ORIGINAL ARTICLE

Correlates of range size variation in the Australian seed-plant flora

Rachael V. Gallagher*

Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

ABSTRACT

Aim To map and analyse range size variation in the terrestrial seed-plant flora of Australia in relation to latitude, habitat availability, climate and soils, and to compare mean range size between biomes and growth forms.

Location Australia.

Methods Range sizes were estimated from herbarium records using alpha-hulls for 19,227 species and mapped into a set of $0.5° \times 0.5°$ grid cells across Australia. Ordinary-least squares regressions were used to test for relationships between mean range size, latitude and habitat availability. Simultaneous autoregressive models (SAR) with spatial error terms were used in a multi-model framework to assess the role of aridity, mean annual temperature (MAT), soil pH, depth and total P concentration in shaping range size variation. Species-level differences between growth forms (graminoids, herbs, trees, shrubs, climbers) and biomes were assessed using one-way analysis of variance (ANOVA).

Results 68% of Australian seed-plant species have ranges which cover < 1% of the continent. Generally, large ranges are characteristic of graminoids and herbs and are associated with arid and grassland biomes. The smallest ranges were found in Mediterranean ecosystems in the SW corner of the continent, and were typically shrub species. Range size peaked at mid-latitudes and was not consistently smaller at lower latitudes (contrary to Rapoport's Rule). Increasing aridity, MAT and soil pH were strong predictors of large range size; however, soil depth and P content had little influence in SAR models.

Main conclusions Aridity and temperature are the primary drivers of range size variation in the Australian flora. Trait syndromes which promote colonization and survival in arid and grassland habitats (e.g. C4 photosynthesis, wind pollination) have allowed grasses and herbs to occupy large areas of the continent. Ranges were not smaller, on average, in the tropics due to the concentration of large-ranged species in the widespread arid biome in the centre of the continent.

Keywords

area of occupancy, aridification, arid zone, climate variability, climatic gradients, extent of occurrence, extinction risk, grasses, null model, wind pollination

*Correspondence: Dr Rachael Gallagher, Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia.
E-mail: rachael.gallagher@mq.edu.au

INTRODUCTION

Range size is a fundamental ecological measure which underpins much of comparative biogeography. For decades, biologists have calculated and compared the geographical extent of species ranges in search of unifying principles to explain emergent patterns of diversity (Willis & Yule, 1922; Dobzhansky, 1950; Rapoport, 1982; Stevens, 1989; Brown *et al.*, 1996; Gaston, 1996). More recently, range size has been used as a proxy for extinction risk and to prioritize

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species for conservation actions in the face of rapid global change (Mace *et al.*, 2008). Large-scale data sets are now routinely used to compare ranges across species occupying entire continents or biogeographical provinces (Manne *et al.*, 1999; Harris & Pimm, 2008; Gallagher *et al.*, 2011; Morueta-Holme *et al.*, 2013). These analyses test and inform ecological theory, and serve more pragmatic needs such as climate change adaptation planning.

The primary aim of this study is to assess how the distribution of range sizes varies across the terrestrial seed-plant flora of Australia and to determine which environmental factors best predict this variation. The terrestrial native seed-plant flora of Australia includes species from 198 families [following the *Australian Plant Census* (Australian Plant Census (APC), 2015)], with several endemic genera and species, which can be ecologically dominant. For instance, species from the genera *Eucalyptus* L'Hér. and *Acacia* Mill. occur across most vegetation types, yet their historic distribution rarely extends beyond the Australian continent. The ubiquity of these two groups has made them the focus of multiple studies of range size, endemism, niche conservatism and dominance (e.g. Hopper & Maslin, 1978; Hughes *et al.*, 1996; Mishler *et al.*, 2014). Similar studies have also been conducted for selected families which are highly diverse within Australia, such as the Proteaceae and subfamily Styphelioideae (formerly Epacridaceae) (Keighery, 1996; Cardillo & Pratt, 2013). While these studies have been fundamental to Australian plant biogeography, a more general understanding of range size variation across the full taxonomic breadth of the terrestrial flora is warranted, particularly for conservation planning purposes.

In this context, I used digitized herbarium specimen data for 19,227 terrestrial seed-plant species native to Australia to define, map and analyse patterns of range size variation. Three complementary questions are addressed: (1) Are there latitudinal trends in range size in the Australian seed-plant flora? (2) Which climate and soil conditions best predict range size variation? and (3) Does range size vary significantly between biomes and growth forms?

I hypothesized that range size, on average, will not increase with latitude. Instead, I expected the relationship between range size and latitude to peak at mid-latitudes, due to the concentration of species with large range sizes in the central arid zone of the continent. This zone covers approximately 70% of the Australian continent and is characterized by large expanses of relatively homogeneous temperature conditions with low topographic relief and poor nutrient availability, but high spatial and temporal variability in rainfall (Byrne *et al.*, 2008; Morton *et al.*, 2011). Environmental conditions in the arid zone have fluctuated through evolutionary time and instability in long-term climate conditions has also been shown to favour the retention of large-ranged species (Stevens, 1989; Sandel *et al.*, 2011). The availability of land can also set limits on the size of species ranges (Colwell & Hurtt, 1994) and, in Australia, the geographical extent of occupiable land is also greatest at mid-latitudes. Therefore, I also explored the role of land availability in determining latitudinal patterns of range size variation in the Australian flora.

Latitude *per se* offers little explanatory power in ecological terms, acting largely as a surrogate for more proximal factors such as temperature, rainfall or soil conditions. Therefore, I tested for a relationship between mean range size and five abiotic variables hypothesized to affect plant range size: mean annual temperature (MAT; °C), an index of aridity (AI; annual rainfall/annual potential evapotranspiration), soil depth to regolith (DEPTH; m), soil pH (pH) and soil total phosphorus (TOTP; %). MAT and AI capture the two major climatic gradients operating at the continental-scale across Australia which may contribute to variation in plant range size. These gradients run orthogonally across the landscape, describing a N-S axis in temperature, and an coastal-inland axis in aridity.

