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A spatially predictive baseline for monitoring multivariate species occurrences and phylogenetic shifts in mediterranean southern Australia

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Keywords
Climate change; Community phylogeny; Distance decay; Flinders Ranges; Gradient analysis; Logistic regression; Mediterranean Biome; Mount Lofty Ranges; Spatial analogues; Species composition

Abbreviations
AIC = Akaike information criterion
APG = Angiosperm Phylogeny Group
NMDS = non-metric multidimensional scaling.

Nomenclature
Census of South Australian Plants (http://www.flora.sa.gov.au/census.shtml)

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Abstract

Question: Climate change is driving shifts in the composition of vegetation but the lack of controls and confounding spatial factors pose challenges for detecting the climate signal in observed changes through time and space. We tested whether climate can be isolated as a driver of spatial vegetation composition at the landscape scale in mediterranean southern Australia by considering landscape factors (e.g. soil gradients) and spatial structure (relative geographic isolation). The aim was to develop principles for selecting spatial analogues for climate change and provide a spatially predictive baseline for monitoring.

Methods: A landscape-scale monitoring transect spanning 550 km was established. Whole community presence/absence of vascular plant species in plots was modelled as a multivariate response to environmental and spatial variables. Species and phylogenetic composition–environment relationships were also explored using indirect gradient approaches, partial correlations and distance decay models.

Results: A total of >2900 occurrences of >400 plant species were recorded. Relative vegetation composition was predicted by mean temperature and soil properties, such as electrical conductivity and texture. Spatial structure was critical, as decay in compositional similarity with geographic distance and spatial autocorrelation of nested plots were involved in turnover patterns. The rate of change in species composition with changes in temperature equated to complete species turnover within the habitats sampled.

Conclusions: The influence of climate on spatial variation in vegetation composition can be quantified, accounting for distance decay. Landscape gradients (particularly soil properties) tended to be orthogonal to climate and explained some turnover. Spatial analogues for climate change would need to be similar in soil properties and not too geographically distant. Composition resulting from more extreme climate change scenarios may have no spatial analogue due to the importance of neutral distance decay at larger spatial scales in determining compositional differences. We illustrate these principles with a sequence of warming, drying analogues. The spatial transect provides a framework for monitoring composition by directly incorporating temporal data and using spatial analysis to inform the expected direction of compositional shifts with climate change.

Introduction

Climate change is believed to be driving shifts in the species composition (presence and relative abundance) of vegetation (Penuelas & Boada 2003; Lloret et al. 2004; Wahren et al. 2013). The Mediterranean Biome has been identified as at particular risk from climate change, in part because of extensive habitat fragmentation and modification (Wade et al. 2003; Abbott & Le Maitre 2010; Prober et al. 2012). The focus of this paper is on spatial drivers of

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species and phylogenetic composition in a mediterranean climate ecosystem in southern Australia as a context for on-going monitoring of the impacts of climate change. We define spatial drivers as factors that influence vegetation composition according to spatial processes or that vary through space, particularly changes in climate, landscape variables and dispersal limitation.

Space-for-time substitution is a valuable tool for assessing the importance of climate and making predictions of species assemblages with future climate change, notwithstanding the potential for no-analogue climates and ecological communities (Emanuel et al. 1985; Williams & Jackson 2007; Guerin et al. 2013). A critical challenge for spatial and temporal analysis is detecting the climate signal in observed composition shifts (Stohlgren et al. 2000). For spatial comparisons of vegetation composition, there may be confounding landscape and historical factors, while for temporal comparisons there are no controls for climate change (Dunne et al. 2004; Abbott & Le Maitre 2010). Accurate prediction of temporal shifts by reference to spatial climate–composition relationships requires knowledge of historical factors and spatio-temporal scales that led to current patterns (Dunne et al. 2004). Responses to climate can be sampled across environments in a way that simultaneously establishes a baseline for monitoring whilst determining spatial climate–response links with controls for confounding factors (Imeson & Lavee 1998; Stohlgren et al. 2000). Future observations can be compared to an established baseline and to expectations of ecosystem shifts with climate change from spatial analysis.

It is widely recognized that the spatial structure (relative geographic isolation) of ecological communities influences patterns of compositional similarity (Nekola & White 1999; Soininen et al. 2007; Tang et al. 2012; Guerin et al. 2013). The influence of spatially structured environmental variables (including those not explicitly included in analysis) and neutral processes on distance decay can be partitioned through sampling that specifically compares environmental vs. geographic distances (Tang et al. 2012). This can be achieved by sampling nearby locations with different environments as well as distant locations with similar environments and inferring patterns from empirical data for specific regions (Tang et al. 2012).

