed fire in the studied landscape is correlated with climatic factors, leading to spatially structured disturbance factors (Murphy et al. 2015). This spatial structuring is evident in the soil-seedbank as averaged richness was lower at sites with higher aridity and more frequent fire. Sites with lower aridity are less productive and have shorter inter-fire intervals (more wildfires and more prescribed fire) than the wettest more productive sites separated by a spatial gradient from east to west (see Table 1 and Fig 1). Further, the strong influences of fire history and climate on above-ground beta-diversity suggests that disturbance and productivity are shaping vegetation patterns in the region. This aligns with the dynamic-equilibrium model (DEM) (Huston 1979) that predicts, and past research that found (Pausas & Bradstock 2007), productivity interacting with disturbance to determine species co-existence through competition. Our understanding of above-ground processes, combined with DEM theory, can explain the soil-seedbank patterns found here. Australian heathy-woodlands generally follow the 'initial floristics model' (Egler 1954) of post-fire change above-ground, which is characterised by high initial diversity and no change (McFarland 1988) or decreases (Specht et al. 1958; Clemens & Franklin 1980; Wark 1987; Franklin et al. 2011; Freestone et al. 2015) with TSF. If fire is infrequent and productivity rates are higher, this initially high above-ground diversity is likely to reach reproductive age quicker and produce more propagules, but also out-compete and decrease faster, whilst soil-seedbank diversity remains constant or increases (Milberg 1995). Inversely, if fire is too frequent and productivity rates are lower, soil-seedbank diversity may not fully replenish (Ooi 2012), whilst above-ground diversity remains high.

The amount of soil-seedbank beta-diversity explained (31.1%), whilst within the range identified in other community studies (Baldeck et al. 2013; Siefert et al. 2013; Murphy et al. 2015), was lower than that explained above-ground (35.1%). The extra-unexplained variance in the soil-seedbank component, and the overall unexplained variance for both pools, may be attributable to unaccounted local stochastic processes (Myers et al. 2013) or abiotic/ biotic coupling processes underlying community assembly (He et al. 1996). Dissimilarity in above-ground vegetation explained most variation in soil-seedbank beta-diversity, suggesting biotic-abiotic coupling processes. Further, total soil phosphorus (P) contributed a small but significant amount to soil-seedbank beta-diversity, suggesting nutritional constraints important. Kasel et al. (2017) also found soil P, along with Mg and N, were edaphic constraints helping to shape beta-diversity in temperate eucalypt forests within the region. Soil P influences the growth of sclerophyllous heathland shrubs (Specht et al. 1958) which in turn influences the above-ground biomass production and seed set of these species (Brys et al. 2005). Increased soil P also facilitates the storage of P in seeds of heathland shrubs, which could increase the chance of seedling establishment post fire (Groves et al. 1986). Our results suggest that P availability influences turnover but may be doing so in interaction with biotic and disturbance variables. When combined, our richness and beta-diversity results indicate broader scale climatic factors are influencing above-ground diversity, which in turn is interacting with local scale processes that mediate soil nutrition and water availability, which in turn influences regeneration success, growth, and seed production and thereby promotes turnover in soil-seedbank composition.

The intensity and severity of fire influences the fire-persistence responses of species (Bradstock & Auld 1995; Bellingham & Sparrow 2000; Keeley 2009) which shape the post-fire productivity driven competition processes and, therefore, the floristic pathway measured in chronosequence studies (Walker et al. 2010). The composition of species fire-persistence traits is different within the three regions of this study (Appendix 2), which may help explain the increased sensitivity of richness and beta-diversity at higher productivity where prescribed fires are likely more intense. Although beyond this research, trait based analysis within mosaics of fire intensity and severity would be an important future step towards better understanding the diversity dynamics of this ecosystem.

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	Anglesea	Forrest	Carlisle River
Rainfall (mm)			
Annual mean	814	1041.2	1070.3
Temp (°C)			
Annual mean max	18.2	17.7	18.5
Annual mean min	10.6	6.9	6.8
Sites (growth-stage, n)			
Juvenile (0 - 3 yrs)	3	2	4
Young (3 - 10 yrs)	8	7	2
Mature (11- 30 yrs)	13	8	7
Old (> 30 yrs)	5	6	6
Growth stage total (n)	29	23	19
Average inter-fire interval	19.1 (± 1.5) SE	30.4 (± 1.6) SE	32.1 (± 2.7) SE
	Low fertility	Moderate fertility	Moderate fertility
Soil texture / fertility	Clay Loam/Clay	Sandy Loam/Loam	Sandy Loam/Loam
Clay content (%)	25.0 (± 2.1) SE	18.8 (± 2.3) SE	13.4 (± 2.0) SE
Sand content (%)	47.8 (± 2.0) SE	52.0 (± 3.0) SE	53.6 (± 1.9) SE

Fig. 1. Study area in the Otways Ranges. (a) Sites, indicated by black dots, within the three heathy-woodland regions (Anglesea, Forrest, and Carlisle River) in south-eastern Australia. (b) Fire history and sites (black dots) within the Anglesea region. (c) Layout of six quadrats (3 x 3m) per site running from ridge to gully (black dashed line indicates transect, undashed line with "Creek" indicates creek). Thirteen soil-seedbank cores and three soil analysis cores within each quadrat.

