ORIGINAL ARTICLE

EFFECTS OF A FIRE RESPONSE TRAIT ON DIVERSIFICATION IN REPLICATED RADIATIONS

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Fire has been proposed as a factor explaining the exceptional plant species richness found in Mediterranean regions. A fire response trait that allows plants to cope with frequent fire by either reseeding or resprouting could differentially affect rates of species diversification. However, little is known about the generality of the effects of differing fire response on species evolution. We study this question in the Restionaceae, a family that radiated in Southern Africa and Australia. These radiations occurred independently and represent evolutionary replicates. We apply Bayesian approaches to estimate trait-specific diversification rates and patterns of climatic niche evolution. We also compare the climatic heterogeneity of South Africa and Australia. Reseeders diversify faster than resprouters in South Africa, but not in Australia. We show that climatic preferences evolve more rapidly in reseeder lineages than in resprouters and that the optima of these climatic preferences differ between the two strategies. We find that South Africa is more climatically heterogeneous than Australia, independent of the spatial scale we consider. We propose that rapid shifts between states of the fire response trait promote speciation by separating species ecologically, but this only happens when the landscape is sufficiently heterogeneous.

KEY WORDS: Climatic heterogeneity, climatic preference evolution, mediterranean climate, Restionaceae, speciation.

Fire impacts the current distribution of plant species in several of the world major's biomes (Bond et al. 2005). Many of the current terrestrial hotspots of biodiversity harbor flammable vegetation (Sauquet et al. 2009), and fire is likely a key factor explaining the high species richness in these regions (Cowling et al. 1996; Linder 2003; Barraclough 2006; Simon et al. 2009). In fire-prone environments, lineages cope with fire through survival of parts of the plant, or through fire-stimulated germination that allows population persistence despite repeated burning (Bond and van Wilgen 1996; Keeley et al. 2012). Adaptive responses to fire can evolve over short evolutionary timescales (e.g., because of the start of anthropogenic fires in the mid-16th century in Chile; Gómez-González et al. 2011), and fire response traits can be extremely labile on species-level phylogenetic trees (Schnitzler et al. 2011). Wells (1969) proposed that fire response traits can impact plant evolution, but their relation with diversity increase is still controversial. For example, rates of species diversification are not associated with fire response traits in five genera of four plant families living in fire-prone regions (Verdú et al. 2007). To the contrary, there is evidence of association between fire response

traits and the species (Ojeda 1998) or genetic (Segarra-Moragues and Ojeda 2010) diversity of *Erica* species. Such contrasting results call for complementary analyses to inform us on whether general statements can be made regarding evolutionary processes in fire prone areas.

Adaptations to fire in Mediterranean climate regions can be classified into two main fire response syndromes (Bell 2001). Resprouter plants survive fire as individuals and then replace the lost structures by resprouting from surviving tissues. In contrast, reseeder individuals die as a result of fire and the population is reestablished by a new generation growing from seeds (Bell 2001). More generally, a vast array of responses to fire exists in plants. A continuum of resprouting typologies depending on the intensity and frequency of fires, exists. For example, bark thickness, meristem position (from basal to axillary), or underground storage organs will allow extremely variable resprouting dynamics among plant taxa (Bond and Midgley 2001; Clarke et al. 2013). There exist also various types of obligate reseeders with seed dispersal and/or germination that is stimulated by fire (Pausas et al. 2004). The dichotomy between reseeders and resprouters is not mutually exclusive as resprouters are generally also able to reseed to some extent (Bond and Midgley 2001). In this article, we use the term reseeder for plant species that is killed by fire and has fire induced germination. Moreover, we do not classify resprouters into finer groups, as these do not exist in our study system.

