

Plant trait–environmental linkages among contrasting landscapes and climate regimes in temperate eucalypt woodlands

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Abstract. Ecological sorting of species along climate and landscape gradients is a fundamental global pattern. However, the extent to which functional traits reflect floristic turnover in response to interactions between climate and landscape gradients is rarely assessed. We tested whether floristic variation among sites within a bioregion was more strongly correlated with soil fertility or climate. We then examined the relationship between floristic composition, environment and the covariation of selected vegetative and regenerative functional traits. This allowed us to assess the ecological sorting of species along soil fertility and rainfall gradients and to detect any resource compensation effects via interactions between these factors. Floristic differences were equally associated with soil fertility and climate contrasts but species' trait patterns were more strongly associated with soil fertility than rainfall. No interactive effects, which would suggest resource compensation, were detected. Instead, more fertile sites consistently had more forbs, annuals and grasses in comparison with less fertile sites which were dominated by woody species and had a higher abundance of graminoids. Three broad mechanisms for sorting of species based on trait patterns are proposed (1) differences in the fundamental regenerative and growth niche, (2) resource competition during establishment and (3) disturbance-mediated sorting.

Introduction

The extent to which the landscape *v.* the climate template influences community level plant trait mixtures is a critical question in understanding the response of communities to environmental change. Numerous studies worldwide have examined relationships between plant traits and environmental conditions, both in terms of the responses of plants (Lavorel *et al.* 1997; Diaz *et al.* 1998; Fonseca *et al.* 2000; Cingolani *et al.* 2007; Garnier *et al.* 2007) and the effects on ecosystem functions (Herbert *et al.* 1999; Epstein *et al.* 2001; Garnier *et al.* 2007; van Wijk 2007). These studies have led to the development of a growing consensus on suites of traits that are useful in examining trait–environment relationships at various scales (Cornelissen *et al.* 2003; Diaz *et al.* 2004; Garnier *et al.* 2007). Both vegetative and regenerative traits are considered essential in devising valid community classifications, as weak relationships between the two have been consistently demonstrated (Diaz *et al.* 1999; Poorter 2007).

Contrasts in the traits of plants across fundamental gradients in plant resources have provided a powerful tool, not only for understanding natural selection, but also in developing functional models of communities (Lavorel *et al.* 1997; Diaz *et al.* 2004; De Bello *et al.* 2005; Cingolani *et al.* 2007; Quetier *et al.* 2007). At the community level, these contrasts have been predominantly comparisons of the relationship of plant traits with either landscape templates or climate templates, e.g. rainfall, with few examples of where climate and landscape are compared or their interactions tested (but see Fonseca *et al.* 2000; Clarke

et al. 2005). Variation in community composition of trait-mixtures may change across geological boundaries, and where the edaphic contrast is strong, both nutrients and soil water potentials covary. Hence, more fertile soils often retain more moisture because they have a higher clay content and fertile soils may provide edaphic compensation for soil water-deficit where rainfall is limiting. Conversely, in higher rainfall regions, nutrient poor soils may be resource compensated by higher rainfall, narrowing the resource difference between infertile and fertile soils. One way of testing this hypothesis is to compare trait-mixture across climate and soil gradients to see whether there are statistical interactions among climate and soil fertility factors.

In Australia, the distribution of the major structural formations of vegetation is influenced predominantly by rainfall and temperature patterns (Cox *et al.* 1976; Beadle 1981). There is, however, considerable floristic variation within communities and local patterns of variation are frequently associated with soil fertility and moisture gradients (Specht and Perry 1948; Beadle 1981; Keith and Sanders 1990; Fonseca *et al.* 2000). Boundaries between community types are usually continuous, although sudden changes in vegetation have been observed in relation to abrupt changes in lithology (e.g. Specht and Perry 1948; Ridley 1962). Such abrupt changes in floristic composition are likely to be accompanied by changes in plant functional traits in terms of resource use and response to perturbations (Gitay and Noble 1997). Hence, these juxtapositions provide an opportunity to compare the relative influence of climate and landscape on community level plant functional composition.

Patterns of association between understorey vegetation and soil fertility in the montane forests and woodlands of eastern Australia are well recognised (Beadle 1981; Clarke *et al.* 1997, 2000a; Benson and Ashby 2000). Open forests and woodlands with a grassy understorey occur predominantly on the finer textured, more fertile soils, derived from basalt and metasediment lithologies, whereas those with a shrubby understorey occur on the coarser textured, less fertile acid granites, such as leucadamellites (Morgan and Terrey 1990; Clarke *et al.* 1997, 2000a; McIntyre and McIvor 1998; Benson and Ashby 2000). However, the extent to which these floristic differences are reflected in turnover in plant trait mixtures has rarely been assessed.