We initiated a landscape-scale monitoring transect in southern Australia spanning 550 km. The aim was to examine spatial drivers of compositional turnover to isolate the influence of climate on whole vegetation community composition and therefore inform on-going monitoring of the impact of climate change. Although remnant vegetation available for monitoring in the study region is limited by historical clearing (87% since 1836 in southern portion; Armstrong et al. 2003), we targeted ecosystems less affected by fragmentation and accounted for confounding spatial factors by the inclusion of a range of environmental data and spatial structure. We recently tested appropriate plot-based methods for monitoring in these habitats (Guerin & Lowe 2012a) and apply comparable methods here. The transect samples spatial climate gradients of 5 °C in mean temperature and 800 mm in mean annual rainfall. The region has a mediterranean climate, with a small pocket of relatively high rainfall in the southern ranges which grades into desert-like conditions to the north (Keith et al. 2013).

Changes in species composition are predicted to occur in the study region with expected near-future warming and drying (Suppiah et al. 2006; Guerin & Lowe 2012b; Guerin et al. 2013). Systematic monitoring is required along with analysis of spatial drivers of turnover and better understanding of landscape factors to test this expectation (Keith et al. 2013). There are good vegetation inventory data for the region, and preliminary studies have been conducted on species and community climate sensitivity based largely on these pre-existing data (Guerin & Lowe 2012b; Guerin et al. 2013; McCallum et al. 2014). However, ecological patterns within the region remain poorly studied. No analysis has been reported on the influence of climate on vegetation based on dedicated, systematic sampling that includes a range of potentially important landscape variables, nor that establishes an informed baseline for climate change monitoring. The new transect enables analysis of ecosystem responses to climate change through space-for-time substitution and on-going monitoring against collected baseline data.

The following research questions are addressed here:

1. What are the most important spatial drivers of species and phylogenetic composition along landscape-scale environmental gradients?
2. Can the answer to Question (1) inform selection of suitable spatial analogues for climate change?
3. How can a framework for assessing spatial drivers be used to monitor and interpret shifts in species composition due to climate change?

Methods

Establishment of field plots

A vegetation community sampling transect was established with 85 plots among 17 sites along the Adelaide Geosyncline between the Fleurieu Peninsula in the southern Mount Lofty Ranges and Mount Hack in the northern Flinders Ranges (Fig. 1, Table S1 of Appendix S1). Transect design was limited by site access and availability of remnant native vegetation but took advantage of linear ranges running parallel to a latitude gradient in temperature. Sampling could therefore compare the influence of

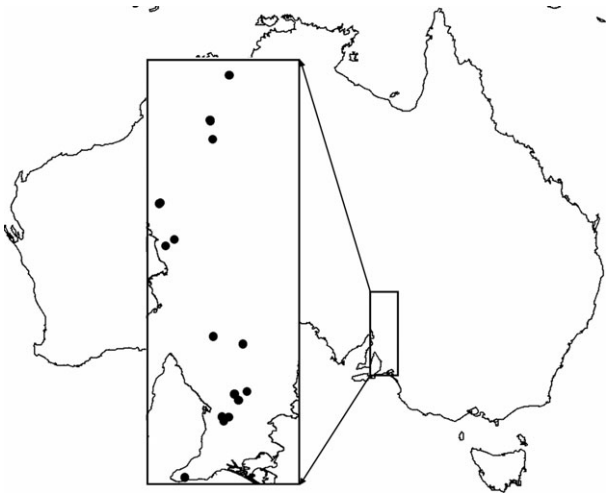

Fig. 1. Location of the species composition sampling transect in the context of Australia. Dots mark location of 85 plots nested among 17 sites. Due to scale, not all plots visible individually. Maximum geographic distance between plots 550 km. Scale: inset 170 km across.

geographic and climate distances on ecosystem composition at a landscape scale. Topographic heterogeneity was used to vary climate between sites over relatively small distances and, conversely, to compare distant sites with similar climate (Fig. 2d).

A nested plot sampling design was implemented, consisting of five replicate plots established at each site within a confined spatial area (e.g. within 500-m radius) on similar topography and soil. The 30 m × 30 m plots were pegged in their southwest corner and their sides (orientated north–south–east–west) marked out using a compass and measuring tape. Aspect was recorded with a compass and converted to 'northness': cos((aspect*pi)/180) and 'eastness': sin((aspect*pi)/180) for analysis. Slope was estimated with the aid of a digital level measure rested on representative, evenly sloped ground on a flat object (e.g. length of timber). Visual estimates were recorded for the percentage surface cover of stones and outcropping rock. Topsoil samples were collected from each plot by removing the surface crust and taking samples from the top 10 cm from each of four holes located randomly across the plot, which were subsequently mixed.