Table 1. Climate, fire, and soil fertility variables describing the
Rainfall and temperature as measured by the Bureau of Meteorology
Soil parameter values (% mean $\pm$ s.e.) based on site particle size
Growth-stages based on time since fire c

Silt content (%)	27.1 (± 0.9) SE	34.1 (± 1.5) SE	32.0 (± 0.7) SE
Organic matter (%)	3.1 (± 0.3) SE	4.0 (± 0.8) SE	4.1 (± 0.5) SE

35.

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Table 2. Top LMM species richness models

Top factor group models (Climatic, Topographic, Disturbance, Edaphic) and constituted significant variables

Random effects used in factor group models: macro = none; meso = region/growth-stage; micro = region/topographic position

Final model = best model when all factors (not in groups) were considered. Full model results include interactions between factors.

F= variable. INT = interactions; X= multiplicative interaction and + = additive interaction

Two measures of fit are presented for each model; marginal r^2 (r^2 (m)) and conditional r^2 (r^2 (c))

TSF = time since last fire, Aridity Index = lower values indicate wetter

Factor relationships									Full model relationships		
Scale	Top model	F1	INT	F2	INT	F3	INT	F4	r ² (m)	r ² (c)	R
Response = above-ground richness											
Macro	Climatic	Avg Temperature (+ + +)	X	Avg Precipitation (- -)					0.36	n/a	0.72
	Full Model	Avg Temperature (+ + +)	+	Avg Precipitation (- -)	+	TSF (- -)	+	Clay Content (- -)	0.41	n/a	0.65
Meso	Climatic	Avg Temperature (+ + +)	+	Avg Precipitation (- -)					0.36	0.47	0.72
	Full Model	Clay Content (- -)	X	Soil pH (- -)	+	Avg Radiation (-)	+	Aridity index (+)	0.39	0.80	0.83
Micro	Disturbance	Avg inter-fire interval (- -)							n/a	0.36	0.61
	Full Model	Avg inter-fire interval (- -)							n/a	0.36	0.61
Response = soil-seedbank richness											

Macro	Disturbance	TSF (++)					n/a	n/a	0.44
	Full Model	TSF (++)	X	Aridity Index (-)	+	Clay Content (-)	0.39	n/a	0.66
Meso	Disturbance	TSF (++)					n/a	0.26	0.51
	Full Model	TSF (++)	X	Avg Temperature (-)			0.26	0.69	0.76
Micro	Disturbance	TSF (++)					n/a	0.22	0.46
	Full Model	TSF (++)	X	Aridity Index (-)			0.19	0.30	0.54

(+) = positive relationship $r^2 < 0.1$ but > 0.05 , (++) = positive relationship $r^2 > 0.1$, (+++) = positive relationship $r^2 > 0.2$

Equal for negative (e.g. (-) = negative relationship $r^2 < 0.1$)

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Table 3. GDM results

Total composition turnover variance explained by environmental and fire disturbance history factors explaining > 4 %		
Total variance explained for full model with geographic location above, relative variance explained by factors separately below		
R = pearsons correlation between observed and model predicted values		
	Above-ground variance explained (%)	Soil-seedbank variance explained (%)
Full model	34.2	31.1
Factors	Relative % explained	Relative % explained
<i>Spatial/ Biotic/Topographic</i>		
Geographic site location*	1	0.2
Aboveground vegetation dissimilarity (nMDS)		10
Topographic wetness index	5.1	
Total spatial/ biotic/topographic	5.2	10.2
<i>Climatic</i>		
Annual precipitation (mm/year)		4.8
Average annual temperature (°C)		7.6
Aridity Index (AI _B)	9.7	-
Total climatic	9.7	12.4
<i>Edaphic</i>		
Total soil phosphorus (%)		4.1
Soil bulk density (g/cm ³)	4.7	
Total edaphic	4.7	4.1
<i>Disturbance</i>		
Time since fire (years)	6.9	
Average inter-fire interval (years)	7.7	
Fire frequency (count)		4.4
Total disturbance	14.6	4.4

*latitude and longitude

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581
582 **Appendices:**

583
584 Appendix 1. Independent soil edaphic, topographic, climatic, and disturbance variables used in linear mixed
585 effects (LMM) and generalised dissimilarity (GDM) modelling

586
587 Appendix 2. Common species above-ground and in the soil-seedbank

588
589 Appendix 3. Complete factor group LM and LMM results

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Author/s:

Chick, MP;Nitschke, CR;Cohn, JS;Penman, TD;York, A

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