The relationship between the plant attributes and the habitats in which they occur, trait–environmental linkages, has been examined extensively for temperate grassy eucalypt communities (grassy woodlands) in Australia (Tremont and McIntyre 1994; Lunt 1997; McIntyre and Lavorel 2001; Clarke 2003), mainly in relation to disturbance gradients driven by herbivory and soil fertility levels. By contrast, for shrubby eucalypt systems (dry sclerophyll forest), the relationship between habitat and plant traits has been explored more in terms of fire disturbance (Morrison 1995; Clarke 2002; Clarke and Knox 2002), with less emphasis on productivity gradients (Clarke and Knox 2002; Vesk and Westoby 2004; but see Clarke *et al.* 2005).

The purpose of this study was to assess ecological sorting by comparing the variation in species' functional traits among communities from contrasting soil fertility and climate zones on the New England Tableland of north-eastern New South Wales. First, we examined whether soil fertility or climate was more strongly correlated with floristic differences among sites. Second, we examined the relationship between floristic composition, environment and the covariation of selected vegetative and regenerative traits. We tested whether the distribution of trait classes varied more among soil fertility or climate groups. Third, we tested whether assemblage means of species numbers and their abundance for each trait were significantly related to soil fertility, climate, or the interaction of soil fertility and climate.

Materials and methods

Study areas

Four regions on the New England Tableland, referred to as Torrington, Booralong, Guyra and Ebor, were selected for study (Fig. 1). Within each region, two survey areas were chosen to allow sampling of open forests and woodlands with contrasting lithologies in areas with similar histories of disturbance. The sediments and metasediments at Torrington and Booralong are mostly fine-grained siliceous sediments that weather to form soils of moderate fertility (0.039% P, 0.413% N), whereas the basic igneous rocks of the Ebor and Guyra regions are dark fine-grained rocks that weather to form soils of moderate to high fertility (0.115% P, 0.556% N) (Clarke *et al.* 2005). Both these soil types were selected to provide the 'high' fertility sites for this study. In contrast, soils derived from leucogranites have rudimentary soil development and poor structure with lower soil fertility (0.038% P, 0.207% N). Details of the survey regions are

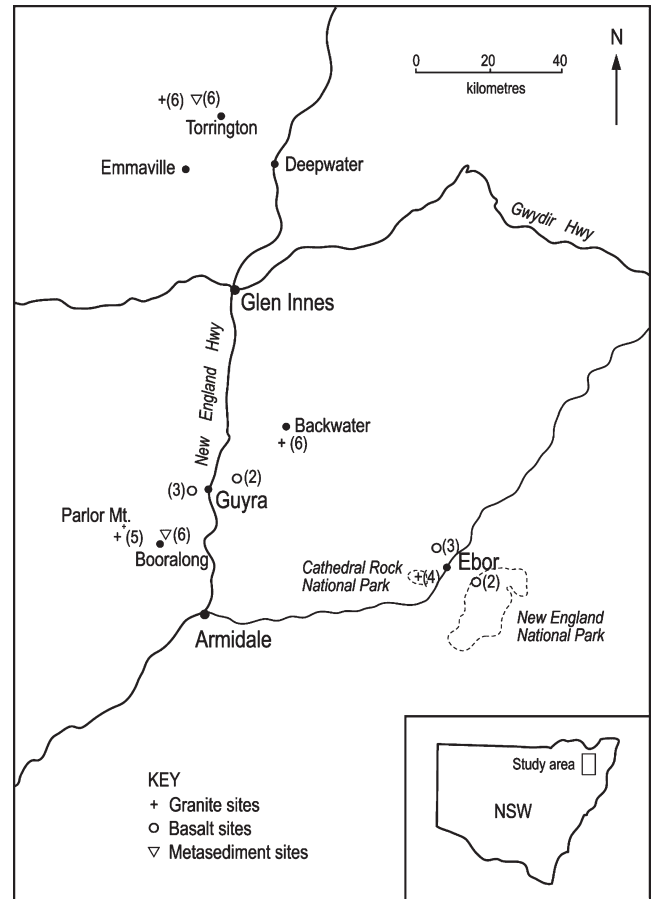


Fig. 1. Location of survey sites on the New England Tableland. Numbers in parentheses are the number of sites sampled.

given in Table 1. Information about strata lithology and age was derived from geological maps (Brunker and Chesnut 1976; Gilligan *et al.* 1992).

Floristic data for the Ebor, Guyra and Booralong granite sites are from a study of the granite flora of the New England Batholith (Hunter 1999), and data for the Torrington granite and three of the Torrington metasediment sites are from the Torrington vegetation survey (Clarke *et al.* 1997). The remaining sites were surveyed between December 1997 and March 1998. In all locations, sampling was undertaken at sites with a history of minimal disturbance from grazing as advised by relevant land managers, and where there was no evidence of recent large-scale disturbance from fire or cattle grazing.