Soils provide the basic matrix from which plants extract nutrients and water essential for growth and are factories for the decomposition of senesced tissues. The challenge faced by plants in extracting nutrients, which are often scarce, from soil has driven the evolution of various adaptations and is known to contribute to the high rates of species diversification and endemism in global plant biodiversity hotspots (Cowling & Holmes, 1992; Hopper & Gioia, 2004). Given the important role that the availability of soil nutrients has played in shaping plant strategy variation, it follows that soil properties should be key determinants of plant distribution. Therefore, I hypothesized that two key soil properties (depth and fertility) should influence range size variation in the Australian flora. Deep soils support a wide breadth of rooting depths and growth forms (Jackson *et al.*, 1996) and I expected a positive relationship between soil depth and range size. Plant species may also become specialized to low nutrient or extreme pH conditions by developing adaptations which increase growth and survival (e.g. cluster roots, mycorrhizae, salt tolerance). However, specialized adaptations of this kind may reduce competitive ability in more benign environments, subsequently restricting range size. Therefore, I expected a positive relationship between soil fertility (TOTP, pH) and range size across Australian seed-plants.

Finally, I explored how seed-plant range size varies among biomes and growth forms (trees, shrubs, climbers, graminoids and herbs). The Australian continent supports a diverse array of biomes – areas supporting similar vegetation types, shaped largely by analogous climate conditions – which exhibit different levels of species endemism. I hypothesize that across all species, mean range size will differ between Australia's seven biomes, independent of species richness or biome area. I expected that smaller mean range sizes will be found in biomes with high levels of endemism, reflecting the adaptation of the constituent species to a restricted set of abiotic conditions. I also hypothesized range size differences between woody (trees, shrubs) and non-woody (graminoids, herbs) growth forms, with shallow rooted, non-woody forms occupying larger ranges than do deep-rooted, woody groups.

MATERIALS AND METHODS

Species data

Occurrence records from vouchered specimens in Australia's Virtual Herbarium (AVH; accessed January 2015 via the Atlas of Living Australia Data API web service; http://collections.ala.org.au/) were used to characterize the distributional range of Australia's plant species. The AVH provides digitized records from vouchered specimens held within Australia's nine major herbaria and is the largest source of occurrence data for this continental flora. All analyses were confined to terrestrial seed-plants (i.e. angiosperms and gymnosperms; $n = 198$ families; $n = 1931$ genera) and taxonomy was standardized to the APC. For full lists of recognized genera and families used in this study see Appendix S1 in the Supporting Information.

A preliminary data set of 5,459,076 species occurrence records was cleaned to remove taxonomic and spatial errors. Taxonomic cleaning removed records that were not identified to species level – including manuscript names and hybrids, records that were not for terrestrial seed-plants (i.e. ferns, fern allies, mosses, bryophytes), and records which were for species not native to Australia (i.e. introduced species identified in both an Australian exotic plant checklist (Randall, 2007) and with the tag 'naturalized' provided in the APC). Records lacking latitude and longitude coordinates were then discarded and the remaining spatially georeferenced records were cleaned by removing occurrences from outside Australia, duplicates (i.e. non-unique combinations of latitude, longitude and species name) and specimens taken from cultivated plants (either flagged as such in the AVH or containing the search terms cultivate*, garden, horticulture* or agricultur*). Finally, all intraspecific ranks were aggregated to species level for analysis.

Following these procedures, the final data set of 3,061,143 occurrence records represented 19,227 species from 1931 genera and 198 families. Across all species, the number of occurrences per species ranged between 1 and 18,710, with a mean of 160 and a median of 73.

Range size calculations

Occurrence records were projected to an Albers equal-area projection and range sizes for each species were calculated as the area in km^2 of the α-hull derived from all occurrences (Burgman & Fox, 2003). The α-hull is a modified minimum convex polygon created by linking all occurrence records with a set of non-intersecting triangles and removing those edges whose length is greater than the mean edge length of all triangles combined, multiplied by α (i.e. $Li > L \times \alpha$; where α = 0.3). The remaining area is taken as the range size in km^2. This method provides a more conservative estimate of range size than does a polygon encompassing all records (i.e. minimum convex polygon) and minimizes the underestimation of range size inherent in area of occupancy calculations (i.e. summing the area within occupied grid cells). These features make α-hull estimation particularly suited to studies using occurrence data collected in a non-systematic way, such as herbarium records (Burgman & Fox, 2003).

For 2686 species, area of occupancy – calculated as the number of 10×10 km grid cells occupied – was used to estimate range size. α-hulls were not appropriate for these species for three potential reasons: (1) there were < 3 occurrences ($n = 1209$) or (2) the configuration of the occurrences was unsuitable (e.g. a linear arrangement; $n = 138$) or (3) the hull estimate was less than the area of occupancy ($n = 1339$).

All range size calculations were made in R (R Core Team 2015) using the *alpha-hull* (Pateiro-López & Rodríguez-Casal, 2010) and *raster* (Hijmans & van Etten, 2012) packages.

Range size mapping

Range size variation among taxa is most commonly compared using frequency histograms – two-dimensional plots where size is displayed as a function of frequency of observation in a group of species (Fig. 1; reviewed in Gaston, 1996). While histograms are a useful tool for characterizing variation among species, the patterns they generate lack an explicit spatial context. To address this, I mapped the mean range size of all species occurring in a set of 3026, $0.5° \times 0.5°$ grid cells across Australia (Fig. 2a) and test for a relationship between mean range size and latitude using grid cell values as replicates.

