



Environmental niche conservatism explains the accumulation of species richness in Mediterranean-hotspot plant genera

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The causes of exceptionally high plant diversity in Mediterranean-climate biodiversity hotspots are not fully understood. We asked whether a mechanism similar to the tropical niche conservatism hypothesis could explain the diversity of four large genera (*Protea*, *Moraea*, *Banksia*, and *Hakea*) with distributions within and adjacent to the Greater Cape Floristic Region (South Africa) or the Southwest Floristic Region (Australia). Using phylogenetic and spatial data we estimated the environmental niche of each species, and reconstructed the mode and dynamics of niche evolution, and the geographic history, of each genus. For three genera, there were strong positive relationships between the diversity of clades within a region and their inferred length of occupation of that region. Within genera, there was evidence for strong evolutionary constraint on niche axes associated with climatic seasonality and aridity, with different niche optima for hotspot and nonhotspot clades. Evolutionary transitions away from hotspots were associated with increases in niche breadth and elevated rates of niche evolution. Our results point to a process of “hotspot niche conservatism” whereby the accumulation of plant diversity in Mediterranean-type ecosystems results from longer time for speciation, with dispersal away from hotspots limited by narrow and phylogenetically conserved environmental niches.

KEY WORDS: Evolutionary model comparison, Mediterranean-type ecosystems, niche conservatism, Ornstein–Uhlenbeck model, Proteaceae.

Mediterranean-type ecosystems (MTEs) contain plant species diversity comparable to some tropical regions, and far greater than expected given their latitude and low primary productivity (Cowling et al. 1996; Linder 2003), making these regions valuable case studies for understanding the processes underlying plant diversity more generally. Five MTEs are recognized as biodiversity hotspots based on high numbers of endemic plant species combined with high levels of habitat loss from anthropogenic disturbance (Myers et al. 2000), but the evolutionary and ecological mechanisms that drive the high diversity of these regions are still incompletely understood. In recent studies of MTE diversity patterns, much of the emphasis has been on the role of elevated diversification rates in driving high plant species richness (Richardson et al. 2001; Latimer et al. 2005; Sauquet et al. 2009; Verboom et al. 2009; Cardillo and Pratt 2013; Valente and Vargas

2013; Onstein et al. 2015; Reyes et al. 2015). However, results have been mixed, with some studies supporting elevated hotspot diversification (Latimer et al. 2005; Sauquet et al. 2009; Onstein et al. 2015; Reyes et al. 2015), but others failing to (Cardillo and Pratt 2013; Valente and Vargas 2013; Cook et al. 2015; Linder and Bouchenak-Khelladi 2015).

The equivocal support for faster diversification within MTE hotspots shifts the focus to other mechanisms that could underlie the high plant diversity of these regions. In this study we investigate whether a process analogous to the Tropical Niche Conservatism Hypothesis (TCH; Wiens and Donoghue 2004) could underlie the diversity of MTEs. The TCH proposes that many large groups of organisms arose during periods when a tropical climate was more extensive (Wiens and Donoghue 2004; Romdal et al. 2013). The retention of a tropical niche limited the

Table 1. The four genera used in this study, with the total species richness and number of species found within an MTE hotspot; the number of species sampled in each phylogeny; and the number of these found in an MTE hotspot, a reference to the original publication of each phylogeny, and TreeBase accession numbers for two genera (*Moraea* and *Protea*).

Genus	Total Species (Hotspot Species)	Species in Phylogeny (Hotspot Species)	Reference	TreeBase TreeID
<i>Banksia</i>	170 (155)	158 (143)	Cardillo and Pratt (2013)	–
<i>Hakea</i>	151 (92)	137 (85)	Cardillo et al. (unpubl. ms.)	–
<i>Moraea</i>	200 (150)	162 (129)	Schnitzler et al. (2011)	Tr26543
<i>Protea</i>	115 (70)	90 (70)	Schnitzler et al. (2011)	Tr26558

dispersal of lineages into temperate regions, and therefore the difference in diversity between tropical and temperate regions may be explained by longer residence times within tropical biomes: the “time-for-speciation” effect (Stephens and Wiens 2003). Subsequent studies have extended the niche conservatism model to nonlatitudinal diversity patterns, such as the disparity in richness between biomes or along climatic gradients (Li et al. 2009; Hutter et al. 2013; Wiens et al. 2013). Could similar processes explain the high plant diversity of MTE hotspots?

Much MTE plant diversity consists of large plant genera that are distributed primarily within MTEs, but are also represented by smaller numbers of species in adjacent non-MTE biomes (Cowling et al. 1996; Beard et al. 2000; Hopper and Gioia 2004). In some studies, the MTE has been reconstructed as the ancestral biome of a genus, with rare dispersal events into other biomes (e.g., *Protea*, Valente et al. 2010; *Banksia*, Cardillo and Pratt 2013), suggesting longer residence times within MTEs. What remains poorly known, however, is whether the high MTE diversity of such genera is purely the result of a time-for-speciation effect, or if this effect is reinforced by environmental niche conservatism that limits the capacity of plant lineages to “break out” from MTE hotspots and adapt to different environments outside the hotspot regions.

It is therefore useful to examine not only whether hotspot plant clades show an overall signature of environmental niche conservatism, but also to ask what may have facilitated the shifts away from hotspots. MTE hotspots are often island-like regions with a distinctive climate characterized by predictable summer drought, surrounded by more arid regions with less regular seasonal cycles (e.g., the Nullarbor Plain and Western Deserts in Australia, the Namib Desert and Nama Karoo in southern Africa). For a lineage adapted to a Mediterranean-type environment to shift away from an MTE region into a more arid region, or to mesic regions beyond, may require the emergence of a temporary corridor of suitable environment, such as may have existed in southern Australia before the origin of the Nullarbor Plain (Crisp and Cook 2007). Alternatively, shifts away from an MTE could occur in the absence of such corridors by the evolution of a broader environmental niche, allowing expansion into adjacent low richness areas (e.g., Che-

janovski and Wiens 2014). A shift may also occur via evolution of the niche mean or optimum environmental tolerance in a particular lineage (Wiens and Donoghue 2004), which is expected to leave a signature of accelerated niche evolution associated with dispersal away from the MTE (Fisher-Reid et al. 2012).