Although both fire responses are viable, they may differentially affect species evolution (Wells 1969). Reseeders experience a new generation after each fire event, creating a complete turnover of the populations, whereas resprouters survive fire events and thus have a much longer life span (Ojeda et al. 2005). The outcome of this direct link between fire events and generations is that reseeders have shorter generation times than resprouters (Wells 1969; Verdú et al. 2007). This important difference in a conspicuous life-history trait could impact the evolution of reseeders and resprouters at both microevolutionary (e.g., Segarra-Moragues and Ojeda 2010) and macroevolutionary scales (Wells 1969; Bond and Midgley 2003). Indeed, generation time is negatively correlated with molecular substitution rates in angiosperms (Smith and Donoghue 2008) which, for example, allows herbaceous species (usually short-lived) to explore a wider climatic space than longer-lived species because of higher rates of evolution of climatic preference (Smith and Beaulieu 2009, but see Kostikova et al., unpubl. ms.). Furthermore, a positive relationship between molecular substitution and diversification rates has been found in birds and reptiles (Eo and Dewoody 2010). This suggests that lineages with short generation times, which usually experience higher rates of molecular substitution (Thomas et al. 2010), may diversify more rapidly than others (Fontanillas et al. 2007). Recombination rates could also differ between reseeder and resprouter species because these responses share common attributes with sexual and asexual reproduction, respectively. More frequent recombination in reseeders could thus lead to more rapid genetic change and also increase the rate of trait evolution (Rieseberg et al. 2003; Glémin et al. 2006). Therefore, different fire response traits likely play an important role in plant species diversification. Comparative study of the evolution of reseeders and resprouters should improve our understanding of the effect of life-history traits on macroevolutionary processes.

Fire regimes are commonly used to help describe how fire impacts ecosystems. Among several other parameters, fire regimes take into account fuel consumption, fire frequency, and intensity (Keeley et al. 2012). The evolutionary response to different fire regimes by reseeders and resprouters could depend on the ecological context (e.g., forest or shrubland), making it difficult to find a single model of life history that can be applied across plant communities (Keeley et al. 2012). Nevertheless, models linking fire regimes and specific fire responses have been successfully applied (e.g., Enright et al. 1998; Pausas 2006). On the contrary, the importance of climate in shaping fire dynamics and, thus, plant distributions is much clearer (Pausas and Keeley 2009; Krawchuk and Moritz 2011). More precisely, in a model simulating microevolutionary (within species) processes, only a mild-Mediterranean climate (moderate summer drought and reliable winter rain) allows the replacement of a resident resprouter population by an invading reseeder phenotype (Ojeda et al. 2005). Observations of post-fire succession in South African fynbos vegetation show that increased soil moisture (presence of seeps) increases growth rates for reseeders, whereas resprouters have a growth advantage in dryer areas (Rutherford et al. 2011). In many South African Cape clades, sister-species differ in their fire response traits (van der Niet and Johnson 2009; Schnitzler et al. 2011). Whether sister species also differ in environmental preferences is not yet clear, but the action of one or both factors could facilitate species diversification by ecologically separating populations having different response to fire.

In this study, we assess the effect of fire response traits on species diversification using the Restionaceae (order Poales) as a study system. The Restionaceae are graminoid plants that are ecologically important in oligotrophic heathlands of the southern regions of the African and Australian continents (Linder et al. 2003). These plants radiated independently in both regions with circa 150 species in Australia and New Zealand (subfamilies Sporadanthoideae and Leptocarpoideae; Briggs and Linder 2009), hereafter referred to as the Australian clade, and 350 species in South African subfamily Restionoideae, which is the third largest clade in the South African Cape flora (Goldblatt and Manning 2000; Linder 2003). The two clades are reciprocally monophyletic and originate from a basal split in the family. Reseeders and resprouters are found in an even ratio among the Restionaceae and only a handful of species display both states of the fire response

trait (Bell 2001). As a speciose and ecologically diverse family, the Restionaceae constitute an ideal study system to examine the effect of fire response traits on species evolution, using a densely sampled phylogeny and modern phylogenetic comparative methods. First, we evaluate whether as predicted, reseeders diversify at a higher rate than do resprouters. After describing the climatic preferences of every species and assessing the climatic heterogeneity found in South Africa and Australia, we test whether reseeders and resprouters are selected toward different climatic optima. Finally, we ask whether reseeders experience a higher rate of evolution of climatic preference than do resprouters, which is expected given their shorter generation time and anticipated higher rate of molecular recombination. All analyses are performed on the South African and Australian clades separately to enable a continental comparison of diversification processes.