Sampling at each site was undertaken with a single 32 m × 32 m (0.1 ha) nested concentric quadrat containing 10 sub-quadrats that increase geometrically in size. This method has proved to be useful in studies of vegetation community patterns, particularly in detecting small variations in pattern (Outhred 1984; Morrison *et al.* 1995). The approximate areas of the sub-quadrats were 2, 4, 8, 16, 32, 65, 128, 255, 512 and 1022 m². In each of the 10 sub-quadrats a list of all species present was compiled enabling both presence or absence and abundance (1–10) scores for each site to be determined. The abundance score was simply the number of sub-quadrats in which

Table 1. Location of sample sites and their main environmental attributes

Region	No. of sites	Map Geology	Lithology	Soil fertility class	Altitude (m)	Latitude, longitude	Mean annual rainfall (mm)	Mean annual temperature (°C)	Mean annual radiation	Mean moisture index
Torrington	6	Torrington Pendant	Mudstones and siltstones	High	980–1140	29°16'S, 151°38'E	868 (lower)	13.2	18.1	0.63
	6	Mole Granite	Coarse grained leucogranite	Low	940–1060	29°14'S, 151°41'E	868 (lower)	13.2	18.1	0.63
Guyra	5	Unnamed volcanics	Basalt	High	1300–1360	30°14'S, 151°43'E	932 (higher)	11.2	17.7	0.75
	6	Oban River Leucoadamellite	Coarse grained leucogranite	Low	1195–1305	29°59'S, 151°55'E	959 (higher)	11.5	17.6	0.77
Booralong	6	Sandon Beds (5 sites) Annalee Pyroclastics (1 site)	Lithic wacke, slate, basalt Felsic volcanics	High	1240–1325	30°19'S, 151°34'E 30°18'S, 151°43'E	825 (lower)	11.5	17.9	0.65
	5	Parlor Mountain Leucoadamellite	Medium-coarse grained granite	Low	1065–1175	30°18'S, 151°26'E	794 (lower)	12.3	18.1	0.60
Ebor	5	Unnamed volcanics	Basalt	High	1290–1550	30°28'S, 152°21'E	1581 (higher)	10.3	16.6	0.97
	4	Round Mountain Leucoadamellite	Biotite leucogranite	High	1220–1350	30°23'S, 152°16'E	1123 (higher)	11.0	17.2	0.91

the species was recorded. Nomenclature follows Harden (1990, 1991, 1992, 1993).

Data on location, altitude, slope, aspect, vegetation structure, lithology and geology were recorded for each site. Soil samples were collected from each site and the percentage sand determined by using the hydrometer method of particle size analysis (Day 1965). The altitude of the sites ranged from 940 m at Torrington in the north of the Tableland to 1550 m near Ebor. The Guyra and Booralong survey regions were the closest sites, ~40 km apart whereas the Torrington and Ebor survey regions were most distant, ~155 km apart. Climate data were also modelled for each site with BIOLCLIM (Busby 1991) and sites were divided into more montane climates of higher (1210 mm) and lower (857 mm) mean annual climate. Mean annual temperature differed by 1.3°C among these sites.

Selection of traits

Each of the 441 species recorded in the vegetation survey was scored for the following vegetative and regenerative plant traits: (1) growth form: climber, epiphyte (includes orchids, mistletoes and ferns), graminoid (including grass trees), grass, forb, shrub, dwarf shrub, tree; (2) longevity: annual, short-lived perennial, perennial; (3) sexual system: bisexual, dioecious, monoecious; (4) dispersal mode: external animal transport (awned/barbed), ant dispersal (eliasome), internal animal transport (fleshy), wind dispersal (wing/pappus), unassisted; (5) vegetative fire response: herbaceous sprouter, herbaceous obligate seeder, woody sprouter, woody obligate seeder; and (6) reproductive fire response: stimulated by fire, unaffected or suppressed by fire. Data were compiled by using field observations, floras (Harden 1990, 1991, 1992, 1993; Wheeler *et al.* 1990) and the scientific literature (McIntyre *et al.* 1995; Benson and McDougall 1996; Clarke *et al.* 2000a, 2000b; Clarke and Knox 2002).

Canonical correspondence analyses

The relationships between species and environmental variables were analysed by canonical correspondence analysis (CCA) with CANOCO (ter Braak and Smilauer 1998), which models the relative abundance of species, and employs a method of ordination in which the axes are constrained to be linear combinations of environmental variables. It focuses on β -diversity, or dissimilarity among sites, and assumes a unimodal response model. The derived synthetic gradients (ordination axes) maximise the niche separation of species by using species centroids (weighted averages) as an estimate of the species optimum (ter Braak and Verdonschot 1995). Each species point is placed at the centroid of the site points in which it is recorded. Eigenvalues indicate the maximum amount of niche separation achieved. They are used to calculate the percentage accounted for of the total inertia (weighted variance) in abundance and of variance in fitted species data (weighted averages) (ter Braak 1994). Eigenvalues greater than 0.3 are considered to indicate strong gradients (ter Braak and Verdonschot 1995). The statistical significance of the relationship was determined by a Monte Carlo permutation test with 199 permutations. The continuous variables included in the analyses were: altitude, slope, aspect, mean annual rainfall, mean annual temperature,

percentage sand and latitude (AMG northing reference). Soil fertility was represented by the nominal variables high and low fertility (Table 1). The climate variables were estimated from interpolation between climate stations with BIOCLIM (Busby 1991) software which should be valid in a landscape of subdued topography. The number and abundance of species with traits in five classes were also plotted as supplementary (passive) variables onto the CCA.