In this article, we test this model of “hotspot niche conservatism,” using four large genera with much of their species richness found in two MTE hotspots, South Africa’s Greater Cape Floristic Region (*Protea* and *Moraea*) and Australia’s Southwest Australian Floristic Region (*Hakea* and *Banksia*). For each genus, we estimate the present-day environmental niche from species distributional and spatial environmental data, and infer the history of environmental niche evolution along the phylogeny of each genus. We ask, first, to what extent differences in species richness between regions can be explained by longer or shorter inferred residence times within different regions. We then test for evidence of niche conservatism along multiple environmental niche axes, and ask whether shifts between MTE hotspots and other regions are associated with shifts in niche optima, niche breadth, or the rate of niche evolution.

Materials and Methods

PHYLOGENETIC AND SPATIAL DATA

Our choice of genera for analysis (*Banksia*, *Hakea*, *Moraea*, and *Protea*) was driven by (1) the availability of high-resolution spatial data and well-sampled, time-calibrated phylogenies, and (2) their representativeness of the kinds of large genera that account for much of the diversity of the Southwest Australian Floristic Region and Greater Cape Floristic Region, as explained above (Table 1).

Occurrence records for these genera were collected from the Australian Virtual Herbarium (<http://avh.chah.org.au/>), South Africa Biodiversity Information Facility (<http://www.sanbi.org/>), and Global Biodiversity Information Facility (<http://www.gbif.org/>). We were able to obtain spatial data for almost all species in each phylogeny with the exception of five *Protea* species (*P. roupelliae*, *P. woenskaensis*, *P. caespitose*, *P. heckmanniana*, and *P. munditeast*), three *Moraea* species (*M. calcicola*, *M. aristata*, *M. rigidifolia*), *Banksia prionophylla*, and *Hakea rubriflora*.

These species were removed from further analysis, resulting in 136 species, or 90% of all *Hakea* species, 85 *Protea* (74%), 159 *Moraea* (~80%), and 157 *Banksia* (92%).

Records judged erroneous were removed after cross-referencing with expert range maps (Goldblatt, 1973, 1976, 1977, 1982; Rourke 1980; Taylor and Hopper 1988; Goldblatt & Manning 1995, 2000, 2002, 2004; Barker et al. 1999; George 1999; Goldblatt et al. 2002; Holliday 2005; Young 2006). This included records that had impossible coordinates (in the ocean), unlikely coordinates (well outside of the known distribution for that species), or were recorded from herbaria and botanical gardens. This resulted in 3445 records of *Moraea* (range: 1–889, mean: 21 records per species), 10,263 records of *Banksia* (range: 1–1659, mean: 55), 18,609 for *Hakea* (range: 1–902, mean: 122), and 93,161 for *Protea* (range: 3–14,690, mean: 1096). Many plant species from the two hotspots are narrowly distributed and (naturally) rare, so their distributions are represented by a small number of occurrence records. We included all species with available data, including those known from fewer than 10 occurrence records (14 species of *Hakea*, 2 *Protea*, 53 *Banksia*, and 85 *Moraea*). This needs to be considered as a caveat on the interpretation of niche estimates based on occurrence records, although it is likely that low numbers of records reduces precision of niche estimates, rather than accuracy.

Climate data were obtained from the CliMond dataset (Kriticos et al. 2012) at a resolution of 10' (approximately 15–20 kms²) and extracted from each occurrence point for each species. We selected eight of the 35 CliMond variables that capture key aspects of the environmental niche important for plant distributions generally, as well as reflecting the climatic conditions that characterize a Mediterranean climate (i.e., strongly seasonal winter precipitation/summer drought with low humidity; Aschmann 1973; Cowling et al. 1996; Linder 2003): mean annual temperature, mean annual precipitation, mean temperature in the warmest quarter, mean temperature in the driest quarter, mean precipitation in warmest quarter, mean precipitation in the driest quarter, temperature seasonality, and precipitation seasonality. We also extracted soil pH data at a 250 m² resolution from the Australian Soil Resource Information Service (<http://www.asris.csiro.au/>) and World Soil Information (<http://www.isric.org/>) for each occurrence record. For each variable, we summarized the data extracted from the set of occurrence records into a measure of niche position (median value) and niche breadth (the standard deviation; Burgman 1989).

INFERENCE OF ANCESTRAL AREAS

To investigate the relative timing and phylogenetic position of transitions between hotspot and nonhotspot regions, we estimated the ancestral geographic distributions at internal nodes of

each phylogeny, using a likelihood-based biogeographic model comparison approach with the BioGeoBEARS R package (Matzke, 2014). We first classified species as either hotspot or nonhotspot. This binary condition is a simplification of the range of biomes and biogeographic regions occupied by different species, but it is appropriate for the questions about hotspot versus nonhotspot lineages that are the focus of our study. Ten species of *Moraea* and six species of *Hakea* are found in both hotspot and nonhotspot regions, but the BioGeoBEARS models allow species to occupy multiple regions, so these species were classified as “widespread.”

We modeled the history of evolutionary transitions between hotspot and nonhotspot regions under six different biogeographic models (DEC, DEC+j, DIVA, DIVA+j, BayArea, and BayArea+j), that model range evolution with different combinations of parameters for dispersal, extinction, vicariance, sympatry, and founder-event speciation. For each genus, we found the best-fitting model using AIC, which we then used to reconstruct the geographic distribution (hotspot or nonhotspot) at each node in the tree, using stochastic character mapping with 50 replications.

RATES OF MODES OF NICHE EVOLUTION

We compared a series of Brownian Motion (BM) and Ornstein–Uhlenbeck (OU) models of niche evolution to compare the tempo and mode of niche evolution between hotspot and nonhotspot lineages. The OU model is a variation of the BM model in which a continuous trait evolves toward an optimal value (θ), where the strength of the selective force toward the optimum (α) and rate of stochastic drift around the optimum (σ^2) are estimated using maximum likelihood (ML; Hansen 1997; Beaulieu et al. 2012). The BM model has only one parameter, σ^2 .

We investigated five different BM and OU models that allowed the parameters of the BM and OU process to differ along the phylogeny based on the inferred geographic state at each node (BMM, OUM, OUMA, OUMV, and OUMVA). To account for uncertainty in the biogeographic state of internal nodes, we took 50 stochastic maps of the best-fitting model from the BioGeoBEARS analysis and labeled the nodes of each tree with the inferred states. However, as BioGeoBEARS allows species to occupy multiple states concurrently, and the regime for the evolutionary model comparisons requires discrete states, we ran each of these five models three times for each stochastic map (150 times each for each different niche trait investigated), first with widespread species designated as “hotspot,” then as “nonhotspot,” then as “widespread.” These three different categorization methods allowed us to incorporate biogeographic uncertainty in the evolution of each niche axis.

