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Environmental associations of abundance-weighted functional traits in Australian plant communities

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Abstract

Predictions of how vegetation responds to spatial and temporal differences in climate rely on established links with plant functional traits and vegetation types that can be encoded into Dynamic Global Vegetation Models. Individual traits have been linked to climate at species level and at community level within regions. However, a recent global assessment of aggregated community level traits found unexpectedly weak links with macroclimate, bringing into question broadscale trait−climate associations and implicating local-scale environmental differences in the filtering of communities. To further evaluate patterns in light of these somewhat contradictory results, we quantified the power of macro-environmental variables to explain aggregated plant community traits, taking advantage of new trait data for leaf area, plant height and seed mass combined with a national survey that records cover-abundance using consistent methods for a large number of plots across Australia. In contrast to the global study, we found that abundance-weighted community mean and variance of leaf area and maximum height were correlated with macroclimate. Height and leaf area were highest in wet (especially warm, wet) environments, with actual evapotranspiration explaining 30% of variation in leaf area and 26% in maximum height. Seed mass was weakly related to environment, with no variable explaining more than 5% of variance. Considering all three traits together in a redundancy analysis, the complete set of environmental variables explained 43% of variation in site-mean traits and 29% of within-site trait variance. While significant trait variation remains unexplained, the trait−environment relationships reported here suggest climatically-driven filtering plays a strong role in assembling these vegetation communities. Regional assessments using standardised species abundances can therefore be used to predict aspects of vegetation function. Our quantification of plant community trait patterns along macroclimatic gradients at continental scale thereby contributes a much-needed functional basis for Australian vegetation.

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Introduction

Plant functional traits provide a key link between the environment, species occurrences and ecosystem function (Jamil et al. 2013). Size traits are important axes of plant ecological strategy and affect competitive ability across their expression in leaves, plant stature and seeds (Westoby 1998; Díaz et al., 2016; Dirks et al. 2017). Leaf size affects leaf temperature and light capture for photosynthesis and, considered across the world's species, generally increases towards the equator where there is a predominance of hot, wet and sunny environments (Wright et al. 2017). Maximum plant height is limited by the ability of canopy leaves to maintain turgor and relates to water availability and competition for light (Moles et al. 2009; Klein et al. 2015; Falster & Westoby 2003; Falster et al. 2017). Seed mass reflects evolutionary history and regeneration strategy (Moles et al. 2005a), and is higher in warm, wet habitats at low latitudes (Moles & Westoby 2003; Moles et al. 2005b) and in shaded habitats (Foster 1986; Westoby et al. 2002). Plants with lower stature and smaller leaves with conservative nutrient acquisition strategies are expected on nutrient-impoverished soils (Hill 1998; McDonald et al. 2003; Ordoñez et al., 2009). Via their influence on function, traits contribute to differential success across environmental gradients, generating a link between traits, species distributions, and environment (Shipley et al. 2006).

If plant communities are environmentally determined, functional differences relating to tolerances and competitive ability should be apparent along macroclimatic gradients (Shipley et al. 2006). Average trait values aggregated at local community level and functional diversity of species within map grid cells have been found to vary predictably with regional climate and elevation (Sandel et al. 2010; Hulshof et al., 2013; Moles et al. 2014; Andrew et al. 2021). Indeed, Dynamic Global Vegetation Models, which model vegetation function in terms of primary production and fluxes of water and nutrients, seek to encode mechanistic links with macroclimate and traits as a basis for predicting vegetation distribution and carbon cycling under climate change (Berzaghi et al. 2020). Theory suggests that environmental conditions filter possible species trait values, leading to community convergence and lowered trait variance (Bernard-Verdier et al. 2012; Bruelheide et al. 2018). Trait convergence has been detected both continuously along environmental gradients and at the resources-scarce extremes of gradients (Bernard-Verdier et al. 2012). These trait-environment relationships for both community mean and variance are strongly influenced by the relative abundances of different species within communities (Bernard-Verdier et al. 2012; Wieczynski et al. 2019), which suggests that incorporating knowledge about relative abundances may strengthen understanding of trait−environment links (Grime 1998).

Previous global analyses found strong trait−environment relationships based on individual species patterns or aggregations of <1,000 vegetation plots (Wright et al. 2004; Wright et al. 2005; Wright et al. 2017; Zanne et al. 2018). In contrast, recent global-scale analyses, combining unprecedented data on plot-based relative abundances and species traits, have revealed unexpectedly weak relationships between mean trait values and environment, bringing into question the importance of biogeographic gradients in traits for understanding global vegetation. Bruelheide et al. (2018) tested a series of hypotheses relating aggregated community traits to macroclimatic controls by analysing >1.1 million field plots with matching species trait data (Kattge et al. 2020). The relationships revealed were weak, suggesting factors such as disturbance, microclimate or small-scale soil differences may shape plant communities (Bátori et al. 2017).