Univariate analyses

Two-way factorial generalised linear models (GLM) were used to test for the fixed effects of soil fertility (high and low) and rainfall (high and low) and their interactions on the following two response variables: (1) the number of species with a particular trait and (2) the summed abundance of each species with each trait. The level of replication was the quadrat with four to six replicates in each combination of soil fertility and rainfall levels. Where the response variable was species number, a Poisson error with a log-link function was used, whereas for abundance data, a normal error structure with an identity link function was used. Data were checked for homogeneity of variance before analyses; no transformations proved necessary.

Results

Floristic composition

In the 43 sites surveyed, 441 species were recorded from 235 genera and 74 families. The largest numbers of species were recorded for the families Asteraceae (59 species), Poaceae (52 species) and Fabaceae (52 species). The most commonly recorded species were from the Poaceae with an average of 6.8 species at each site.

Correlation with environmental variables and species traits

The eigenvalues of the first two axes in the CCA biplot of sites and environmental variables (Fig. 2) are high (0.48 and 0.34) and are indicative of strong gradients. A Monte Carlo permutation test of the first canonical axis was significant ($P < 0.01$). The ordination plot in two dimensions accounts for 42% of the variance in the fitted species data. The significance of the relationship between each environmental variable and the species data was tested by using the forward selection procedure. The Monte Carlo permutation tests with 199 permutations were significant at the 5% level for eight of the nine environmental variables. Percentage sand was not significant and is not shown on the plot of sites and environmental variables. The relative importance of environmental variables was assessed by examining the correlation coefficient (intraset correlation) where the ordination axes with higher intraset correlations indicate an increased rate of change in community composition across the environmental gradient (ter Braak 1986). High and low soil fertility are the variables most strongly related to Axis 1 (intraset correlations of -0.95 and 0.90 , respectively) with the low fertility sites towards the left of the plot, and the high fertility sites located on the right (Fig. 2). Rainfall, altitude and temperature are most strongly related to Axis 2 (intraset correlations of 0.85 , 0.64 and -0.751 , respectively). Sites from Ebor and Guyra, with the highest annual rainfall and altitude, are in the upper right portion of the plot, whilst the drier, low altitude

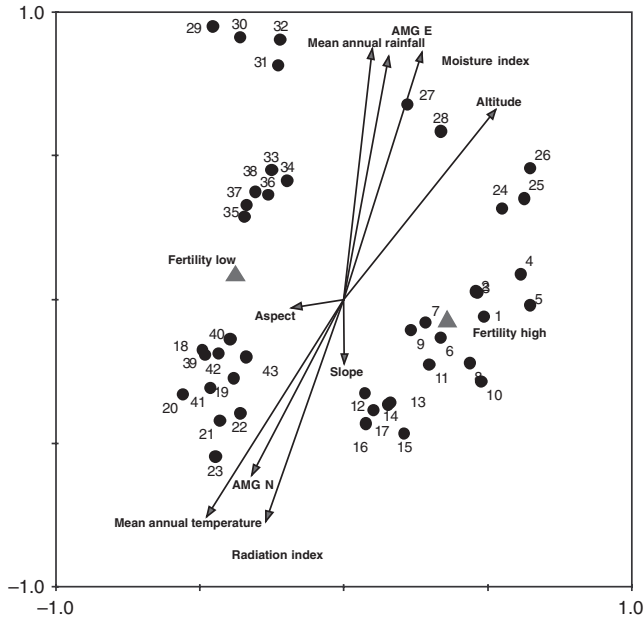


Fig. 2. Canonical correspondence analysis biplot of sites and environmental variables displaying 42% of the variance in the fitted species data. Eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.57 and 0.44, respectively; the sum of all canonical eigenvalues is 2.36. Increasing values for each environmental variable are in the direction of the arrowhead. Note that the higher soil fertility sites are more closely arranged than the lower soil fertility sites. Symbols: circles = sites; triangles = nominal environmental variables; arrows = continuous variables.

Torrington and Booralong sites are in the lower left portion. The two basalt sites in New England National Park, with both the highest rainfall and altitude, are substantially separated from the remaining Ebor and Guyra basalt sites in the upper right portion of the ordination space. The arrow representing latitude (AMGE) shows a progression from the southernmost sites at Ebor in the upper and right portions of the plot through to Guyra and Booralong and to the northernmost sites at Torrington in the lower left portion of the plot. Overall, there was less spread in ordination space from sites sampled on more fertile sites than those sites from low soil fertility.