The OUM model allows the optimal niche value (θ) to differ between hotspot and nonhotspot regions to test if species in each region occupy different niche positions. The OUMV model

allows both θ and the rate parameter (σ^2) to vary, the OUMA model allows θ and the strength of selection (α) to vary, while the OUMVA allows all three parameters to vary. The BMM model allows the evolutionary rate parameter (σ^2) to vary. We also investigated a further two single-rate models that modeled the BM and OU process independent of hotspot occupancy (BM1 and OU1). We fitted all evolutionary models using the R package OUwie (Beaulieu et al. 2012).

Models that estimate a number of parameters are often more complex than the information contained within the data and, as a result, fail to converge on an ML outcome (Beaulieu et al. 2012). We analyzed the eigendecomposition of the Hessian matrix of each model to determine convergence. If eigenvalues are negative, then the Hessian matrix is not positive definite and this indicates the model did not arrive at an ML estimate of each parameter (Beaulieu et al. 2012). Any individual model that failed to converge was excluded from the assessment of model fit and model averaging (see below).

To assess relative model fit we used Akaike weights, and to incorporate model selection uncertainty into the parameter estimates from the models we used a model averaging procedure (Burnham and Anderson 2002; Johnson and Omland 2004) across all successfully converged simulations for each genus. For each genus and niche variable combination, we obtained the goodness of fit of each model using Akaike weights, derived from the size-corrected Akaike information criteria (AICc). In cases where multiple-rate OU models were the best fit and no single model provided an unequivocally better fit (Akaike weights > 0.9) we found model-averaged parameter values of θ , α , and σ^2 . We also obtained the stationary variance ($\sigma^2/2\alpha$), an estimate of the relative contribution of stochastic drift versus constraint in the evolution of a niche axis. A lower stationary variance indicates a greater relative influence of the constraining parameter (α) compared to stochastic drift (σ^2) on the evolution of a niche axis. This implies stronger attraction to the niche optimum, and may be interpreted as the niche axis being more conserved. Conversely, a higher value of stationary variance indicates a greater influence of σ^2 rather than α , suggesting greater lability in that niche axis (Münkemüller et al. 2015).

NICHE BREADTH DIFFERENCES

To determine if nonhotspot species were characterized by greater niche breadth than hotspot species, values for all nine niche axes were compared between hotspot and nonhotspot species using phylogenetic MANOVA (multivariate analysis of variance), a multivariate application of the phylogenetic ANOVA developed by Garland et al. (1993), using the R package GEIGER version 2.0.6 (Harmon et al. 2008). A MANOVA determines whether the means of multiple dependent variables (niche axes) differ with a change in an independent variable (region). Phylogenetic

MANOVA takes into account phylogenetic non-independence when determining the significance of the MANOVA test statistic (here we used Wilk's λ), as differences between hotspot and non-hotspot species may be due to shared ancestry, and species may therefore not be independent (Garland et al. 1993). Phylogenetic MANOVA tests whether the test statistic is significantly different than expected under a BM model of trait evolution, using 1000 Monte Carlo simulations of traits on the phylogeny. To explore which variables drive the multivariate differences between hotspot and nonhotspot lineages, we also used a univariate phylogenetic ANOVA (Garland et al. 1993) on each niche axis separately, also using GEIGER. Again, for these analyses we consider species found in multiple regions first as hotspot species then as non-hotspot species.

PHYLOGENETIC STRUCTURE OF ASSEMBLAGES

If dispersal events away from the hotspot regions into other biomes were rare, we would expect species descending from lineages that moved away from hotspots to be phylogenetically clustered (i.e., more closely related to one another than to a random sample of species from across the phylogeny). We tested whether hotspot and nonhotspot species were significantly clustered on the phylogeny using phylogenetic species variability (PSV; Helmus et al. 2007). To determine whether PSV values for hotspot and non-hotspot groups were significantly different from what we would expect by chance, values were compared to a null model, where species were randomized on the tips of the phylogeny 999 times. Observed PSV values were compared to the distribution from the simulations and were considered clustered if $P < 0.025$ or overdispersed if $P > 0.975$.

TIME-FOR-SPECIATION EFFECT

Under the "hotspot niche conservatism" hypothesis, we expect two observable relationships between species richness and time within each genus. The first is a positive relationship between clade age and species richness across clades generally, if diversification rates are equal between hotspot and nonhotspot lineages. The second is a positive relationship between the age of colonization of a biogeographic region and the number of species descended from that colonization (the time for speciation effect).

To investigate the overall relationship between clade age and species richness, for each genus we plotted the crown ages of sets of phylogenetically nonnested subclades against the natural logarithm of their extant species richness. Subclades within each genus were chosen systematically by starting at the root node and selecting all clades obtained by counting a given number of nodes below the root. The number of nodes from the root was selected to provide a balance between maximizing the number of clades chosen ($n > 10$), while also ensuring that clades of a range of sizes and ages were chosen (for example, counting too many

nodes below the root would result in only small, shallow clades being selected).

To investigate the time-for-speciation effect we identified the crown nodes of clades for which the branch subtending the node was inferred to exist in a different biogeographic state (i.e., the node at which a transition between hotspot and non-hotspot regions was inferred from the best fitting BioGeoBEARS model). We found the age of these nodes using the “branching.times” function in GEIGER (Harmon et al. 2008), and plotted this age against the log number of species in that clade that are found in the same geographic region at that node. For *Moraea*, *Protea*, and *Banksia*, the number of inferred transitions between biogeographic regions was too small to test the relationship statistically, so we pooled the data for all genera and plotted the relative age of nodes against log (species richness). For *Hakea*, there were a number of nodes not assigned a high probability to any one state. For this genus, we repeated the time for speciation tests under two criteria for accepting a nodal probability value as a transition to a given geographic state: “strict” (>90%) and “relaxed” (>60%).

Results

INFERENCE OF ANCESTRAL BIOMES

MTE hotspot origins were strongly supported for the crown nodes of *Banksia*, *Protea*, and *Moraea*. For *Hakea* we were unable to confidently assign the crown node to either a hotspot or non-hotspot as neither of the probabilities of hotspot and nonhotspot states under the best-fitting BioGeoBEARS model were very high (0.33 and 0.1, respectively; Fig. 1). For all genera the DEC+j model was the best fit, suggesting a role of founder speciation (represented by the parameter j) in all groups. Estimates of nodal geographic states under the DEC+j model for each genus are shown in Figure 1.