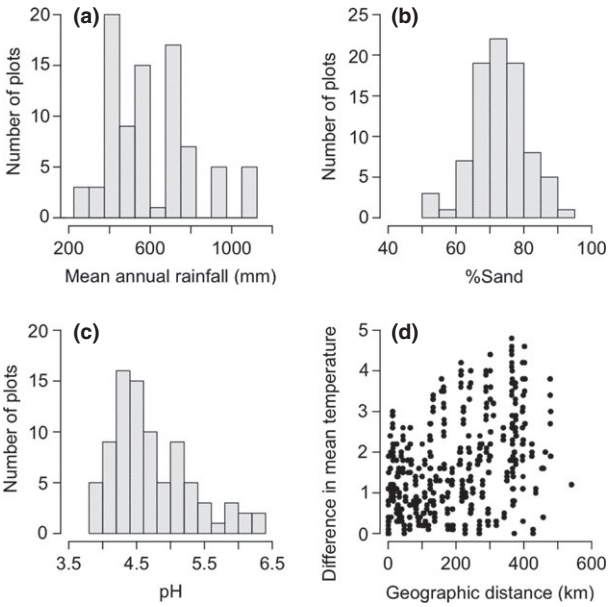

Fig. 2. Histograms summarizing sampling design and examples of gradients sampled in plots. (**a**) Rainfall; (**b**) soil texture; (**c**) soil pH ($CaCl_2$); (**d**) sampling design reflecting a range of climatic habitats sampled at a range of geographic distances to isolate the effects of climate vs. geographic isolation.

All visible, living vascular plant species were recorded, with detection through an exhaustive visual search of plots. Plants rooted in, or with foliage overhanging, the plot, were included. Dead plants were not recorded, with the exception of obviously recently senescent foliage of annuals and geophytes. Species were recorded along with a visual estimate of projected foliage cover to the nearest 5% or scored 1% as present but low cover. The first occurrence of each taxon at each site (within a set of five replicate plots) was vouchered. Additional voucher material was sometimes collected for later occurrences to improve material available for identification. Species identifications were verified mostly by GRG using literature, herbarium resources and specialist consultation. Nomenclature follows the Census of South Australian Plants (see http://www.flora.sa.gov.au/census.shtml).

Environmental and spatial data

Data for mean temperature and annual rainfall were extracted for plot coordinates in DIVA-GIS (Hijmans et al. 2012) from WorldClim (Hijmans et al. 2005). Gradients of 800 mm in mean annual rainfall and 5 °C in mean temperature were sampled (Fig. 2a, Table 1, Appendix S3). DIVA-GIS was also used to extract pair-wise geographic distances between plots (Appendix S4).

Plots were situated on typically sandy, low-nutrient, slightly acidic soils (Fig. 2b,c, Table 1, Appendix S3). Soil texture was measured for each plot using ~35 ml of soil cleaned of coarse material and lightly rolled to break up soil lumps. Soil was added to 100 ml ~0.5% w/w sodium hexametaphosphate ('Calgon') and agitated for 5 min. The mixture was then topped up to 200 ml with tap water. Soil was allowed to settle and the percentage sand calculated by measuring volume. Levels of soil nitrogen (ammonium and nitrate), phosphate (Colwell P), potassium (Colwell K), pH ($CaCl_2$) and electrical conductivity were analysed

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Table 1. Environmental variables and their ranges recorded from 85 vegetation monitoring plots. Partial correlations of phylogenetic distance metrics with pair-wise distances based on individual variables (given other correlated variables and geographic distance but with non-significant variables excluded).

Variable	Range	Source	Partial correlation with phylogenetic distance metrics			
			UniFrac	PCD	PCDp	PCPc
%Outcrop	0–60	Visual estimate	0.04**			
%Sand	53–91	Analysis of soils samples	0.15***	0.14***	0.06***	0.13***
%Surface stones	0–90	Visual estimate				0.03*
Aspect (°)	0–360	Compass	0.25 (N)***, 0.05 (E)**	0.28 (N)***	0.22 (N)***	0.16 (N), 0.08 (E)***
Mean annual rainfall (mm)	300–1100	WordClim				
Mean temperature (°C)	13–18	WorldClim	0.30***	0.28***	0.12***	0.28***
Slope (°)	0–33	Visual estimate/digital level	0.11***	0.05**		0.06***
Soil electrical conductivity (dS m^{-1})	0.011–0.113	Analysis of soils samples	0.20***	0.21***	0.11**	0.18***
Soil nitrate nitrogen (mg kg^{-1})	<1–30	Analysis of soils samples				
Soil ammonium nitrogen (mg kg^{-1})	2–19	Analysis of soils samples				0.07***
Soil pH ($CaCl_2$)	3.9–6.4	Analysis of soils samples	0.06**	0.06***	0.10***	
Soil potassium (Colwell K; mg kg^{-1})	22–314	Analysis of soils samples	0.08***	0.08***		0.04**
Soil phosphorus (Colwell P; mg kg^{-1})	1–15	Analysis of soils samples			0.09***	

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$, based on 1000 permutations.

externally at the CSBP Soil & Plant Analysis Laboratory (Bibra Lake, WA, Australia).

Analysis

Four analyses were conducted: (1) initial exploratory visualisation of data using ordination methods; (2) distance-based regression based on species composition; (3) distance-based correlations based on phylogenetic composition; and (4) models based on raw gradients and multivariate species presence/absence.