Plotting the association of species traits onto the CCA showed distinct trends relating to both the first axis, associated with soil fertility, and the second axis, associated with rainfall or temperature (Fig. 3). These relationships were tested quantitatively by GLM analyses that follow. Plots of passive ordination variables (species traits) in CCA were similar for those based on species richness and those based on species abundance; hence, richness data are presented. Plots of the major trait variation show the strong relationship of growth form, longevity and diaspore type with lithology, while only epiphyte abundance correlates with rainfall (Fig. 3). Forbs were more prominent on the more fertile lithologies, as were annuals and short-lived perennials and wind-dispersed species. On the less fertile lithologies, shrubs and dwarf shrubs were more prominent as were species with internal animal and ant assisted seed dispersal modes (Fig. 3). Overall, the suites of traits prominently covary among diaspore type and growth form.

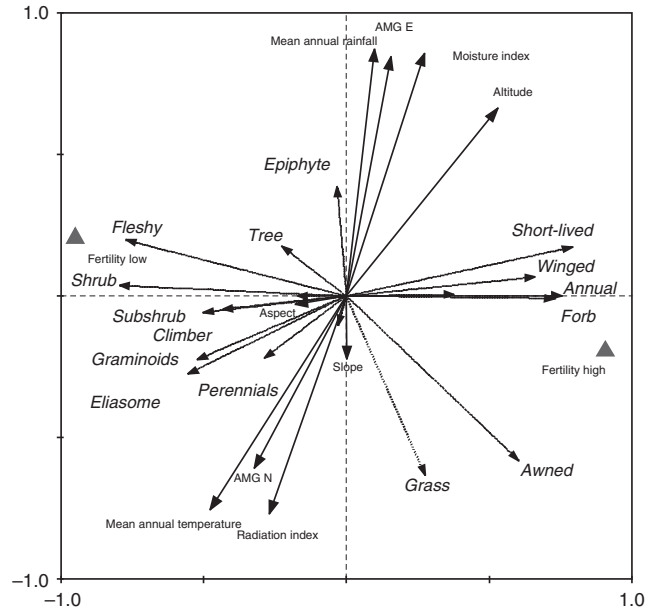


Fig. 3. Canonical correspondence analysis biplot of environmental variables and covarying species traits. Symbols: triangles = nominal environmental variables; arrows = continuous variables. Site symbols removed for ease of presentation.

GLM trait analyses

All trait classes were represented in every combination of soil fertility and climate class, but their magnitude of presence varied with the exception of sexual system (Tables 2 and 3). Soil fertility showed the strongest effect on the variation in traits with 15 of 22 traits being significantly different in species richness proportions and 14 of 22 traits for abundance. Climate variation was detected in 6 of the 22 trait contrasts for species richness and 7 of the 22 trait contrasts for abundance proportions (Tables 2 and 3). No interactive effects were detected for either richness or abundance data.

The most prominent trends were forbs and grasses being more abundant and species rich on the more fertile sites. Conversely, graminoids, climbers, dwarf shrubs and shrubs were more abundant in the less fertile sites (Tables 2 and 3). Both grasses and graminoids were more abundant and species rich in the lower rainfall sites (Tables 2 and 3). The results of the growth form analyses were mirrored in the longevity analyses, where annual and short-lived herbaceous species were more abundant and species rich on high fertility sites (Table 3, Fig. 3).

Dispersal traits were also strongly related to soil fertility with higher species richness and abundance of species with wind-assisted dispersal modes (awned and winged diaspores) on more fertile sites. Conversely, species with internal animal (fleshy diaspores) and ant assisted (with eliasomes) dispersal modes were more abundant on low fertility sites (Tables 2 and 3). Variation in these traits was also associated with rainfall differences with higher presences of species with awned and eliasome diaspores associated with lower rainfall, whereas winged diaspores were more prevalent in higher rainfall sites (Tables 2 and 3). Neither richness nor abundance in resprouting varied with soil fertility and climate for woody species, although

Table 2. Relative proportion of species with trait classes among soil fertility and climate groups where there were significant differences as detected by GLM analyses