The degree to which macroclimate controls trait variation, as revealed via plot-based inventories, is important for forecasting vegetation form and function. Conflicting results bring into question our ability to map traits at community level based on macroenvironment, indicating more data are needed to resolve this question. Historically, an impediment has been a paucity of plot and trait data covering large spatial scales (Stahl et al. 2014). Recent efforts to aggregate global data have reduced this barrier (Bruelheide et al. 2018), and continental-scale assessments are now emerging (Buzzard et al. 2019). For example, a recent analysis of 201 forest plots in Italy reported stronger relationships for leaf, plant stature and seed traits than reported globally, with a set of environmental variables explaining 16−36% of variance in these traits at community level (Chelli et al. 2019). Traits are expected to influence species ranges across climatic gradients (Stahl et al. 2017), while soil properties mediate those relationships by altering the costs of nutrient and water-use (Paillassa et al. 2020).

Here, we examine macroclimatic controls on the functional traits of Australia's diverse vegetation, linking aggregated community plant traits to environment by combining species composition, functional trait and environmental datasets. As part of an emerging global picture, we seek to present basic patterns of functional traits at continental scale using the biogeographically distinct plant communities of Australia. Such analyses represent a major knowledge gap in Australian vegetation science (Andrew *et al.* 2021). We posit that key functional traits of Australian plant communities are primarily constrained by macroclimate. We used standardised abundance data collected using precise and consistent methods to explore these patterns and to determine whether the abundance-weighted community mean and variance of key functional traits are related to macroenvironmental gradients of temperature, moisture availability and soil fertility across Australia.

Materials and methods

Datasets

We combined plant species composition data from TERN Ausplots, which includes standardised abundances across

environmentally diverse sites (Guerin et al. 2017; Cleverly et al. 2019; Sparrow et al. 2020), with species-level data for key functional traits from the AusTraits database, which aggregates trait measurements for the Australian flora (Falster et al. 2021). This new dataset enables the first comprehensive assessment of trait−environment relationships at local community level using plot data from across Australia's major terrestrial biomes by combining robust measures of relative abundance with high trait coverage.

We calculated species abundances (% cover) from the point-intercept module of TERN Ausplots (Guerin et al. 2019; Sparrow et al. 2020; TERN 2020; Munroe et al. 2021). This nationally distributed network of one hectare plots is a key component of Australia's terrestrial ecosystem observatory (Fig. 1A; Cleverly et al. 2019). All vascular plant species including trees, where present, and associated understorey, are recorded where they intersect points at one-metre intervals along 10 × 100 m transects in each plot, giving accurate measures of cover over the total of 1010 point-intercept hits (Sparrow et al. 2020). The plots are stratified to represent the major environments and vegetation types of the Australian continent, excluding the wet tropics and 'tall eucalypt' forests, and have high ecological coverage (Guerin et al. 2017; Guerin et al. 2020a; Guerin et al. 2020c). Key Australian vegetation types sampled include eucalypt woodlands, mallee and forests, *Acacia* shrublands and woodlands, tussock and hummock (spinifex) grasslands, and chenopod shrublands (Thackway et al. 2007; Sparrow et al. 2020; Fig. 1B).

We matched species occurrences to log-scaled trait values for leaf area (mm^2), seed mass (mg) and maximum height (m), from AusTraits (v0.9.1; http://doi.org/10.5281/zenodo.3568417; Appendix S2; Falster et al. 2021; Guerin et al. 2020b), capturing different aspects of plant function (Westoby 1998; Garnier & Navas 2012). AusTraits is a database in which plant traits for the Australian flora have been compiled from literature, field and herbarium sources, comprising > 900,000 trait × species combinations (Falster et al. 2021).

While our selected focal traits broadly represent the 'leaf-height-seed' (LHS) scheme (Westoby 1998; Chelli et al. 2019) of plant function, the original scheme specified specific leaf area (SLA) rather than the trait leaf area (LA) used in our study. Like SLA, LA is expected to be highly associated with macro-climate (Bruelheide et al. 2018), but LA especially influences leaf energy balance and light interception (Wright et al. 2017). Leaf size measurements are also available for most Australian species, whereas dry weight measurements (required to calculate SLA, which is fresh leaf area divided by dry weight) are not (Andrew et al. 2021).