1 Species composition was plotted using two-dimensional non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities with up to 20 random starts and the configuration rotated to its principal components. Environmental variables were fitted to the NMDS configuration as linear correlation vectors (with 1000 permutations to test significance) and as contours using GAM regression splines to test for more complex responses. Only variables with statistically significant fit to the configuration and high linear correlations are reported. NMDS has been widely reported to be a robust method for mapping environmental gradients underlying compositional patterns (Laughlin & Abella 2007; Oksanen et al. 2011). A limitation to this analysis was that the nesting of replicate plots among sites was not explicitly acknowledged when calculating vectors and statistical significance.

2 A distance-based regression treated Bray–Curtis dissimilarity in species composition as the response to environmental and geographic distances. Euclidean pair-wise distances between plots were calculated based on each environmental variable. The non-linear response was accounted for by using the following transformation of linear predictors to constrain predicted values between zero and one: $1 - e^{-x}$ (Guerin et al. 2013). As 9% of Bray–Curtis scores were 1 (which the model transformation cannot take), the inverse of geographic distance (which had a mean value of 0.0003) was subtracted from the scores. Linear coefficients were estimated using multiple distance matrix regression (Lichstein 2007) with 10 000 permutations to test statistical significance. Terms that were not statistically significant or generated negative coefficients were sequentially removed. Coefficients from the model were used to predict the Bray–Curtis scores resulting from the maximum sampled distance for each variable in isolation to compare their relative influence on species turnover across the transect.

3 The online phylogeny database Phylomatic (http://www.phylodiversity.net/phylomatic) was used to derive a phylogenetic hypothesis for the majority of vascular plants recorded within plots by matching species to the consensus view of relationships according to The Angiosperm Phylogeny Group (APG III 2009). Pair-wise phylogenetic distances between plots were calculated based on the metrics unweighted 'UniFrac' and Phylogenetic Community Dissimilarity ('PCD'), which includes phylogenetic, species composition and combined distance components (Ives & Helmus 2010). We calculated the partial correlations of the phylogenetic distance metrics with pair-wise distances for each environmental variable, given the other variables and geographic distance. We tested the significance of partial correlations via 1000 permutations of the environmental and geographic distance variables to test whether the partial correlations were significantly higher than expected at random. Since only positive correlations between phylogenetic and environmental distances are expected for important variables, P-values were calculated based on the proportion of permutations for which higher partial

correlation coefficients were obtained. Variables with non-significant partial correlation to phylogenetic distance were sequentially removed.

4 A binomial generalized linear mixed model (GLMM) was fitted using maximum likelihood to the combined presence/absence of all species in plots. Species and sites were treated as random effects to account for pseudo-replication and to allow responses to differ between species, and environmental variables were treated as fixed effects. Using R package 'lme4' (R Foundation for Statistical Computing, Vienna, Austria) the generic structure of this model was expressed as:

$$\begin{aligned}&\text{lmer}(\text{response} \sim \text{variable1} + \text{variable2} + \text{variable3}\\&\quad + (1|\text{site}) + (1 + \text{variable1} + \text{variable2}\\&\quad + \text{variable3}|\text{species}), \text{family}\\&\quad = \text{binomial, data})\end{aligned}$$

Initially, terms were tested individually and terms with no significant effect were excluded. We trialled the inclusion of quadratic terms for climate variables to allow the mode to occur within the sampled portion of the gradients (as linear terms assume the mode occurs outside the sampled portion) but found that these terms were not a good fit. Models were built with forward selection of linear terms. Successive terms were included until additional terms provided no statistically significant improvement and a minimum AIC (Akaike information criterion) had been reached. The data structure finds variables that significantly contribute to species composition in terms of determining the presence and absence of multiple species. To improve efficiency and decrease noise, we only included data for species recorded five or more times across the transect (about 200 species accounting for 84% of all presence records).

Analyses were conducted in R (v. 2.11.1, R Foundation for Statistical Computing, Vienna, Austria; Appendix S1) using functions from packages 'ecodist' (multiple regression of distance matrices, linear vector fitting; Goslee & Urban 2007), 'lme4' (GLMM) and 'Vegan' (ordination). We also specifically developed a function 'parCorPerm' to calculate the permutational significance of multivariate partial correlations (Appendix S1) after Ives & Helmus (2010), with coefficients calculated using package 'ppcor'.