As sampling effort and species richness may affect mean range size patterns, a null model was used to determine where in the landscape the mean range size is larger, or smaller, than expected due to chance alone. Specifically, I
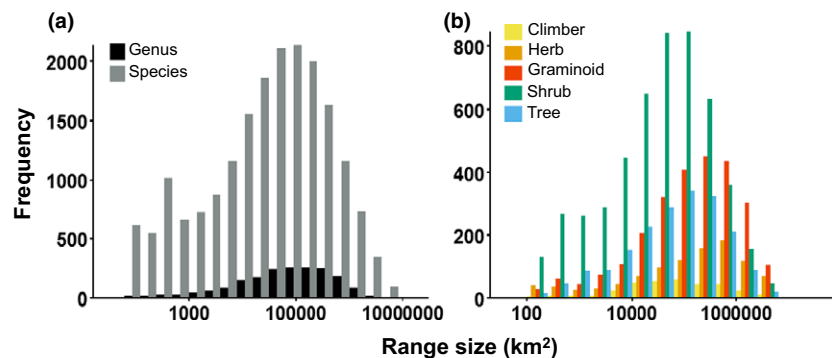

Figure 1 Frequency distributions of $\log_{10}$ range size (km^2) in the seed-plant flora of Australia in (a) species ($n = 19,227$) and genera ($n = 1930$) and (b) five major growth forms in 10,694 species of: climber ($n = 339$), graminoid ($n = 991$), herbs ($n = 2543$), shrubs ($n = 4,923$), trees ($n = 1,898$).
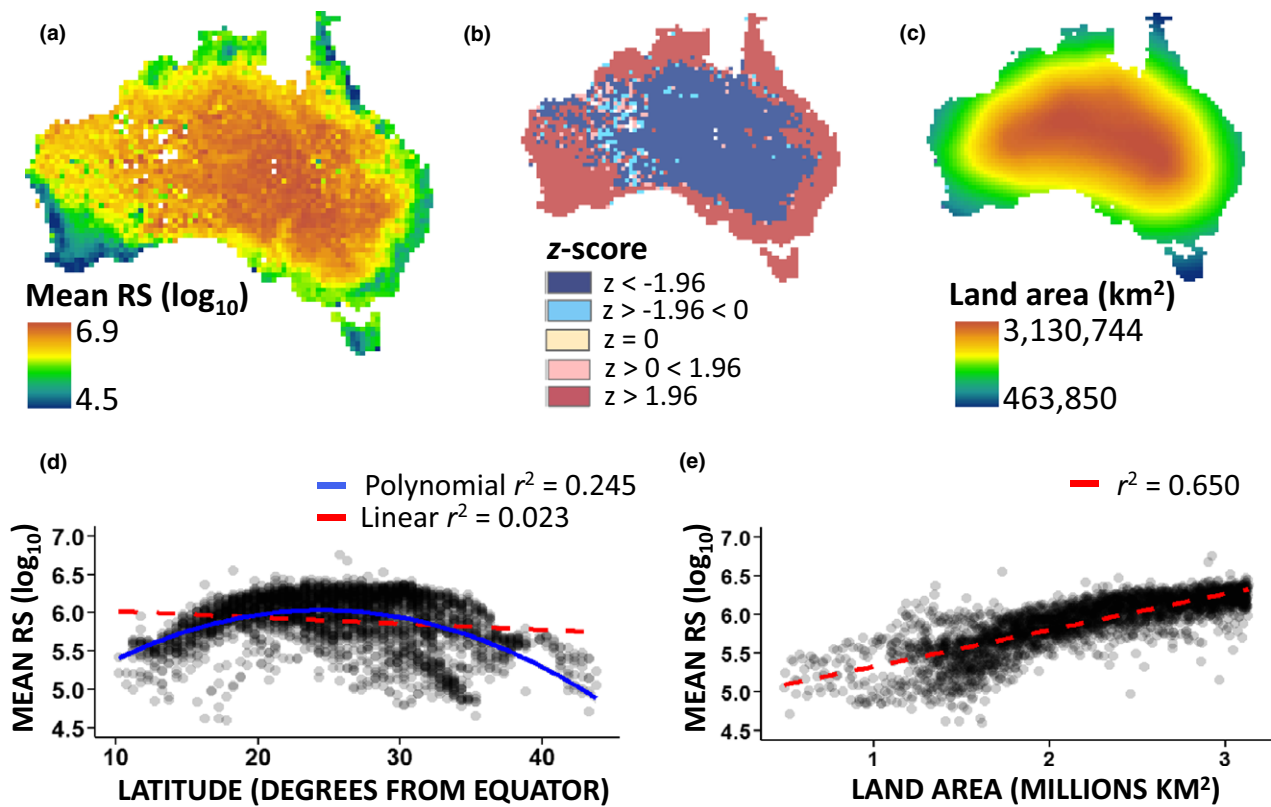
Figure 2 Range size variation in the Australian flora. (a) Map of mean range size (RS) across all terrestrial seed-plant species co-occurring in a series of 0.5° × 0.5° grid cells; (b) Map of the deviation of the observed mean from random expectation (z score) under a null model using 1000 reassignments of range size. Red and blue represent grid cells where mean range size is lower or higher than expected, respectively, given observed species richness; (c) Map of land availability as measured by the amount of land surrounding each cell falling within a 1900 km radius; (d) Relationship between $\log_{10}$ mean range size (km^2) and latitude (distance from the equator in °); (e) Relationship between $\log_{10}$ mean range size (km^2) and land availability (millions of km^2). In (d) and (e) dashed, red lines depict line of best fit in an ordinary least squares (OLS) regression model. In (d) blue, solid line depicts line of best fit in an OLS regression model with a polynomial term.

calculated the expected mean of range size for each grid cell under 1000 random assignments of range size across the entire species pool. Species richness in each grid cell was maintained, but the probability of drawing each range size was weighted by its own area to reflect the increased likelihood of drawing large-ranged species in each cell. A z score summarizing the difference in observed and expected mean range size and standard deviation in each cell was then calculated and mapped (Fig. 2b).