Within each genus, a significant positive correlation between the age of clades and log (species richness) was evident across sets of phylogenetically independent subclades (Fig. 1). There were also positive correlations between the age of geographic colonization events and log (species richness) for three genera (*Protea*, *Moraea*, *Banksia*; Fig. 2). For *Hakea*, the timing of transitions between hotspot and nonhotspot regions differed depending on the criteria for accepting the geographic state of each internal node (strict vs. relaxed). Under both criteria there was a positive but nonsignificant relationship between the timing of a colonization and the log (species richness, Fig. 2).

HOTSPOT/NONHOTSPOT DIFFERENCES IN NICHE BREADTH

Phylogenetic MANOVA revealed significant differences in environmental niche breadths (across all nine niche axes) between hotspot and nonhotspot species, over and above that expected

given their phylogenetic relationships. The pattern clearly demonstrates broader environmental niches for nonhotspot species within each genus (Table 2). When niche axes were analyzed individually using phylogenetic ANOVA, many axes showed significantly greater niche breadth in nonhotspot species, and none showed significantly greater breadth in hotspot species (Table 3). Results were very similar regardless of whether widespread species (those found both inside and outside hotspots) were considered hotspot or nonhotspot species. The results we present are based on the designation of widespread species as non-hotspot.

RATES AND MODE OF NICHE EVOLUTION

Comparisons of alternative models of niche evolution (Table 4) reveal a pattern of evolution toward divergent environmental optima in hotspot and nonhotspot species, with multiple-optima OU models (OUM, OUMV, OUMA, OUMVA) nearly always showing stronger support than both BM models and a single-optimum OU model. The major exception to this pattern was in *Banksia*, as all OU models failed to converge in all replicate runs for three variables (mean annual temperature, mean temperature of the wettest quarter, Soil pH) leaving a comparison between only BM models for these niche axes. For temperature seasonality a single-optimum OU model (OU1) was preferred over those multiple-optima models that did succeed in converging. For all genera, in only a few cases was there unequivocal support for any one OU model (Akaike weight > 0.9), so our estimates of the OU parameters (θ , α , and σ^2) for each genus and niche axis combination were calculated using a model-averaging procedure (Burnham and Anderson 2002; Johnson and Omland 2004). Model averaged OU parameter estimates for all genera are included in Table S1 in Supporting Information.

The stationary variance ($\sigma^2/2\alpha$) reveals variation in the relative importance of the rate of evolutionary drift (σ^2) and the strength of attraction toward an optimum (α), between hotspot and nonhotspot lineages, for different niche axes (Fig. 3). The most striking differences between hotspot and nonhotspot species are in mean rainfall in the warmest and driest quarter of the year in *Hakea*, *Banksia*, and *Moraea*, in mean annual temperature, and temperature in the warmest quarter of the year for *Protea*, *Hakea*, and *Moraea*, and in mean annual precipitation and temperature in the driest quarter for *Banksia* and *Hakea*. These results are consistent with our hypothesis that niche evolution is less constrained toward niche optima (a higher stationary variance) in nonhotspot lineages.

In *Hakea*, the parameter estimates were robust to the geographic designation of widespread species. In *Moraea*, when widespread species were considered nonhotspot species, the non-hotspot stationary variance was much higher, but when treated as hotspot species, four of the nine variables (mean annual precipitation, precipitation in the driest quarter, precipitation in the wettest