Results

Field data

The field surveys resulted in >2900 individual species presence records of >400 species at an average species richness of 34 plot^{-1} (Fig. 3d, Appendix S2). Over 97% of records were identified to species or infraspecific level. The remainder, for which insufficient material was available, were excluded from analysis. The 20 most frequently recorded species represented families including Asparagaceae, Asteraceae, Xanthorrhoeaceae, Poaceae, Dilleniaceae and Haloragaceae (Table 2). Typical vegetation structure within plots consisted of mallee, woodland and forest dominated by *Eucalyptus* spp. (± *Allocasuarina verticillata*,

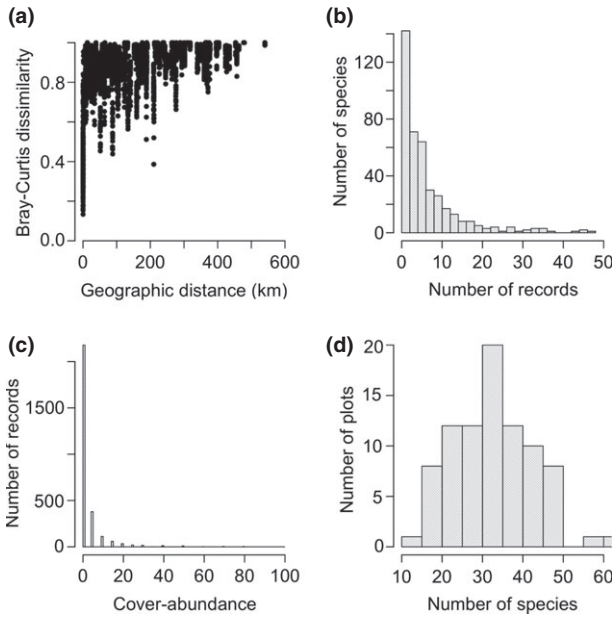

Fig. 3. Histograms summarizing species records from plots. (**a**) Scatterplot of distance decay in compositional similarity; (**b**) species frequency; (**c**) cover-abundance frequency; (**d**) species richness.

Table 2. Twenty most frequently recorded species along the transect within 85 vegetation monitoring plots

Family	Species	No. records
Xanthorrhoeaceae	*Dianella revoluta* var. *revoluta*	47
Ericaceae	*Astroloma humifusum*	46
Asparagaceae	*Arthropodium strictum*	46
Myrtaceae	*Calytrix tetragona*	44
Dilleniaceae	*Hibbertia crinita*	40
Haloragaceae	*Gonocarpus elatus*	37
Xanthorrhoeaceae	*Xanthorrhoea quadrangulata*	36
Casuarinaceae	*Allocasuarina verticillata*	35
Leguminosae	*Acacia pycnantha*	34
Asteraceae	*Hypochaeris glabra*	34
Asteraceae	*Cassinia laevis*	33
Oxalidaceae	*Oxalis perennans*	32
Haloragaceae	*Gonocarpus tetragynus*	31
Asparagaceae	*Lomandra densiflora*	30
Sapindaceae	*Dodonaea viscosa* subsp. *angustissima*	28
Poaceae	*Austrodanthonia setacea*	27
Dilleniaceae	*Hibbertia exutiacies*	27
Asparagaceae	*Lomandra multiflora* subsp. *dura*	27
Poaceae	*Poa crassicaudex*	25
Asteraceae	*Olearia decurrens*	24

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Callitris spp.), typically with a heathy or open shrub understorey. Dominant species (i.e. highest cover-abundance within highest vegetation strata) turned over rapidly. Twelve eucalypt species were recorded as dominants across the 17 sites, and the most frequent, *E. fasiculosa,* occurred at a frequency of 0.2 across all 85 plots. Rapid turnover was also demonstrated as the high proportion of species with few records (Fig. 3b). Most of the species richness was due to non-dominant species (i.e. species recorded as present only; Fig. 3c).

Ordination and gradient analysis

Ordination of species composition data with NMDS followed by indirect gradient analysis revealed strong linear correlations between composition (NMDS configuration) and soil texture, pH, temperature and rainfall (Fig. 4). Of these environmental gradients, landscape and climate variables were largely orthogonal.

Regression, partial correlations and models

The distance-based regression suggested species turnover among plots responds to a combination of geographic distance (see Fig. 3a), mean temperature, ammonium N levels, electrical conductivity and aspect (Table 3). Turnover attributed to mean temperature was higher than for soil and landscape factors and when linear predictions were transformed into Bray–Curtis dissimilarities, temperature generated complete species turnover between plots at extremes of the sampled gradient (Fig. 5).

Turnover in species composition among sites was associated with shifts in represented phylogenetic branches (Table 1). While controlling for geographic distance and partial correlations with other variables, differences in mean temperature, aspect ('northness'), soil texture and electrical conductivity were revealed as the environmental factors most strongly and frequently correlated with phylogenetic (and species) turnover.

The logistic GLMM predicting the multivariate presence/absence of species also showed that community composition is best explained (in order of importance) by spatial structure, climate (mean temperature) and the soil properties of ammonium N, Colwell P and electrical conductivity (Table 3). The distribution of random effects is shown in Figs S1–S2 of Appendix S1.