Statistical analyses

In all analyses, variables were $\log_{10}$ transformed prior to analysis to approximate normality where necessary. Collinearity between predictor variables was checked using Spearman rank correlations; R was < 0.5 in all pairwise comparisons (Table 1). Analyses were executed in R using the *raster* (Hijmans & van Etten, 2012), *rgdal* (Bivand *et al.*, 2015), *multcomp* (Hothorn *et al.*, 2008), *car* (Fox & Weisberg, 2011) packages. Statistical tests were considered significant at an alpha-level of $P = 0.05$.

Mean range size versus latitude and land area

The latitude at the centroid of each grid cell was determined and converted to an absolute value (i.e. distance from the equator in decimal degrees). To calculate the land area available for species to occupy around each grid cell, I placed a circle of radius 1900 km at the centroid of each cell and measured the land area to the coastline in km^2 (Fig. 2c). This radius corresponded to the largest possible circle fitting inside the continental boundary. The relationship between mean range size and these two variables was then modelled using ordinary least squares (OLS) regression.

Mean range size versus climate and soils

Data for climate (MAT, AI) at the centroid of each cell was extracted from ANUCLIM1.0 via e-MAST (http://www.emast.org.au/models/anuclimate-1-0/) and the CGIAR-CSI (http://www.cgiar-csi.org/data/global-aridity-and-pet-database) respectively. AI is calculated as the ratio of mean

Table 1 Spearman-rank correlations between pairwise combinations of soil and climate variables in $n = 3026$, $0.5° \times 0.5°$ grid cells across Australia. All correlations were significant ($P < 0.01$). AI, aridity index; MAT, mean annual temperature (°C); pH, pH of soil in a $CaCO_3$ solution; Depth, depth of the soil to the regolith (m); Total P, total available soil P (%).

	AI	MAT	pH	Depth
MAT	−0.221			
pH	−0.473	−0.117		
Depth	−0.538	0.169	0.537	
Total P	0.304	−0.311	0.149	−0.187

annual precipitation to mean annual potential evapotranspiration, where higher values represent regions of greater humidity (i.e. lower aridity). Values of AI < 0.5 are considered indicative of arid conditions. Soil values (DEPTH, pH, TOTP) were extracted from the National Soil Attribute Maps available in the Soil and Landscape Grid of Australia (http://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html).

Complementary non-spatial and spatial modelling techniques were used to explore mean range size variation in relation climate and soils. Univariate OLS regression was used to illustrate trends in how mean range size varied with each predictor variable (Fig. 3). Multiple OLS regression with all predictors was performed; however, tests of model residuals showed strong evidence of spatial autocorrelation. Spatial autocorrelation (i.e. the similarity of observations as a function of their distance from each other in space) violates the key assumption of independence in model residuals in statistical analysis (F Dormann et al., 2007). Therefore, I used simultaneous autoregressive (SAR) models to test the relationship between the five environmental predictors and mean range size, adding an autoregressive process to the error term.

SAR models use a matrix of spatial weights calculated on a given neighbourhood distance to account for patterns in response variables related to spatial location, rather than to the predictor variables in the model (Kissling & Carl, 2008). The spatial weights matrix was calibrated using a neighbourhood distance of 1° (approximately 100 km) and a row-standardized coding scheme. These parameters were chosen through a preliminary analysis of multiple neighbourhood distances and coding schemes as they were shown to have consistently low values of Moran's I over the first twenty distance groupings.

SAR models were run for all possible subsets of the five predictor variables ($n = 32$ models) under a multi-model inference approach. For each subset model, an Akaike's information criterion (AIC) score was calculated and used to select the most parsimonious model (Akaike, 1987) and model fit was assessed using pseudo-R^2 (Pearson correlation of observed and predicted values). The relative importance of each climate and soil variable for explaining mean range size variation was determined by summing the Akaike

weights (w) across all models containing the target variable. Akaike weights assess the relative likelihood of each model allowing for comparisons based on the model probability (Burnham & Anderson, 2004). Higher summed values of w indicate a greater probability of the model containing the variables being a good predictor of range size variation. Average model coefficients and their standard errors were also used to characterize the effect of individual climate and soil variables on range size.

Mean range size versus biomes and growth forms

Biome representation in Australia was derived from the World Wildlife Fund Ecoregions data set (Olson et al., 2001), which subdivides the world into 13 biomes, seven of which are found in Australia (Fig. 4). Four parameters were estimated for each biome – species richness (n), the mean range size of all species present (km^2), the mean range size of endemic species (km^2) and area (km^2). Species richness was derived by overlaying a map of cleaned occurrence records with a polygon shapefile of ecoregions and extracting a vector of species present. Mean range size estimates for each biome were then created by averaging range size for all species in each biome. Quantitative estimates of seed-plant richness in each biome (% of all Australian species) were also calculated.

Growth form data for 10,694 species was collated from published floras and taxonomic treatments. A full list of sources is provided in Appendix S2. Recognized growth forms were: climber ($n = 339$), graminoid ($n = 991$), herbs ($n = 2,543$), shrubs ($n = 4,923$), trees ($n = 1,898$). Where a species had multiple growth forms across different data sets it was omitted from analysis.

One-way analysis of variance (ANOVA) and post hoc multiple comparisons were used to test for significant differences in mean range size between biomes and growth forms.