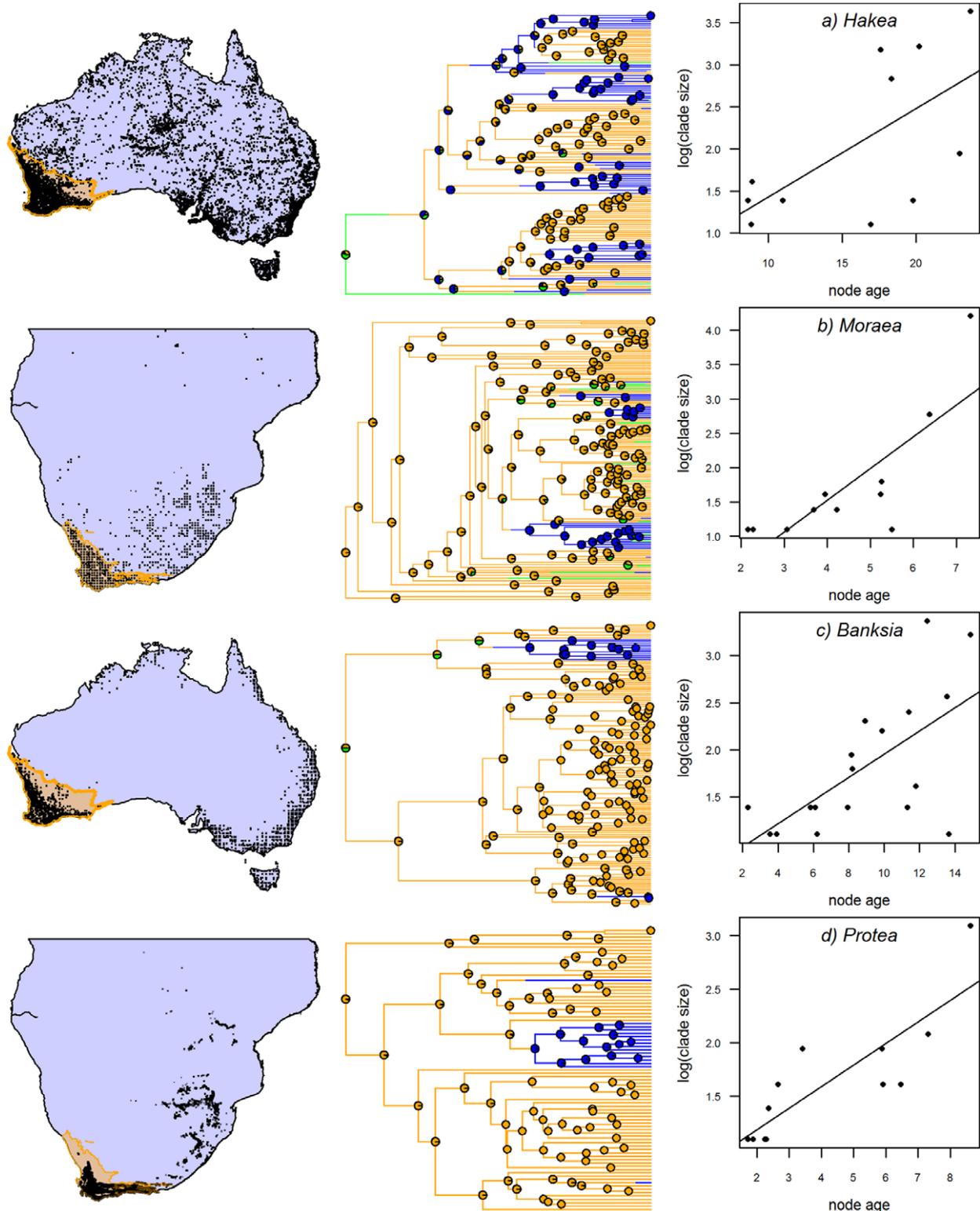


Figure 1. The distribution of occurrence data, reconstruction of ancestral biome, and clade age versus species richness relationships of four hotspot genera; (A) *Hakea*, (B) *Moraea*, (C) *Banksia*, and (D) *Protea*. In each map, biodiversity hotspots (the Southwest Australian Floristic Region and Greater Cape Floristic Region) are orange and nonhotspot regions are blue. On each phylogeny, orange branches are reconstructed as occurring in the hotspot, blue branches are reconstructed as occurring outside the hotspot, while green branches are reconstructed as being both hotspot and nonhotspot. Node panels show the probability of each geographic state from BioGeoBEARS analysis. Clade size in the regression panels is log (species richness +1), and all four clades show a positive relationship (*Hakea* $R^2 = 0.34^*$; *Moraea* $R^2 = 0.60^{**}$; *Banksia* $R^2 = 0.38^{**}$; *Protea* $R^2 = 0.68^{***}$; $^{***}P < 0.001$, $^{**}P < 0.005$, $^*P < 0.05$).

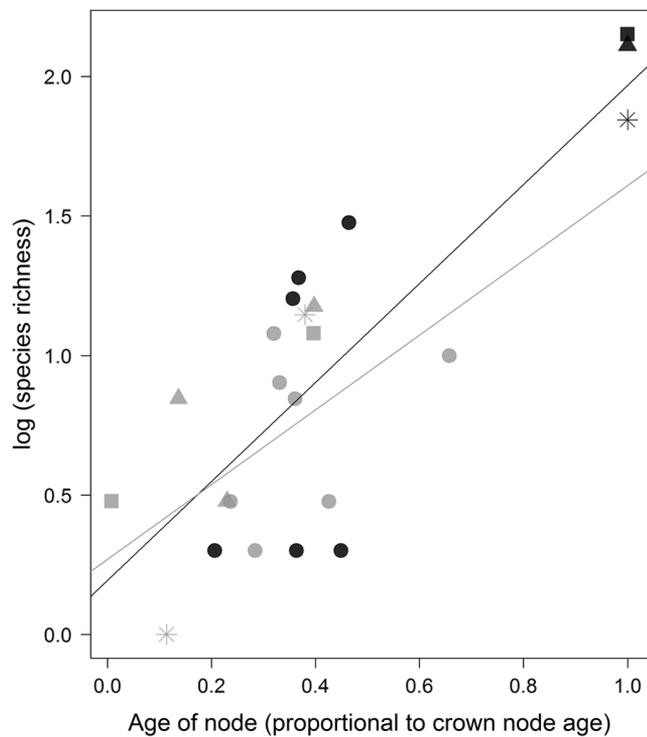


Figure 2. The time-for speciation effect. A regression between the age of a colonization event, relative to the age of each genus, against the log of the number of species descended from that colonization event. The slope in black is the model when all genera are pooled together ($R^2 = 0.63$, $P < 0.001$), the line in grey was determined for only *Hakea* ($R^2 = 0.05$, $P > 0.05$). Symbols in black represent hotspot clades, while symbols in grey represent clades found outside the hotspot; *Banksia* = ■, *Moraea* = ▲, *Hakea* = ●, *Protea* = *.

Table 2. Phylogenetic MANOVA results for multivariate comparison of niche breadths for nine niche axes between hotspot and nonhotspot groups of *Moraea*, *Protea*, *Banksia*, and *Hakea*.

Genus	Wilk's λ	F
<i>Moraea</i>	0.26	17.72***
<i>Protea</i>	0.27	25.30*
<i>Banksia</i>	0.26	54.45***
<i>Hakea</i>	0.43	20.63***

All results indicate significantly broader niches for nonhotspot species.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

quarter, and mean temperature in the driest quarter) showed the opposite pattern. When widespread species were put into a third “widespread” geographic category, the stationary variance of only two niche axes (mean annual precipitation and precipitation seasonality) was greater in hotspot species. This suggests that hotspot lineages of *Moraea* show less stochastic drift and/or attraction to niche optima when only regional endemics are considered.

PHYLOGENETIC STRUCTURE OF ASSEMBLAGES

Within *Banksia*, *Protea*, and *Moraea*, nonhotspot lineages were significantly phylogenetically clustered, with PSV values in the lower tail of the null distributions (Table 4). For *Hakea*, the pattern was reversed: hotspot lineages were significantly clustered, but the phylogenetic structure of nonhotspot lineages was consistent with the null model (Table 5).

Discussion

Biodiversity hotspots in MTEs are potentially valuable case studies for understanding geographic disparities in species richness, precisely because they lie outside the major global pattern of variation in species numbers with climate. Our reconstruction of the biogeographic and niche-evolution histories of four large MTE plant genera point to an important role for niche conservatism and long residence times in generating the high botanical diversity of MTE regions.

Inference of ancestral regions from phylogenetic and distributional data indicates that the common ancestors of present-day *Banksia*, *Protea*, and *Moraea* occupied and began diversifying within the Greater Cape Floristic region or Southwest Australian Floristic Region biodiversity hotspots. This would suggest that present-day nonhotspot species within these genera were derived from comparatively few lineages that “broke out” and dispersed away from hotspot regions into adjacent biomes, consistent with previous findings for these genera (Goldblatt et al. 2002; Valente et al. 2010; Cardillo and Pratt 2013). This has resulted in a present-day pattern of phylogenetic clustering among the nonhotspot members of these three genera. In contrast, the genus *Hakea* seems to have been more geographically mobile, undergoing a large number of biome shifts, and is the only genus that appears to have secondarily recolonized an MTE region from outside. However, the inference of a hotspot origin for the common ancestor of *Hakea* is more ambiguous than for the other genera, and together with the existence of a number of widespread species this means there is more uncertainty in the number and timing of evolutionary transitions between hotspot and non-hotspot regions. To fully understand the more complex biogeographic history of *Hakea* it will be necessary to model transitions between all major biomes in which the genus occurs, rather than assume a simple hotspot/nonhotspot binary state (Cardillo et al. unpubl. ms.).