For species with multiple values in AusTraits, the highest plant height was taken to represent the trait 'maximum height' (associated with growth form, light competition, and potential lifespan; Perez-Harguindeguy et al. 2013), while for other traits the mean was taken. To more effectively use all available trait data, leaf area and seed mass were, in some instances, estimated from length and width dimensions using a Linear Mixed Model (LMM). The leaf area model used leaf length and width as fixed effects and family taxon as a random factor with an interaction with leaf length so random factor levels (families) had independent intercepts and slopes. Similarly, seed mass was estimated using seed length as a fixed effect with an interaction with the random factor of plant taxonomic family. The LMMs were run using the R package *lme4* (Bates et al. 2015) and the *predict()* function was used with models to estimate leaf area and seed mass. Models with family as a random factor explained the most variation in leaf area and seed mass for the training data, the leaf area model conditional $R^2 = 0.82$ (marginal $R^2 = 0.74$), and for the seed mass model conditional $R^2 = 0.82$ (marginal $R^2 = 0.63$). Conditional R^2 is the
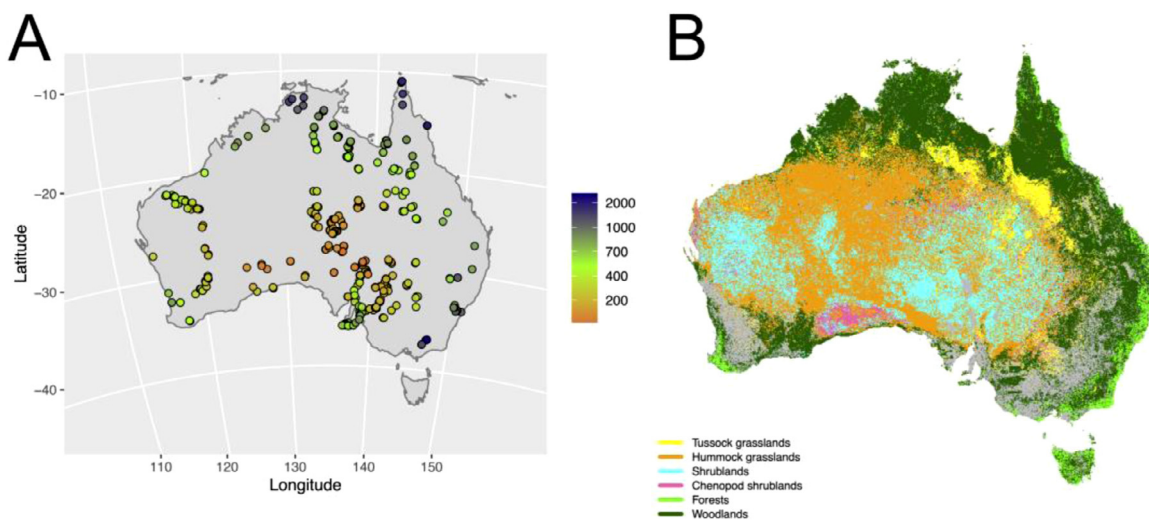

Fig. 1. Maps of Australia showing; A) location of 415 TERN Ausplots for which community trait moments (CWM, CWV) were analysed, colour-coded by annual precipitation (PTA); B) broad vegetation types (simplified from Lymburner et al. 2010).

proportion of variance explained by both fixed and random factors and marginal R^2 is for fixed effects only (Johnson 2014).

To circumvent bias in trait data availability, species with incomplete trait data were gap-filled using Bayesian Hierarchical Probabilistic Matrix Factorization (BHPMF; Schrodt et al. 2015). The machine learning approach of BHPMF uses the correlation structure in sparse matrices of trait data along with taxonomic structure to gap fill missing values. BHPMF was run with a matrix of all traits (i.e., maximum plant height, combined leaf area, leaf length, leaf width, combined seed mass and seed length). All gap-filled values outside the original range of transformed trait values were removed. A total of 13, 21 and 29% of species were gap-filled for maximum height, seed mass and leaf area, respectively.

We included 2,031 species recorded in 415 sites which met the criterion of at least 80% trait coverage by abundance, which has been shown to be a suitable standard for producing unbiased estimates of community traits (Pakeman & Quested 2007; Borgy et al. 2017; Fig. S1 in Appendix S1). A comprehensive set of climate, soil and landscape variables were sourced from 9-second resolution (i.e., approximately 250 m pixels) spatial layers (Grundy et al. 2015; Harwood et al. 2016; Gallant et al. 2018; Table 1). Selected variables were log-transformed to linearise relationships. The selected sites range in mean annual precipitation from 155 to 2,190 mm/yr (Fig. 1A), and span mean annual temperature minima of 2 to 23°C and maxima of 9 to 36°C.

Statistical analysis

We calculated the community weighted mean (CWM; abundance-weighted mean; Equation 1 of both Bernard-Verdier et al. 2012; Hulshof et al. 2013) and variance (CWV; abundance-weighted sum of squares; Equation 2 of both Bernard-Verdier et al. 2012; Hulshof et al. 2013) by trait and site. Trait−environment associations were assessed using Pearson correlations (Wei & Simko 2021) and regression against explanatory environmental variables and latitude using Ordinary Least Squares regression (OLS). Quadratic terms were added where appropriate.

A trait−environment relationship was considered present if two conditions were met: (i) $p < 0.05$ after Bonferroni correction for multiple hypotheses (Rice 1989); and (ii) regressions of species trait values onto species niche centroids (SNC) along corresponding gradients were significant ($p < 0.05$). The latter test is required to avoid common type I errors in which random traits can yield significant environmental correlations, as well as the potential sensitivity of CWM to the abundance patterns of one or a few species, irrespective of functional constraints (ter Braak et al. 2018). SNCs were calculated for each variable as the abundance-weighted mean environment where the species occurs. For each variable−trait combination, SNCs were regressed

Table 1. Climate (Harwood et al. 2016), soil and landform (Gallant et al. 2018) variables used in the analysis.