RESULTS

Among species, range size varied over four orders of magnitude in the Australian seed-plant flora (mean: 235,829 km^2; range: 100–7,114,754 km^2; Fig. 1) and there was a distinct skew towards smaller range sizes (median: 38,395 km^2). The perennial grass species *Themeda triandra* Forssk. had the largest range estimate of any species, occurring across 7,114,754 km^2 of the continent and the graminoids and herbs had significantly larger range sizes than did all other growth forms ($F_{4,10689} = 184$; $P < 0.01$; Table 2). Ranges were smallest in shrubs, supporting the expectation that non-woody growth forms would possess larger ranges, on average, than their woody counterparts. A number of species had only one unique occurrence record per grid cell ($n = 308$) and therefore shared the smallest range size estimate of 100 km^2. While these small-ranged species were drawn from 63 plant families, 27% were orchids (Orchidaceae: $n = 83$ species). The majority of species (68%) have
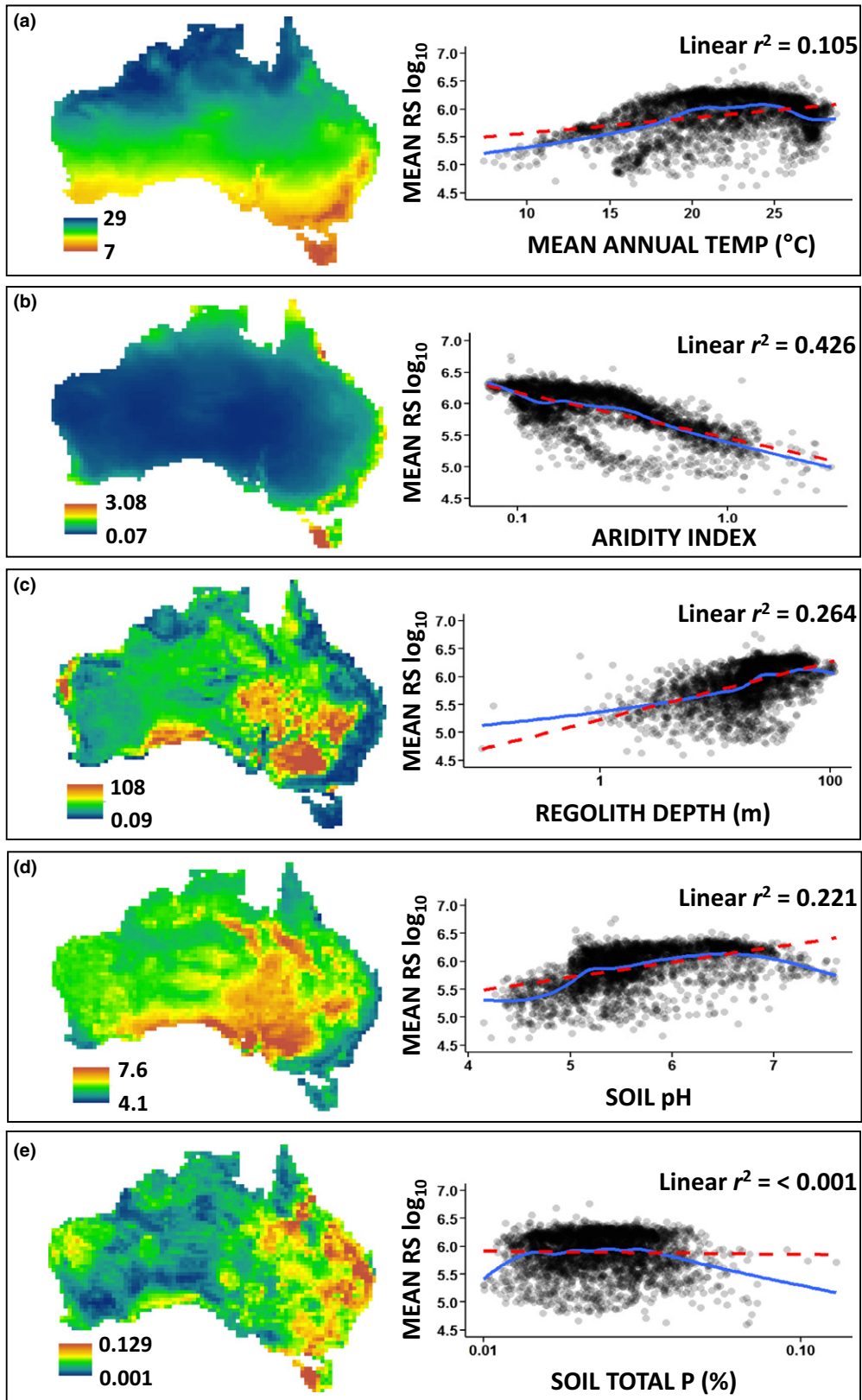
Figure 3 Climatic and edaphic predictors of range size variation in the Australia flora. In (a–e), maps depict the spatial variation in each environmental predictor and graphs show the relationship between the predictor and $\log_{10}$ mean range size across 3026, 0.5° × 0.5° grid cells in Australia. Red dashed lines depict the line of best fit in an ordinary least squares regression. Blue solid lines depict line of best fit from localized regression models (LOESS).
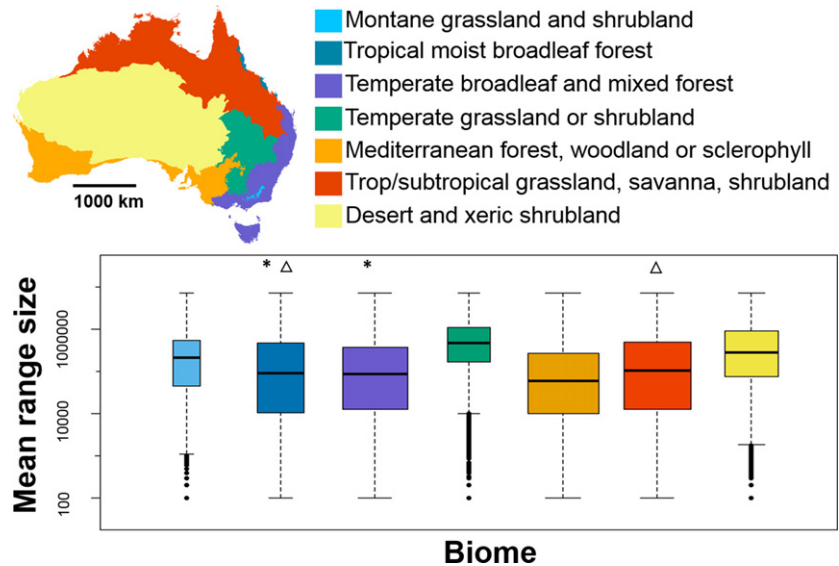
Figure 4 Boxplots depicting variation in mean range size between species occurring in Australia's seven biomes. Plots are arranged in the order of increasing biome area and their width is proportional to species richness (*n*). Symbols indicate biomes which did not differ significantly in mean range size by post hoc multiple comparison tests ($P < 0.05$).