The inference of hotspot origins for the common ancestor of *Banksia*, *Protea*, and *Moraea* and the strong positive associations between crown ages of subclades and their species numbers suggest that a simple time-for-speciation effect can go a long way to explaining the disparity in species richness between hotspot and nonhotspot lineages in these genera, as was also found for two large genera of Fabaceae (Cook et al. 2015). Under a simple constant-rates diversification process, we expect a positive

Table 3. Phylogenetic ANOVA results and species niche breadth (mean \pm SD across species) for hotspot and nonhotspot species of *Protea*, *Moraea*, *Banksia*, and *Hakea*.

Genus	Niche Axis	<i>F</i>	Hotspot	Nonhotspot
<i>Moraea</i>	MAT	46.52**	0.96 \pm 0.59	1.84 \pm 0.98
	TS	6.26	0.001 \pm 0.00	0.002 \pm 0.00
	MTD	19.25*	1.53 \pm 1.5	2.70 \pm 1.4
	MTW	36.0**	1.05 \pm 0.59	1.79 \pm 0.89
	MAP	0.73	116.5 \pm 102.2	131.2 \pm 80.1
	PS	9.26	0.07 \pm 0.06	0.11 \pm 0.07
	MPD	4.70	13.70 \pm 12.73	18.43 \pm 13.02
	MPW	120.95***	15.15 \pm 14.28	56.15 \pm 34.03
	Soil pH	16.43	3.55 \pm 2.18	2.99 \pm 1.43
	<i>Protea</i>	MAT	12.51	0.69 \pm 0.34
TS		0.02	0.001 \pm 0.00	0.001 \pm 0.00
MTD		0.53	1.56 \pm 1.28	1.28 \pm 1.02
MTW		11.30	0.74 \pm 0.35	1.19 \pm 0.81
MAP		0.15	110.20 \pm 66.32	117.67 \pm 78.98
PS		2.2447	0.08 \pm 0.06	0.05 \pm 0.06
MPD		0.20	13.88 \pm 10.47	12.51 \pm 11.22
MPW		65.57**	16.17 \pm 13.57	68.21 \pm 46.00
Soil pH		1010.6***	2.22 \pm 0.76	2.36 \pm 0.58
<i>Banksia</i>		MAT	74.68**	0.59 \pm 0.44
	TS	3.25	0.001 \pm 0.00	0.001 \pm 0.00
	MTD	83.44**	0.75 \pm 0.57	2.44 \pm 1.36
	MTW	21.60	0.83 \pm 0.59	1.59 \pm 0.71
	MAP	65.7*	89.49 \pm 63.45	233.18 \pm 81.53
	PS	1.973	0.07 \pm 0.04	0.09 \pm 0.05
	MPD	170.07***	7.38 \pm 6.19	34.13 \pm 15.67
	MPW	294.09***	8.62 \pm 11.47	92.32 \pm 47.44
	Soil pH	19.08***	0.43 \pm 0.23	0.68 \pm 0.23
	<i>Hakea</i>	MAT	31.48**	0.73 \pm 0.43
TS		0.26	0.001 \pm 0.00	0.001 \pm 0.00
MTD		47.33**	0.90 \pm 0.57	1.81 \pm 1.25
MTW		5.78	1.00 \pm 0.56	1.11 \pm 0.64
MAP		7.43	97.88 \pm 61.89	147.62 \pm 111.11
PS		0.05	0.08 \pm 0.06	0.08 \pm 0.05
MPD		37.99**	8.07 \pm 4.32	20.14 \pm 15.39
MPW		70.92**	8.54 \pm 5.81	49.80 \pm 41.36
Soil pH		25.16***	0.48 \pm 0.22	0.69 \pm 0.23

MAT, mean annual temperature; TS, temperature seasonality; MTD, mean temperature in the driest quarter; MTW, mean temperature in the warmest quarter; MAP, mean annual precipitation; PS, precipitation seasonality; MPD, mean precipitation in the driest quarter; MPW, mean precipitation in warmest quarter.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

association between clade age and species richness (McPeck and Brown 2007; Wiens 2011), or between the length of a clade's occupation of a geographic region and its species richness within that region (Stephens and Wiens 2003; Wiens 2011). The association between occupation time and species accumulation is likely to have been facilitated in the two hotspot regions we have examined by their relatively stable geological histories. The Southwest Australian Floristic Region and Greater Cape Floristic Region have been referred to as "old, climatically buffered, infertile landscapes," with comparative geological and climatic stability since

before the Pliocene (Hopper 2009). Persistence of a maritime climate and few major recent orogenic events have maintained a gradual climatic change in these regions despite increasing aridification of the surrounding regions over the past 15 My (Hopper 2009; Cowling et al. 2015; Hopper et al. 2016). This long-term environmental stability may have promoted a steady accumulation of plant species from old lineages over a long period (Cardillo and Pratt 2013; Cowling et al. 2015; Linder and Bouchenak-Khelladi 2015), as opposed to a series of short, rapid radiations. Such a diversification process would be consistent with our

Table 4. Model support (Akaike Weights) for alternative models of environmental niche evolution in four genera averaged across 50 stochastic maps.

Genus	Niche Axis	Niche Evolution Model						
		BM1	BMM	OU1	OUM	OUMV	OUMA	OUMVA
<i>Banksia</i>	MAT	0.119	0.881	–	–	–	–	–
	TS	0	0	0.448	0.324	0.112	0.04	0.075
	MTD	0	0	0	–	1	–	–
	MTW	0.854	0.146	–	–	–	–	–
	MAP	0	0	0	0	1	–	–
	PS	0	0	0.001	0.339	0.66	–	–
	MPD	0	0	0	0	1	–	–
	MPW	0	0	0	0	1	–	–
	Soil pH	0.886	0.114	–	–	–	–	–
<i>Hakea</i>	MAT	0	0	0	0	0.396	0	0.603
	TS	0.005	0.011	0.057	0.035	0.535	0.137	0.221
	MTD	0	0	0	0	0.604	0	0.396
	MTW	0	0.001	0	0	0.516	0	0.483
	MAP	0	0	0	0	0.663	0.004	0.333
	PS	0	0	0.043	0.067	0.405	0.048	0.437
	MPD	0	0	0	0	0.788	0	0.212
	MPW	0	0	0	0	0.693	0	0.307
	Soil pH	0	0.036	0	0	0.716	0.007	0.242
<i>Moraea</i>	MAT	0	0.048	0	0	0.304	0.493	0.155
	TS	0	0	0.04	0.397	0.263	0.206	0.095
	MTD	0.001	0.045	0.005	0.142	0.209	0.358	0.24
	MTW	0	0.196	0	0	0.804	–	–
	MAP	0	0	0	0.479	0.223	0.223	0.075
	PS	0	0	0.001	0.174	0.178	0.073	0.574
	MPD	0.004	0.001	0.352	0.296	0.096	0.101	0.15
	MPW	0	0.009	0	0	0.082	0.621	0.287
	Soil pH	0	0	0	0.513	0.281	0.204	0.001
<i>Protea</i>	MAT	0	0	0	0	0.118	0	0.882
	TS	0	0	0	0	0.607	0.041	0.352
	MTD	0	0	0	0	0.64	0.131	0.229
	MTW	0	0	0	0.001	0.628	0.021	0.349
	MAP	0	0	0	0.515	0.338	0.029	0.118
	PS	0	0	0	0.299	0.375	0.196	0.131
	MPD	0	0	0	0	0.906	0	0.094
	MPW	0	0	0	0	0.906	0	0.094
	Soil pH	0	0	–	0.037	0.963	–	–