Code	Name	Unit
TXM	Maximum temperature − Annual mean	°C
TXI	Maximum temperature − monthly minimum	°C
TXX	Maximum temperature − monthly maximum	°C
TNM	Minimum temperature − Annual mean	°C
TNI	Minimum temperature − monthly minimum	°C
TNX	Minimum temperature − monthly maximum	°C
TRI	Minimum monthly mean diurnal temperature range	°C
TRX	Maximum monthly mean diurnal temperature range	°C
TRA	Annual temperature range (TXX − TNI)	°C
ADM	Mean annual aridity index (annual precipitation/ annual potential evaporation)	proportion
ADI	Minimum monthly aridity index	proportion
ADX	Maximum monthly aridity index	proportion
EPA	Annual potential evaporation	mm
EPI	Minimum monthly potential evaporation	mm
EPX	Maximum monthly potential evaporation	mm
EAA	Annual total actual evapotranspiration terrain scaled using MODIS	mm
EAAS	Annual total actual evapotranspiration modelled using terrain-scaled water holding capacity	mm
PTA	Annual precipitation	mm
PTI	Minimum monthly precipitation	mm
PTX	Maximum monthly precipitation	mm
PTS1	Precipitation seasonality 1- solstice seasonality composite factor ratio	ratio
PTS2	Precipitation seasonality 2- equinox seasonality composite factor ratio	ratio
WDA	Annual atmospheric water deficit (annual precipitation − annual potential evaporation)	mm
WDI	Minimum monthly atmospheric water deficit (precipitation − potential evaporation)	mm
WDX	Maximum monthly atmospheric water deficit (precipitation − potential evaporation)	mm
AWC	Available Water Capacity	%
BDW	Bulk Density − Whole Earth	g/cm3
CLY	Clay	%
DER	Depth of Regolith	m
DES	Depth of Soil	m
ECE	Effective Cation Exchange Capacity	meq/100g
NTO	Total Nitrogen	%
PHC	pH − CaCl2	None
PTO	Total Phosphorus	%
SLT	Silt	%

(continued)

Table 1 (*Continued*)

Code	Name	Unit
SND	Sand	%
SOC	Organic Carbon	%
TWI3S	Topographic wetness index	index
SLOPEDEG	Slope	degrees
PROFCURV	Profile curvature	index
PLANCURV	Plan curvature	index
ELVR1000	Elevation focal range within 1000m moving window	index
CONAREA	Contributing area	index
SLPFM300	300m focal median of percent slope	%

against corresponding species trait values using a linear model. SNC results were considered only as a vetting procedure for CWM models and hence are not reported in further detail.

Because OLS residuals were spatially autocorrelated (Moran's I; Paradis et al. 2004) and were often found to be heteroskedastic, we repeated regressions using Generalised Least Squares (GLS; Pinheiro et al. 2016). A Gaussian spatial correlation structure was specified (Dormann et al. 2007; Pinheiro et al. 2016) and when heteroskedastic residuals were detected (Breusch & Pagan 1979), models were encoded with a fixed change in variance along the predictor. Model fit was compared using pseudo-R^2 using the method of Nagelkerke (1991), a modification of the McFadden and Cox-Snell methods, as implemented in Lefcheck (2015).

We report both OLS and GLS models to maximise comparability with similar studies.

To assess variance explained by multiple environmental variables collectively for all three traits, we performed redundancy analysis (RDA; Oksanen et al. 2018) on the response traits constrained by all environmental variables. We repeated the RDA using a subset of environmental variables as constraints that had variance inflation factors <10, to reduce collinearity (Dormann et al. 2013; pairwise variable correlations shown in Fig. S7). Analyses were performed in R version 3.3.0 (Appendix S3; R Core Team 2016).