Trait	Class	Fertility	Climate	Soil fertility class		Climate class		All classes
				Higher	Lower	Higher rainfall	Lower rainfall	
Growth form	Forb	$F = 63.3^{***}$	$F = 9.5^{**}$	0.59	0.36	0.52	0.44	0.47
	Grass	$F = 4.3^*$	$F = 7.9^{**}$	0.13	0.11	0.11	0.14	0.12
	Graminoid	NS	$F = 10.8^{**}$	–	–	0.04	0.07	0.05
	Climber	$F = 13.9^{**}$	NS	0.02	0.03	–	–	0.02
	Dwarf shrub	$F = 13.5^{**}$	NS	0.04	0.08	–	–	0.06
	Shrub	$F = 55.1^{***}$	NS	0.09	0.26	–	–	0.17
	Tree	$F = 7.5^{**}$	NS	0.06	0.08	–	–	0.07
Longevity	Annual	$F = 29.7^*$	NS	0.12	0.04	–	–	0.08
	Short-lived	$F = 22.2^{**}$	$F = 19.4^{**}$	0.03	<0.01	0.03	<0.00	0.01
	Perennial	$F = 42.3^{***}$	$F = 8.4^{**}$	0.83	0.98	0.86	0.96	0.88
Sexual system	Bisexual	NS	NS	–	–	–	–	0.92
	Monoecious	NS	NS	–	–	–	–	0.002
	Dioecious	NS	NS	–	–	–	–	0.05
	Unknown	NS	NS	–	–	–	–	0.02
Dispersal mode	Awned	$F = 27.7^{***}$	NS	0.13	0.07	–	–	0.10
	Eliasome	$F = 32.7^{***}$	$F = 17.7^{***}$	0.05	0.09	0.06	0.08	0.07
	Fleshy	$F = 50.4^*$	NS	0.09	0.19	–	–	0.14
	Winged	$F = 19.6^{***}$	NS	0.14	0.08	–	–	0.12
	Unassisted	NS	NS	–	–	–	–	0.57
Resprouting rich, ratios woody	NS	NS	–	–	–	–	0.89	
Resprouting rich, ratios herb.	$F = 11.0^{**}$	NS	0.86	0.91	–	–	0.88	
Fire-cued reproduction	$F = 23.5^{***}$	NS	0.15	0.08	–	–	0.11	

there was a greater proportion of resprouting herbaceous species in sites of low soil fertility (Tables 2 and 3). Fire-cued germination was also more prominent in the low soil-fertility sites.

Discussion

Floristic patterns, landscapes, climate and dispersal

It is remarkable that in a total sample area of 4.3 ha we were able to sample some 441 plant taxa representing ~20% of the region's floristic composition. Of the variance in species–environmental relationships, 42% was represented in two ordination dimensions; one strongly associated with landscape (soil fertility) and the other strongly associated with climate (rainfall and temperature). Such patterns are consistent with previous classifications of regional vegetation (Clarke *et al.* 1997, 2000a; Benson and Ashby 2000) and they conform more broadly to the widespread pattern of soil fertility and eucalypt forest understorey type in eastern Australia (Keith 1994; Le Brocque and Buckney 1994; McIntyre and McIvor 1998).

Although the floristic difference between 'shrubby' and 'grassy' vegetation is pronounced in composition, a similar order of floristic difference was shown along the climate gradient. The latter difference could conceivably be maintained by lack of dispersal; however, some of the most distant sites

(Torrington v. Booralong or Parlor Mountain) were clustered together on the ordination diagram, suggesting dispersal distance is not strongly affecting floristic patterns relative to climate and soil fertility effects. The juxtaposition of high and low soil fertility sites also points strongly to ecological sorting effects as dispersal should not limit the distribution of species across geological boundaries that change over tens of metres.

Trait spectra and environment linkages

Trait spectra differed more strongly between soil fertility contrasts than between climate types, despite there being high floristic turnover in climate contrasts. Nevertheless, all trait classes are represented in both high and low soil fertility sites and between sites with differing climates; in other words neither the landscape nor climate domain is precluding the presence of any major group. Instead, differences in the mean richness and abundance of traits shift among environments at the landscape and quadrat scale. These differences vary more in relation to the landscape pattern (soil fertility) than climate and no interactive effects of landscape and climate were detected. This suggests that any compensatory effect of soil fertility or climate is not manifested in the sorting of species with different traits. For example, the expectation that sites with lower rainfall and more fertile soils would have drought tolerant functional groups

Table 3. The abundance of species with trait classes among soil fertility and climate groups where there were significant differences as detected by GLM analyses

Trait	Classes	Fertility	Climate	Soil fertility class		Climate class		All classes
				Higher	Lower	Higher rainfall	Lower rainfall	
Growth form	Forb	$F = 16.9^*$	NS	133.3	85.4	–	–	109.7
	Grass	$F = 4.8^*$	$F = 7.5^{**}$	36.1	29.4	28	37.4	32.8
	Graminoid	$F = 3.9^*$	$F = 11.3^{**}$	9.3	15.4	10.3	13.6	12.1
	Climber	$F = 9.6^{**}$	NS	2.6	6.0	–	–	4.3
	Dwarf shrub	$F = 7.8^{**}$	NS	8.6	16.5	–	–	12.5
	Shrub	$F = 74.8^{**}$	NS	16	57.4	–	–	36.2
	Tree	NS	NS	–	–	–	–	15.5
Longevity	Annual	$F = 17.7^{***}$	$F = 5.7^*$	24.7	9.4	22.1	13.3	17.4
	Short-lived	$F = 13.7^{**}$	$F = 8.2^{**}$	4.8	0.7	4.9	1	2.8
	Perennial	$F = 5.8^{**}$	NS	189.1	215.5	–	–	201.9
Sexual system	Bisexual	NS	NS	–	–	–	–	204.8
	Monoecious	NS	NS	–	–	–	–	0.37
	Dioecious	NS	NS	–	–	–	–	13.3
	Unknown	NS	NS	–	–	–	–	5.0
Dispersal mode	Awned	$F = 22.9^{**}$	$F = 8.2^*$	30.7	15.6	18.3	27.7	23.3
	Eliasome	$F = 17.7^{**}$	$F = 17.0^*$	10.5	19.5	10	19.2	14.9
	Fleshy	$F = 76.2^*$	NS	17.2	41.3	–	–	26.9
	Winged	$F = 9.0^{**}$	$F = 4.8^*$	29.0	18.7	27.9	20.5	24.0
	Unassisted	NS	NS	–	–	–	–	133.5
Resprouting ratios woody	NS	NS	–	–	–	–	0.89	
Resprouting ratios herb.	NS	NS	–	–	–	–	0.88	
Fire-cued reproduction		$F = 27.7^{***}$	NS	23.4	16.8	–	–	20.1