A dash indicates the model failed to converge. OU1, OUM, OUMA, OUMV, OUMVA refer to Ornstein-Uhlenbeck models, BM1 and BMM refer to Brownian motion models; see text for details.

MAT, mean annual temperature; TS, temperature seasonality; MTD, mean temperature in the driest quarter; MTW, mean temperature in the warmest quarter; MAP, mean annual precipitation; PS, precipitation seasonality; MPD, mean precipitation in the driest quarter; MPW, mean precipitation in warmest quarter.

observation that hotspot lineages tend to be both older and more diverse.

If hotspot lineages tend to have deeper origins than non-hotspot lineages, with occupancy times within hotspots extending back tens of millions of years, the next question to answer is why dispersal events away from MTE hotspots (at least ones that gave rise to present-day descendants) have been so rare. Our analy-

ses of the patterns of environmental niche evolution in a number of MTE plant genera suggest that one reason for this is that the environmental niche of hotspot species is phylogenetically conserved, with strong evolutionary attraction to environmental niche optima along multiple environmental axes. This is indicated by three of our findings: (1) generally narrower environmental niches in hotspot species, (2) stronger support for OU over BM models,

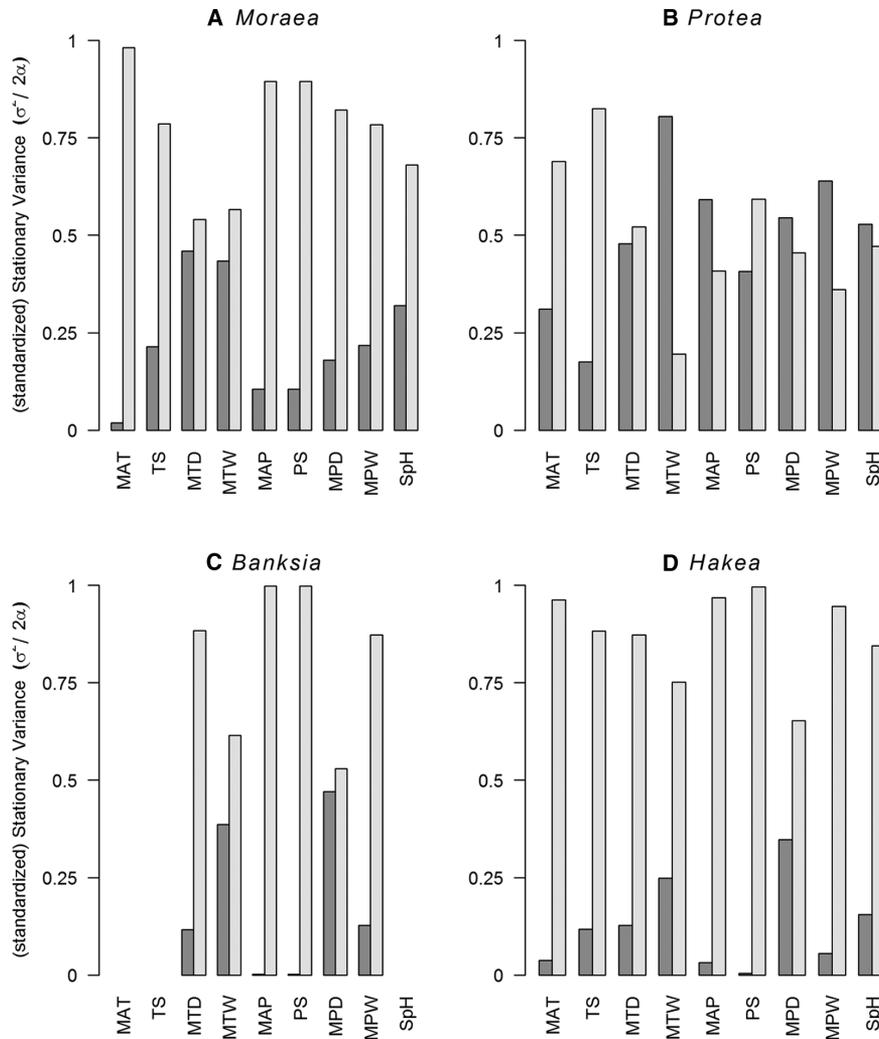


Figure 3. Stationary variance (SV) of the model-averaged parameter values across four Ornstein-Uhlenbeck models of trait evolution (OU1, OUM, OUMA, OUMV, OUMVA) for (A) *Moraea*, (B) *Protea*, (C) *Banksia*, and (D) *Hakea* (units are scaled so hotspot SV + non-hotspot SV = 1). Stationary variance is the ratio of the relative effect of stochastic drift (σ^2) to the strength of attraction to an optimum (α) in the OU process. Bars in black represent hotspot clades, while bars in grey represent clades found outside the hotspot. MAT, mean annual temperature; TS, temperature seasonality; MTD, mean temperature in the driest quarter; MTW, mean temperature in the warmest quarter; MAP, mean annual precipitation; PS, precipitation seasonality; MPD, mean precipitation in the driest quarter; MPW, mean precipitation in warmest quarter.

Table 5. The phylogenetic structure (PSV) of the present-day species assemblage within each region.