Results

Leaf area CWM was correlated with environmental setting (Figs 2; 3; S3 in Appendix S1), increasing with actual evapotranspiration (EAA; OLS R^2 = 0.30; GLS pR^2 = 0.31), monthly maximum rainfall (PTX; R^2 = 0.26; pR^2 = 0.32), monthly minimum temperature (TNI; R^2 = 0.15; pR^2 = 0.17) and summer rainfall seasonality (PTS1; R^2 = 0.18; pR^2 = 0.15). Average leaf area was highest across northern Australia, in environments that are seasonally wet in summer, with mild minimum temperatures. While the relationship with annual precipitation (PTA; R^2 = 0.22; pR^2 = 0.28) was weaker than with actual evapotranspiration, slope and fit strengthened when outlying sites on the island of Tasmania, which had high rainfall but small leaf area, were excluded from the analysis (R^2 =0.31; pR^2 =0.38). Leaf area CWV was related negatively to annual potential
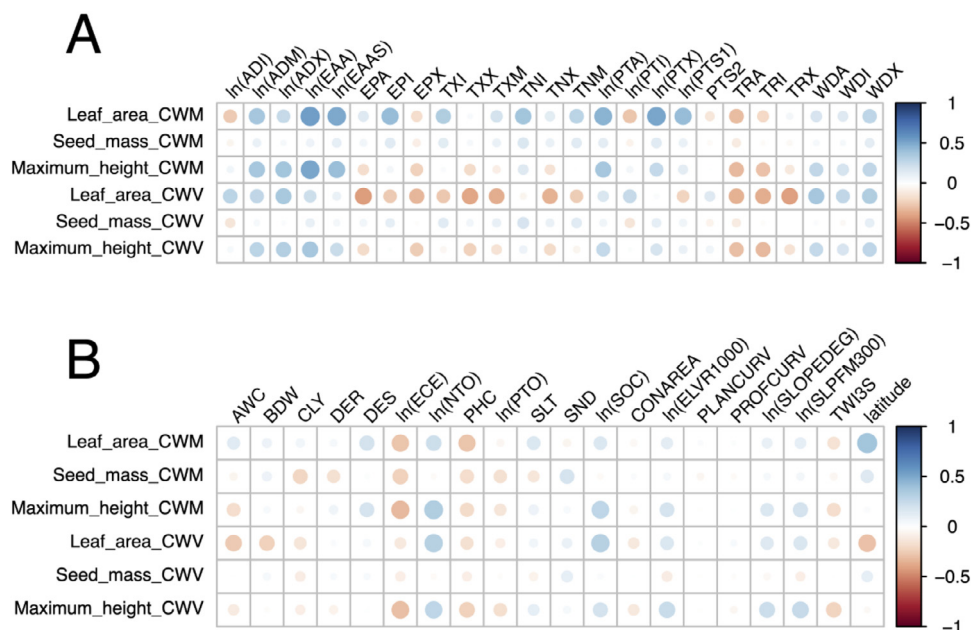

Fig. 2. Plant community functional trait variation across Australia: Pearson correlations between log-scaled community weighted mean (CWM) and variance (CWV) of traits and environmental variables; (A) climate; (B) soil and landscape. Circle size and colour are proportional to the strength and sign of the correlation (value of Pearson's r; legend) to make patterns visually distinguishable. See Table 1 for variable codes.
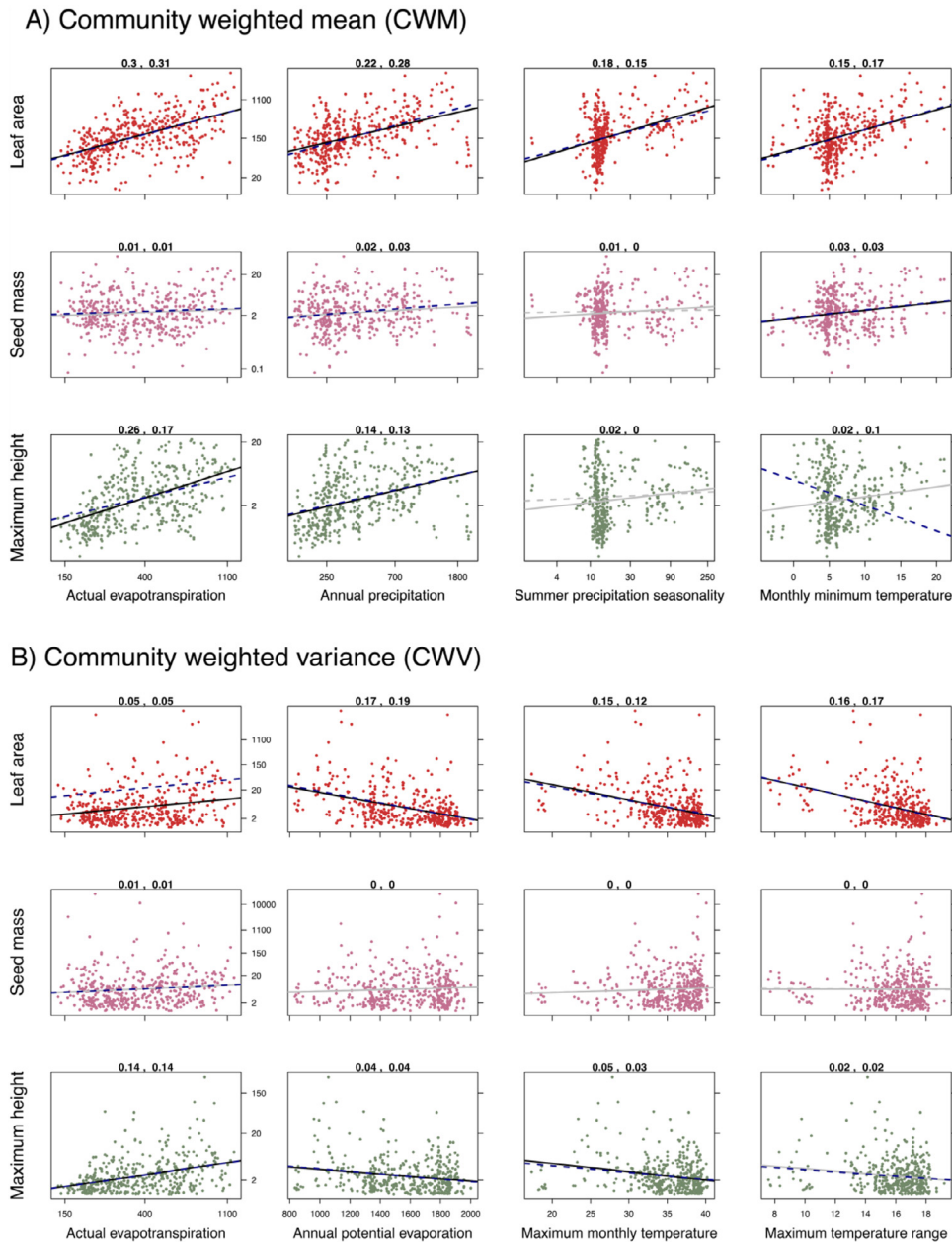
Fig. 3. Selected community trait−environment regressions. Environmental gradients depicted include those with the highest associations to individual traits (see Fig. S3 in Appendix S1 for all significant trait−environment combinations): (A) Community weighted mean (CWM) of leaf area (mm^2), seed mass (mg) and maximum height (m) for 415 Ausplots along gradients of actual evapotranspiration (EAA), annual precipitation (PTA), summer precipitation seasonality (PTS1) and minimum monthly temperature (TNI; Table 1); (B) Community weighted variance (CWV) along gradients of actual evapotranspiration (EAA), annual potential evaporation (EPA), maximum temperature − monthly maximum (TXX) and maximum monthly mean diurnal temperature range (TRX). All axes are plotted on their original, untransformed scales. Solid lines are OLS and dashed lines GLS models. Grey models were not statistically significant (OLS) or had non-positive pseudo-R^2 values (GLS). Numbers above denote R^2 (OLS) and pseudo-R^2 (GLS), respectively.