(perennial forbs) was rejected. Similarly, infertile soils did not appear to be compensated for low resource levels by higher rainfall as forbs and annuals were not enhanced at higher rainfall sites on infertile soils.

Forbs and grasses with high relative growth rates varied more among soil fertility than rainfall gradients and were favoured on more fertile soils, whereas slower growing graminoids and shrubs were more abundant on infertile soils, irrespective of the climate gradient. This is consistent with models which propose that plants with faster growth rates will thrive in productive habitats (e.g. Chapin 1980; Van der Werf *et al.* 1993; Grime 2001). The climate gradient, however, appeared to influence the longevity of herbaceous species with annuals being more abundant in cooler higher rainfall sites. Grasses also increased in prominence with decreasing rainfall and increasing temperature which possibly reflects decreased canopy cover of eucalypts. These patterns in growth form and longevity differences are likely to be linked with more direct measures of resource capture such as leaf mass per area, leaf lifespan and seed size (Westoby *et al.* 2002; Westoby and Wright 2006). The use of more precise physiological traits may also reveal stronger patterns associated with the climate contrast; for example, Fonseca *et al.* (2000) found that both canopy height and specific leaf area of woody species decrease across climate and soil phosphate gradients concurrently.

Regenerative traits associated with mode of dispersal and response to fire also vary more across the fertility than the climate contrast. Strong differences in dispersal traits between soils of contrasting fertilities have previously been reported but

their evolutionary explanation remains elusive (Westoby *et al.* 1991). Like Westoby *et al.* (1991), we found more species with eliasome endowed seed on infertile soils than on fertile soils and this pattern was linked with growth form. A similar order of difference was found across the rainfall gradient, with drier sites also having higher abundances and numbers of species with eliasome endowed seed. In contrast to Westoby *et al.* (1991), we found higher numbers and abundances of species with fleshy diaspores on low fertility soils, which again, is strongly related to covariation in growth form rather than constraints of nutrient availability and canopy height and/or seed mass. Overall, those species with fleshy and eliasome endowed diaspores are often woody, whereas many herbaceous species have awned and winged diaspores. This functional difference in the floras may account for the floristic homogeneity (less spread in ordination space) of sites on fertile soils. Hence, sites on fertile soil have less floristic turnover because their rich herbaceous component has more generalist dispersal traits. Species varied little in classes of sexual systems, possibly reflecting trait conservatism for our relatively narrow range of landscape and climate contrasts.

Fire responses differed little in woody species among contrasting habitats. This was unexpected as Clarke *et al.* (2005) found that there was generally a higher proportion of woody resprouting species on fertile *v.* infertile soils. In contrast, slightly higher proportions of resprouting herbaceous species were also found on infertile soils than on fertile soils which may reflect a trade-off in herbaceous species for allocation to persistence rather than reproduction on infertile soils. There was, however, a higher proportion of species with fire-cued

germination in the infertile *v.* the fertile habitat. This is consistent with Knox and Clarke (2006) who found very low levels of fire-related shrub recruitment in grassy woodlands.

Models for ecological sorting across contrasting lithologies

Differences in floristic composition and associated coarse scale trait variation among adjacent communities are driven by abiotic and biotic factors in ecological sorting. Contrasts in the trait-spectrum provide some clues as to the processes driving these differences given that they reflect functional attributes of species. The simplest explanation of species trait differences is based on resource use; hence germination, growth and reproduction in herbaceous species may be inhibited by lack of resources on low fertility soils, whereas high fertility soils may inhibit growth for a range of woody species because they are adapted to low soil nutrient levels, especially phosphate (Beadle 1966; Handreck 1997; Denton *et al.* 2007) and are thus unable to take advantage of available nutrients (Grime 2001; Hanley *et al.* 2007). Experimental studies have consistently demonstrated reduced survival and growth for woody species when exposed to high levels of added nutrients, particularly phosphorus and nitrogen (Specht 1963; Groves and Keraitis 1976; Milberg *et al.* 1998; Graves *et al.* 2006). In contrast, herbaceous species have been shown to thrive under conditions of high resources (Specht 1963; Wilson 1998; Graves *et al.* 2006).