Genus	PSV	
	Hotspot	Nonhotspot
<i>Banksia</i>	0.68	0.526*
<i>Moraea</i>	0.658	0.435*
<i>Protea</i>	0.743	0.42*
<i>Hakea</i>	0.829*	0.87

All PSV values marked with an asterisk are lower than expected under a null model ($P \leq 0.05$), indicating significant phylogenetic clustering. PSV, phylogenetic species variance.

for the majority of environmental niche axes, and (3) lower stationary variance (relative contribution of random drift vs. strength of attraction to an optimum value) of hotspot compared to non-hotspot lineages, on several key niche axes. These findings are also consistent with a long-held view that MTE plant species tend to occupy both smaller ranges and narrower environmental niches (Cowling et al. 1996; Cook et al. 2015), and with recent evidence that high levels of endemism in MTE hotspots may be promoted by specialization to local climatic regimes, limiting dispersal and geographic spread of plant species (Schnitzler et al. 2012).

In *Moraea*, when widespread species are designated as hotspot species, some of the patterns are reversed, with mean temperature and precipitation of the driest quarters, mean annual

precipitation, precipitation seasonality, and mean precipitation of the wettest quarter becoming more labile (higher stationary variance) for hotspot species. This is not surprising given that the widespread species, by definition, occupy a wide range of environments found within and outside hotspots. However, in *Protea*, which has no widespread species, stationary variance was also higher for hotspot species on some of the niche axes (most clearly for mean temperature in the wettest quarter and mean precipitation in the wettest quarter), the opposite of the general pattern. *Protea* species in the Greater Cape Floristic Region are found in a range of different habitats, as topographical heterogeneity provides a range of precipitation and temperature microclimates, due to rain shadow effects and altitudinal variation (Rourke 1980). This result is supported by experimental evidence that many *Protea* species are differentiated along environmental gradients, with adaptive traits strongly correlating with the level and seasonality of precipitation, and drought stress in the Cape (Carlson et al. 2011; Prunier et al. 2012; Mitchell et al. 2015). In this way, hotspot lineages of *Protea* may be diversifying along environmental gradients related to mean annual rainfall and the severity of the summer drought period.

The corollary of the hotspot niche conservatism model is that “breakouts” from hotspots—rare dispersal events away from a hotspot into adjacent biomes that have given rise to present-day descendant species—were facilitated by the evolution of broader environmental niches, and shifts toward new niche optima, in certain lineages. It may not be surprising that niche breadth and niche shifts are closely associated: species are likely to be constrained by conditions for which they show narrow tolerance, while diverging along axes for which they show a broader tolerance (Ackerly 2003). The relaxation of stabilizing selection toward environmental conditions associated with MTE regions (especially a strongly seasonal temperature and rainfall cycle) could promote not only broader environmental tolerances, but larger geographic ranges and elevated rates of niche evolution, as species expand to fill newly available geographic and ecological space. Larger geographic ranges do indeed seem to be a common feature of non-hotspot members of plant genera that are largely confined to hotspots (Valente et al. 2010; Cardillo and Pratt 2013; Cook et al. 2015). However, it should be kept in mind that sampling effects can generate spurious positive associations between environmental niche breadth and range size (Cardillo and McAlister, unpubl. ms.), so an ecological link between niche breadth and range size should not be assumed without accounting for sampling effects.

One important question is the extent to which geographic proximity can overcome the limitations on dispersal between biomes set by the conservatism of environmental niches. In the African genera, our results point to selection toward divergent niche optima between hotspot and nonhotspot lineages, in the absence of any major geographic barriers between these re-

gions. Summer drought is a defining climatic feature of the Cape and western southern Africa, whereas adjacent Afrotropical and grassland biomes are characterized by summer rainfall, cooler temperatures in sub-alpine regions, higher radiation at higher altitudes, more acidic soils, a different fire regime, and low winter rainfall (Carbutt and Edwards 2001; Lamont et al. 2013). Steep environmental gradients across relatively small geographic distances therefore probably play an important role in maintaining the comparative isolation of the Cape lineages. In Australia, the Southwest Australian Floristic Region is geographically isolated as well as environmentally distinct: The Nullarbor Plain forms a major aridity and edaphic barrier between the MTE regions of south-western and south-eastern Australia. Although one of the two *Banksia* dispersal events from south-western to south-eastern Australia is likely to postdate the formation of the Nullarbor Plain (Cardillo and Pratt 2013), it does seem to have acted as an effective barrier to dispersal, not only for *Banksia* but a range of plant clades (Crisp and Cook 2007). For both Australian genera, dramatically increased lability on niche axes associated with aridity (temperature and precipitation in the warmest and driest parts of the year) is a characteristic feature of nonhotspot lineages. It seems likely that this was a key development allowing lineages to traverse the Nullarbor Plain from west to east, or to disperse through the arid interior north of the Nullarbor. However, the frequency of biome shifts is much greater in *Hakea* than in *Banksia*, suggesting that the inherent capacity of some clades to traverse steep environmental gradients and the degree of biome conservatism is not necessarily a shared feature of diverse hotspot groups. Similarly, despite a prevailing pattern of niche conservatism, many closely related *Banksia* species within the Southwest are distributed across the boundary between the semiarid sandplains and the high-rainfall forest zone of the coastal margins (Cardillo and Pratt 2013). This suggests the possibility that geographic proximity can overcome, at least to some extent, the dispersal barriers that result from environmental niche conservatism. In the face of continual dispersal attempts from a nearby region, the chance of a lineage developing adaptations to a new climatic regime must be substantially higher than would be the case if a large geographic distance also had to be overcome. This is analogous to the phenomenon of “propagule pressure” in invasion biology, whereby the chance of a translocated population establishing successfully is determined largely by the number of establishment attempts (Simberloff 2009).

Environmental niche conservatism is emerging as a key phenomenon associated with some of the world’s major geographic patterns of biodiversity, including the latitudinal diversity gradient (Wiens and Donoghue 2004; Duchene and Cardillo 2015; Kerkhoff et al. 2014), as well as other regional disparities in diversity between biomes (Li et al. 2009; Hutter et al. 2013; Wiens et al. 2013). Together with other recent work (Schnitzler et al. 2012; Cook et al. 2015), our findings show that niche conservatism also

underlies the exceptional plant diversity of MTEs, another of the world's major biodiversity patterns, by reinforcing and enhancing the effect of time in allowing species richness to accumulate. The importance of niche conservatism and time in generating geographic biodiversity patterns is a clear indication that biodiversity patterns (at least on large scales) are the result of history, at least as much as they are the product of ecological responses to present-day environments (Jablonksi et al. 2016). A challenge for future research will be to distinguish the historical and ecological signals in biodiversity data, and quantify their relative importance in shaping the biodiversity patterns that we see today.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Model averaged OU parameter estimates for all genera.