evaporation (EPA; R^2 = 0.17; pR^2 = 0.19), maximum monthly maximum temperature (TXX; R^2 = 0.15; pR^2 = 0.12) and maximum monthly diurnal temperature range (TRX; R^2 = 0.16; pR^2 = 0.17), all of which are higher inland. The mean and variance of leaf area exhibited a quadratic association with latitude (Fig. S4 in Appendix S1; R^2 = 0.24, 0.19, respectively). For maximum height, CWM

and CWV were most strongly associated with actual evapotranspiration, with taller plants more typical of sites with higher evapotranspiration (EAA; R^2 = 0.26; pR^2 = 0.17 for CWM; R^2 = 0.14; pR^2 = 0.14 for CWV; Figs 2; 3; S3 in Appendix S1). Maximum height was also correlated with leaf area (Fig. S6 in Appendix S1), and had quadratic relationships with latitude (Fig. S4 in Appendix S1; R^2 = 0.1 for
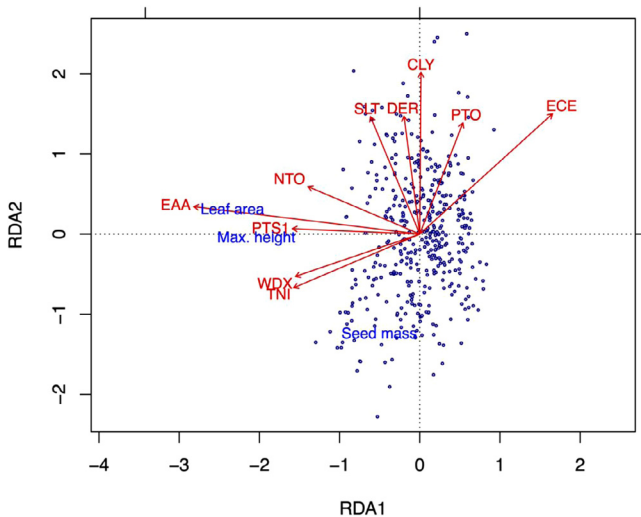
Fig. 4. Plant community functional trait variation across Australia: first two axes of a redundancy analysis with community weighted means (CWM) of leaf area, seed mass and maximum height constrained by environmental variables (Table 1), cumulatively explaining 33% of variance (27% and 4% for RDA1 & 2, respectively). Selected, scaled vectors are plotted for clarity. See Table 1 for variable codes.

each). The CWM and CWV of seed mass were weakly related to the environment and latitude, with no predictor explaining more than 10% of variance (Figs 2; S3; S4 in Appendix S1). Although trait variance in general reflects species richness to some degree, removing this effect through regression residuals did not substantially alter relationships.