Differences in the plant-trait spectrum across the soil fertility gradient may also be driven by competitive interactions among growth forms. In this model herbaceous species competitively exclude shrubs from sites of high fertility because of their higher relative growth rates (Grime and Hunt 1975; Van der Werf *et al.* 1993; Wilson 1998). In contrast, at sites with infertile soils, shrubs may be competitively advantaged by (1) having larger seed reserves to establish on resource poor soils (Stock *et al.* 1990; Hanley *et al.* 2007) and (2) having deeper roots which allow access to resources stored at deeper levels in the soil (Knoop and Walker 1985; Sala *et al.* 1989; Harrington 1991; Dodd and Lauenroth 1997; Dodd *et al.* 2002).

Seed mass is strongly correlated with growth form at the global scale (Leishman *et al.* 1995; Moles *et al.* 2007), supporting evolutionary theory that growth form and seed size have evolved together (Moles *et al.* 2005). Although seed mass is more often related to seedling size than seedling survival (Stock *et al.* 1990), there is evidence that seedling growth for species with larger seeds is less dependent on soil nutrients (Milberg *et al.* 1998; Hanley *et al.* 2007). Efforts to link seed size with soil nutrients have been inconclusive; however, seed mass has been shown to be a good predictor of seedling response to low nutrients for some Australian shrub species (Hanley *et al.* 2007). Seed mass may therefore be a contributing factor in the establishment and maintenance of trait-mixture variation across fertility gradients. Early seedling growth may be less dependent on soil nutrients for species with larger seeds (Hanley *et al.* 2007), thus shrubs should have higher survival rates on infertile soils than many herbaceous species.

Herbaceous species, and grasses in particular, have high root to shoot ratios enabling them able to rapidly utilise soil resources, resulting in faster growth rates (Grime and Hunt 1975; Van der Werf *et al.* 1993; Wilson 1998). Soil texture is also considered an

important determinant of the relative abundance of woody and herbaceous species through the relationship with moisture availability (Sala *et al.* 1989; Dodd *et al.* 2002). It is proposed that grasses with a shallower root system utilise water near the soil surface, whereas shrubs access water from deeper in the soil profile (Sala *et al.* 1997). Grasses are more abundant than shrubs at sites with more water available near the surface, through rainfall in the growing season or on finer textured soils with lower infiltration rates. Conversely, shrubs are predicted to be more dominant at sites with more water available at deeper levels, through winter precipitation or on coarser textured soils with high infiltration rates (Knoop and Walker 1985; Sala *et al.* 1989; Harrington 1991; Dodd and Lauenroth 1997; Dodd *et al.* 2002).

More complex models involve differences in response to disturbance across landscapes such as herbivory and/or fire. Differences in herbivory driven by patch selection may be important in our landscape because herbivores forage where they experience the highest-quality resource (Stephens and Krebs 1986). Thus, marsupial herbivores may forage more frequently on the higher-fertility sites with resulting reduction of woody plants through browsing. Another difference may be related to higher fire severity in shrubby landscapes. On the New England Tableland, low-intensity fires are more common in grassy woodlands than in adjacent sclerophyll forests, and recent experiments have found that low-intensity fires rarely generate enough soil heating to break the dormancy of shrub species (Knox and Clarke 2006). It is thought that more intense fires can favour large-seeded fire-cued species (mostly shrubs), whereas lower-intensity fires can favour small-seeded species because large-seeded species emerge from greater soil depths (Bond *et al.* 1999). Recently, it has been suggested that the relationship between seed size, emergence depth and temperature may be more complex and species specific, as some smaller-seeded species have enhanced germination rates in response to higher temperatures and indeed a greater ability to germinate than many large-seeded species (Hanley *et al.* 2003). Other disturbances, such as fire feedback, may also be important where fire and herbivory interact (e.g. Archibald *et al.* 2005). In this model, grazing may prevent the spread or intensity of fire, reducing shrub recruitment in grassy landscapes.

Conclusion

We have used a simple trait based approach to highlight the ecological sorting of species along two well known environmental gradients. Unexpectedly, no edaphic compensation effects were detected across our gradients, with high soil fertility sites consistently having more forbs, annuals and grasses in comparison with low soil fertility sites which were dominated by woody species. The lack of strong trait differences between the climate contrasts probably reflects the short gradient that we sampled and may be better resolved by using traits such as specific leaf area and seed size. We think, however, that although trait-based approaches provide a framework for understanding community assembly, an experimental approach is required to test the competing hypotheses that explain the widespread, but as yet poorly explained, grassy *v.* shrubby phenomenon in temperate eucalypt vegetation.

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