Methods
PHYLOGENETIC INFERENCE

We assembled four available plastid gene regions (*atpB*, *matK*, *rbcL*, and *trnL-F*) for 382 of the 496 Restionaceae species and four *Anarthria* species (Anarthriaceae), designated as outgroup taxa following Linder et al. (2003), to infer the phylogenetic tree of the Restionaceae (Table S1). We broadened this data set by sequencing a nuclear gene (*phyB*) for 99 species to verify cytonuclear concordance (Table S1; for primers used see Christin et al. 2012). The 50 mL PCR reaction mixture contained ∼100 ng of genomic DNA template, 8 mL of GoTaq Reaction Buffer, 3 mL of each dNTP (2.5 μmol/L), 1 mL of each primer (10 μmol/L), 2.5 mL DMSO, and 1 unit of Taq polymerase (GoTaq DNA Polymerase, Promega, Madison, WI). The samples were incubated for 3 min at 94°C, followed by 39 cycles of 40 sec at 94°C, 70 sec of annealing at 57.5°C, and 75 sec at 72°C. The last cycle was followed by a 7 min extension at 72°C. PCR products were purified with the QIAquick PCR Purification Kit (QIAGEN GmbH, Germany) and sequenced using the Big Dye 3.1 Terminator cycle sequencing kit (Applied Biosystems, Foster City, CA), according to the manufacturer's instructions, and were separated on an ABI Prism 3100 genetic analyzer (Applied Biosystems). All newly generated sequences have been deposited in the EMBL database (accession numbers indicated in Table S1).

DNA sequences were aligned using MAFFT (Katoh et al. 2002) and ambiguously aligned nucleotides were removed using Gblocks with default settings (Talavera and Castresana 2007). The single gene alignments were concatenated into a combined matrix of 386 species and 7246 nucleotides. We reconstructed the phylogenetic tree with BEAST (Drummond and Rambaut 2007), which allows the estimation of substitution rates jointly with divergence times. Absolute dates are not required in this study, but we nevertheless chose to apply an uncorrelated molecular clock using a calibration point (Scholtz 1985; Linder et al. 2003) on the crown node of the Restionaceae with a lognormal prior. The lognormal distribution was parameterized with a mean of 2 and a standard deviation of 1. The age of the available fossil (64 million years) was used as offset. The outcome was a lognormal distribution with the 5% quantile at 64.43 million years and the 95% at 102.3 million years. The best model of substitution for each partition (Table S2) was identified using MrAIC (Nylander 2004). Four analyses were run independently in BEAST 1.7.4 for 50×10^6 generations each. Convergence was verified using Tracer (Drummond and Rambaut 2007) to ensure that the effective sample size (ESS) of each parameter was always higher than 200 and that the four runs converged adequately. The first 10,000 trees were removed as the burn-in period and a maximum credibility tree was inferred using TreeAnnotator (Drummond and Rambaut 2007).

DIVERSIFICATION RATE

Of the 382 Restionaceae species present in the present data set, 275 had available information concerning their fire response traits (Australia: 45 reseeders and 30 resprouters of 146 existing species; South Africa: 104 reseeders and 96 resprouters of 350 existing species). We extracted the fire response trait from the interactive key of Linder (2011) for the South African species and from the literature for the Australian taxa (Meney and Pate 1999). To our knowledge, no species included in our analysis show both fire response traits in wild populations.