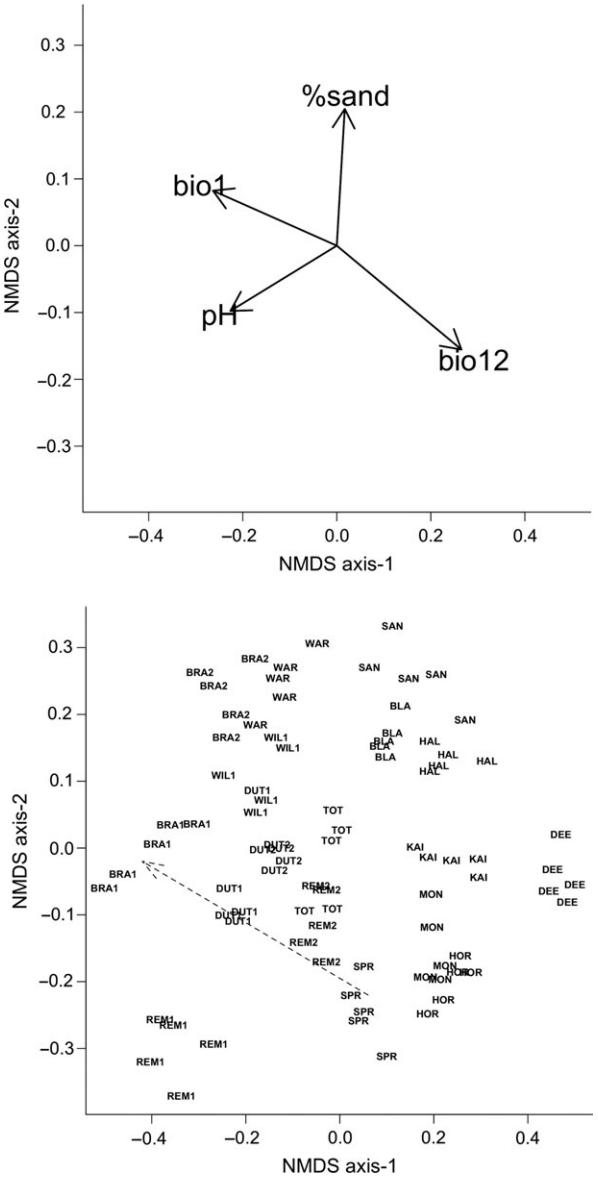

Fig. 4. Two-dimensional NMDS ordination visualizing species composition across spatial gradients based on Bray–Curtis dissimilarities weighted by cover-abundance. Text labels represent replicate plots labelled with site code (Table S1). Linear correlation vectors for the same ordination plot are shown above (bio1: mean temperature; bio12: mean annual rainfall) with vector length proportional to correlation coefficient ($P < 0.01$ for all based on 1000 permutations). Changes in vegetation composition driven by climate change would be expected to manifest as movement of plots along mapped climate gradients with temporal re-sampling. Predicted movement of individual sites towards their spatial climate change analogues is shown with a dashed arrow for a selected set of plots (SPR, REM2, DUT1, BRA1), representing incremental warming and drying of similar landscapes (see Fig. 6).

Discussion

Spatial drivers of species and phylogenetic composition

At broad spatial scales, the sorting of species along abiotic gradients, and dispersal limitation as dictated by spatial structure, can be important determinants of vegetation composition (Soininen et al. 2007). We partitioned the effects of climate and landscape gradients vs. space as drivers of vegetation composition along a landscape-scale

Table 3. Regression term/model forward selection statistics for species turnover and composition as predicted by environmental and spatial variables. Delta AIC represents the change in AIC with the addition of the term where lower values indicate better models (addition of each listed term was statistically significant). R^2 for distance model = 0.34.

Response variable – model	Explanatory variables/fixed effects (GLMM)	Term statistic
Bray–Curtis dissimilarity – exponential distance decay with linear distance predictors		Coefficient
	Geographic distance	$7.56e^{-6}$***
	Mean temperature	0.73***
	Ammonium N	0.09*
	Electrical conductivity	11.52*
	Aspect (N)	0.66***
Multivariate species occurrences – GLMM with site and species as random effects		Delta AIC
	First spatial eigenvector (PCNM axis-1)	−1353
	Mean temperature	−719
	Ammonium N	−130
	Electrical conductivity	−81
	Colwell P	−120

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$, based on 10000 permutations.

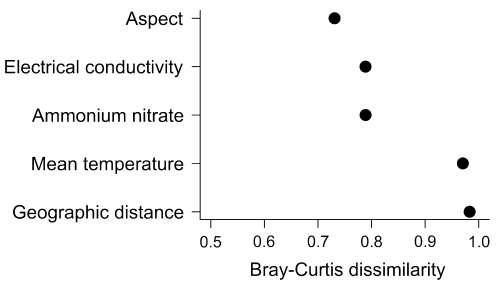

Fig. 5. Predicted species turnover among plots with environmental and geographic distance. Bray–Curtis dissimilarity (horizontal axis) generated by each variable in isolation (vertical axis) based on maximum distances (differences) observed between plots; a comparison of the rate of turnover along each gradient in the context of the sampled gradient breadth. Predictions are based on model transformations of linear predictors. The predicted amount of change in Bray–Curtis scores per unit of environmental distance of a given variable depends on the starting position.

transect and found that mean temperature and selected soil properties were important determinants of species and phylogenetic turnover. Spatial structure was also a strong explanatory variable, and decreased the importance of environmental variables when included. Geographic distance is a proxy for dispersal limitation and also other potentially relevant factors not directly considered here that could be expected to have some spatial structure, such as proximity to human activity, fire regimes and faunal communities. The broad agreement for our data among ordination methods, distance-based analysis and multivariate logistic models provides support for the conclusion that climate is a critical spatial driver of vegetation composition.