For the RDA constrained ordination based on a non-collinear subset of explanatory variables, cumulative variance explained in the CWM of the three traits was 36% (adjusted-R^2 = 0.32; Fig. 4). For CWV, 24% (adjusted-R^2 = 0.20) of variance was cumulatively explained (Fig. S2 in Appendix S1). CWM leaf area and plant height were positively related to moisture availability along the first axis (see also Fig. S5 in Appendix S1), which explained 28% of variance, and was defined mostly by actual evapotranspiration and summer precipitation seasonality. The second axis represented edaphic variation, defined by soil depth and texture, and was most correlated with seed mass but explained only 5% of variance. With all environmental variables included, 43% (adjusted-R^2 = 0.37) of variance in CWMs and 33% (adjusted-R^2 = 0.25) of variance in CWV was explained.

Discussion

Australia is a megadiverse, biologically unique and environmentally varied continent (Crisp and Cook, 2013). A large body of work continues to grow, describing, classifying and mapping Australian vegetation systems and their physiognomy, environmental contexts and history

(Barlow 1994). Still, comparatively little quantitative analysis has been done to understand basic functional patterns and their environmental drivers at continental scale (Andrew et al. 2021). Data resources emerging over the last decade, including species occurrence datasets, standardised plot and trait databases, interpolated environmental layers and online data portals, have enabled broadscale analysis (Wright *et al.* 2017; Bruelheide et al. 2018; Gallagher et al. 2019; Sparrow et al. 2020). For example, Andrew et al. (2021) showed that plant functional diversity increases with annual precipitation across Australia when considering suitable habitat for species aggregated to 10 × 10 km grid cells.

Our results support regional-scale macroclimatic associations with mean leaf area and maximum height in Australian plant communities, contrasting with weak global relationships identified by Bruelheide et al. (2018). Our study adds to a growing body of literature that is identifying the existence of stronger macroclimatic associations at the regional level (Buzzard et al. 2019; Chelli et al. 2019) or at the global level (based on individual species patterns or aggregations of <1,000 vegetation plots; Wright et al. 2004; Wright et al. 2005; Moles et al. 2009; Wright et al. 2017; Zanne et al. 2018).

The relationships between size traits (except seed mass) and climate reported in our continental analysis are stronger than from those in the global data. For example, here 24 different trait−climate combinations had R^2 > 0.1 and all variables cumulatively explained 43% of variance. By contrast, in the global analysis of Bruelheide et al. (2018), variables individually explained no more than 10% of variance in plot mean trait values, and cumulatively explained just 14%. While it is possible that macroecological patterns are stronger in Australia than they are globally, methodological differences may also have contributed to differences in relationships compared to the global data. For example, the Australian plot data we used employed a consistent plot size and a consistent and precise measure of abundance across all sites, whereas global analysis pooled a variety of different plot sizes and abundance measures, including cover, basal area, individual counts, importance value and percentage frequency in subplots, in order to maximise coverage. Added to these methodological differences, Australia has a biogeographically distinct flora that may respond differently compared to globally aggregated communities, due to a long evolutionary and environmental history in isolation from other floras associated with high endemism (Crisp and Cook, 2013).

At the plant community level, although species with a wide range of trait values coexist, the weighted-mean approach shows that traits shift along environmental gradients. Leaf area increased markedly with increasing evapotranspiration. That is, mean log-scaled leaf area increased by approximately 50% (∼12-fold on original scale) over the sampled range of actual evapotranspiration. This pattern of larger leaves in warm, seasonally wet environments

confirms expectations from species-level studies for aggregated plant communities (Garnier & Navas 2012; Wright et al. 2017; Richards et al. 2021). The curvilinear relationship with latitude corresponds to larger leaves being present in plant communities at the mesic coastal fringes of Australia relative to the arid interior, consistent with patterns identified at the species level (Guerin & Lowe 2013). However, vegetation in mesic environments subject to subzero winter temperatures had smaller leaves (Wright et al. 2017), and this weakened the relationship with rainfall.

Competition for light is predicted to favour tall species in mesic environments (Falster & Westoby 2003; Falster et al. 2017). However, limitations of water availability and the potential for cavitation and hydraulic failure shorten plant stature in arid and semi-arid environments (Koch et al. 2004). Physiological limits on plant height are reflected in the decrease in mean and variance of maximum height with decreasing evapotranspiration shown here. Even so, the data suggest variation in the average height of vegetation remains regardless of gradients in macroclimatic conditions, which is likely related to competitive setting and time since disturbance.

We found no evidence that macro-scale soil differences drive variation at the community level in the three traits analysed. The few associations between soil conditions and traits detected were weak and confounded by rainfall, which correlates positively with soil carbon and nitrogen, and negatively with pH. Weak associations with soil are surprising, given evidence for the role of soil nutrition in shaping adaptations such as scleromorphy in Australian vegetation (Hopper 1979; Hill 1998), and driving variation in leaf width, SLA and plant height in eastern Australia (Fonseca et al. 2000). This aspect warrants further investigation as to whether micro-scale soil conditions and alternative traits such as leaf life span or SLA, which is typically lower in hot, dry environments (Wright & Westoby 2003; Wright et al. 2004; Wright et al. 2005; Kattge et al. 2020) are more strongly associated than patterns detected here. Additionally, edaphic data were sourced from continental layers intended for broadscale comparisons. Local differences in soil are likely to influence observed species composition and therefore trait moments (Ewald 2000).