We compared the rates of diversification between reseeder and resprouter species of the monophyletic Australian and South African Restionaceae clades by performing two independent analyses using the BiSSE model, as implemented in the R package Diversitree (FitzJohn et al. 2009; R Development Core Team 2013). The method allowed estimation of rates of speciation and extinction of reseeders and resprouters while taking into account the transitions between states of the fire response trait. Six parameters were estimated, speciation rates for reseeders and resprouters, extinction rates for reseeders and resprouters, and character transition rates between states (Maddison et al. 2007). Incomplete taxon or trait sampling could bias our analysis. We corrected for potential effects of incomplete taxon sampling in the BiSSE analysis using the method presented in FitzJohn et al. (2009). This accounted for the fact that we only had a full sampling (trait + phylogeny) of 75 Australian and 200 South African species out of respectively 146 and 350. The fire strategy of the missing species remained unknown and thus was not specified in the model. The BiSSE models were run under a Bayesian framework for 10^6 generations using exponential priors for the rates. We checked for optimal convergence of the runs by verifying the trace files and by using diagnostic metrics available in the R package Coda (Plummer et al. 2010). We calculated the diversification rate by

subtracting the extinction rate from the speciation rate. In parallel, we applied the "split" model, available in the BiSSE suite, which estimates different parameters for given partitions in the phylogeny. The aim was the estimation of all parameters for Australia and South Africa in a single analysis. Sadly, the method doubles the size of the parameter space that caused convergence problems. We thus report only results from the BiSSE model.

Although reseeders and resprouters in Australian Restionaceae show easily identifiable morphological differences (Meney and Pate 1999), the fire survival strategy of South African Restionaceae is difficult to diagnose in the field. The data on fire survival strategy was compiled by one of the authors (H.P.L.) using field observations, herbarium specimens, and literature comments (Linder 2011). To measure the impact of a potential bias in trait determination, we performed a sensitivity analysis (following Wüest et al., unpubl. ms.). The analysis consisted in running the BiSSE analysis on data sets obtained by randomly permuting the state of the fire response trait of a given percentage of species, which ranged from 2% to 20% in 2% increments, with each replicated 1000 times.

CLIMATIC PREFERENCE DESCRIPTION AND CONTINENTAL HETEROGENEITY

We retrieved occurrence records for Australia and New Zealand from the Global Biodiversity Information Facility (GBIF) web portal (http://www.gbif.org/). One of us (H.P.L.) assembled the records of Southern Africa species by using geo-referenced herbarium specimens from the herbaria BOL and NBG. The data set consisted of 23,859 occurrences (12,266 for South Africa and 11,593 for Australia and New Zealand) with an average of 39 records per species. We used the 19 bioclimatic variables from the WorldClim database at a resolution of 2.5 min (Hijmans et al. 2005) to describe the climatic preference of species. Those variables represented the average and variation of temperature and precipitation. In addition, we created a layer for potential evapotranspiration (PET). Potential evapotranspiration is often used to study the effects of climate and energy supply on species diversity (Fisher et al. 2011). We derived the PET layer from radiation layers created in GRASS GIS (GRASS Development Team 2010) using the empirical equation of Jensen and Haise (1963) We used the "Raster" package (Hijmans and Etten 2012) in R to extract the climatic values for all Restionaceae occurrences and used these data to perform an Outlying Mean Index ordination (OMI; Dolédec et al. 2000). We kept only one occurrence per species per pixel in the analysis to avoid overweighting locations with multiple data points. Outlying Mean Index ordination assumed neither a specific shape of species response curves along climatic gradients nor down-weights species with low abundances. Therefore, OMI is well suited for estimating species climatic preferences (Dolédec et al. 2000). We projected the species centroids onto the first two ordination axes to obtain scores of species climate niche preferences on each axis.