The use of altitude to compare climates between local and distant sites to isolate the influence of geographic distance assumes that dispersal limitation with distance is equivalent regardless of topography. While the highest sampled sites were just 900 m a.s.l. and many sampled species occur at different altitudes, we acknowledge that for some species dispersal between sites at different altitudes may be restricted even over relatively short distances. Despite the strong influence of geographic distance on turnover, exploratory patterns revealed by indirect gradient analysis, such as correlations between climate and vegetation composition, remained after accounting for spatial structure. Different soil properties were highlighted as important, depending on method and whether explicit spatial controls were included.

Multivariate binomial/logistic mixed models that predict species occurrences within whole communities are a recent advance in the application of ecological tools (Jamil et al. 2012). They allow community composition to be modelled against environmental variables without transformation of data. While creating a complex response variable and imposing a model, this makes more transparent use of data, is presumably less vulnerable to distortions than transformed data and in theory enables predictions simultaneously at the species and community level. One limitation of multivariate logistic models is that although responses are allowed to differ between species, the same model is imposed on all species. While we expect that the selected model and terms account for the most frequent response to the sampled environmental gradients, clearly there will be some species for which the model is not the best possible fit and for which more flexible approaches would need to be developed.

A problem encountered in further teasing apart the influence of particular climate variables on species composition was the strong negative correlation between temperature and rainfall (< -0.5 Pearson r). We could not fit statistically significant model or partial correlation terms for rainfall to our data when temperature was included. While temperature was a stronger candidate for inclusion based on these statistics, rainfall must of course be ecologically important. However, we note that a number of species sampled do appear to span large rainfall gradients but limited temperature gradients.

We principally considered the effects of neutral (e.g. dispersal limitation) and more deterministic filtering processes through the influence of selected abiotic gradients and spatial structure. Additional factors that may influence relative species composition were either included only indirectly, via geographic distance decay, or not considered

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at all. These include biotic interactions, such as herbivory, pollination, symbioses (e.g. host–hemiparasite relationships) and inter-specific competition, disturbance levels such as human activity, fragmentation and fire regimes, and small-scale patchiness (Stohlgren et al. 2000). Further understanding of these factors and their inclusion in analysis where possible may improve predictive power, although climate typically accounts for a large portion of composition patterns observed at larger scales (Stohlgren et al. 2000).

Spatial analogues for climate change

Our second stated aim was space-for-time substitution to determine suitable analogues for future climate change. The importance of climate as a spatial driver of vegetation composition can be interpreted as a prediction of temporal composition shifts with changing climate (White et al. 2010; Guerin et al. 2013). While we did not directly make predictions against specific future climate scenarios, our framework allows selection of sites as potential spatial analogues for future climate change. According to our results, future climate analogues should be similar in soil properties and terrain and not too geographically distant, as these factors inflate compositional differences. In practice, this is not a straight-forward task as there are complex combinations of soil properties among sites. Additionally, even the softer interpretation of a future climate analogue as a state towards which composition may become more similar invokes an assumption of equal opportunity for species to migrate and establish at different sites, despite habitat fragmentation (Pitelka 1997). Nevertheless, we illustrate here the selection of a series of plots that represent progressively warmer and drier conditions whilst largely meeting the condition of having similar landscape and soil properties.

We chose the transect sites MON, REM2, DUT1 and BRA1 as progressive climate change (warming and drying) analogues (Appendix S1, Fig. 6). The selected sites incrementally span gradients of 3.6 °C in mean temperature and 400 mm in mean annual rainfall. Climate differences between progressively warmer and drier plots in the analogue series range from +0.4 °C and −17% rainfall to +2.4 °C and −32% rainfall. These comparisons are relevant because changes in climate for the region by 2070 have been predicted to potentially be as high as +3.8 °C and −30% rainfall (Suppiah et al. 2006). The sites have similar soil texture and topography and progressive analogues are a minimum of 50 km and a maximum of 140 km apart.