Previous models predict higher mean seed mass with increasing resource availability, due to a trade-off between relative growth rate and competition for light (DeMalach et al. 2019). Empirical data suggest seed mass has associations with rainfall, latitude and productivity at species, community or aggregated grid cell levels (Moles and Westoby 2003; Sandel et al. 2010; DeMalach et al. 2019). Reported patterns have been somewhat contradictory, however, with cases of positive, negative or neutral associations between soil fertility and seed size (Westoby et al. 2002). In agreement with Bruelheide et al. (2018), we found no evidence of macroclimatic controls on mean seed mass. No environmental variable explained more than 5% of variance, as compared to

Chelli et al. (2019), who reported that 16% of variance in CWM of seed mass in Italian forests was explained by a vetted set of environmental variables, albeit using the non-linear GAM regression method, which may not be completely comparable to linear methods. This result deserves further investigation, for example as to whether the inclusion of habitats in Australia's wet tropics bioregion would change observed patterns. Tropical rainforests are typically characterised by large-seeded species (Foster 1986; Grubb & Coomes 1997; Moles & Westoby 2003; Moles et al. 2005b) and, while making up a small land area in Australia, are not represented in the plot dataset (Guerin et al. 2020a). Close associations between large seeds and vertebrate dispersers which occur in rainforests may also limit the occurrence of many large-seeded plant species outside Australian tropical rainforests (Westcott et al. 2005). Alternatively, phylogenetic conservatism in seed size (Lord et al. 1995) and the coexistence of species with very different seed sizes may explain the lack of strong signals along environmental gradients (Westoby et al. 2002).

The increasing community variance in leaf area and maximum plant height along gradients of moisture availability suggest convergence of community traits with increasing aridity consistent with trait-based environmental filtering of communities under harsher environmental conditions (Bernard-Verdier et al. 2012; Andrew et al. 2021). Even so, environmental variation was a poorer predictor of the variance than the mean, reflecting the fact that species with different functional trait values can coexist in a range of environments, despite filtering and a shifting mean (Bruelheide et al. 2018).

The scaling of functional community responses to climate from locally co-occurring species in plots (including measures of relative abundance) to communities across larger regions is a remaining knowledge gap, as are the roles of local factors (e.g., disturbance and microclimate) and intraspecific trait variation in determining trait moments (i.e., their unexplained variation) and other properties of vegetation communities. Meanwhile, questions remain concerning the role of environmental gradients in driving aggregated community traits at different scales. In future studies, globally aggregating regional calculations of functional responses to macroclimate could be one way to test and account for different responses among biogeographical regions compared to global patterns. Given that leaf size and plant height have been shown to influence differences in ecosystem function, notably carbon assimilation and storage, across species and vegetation types (Luo et al. 2019; Moles et al. 2009; Li et al. 2020), the macroecological patterns of variation developed here can potentially be integrated into Dynamic Global Vegetation Models for Australia.

Conclusion

The trait patterns of plant communities along macroclimatic gradients reported here contribute to a much needed

quantitative baseline understanding of the basic functional properties of the Australian vegetation at continental scale. Moisture availability, as indicated by actual evapotranspiration, was found to be an important driver of community level leaf size and plant height in Australia when considering the relative abundance of species in plot-based samples. This confirms expectations from species-level and regional studies but contrasts with weaker global trait−macro-environment relationships. The results suggest key aspects of vegetation form and function, related to structure, light interception and carbon assimilation, can be predicted from macroclimate, potentially informing regional models of vegetation dynamics. Further analysis is needed to interpret the scaling of responses from local to regional samples and to better account for the influence of local factors such as disturbance and microclimate on trait moments, as well as the role of intraspecific trait variance in mediating responses to environmental change.

Declaration of Competing Interest

The authors have declared that no competing interests.

Acknowledgements

Authors' contributions

GRG, RVG & IJW conceived and designed the study, BS & AJL coordinated the study, GRG, BS, DSF, EHW, SCA & RVG compiled data, GRG, SCA & DSF performed analysis, GRG drafted the manuscript. All authors critically revised the manuscript, gave final approval for publication and agree to be held accountable for the work performed therein.

Data Availability

TERN Ausplots data were sourced and are available through ausplotsR (Guerin et al. 2019; TERN 2020; Munroe et al. 2021). Trait data were sourced from v0.9.1 of AusTraits, available at http://doi.org/10.5281/zenodo.3568417. Trait−environment datasets are included in the Supporting Information and are archived (Guerin et al. 2020b).

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.11.008.

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