Table 2 Range size variation across growth forms in the terrestrial seed-plant flora Australia. Growth form analyses are based on 10,694 species for which habit information was available from published floras and taxonomic treatments. Mean and standard deviation in range size (km^2) across species in each growth form and family are based on range size estimates from α-hull and area of occurrence calculations based on cleaned occurrence records from the Australian Virtual Herbarium (AVH; http://avh.chah.org.au/).

Growth form	Mean range size (1000s km^2)	Median range size (1000s km^2)	*n* (species)
Climber	345.6 ± 6657.9[b]	75.3	339
Graminoid	652.7 ± 10637.6[a]	195.9	991
Herb	521.5 ± 8763.6[a]	167.1	2543
Shrub	188.2 ± 4763.6	40.5	4923
Tree	249.4 ± 4965.9[b]	71.1	1898

N.B. For growth forms, means with similar superscript letters are not significantly different ($P < 0.05$) by post hoc Tukey multiple comparison tests.

ranges which cover < 1% of the Australian continent (76,920 km^2; Fig. 1). A number of these small-ranged species are rain forest specialists, clustered within families endemic to the Wet Tropics bioregion (e.g. Austrobaileyaceae, Cardiopteridaceae, Corsiaceae). Across all families, the largest and smallest mean range sizes were recorded for Hypericaceae and Hamamelidaceae, respectively; however, it should be noted that these families have low species richness in Australia with only three recognized native species apiece (Table 3). Mean range sizes for all families are provided in Appendix S3 in the Supporting Information.

The most consistent environmental predictors of mean range size variation in the Australian seed-plant flora were aridity, temperature and soil pH (Table 4). The SAR model containing these variables explained 94% of the variation in mean range size. These results indicate that hotter, drier locations with pH values approaching neutral support species

with the largest range size, on average, in this flora. These findings supported hypotheses about the importance of climatic gradients in shaping range size variation; however, the role of soil conditions is less clear. Soil depth and total P concentration were poor predictors of range size variation in SAR models (Akaike weights 0.495 and 0.278 respectively), providing little support for *a priori* hypotheses. This was despite the increasing soil pH being associated with larger range size (Table 4).

Across Australia, one quarter of the variation in mean range size of species sharing $0.5° × 0.5°$ grid cells could be explained by latitude, and there was no evidence that range size increased with latitude (Fig. 2d). Rather, mean range size peaked at mid-latitudes and was best approximated by adding a quadratic term to the least-squares regression model (R^2 quadratic = 0.25 cf. R^2 linear = 0.02; $P < 0.01$; $n = 3026$). This finding supported the hypothesis that large-ranged species would be well-represented in the arid centre of the continent (Fig. 2), rather than in high latitude regions as proposed under Rapoport's Rule (Stevens, 1989). While Australian regions closer to the equator were characterized by relatively small range sizes, so too were temperate regions in the south of the continent, particularly in Tasmania where many species are endemic ($n = 308$ species; 15% of the total richness; Fig. 2a). Land area was a greater predictor of range size variation ($R^2 = 0.65$; $P < 0.01$); however, this variable showed the same qualitative relationship to latitude by capturing the trend for larger-ranged species in the mid-latitudes at the centre of the continent.

Null modelling indicated that in the majority of grid cells across Australia (94%), the observed mean range size was much larger, or smaller, than likely under random expectation (Fig. 2b). In these cells, after comparing the observed mean to an expected mean derived from 1000 randomizations of range size, the comparative chance of detecting the observed mean range size was < 5% (i.e. *z* score = < −1.96, or > 1.96).

Table 3 Range size variation in major groups of the terrestrial seed-plant flora Australia. Mean and standard deviation in range size (1000s km^2) are shown for the top five most species-rich genera and families, and for the top five genera and families with the smallest- and largest ranges respectively.

	Mean range size (1000s km^2)	n (sp)		Mean range size (1000s km^2)	n (sp)
Genus			Family		
Most speciose			Most speciose		
Acacia	221.3 ± 486.3	1031	Fabaceae	237.9 ± 532.5	2481
Eucalyptus	134.7 ± 330.6	727	Myrtaceae	112.6 ± 272.8	2154
Grevillea	109.2 ± 350.4	367	Orchidaceae	74.2 ± 8763.6	1454
Caladenia	62.6 ± 131.7	269	Poaceae	625.0 ± 1049.2	1151
Stylidium	79.1 ± 163.6	260	Proteaceae	80.9 ± 265.7	1037
Largest range size			Largest range size		
Evolvulus	5742.4 ± 0	1	Hypericaceae	1761.6 ± 2334.8	3
Trichodesma	5283.2 ± 0	1	Nitrariaceae	1532.8 ± 0	1
Tripogon	5002.2 ± 0	1	Molluginaceae	1417.0 ± 1576.3	7
Daucus	4704.9 ± 0	1	Nyctaginaceae	1147.0 ± 1610.0	17
Triraphis	4510.2 ± 0	1	Crassulaceae	1141.0 ± 1025.6	11
Smallest range size*			Smallest range size		
			Hamamelidaceae	2.1 ± 2.7	3
			Corsiaceae	2.3 ± 0	1
			Calycanthaceae	4.7 ± 0	1
			Musaceae	5.1 ± 8.0	3
			Dichapetalaceae	5.3 ± 4.3	2

*N.B. 26 monophyletic genera share the smallest range size estimate (100 km^2).

Table 4 Variable importance for explaining range size. Mean and standard error of regression coefficients and relative importance of each predictor as measured by summed Akaike weights (W_{AIC}) for five climate and soil variables from spatially autoregressive models of range size. AI, aridity index; MAT, mean annual temperature (°C); pH, pH of soil in a CaCO3 solution; SAR, Simultaneous autoregressive; Depth, depth of the soil to the regolith (m); Total P, total available soil P (%).