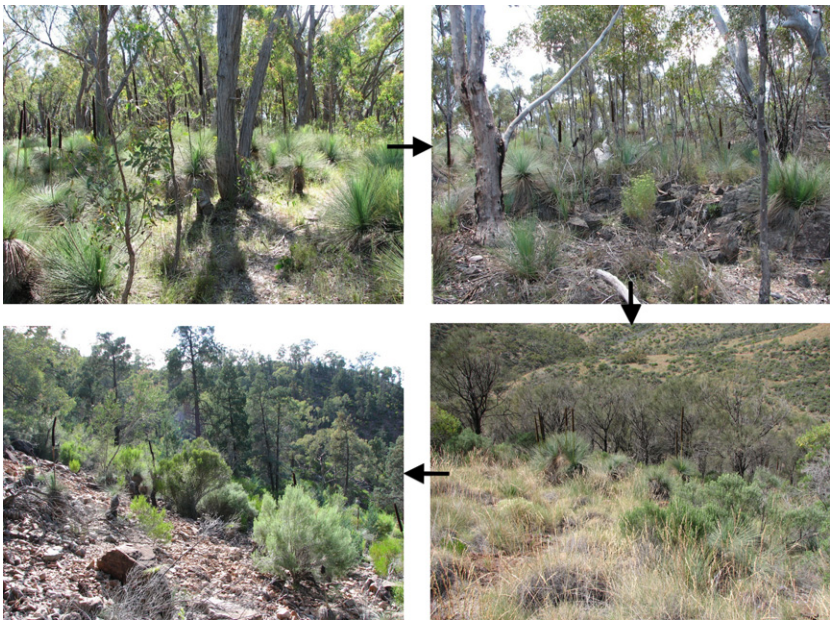

Fig. 6. Illustration of a series of spatial climate change analogues representing incrementally warmer and drier conditions and shifts in species and phylogenetic composition (clockwise from top left; see also Fig. 4): photos of monitoring plots at sites SPR (Spring Gully), REM2 (Mount Remarkable Range), DUT1 (Dutchman's Stern) and BRA1 (Heysen Range). Although confounding spatial factors between these sites were minimized by site selection, the temporal translation of differences in vegetation with climate is further limited by historical factors, temporal scale and opportunities for species to migrate across modified landscapes. These analogues inform the expected direction and ultimate magnitude of shifts in the species and phylogenetic composition of vegetation with climate change rather than the precise composition.

Our results reinforce the notion that spatial analogues for climate change must be considered in the context of spatial structure, in order not to overestimate the importance of climate in driving species turnover. Finding suitable spatial analogues for more extreme climate change scenarios is problematic as vegetation at sites with very different climate may be too geographically distant and therefore ecologically different due to neutral processes. This interpretation differs from the expectation of species composition with no contemporary analogue due to the emergence of novel climates (Williams & Jackson 2007).

A spatial and predictive framework for monitoring

There are opportunities for hierarchical monitoring of species occurrences and community composition (i.e. at site and regional levels) using these – or comparable – data as a baseline and in a way that partly compensates for the absence of controls for climate change. For example, ordination and indirect gradient analysis of species composition (Fig. 4) can be extended to include temporal replicates (Philippi et al. 1998; Wahren et al. 2013). Composition shifts associated with climate change would be expected to produce a response along mapped climate gradients, or to shift a plot from its baseline position towards its climate change analogue (Figs 4, 6).

The spatial sampling design generates predictions of expected compositional shifts with climate change. Observed real time changes can be mapped against these predictions to assess the climate signal. For example, if vegetation composition of plots at site SPR trends towards the baseline of plots at site REM2 with periodic re-sampling, we may infer a high likelihood of a climate change influence. If significant shifts occur with time in a different direction, we may suspect that other drivers are involved.

In addition to visualisation approaches, the nested sampling design of the transect enables numerical detection of significant temporal changes in vegetation composition with periodic re-sampling, which is made possible by replication at the site and landscape level (Philippi et al. 1998). There are several ways temporal changes could be tested within the spatial framework. Changes in the frequency of species, either individually or as multivariate responses, could be tested using binomial models with time as an additional predictor, at the scale of one or several sites or across the entire transect. Significant shifts in composition can also be tested using multivariate analysis of variance based on dissimilarities (Ruokolainen & Salo 2009). These tests could be further compared to climate change predictions of relative composition from spatial models.

The relatively low number of species that were recorded frequently across the transect or that had significant cover-abundance (i.e. >1%) suggests most of the species richness in the system is due to non-dominant species. Given that these species may respond differently to environmental change than the overstorey dominants, effective methods for assessing drivers of species composition should focus more on capturing species richness and patchiness between replicate plots than on precise measurements of structural characteristics (Stohlgren et al. 2000; Guerin & Lowe 2012a). The implemented transect design is a balance between replication and coverage of spatial gradients, given available current and likely future resources (Guerin & Lowe 2012a). Spatial coverage could be increased to broaden the area to which monitoring data can be extrapolated, while increasing site-level replication in space and time could allow detection of smaller shifts, or earlier detection of shifts (Field et al. 2007).

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Supporting Information

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

Appendix S1. Location of 85 plots in the monitoring transect; plots of model random effects; R code for analysis and plotting of data.

Appendix S2. Species data.

Appendix S3. Environmental data.

Appendix S4. Geographic distance matrix.

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