Variable	Mean (± s.e.) SAR model coefficients	W_{AIC}
AI	−0.712 ± 0.022	1.000
MAT	0.058 ± 0.004	1.000
pH	0.097 ± 0.006	0.999
Depth	0.056 ± 0.008	0.495
Total P	0.003 ± 0.018	0.278

There were statistically significant differences in mean range size between biomes as determined by one-way ANOVA ($F_{6, 37974}$ = 476.3; $P < 0.01$) independent of species richness and biome area as hypothesized (Figure 4; Table 5). Of the seven biomes present in Australia, the Temperate grassland and shrublands had the highest mean range size across all species present (861.7 ± 1072.5 km^2) and Mediterranean forest/ woodland/sclerophyll forest the smallest (326.4 ± 727.3 km^2). The Mediterranean biome covers south-west Western Australia which is a known centre of high endemicity (Hopper & Gioia, 2004); 48.8% of species in this biome occurred in no other (Table 5). This biome also had the highest richness (46.6% of all seed-plants examined). Notably, the arid zone supports just over one-quarter (26.2%) of Australia's seed-plant flora, which is more than double previous estimates of

richness from the *Flora of Central Australia* (Jessop, 1981; see also Barker & Greenslade, 1982).

For species endemic within biomes, there were also significant differences in the mean range size ($F_{6, 9303}$ = 132.2; $P < 0.01$; Table 5); however, while the areal extent of the biome necessarily constrained range size in these species the richness of endemics in each biome was not associated with range size differences.

DISCUSSION

Range size varies markedly across the seed-plant flora of Australia; however, more than two-thirds of species have ranges which cover < 1% of the continent. On average, large ranges are characteristic of non-woody growth forms and are broadly associated with the arid and grassland biomes which dominate at mid-latitudes. Equally, small-ranged taxa tend to dominate in previously identified hotspots of endemicity and are more often woody trees and shrubs. There is no evidence that ranges are smaller at lower latitudes (Rapoport's Rule) in Australia, which is in contrast to other well-studied continental floras [e.g. North America (Morueta-Holme et al., 2013), New Zealand (McGlone et al., 2010)] which have been subject to extensive past-glaciations at higher latitudes, which may have driven selection for large range size. There is a strong trend towards smaller ranges along some coastal margins which was associated with decreased habitat availability. However, key environmental correlates of range size identified here (aridity, temperature and to a lesser extent soil pH) are also strongly structured along inland to coastal gradients and provide evidence for the role of evolu-

Table 5 Range size variation across biomes for the terrestrial seed-plant flora Australia. Estimates of the areal extent of each biome (km^2) are based on the Ecoregions of the World classification presented in Olson *et al.* (2001). Percentage of species present in each biome (Richness %) and the percentage of species endemic in each biome (Endemic species %) are based on cleaned occurrence records from the Australian Virtual Herbarium (AVH; http://avh.chah.org.au/). Mean and standard deviation in range size (km^2) across species in each biome are based on range size estimates from α-hull and area of occurrence calculations for 19,227 species. Statistics for all species in each biome (All species) and those occurring exclusively in one biome (Endemic species) are presented separately.

Biome	Area (1000s km^2)	Richness (%)	Endemic species (%)	All species Mean range size (1000s km^2)	n	Endemic species Mean range size (1000s km^2)	n
Montane grassland and shrubland	12.0	7.1	1.3	439.9 ± 697.2	1368	0.8 ± 2.1[ac]	18
Tropical moist broadleaf forest	32.6	19.7	8.6	446.7 ± 878.1[ab]	3796	1.4 ± 2.1[bc]	327
Temperate broadleaf and mixed forest	562.4	39.4	25.4	387.3 ± 784.6[a]	7568	14.3 ± 25.2	1923
Temperate grassland or shrubland	575.5	17.1	0.82	861.7 ± 1072.5	3279	2.9 ± 4.9[ab]	27
Mediterranean forest, woodland or sclerophyll	803.2	46.6	48.8	326.4 ± 727.3	8959	34.2 ± 47.1	4373
Tropical/subtropical grassland, savanna, shrubland	2132.5	41.5	26.1	441.1 ± 812.3[b]	7976	53.1 ± 106.5	2080
Desert and xeric shrubland	3565.2	26.2	11.2	674.3 ± 954.8	5035	74.4 ± 129.1	562

Means with similar superscript letters are not significantly different ($P < 0.05$) by *post hoc* Tukey multiple comparison tests.

tionary adaptation to abiotic conditions in driving range size variation in the seed-plant flora.

Aridification as a driver of large range size

Aridity and high MAT were both consistently associated with large range size, and the arid biome had species with significantly higher mean range size relative to other biomes. In addition, null models indicated a low probability of finding ranges as large as those found in the arid zone by chance alone, supporting the idea that large ranges are an adaptive response to the abiotic conditions and extent of arid conditions. Notably, Australia's arid biome supports a greater richness of endemic species than its tropical rain forests implying a high degree of specialization in the arid-adapted flora (Table 5). However, it should be noted that the areal extent of tropical closed forests in Australia may be underestimated by the WWF ecoregion classification. This may affect measures of endemism, which have previously been shown to be as high as 31% in the Wet Tropics Bioregion (Wet Tropics Management Authority, 2014).

This study demonstrates clearly the importance of arid conditions in selecting for large range size. Climatic instability has been shown to select for large range size by increasing extinctions of species with small climate niches and poor dispersal capacity (Sandel *et al.*, 2011; Morueta-Holme *et al.*, 2013). The retention of widespread taxa in response to climate oscillations has left the signature of large range size in current-day assemblages across the globe and may contribute to large range size in the Australian arid zone flora (Sandel *et al.*, 2011; Miller *et al.*, 2013; Morueta-Holme *et al.*, 2013; Kearns *et al.*, 2014). That is, climatic fluctuations during the evolution of the Australian arid biome may have provided similarly appropriate settings for the retention of large-ranged species.

The Australian arid flora arose via both adaptation of mesic ancestors and via diversification of arid taxa *in situ* (Beadle, 1966; Byrne *et al.*, 2008). Mesic ancestors with traits conferring pre-adaptation to dry conditions are thought to have spread into the expanding arid zone after the Mid-Miocene 15MYA (Byrne *et al.*, 2008; Morton *et al.*, 2011). Although there is little evidence of widespread glaciation in Australia which was largely restricted to Tasmania and mountain ranges in the south-east, cycles of aridification have produced analogous effects on the vegetation over evolutionary time-scales and were most pronounced in the centre of the continent (Hope *et al.*, 2004; Martin, 2006). During palaeoclimate fluctuations, large range size may have shielded some taxa from extinction by occupying more thermal or topographic refugia, or conferred greater resilience to stochastic events through higher population numbers (Davies *et al.*, 2009).

Variability in contemporary climate conditions across the arid zone may also reinforce the advantages of large range sizes for long-term population persistence in harsh environments. In particular, temporal and spatial variation in rainfall across the arid zone may lead to complex meta-population dynamics over large areas which buffer against environmental stochasticity (Morton *et al.*, 2011). Although not all suitable habitat within the range of a species may be occupied through time, an ability to successfully colonize and retain sites contributes to the maintenance of larger range sizes and promotes range-filling (Schurr *et al.*, 2007). Growth forms which can rapidly colonize and capitalize on unpredictable rainfall patterns to fill available habitat, such as grasses and ephemeral herbs, are key features of arid landscapes.

Growth form as a predictor of large range size variation

Non-woody species (graminoids and herbs) had ranges which were significantly larger across Australia than the ranges of their woody counterparts (trees, shrubs or woody climbers) (Table 2). This contrasts with earlier findings that found no difference in range size between 254 tree and

understorey species (forbs, graminoids, shrubs, climbers) in the south-east region of Australia (Murray *et al.*, 2002). Grasses and herbs dominate across the large arid biome and key differences in the morphology, physiology and reproductive biology of these growth forms may confer superior ecological performance under dry and hot conditions. In particular, a C4 photosynthesis, shallow roots and wind pollination and dispersal should facilitate occupation of Australia's large arid zone by increasing water-use efficiency, improving rapid water uptake following rainfall and permitting long-distance pollen and seed transfer across open habitats respectively.

C4 photosynthesis confers major plant productivity benefits in arid and hot environments, where photorespiration is typically high (Sage, 2004). Water-loss via stomatal opening is reduced as a result of CO_2 concentrating mechanisms and C4 species can remain photosynthetically active at high temperatures. The development of C4 photosynthesis in grasses has been implicated in their dominance in arid and savanna biomes throughout the globe (Jacobs *et al.*, 1999; Lundgren *et al.*, 2015) and may help maintain large range sizes across the widespread Australian arid zone. Grasses and herbs also typically lack a taproot for accessing deep soil water, instead relying on surface rainfall and infiltration to meet their water needs (Jackson *et al.*, 1996). Shallow roots may allow for more immediate use of intermittent rainfall for growth. Where permanent soil water is absent, rooting strategies which maximize the use of rainfall in the upper levels of the soil profile, such as allocation to fine root biomass in top soil layers, may be favourable (February *et al.*, 2013).

Wind pollination – which is widespread in grasses (Friedman & Barrett, 2009) – may promote large range size by allowing founding populations on the expanding range boundary to remain in genetic contact with range centres. Wind pollination also liberates species from dependence on specific animal-pollinators and retains the evolutionary benefits of gametic exchange, both of which may be advantageous as ranges expand into novel habitats (Givnish *et al.*, 2010). A recent study showed that the ability to self-fertilize is strongly associated with large range size (Grossenbacher *et al.*, 2015), presumably because single-parent reproduction allows lone individuals to found populations beyond current range boundaries. However, the prevalence of selfing as a breeding system across Australian graminoids is, as yet, unquantified, so hypotheses about this mechanism remain untested. Importantly, self-incompatibility – which promotes outbreeding – is known to also have been instrumental during grass evolution (Yang *et al.*, 2008) implying that interactions between large range size, breeding system and wind pollination in grasses requires more scrutiny. Equally, wind dispersal is common in central Australia graminoids species (Jurado *et al.*, 1991) and other arid-adapted families such as Asteraceae (Andersen, 1993), facilitating long-distance dispersal across the vast arid zone.

Although not all arid-adapted graminoids and herbs will possess the full suite of these traits, their ubiquity in arid floras from across the globe underscores their adaptive significance (Jacobs *et al.*, 1999).

CONCLUSION

Large-scale investment in biodiversity informatics since the 1990s has revolutionized the study of macroecology and biogeography. Unprecedented availability of occurrence data in online natural history collections means it is now possible to test previously intractable hypotheses at continental and global scales (Crisp *et al.*, 2011; Parenti & Ebach, 2013). This study has provided a taxonomically and spatially comprehensive understanding of how range size varies across a large proportion of the Australian flora. This type of baseline information could be applied to improve conservation planning and decision-making at the continental scale. Given that range size is inversely proportional to extinction risk (Mace *et al.*, 2008) data provided here detailing which taxa and landscape locations have the smallest range sizes could be instrumental in identifying conservation priorities. Given the finding that 68% of Australian plant species have ranges which cover < 1% of the continent, a wider portion of the Australian flora may be more vulnerable to human-threats, such as habitat fragmentation and climate change, than previously acknowledged.

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SUPPORTING INFORMATION

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

Appendix S1 Genera and families in this study according to the Australian Plant Census.
Appendix S2 Sources of growth form data.
Appendix S3 Range size estimates for 198 families in this study.

BIOSKETCH

Rachael Gallagher is a plant ecologist and postdoctoral research fellow at Macquarie University in Sydney with interests in functional biogeography and climate change adaptation in the Australian flora.

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