We compared climatic heterogeneity in South Africa and Australia by first projecting the climatic layers (both OMI axes and PET) in space. We then used a moving window analysis that took for each focal pixel the standard deviation of values in a number of adjacent pixels (i.e., within the window). This standard deviation gave a measure of local climatic heterogeneity. The local heterogeneity (at the level of the focal pixel) was then divided by the mean heterogeneity calculated as the standard deviation of the climate values of every pixel of a continent. This provided a measure of the relative spatial heterogeneity available in each pixel at the spatial scale analyzed (i.e., window size). Our use of relative heterogeneity conveyed the advantage of describing the heterogeneity of a pixel independently of the global heterogeneity of a continent and provided a more robust index in the case where, for example, heterogeneity is spatially aggregated. Moreover, this measure provided information on the slope of local gradients (i.e., dependent on moving window size), and which might be more relevant when studying ecological speciation. The fact that the Restionaceae do not inhabit all regions of South Africa and Australia could have led to estimates of climatic heterogeneity from areas that were irrelevant for environments in which the family radiated. Therefore, we restricted comparison of climatic heterogeneity between continents to pixels that were located in quarter degree squares with known Restionaceae occurrences. We performed this analysis using multiple window sizes (3–103 pixels, corresponding to 7.5 arc min to ∼4.3°) to understand whether local climatic heterogeneity changed with spatial scale.

EVOLUTIONARY PROCESSES

We assessed the effect of the state of the fire response trait on the evolution of climatic preferences of the Restionaceae by fitting seven models of character evolution using the "OUwie" R package (Beaulieu et al. 2012). Two initial models were based on Brownian Motion (BM), the first a BM model with a single evolutionary rate σ^2 (BM1 thereafter), and the second a BM model with a separate rate for each trait state (BMS; O'Meara et al. 2006) The five additional models were based on the Ornstein–Uhlenbeck (OU) model, which represented the evolution of a character that was pulled with a selective strength α, toward a modal value or optimum θ (Hansen 1997; Butler and King 2004). Although BM models represented neutral evolution, OU models were used to test for directional evolution in climate preferences and were especially well suited for studying the evolutionary dynamics of relationships between climate and species distributions (Salamin et al. 2010). The first OU model assumed a single climate preference optimum for all Restionaceae species (OU1). The second OU model (OU$_M$) estimated separate climatic preference optima for each state of the fire response trait, while keeping

rate parameter σ^2 and selective strength parameter α constant. Two of the remaining models optimized a separate selective optimum for each fire trait state and either a corresponding rate (OU_{MV}) or selective strength (OU_{MA}) parameter. Finally, the last model optimized for each trait state all of the possible parameters of the OU model (OU_{MVA}). All models were applied using the "noncensored" approach (O'Meara et al. 2006) that relied on phylogenetic trees having the evolutionary history of a binary character mapped on all branches (Bollback 2006). We used the "make.simmap" function available in the R package "Phytools" (Revell 2012) to stochastically map (Huelsenbeck et al. 2003) the evolution of the fire response trait onto the maximum credibility dated tree from the BEAST analysis. Transition rates between states were symmetrical. To take into account the uncertainty in the reconstructed trait states, we replicated the inference 100 times. We analyzed sequentially and independently for the Australian and South African clades each climatic variable (OMI-axis 1, OMI-axis 2, and PET), which together described the main climatic gradients of both continents. We recorded the likelihoods for each model and used the Akaike Information Criterion (AIC) and Akaike weights to identify the model that best described our data.

Results
PHYLOGENETIC INFERENCE
The inferred phylogenetic tree (Fig. 1A) is highly similar to previous analyses of the Restionaceae (Hardy et al. 2008) and we find that the topology inferred with phyB is congruent with the one inferred from cpDNA. As previously found (Johnson and Briggs 1981; Briggs et al. 2000; Linder et al. 2000, 2003), the tree splits at the root of the family in two monophyletic clades containing Australian and South African species, respectively. The estimated age of the root of the Restionaceae in this study ($\sim$80 million years) is at the upper end of the range of estimates published elsewhere (Wikström et al. 2001; Bremer 2002; Janssen and Bremer 2004). The phylogeny is generally highly supported with the majority of nodes having posterior probabilities higher than 0.95 (Fig. 1B,C).

DIVERSIFICATION RATE
The MCMC chains from independent runs converge adequately, and the effective sample sizes of the estimated parameters are high (>10,000 for every parameter), which indicates only little autocorrelation between the samples. In the South African clade, the 95% credible intervals of the posterior distributions of speciation rates do not overlap, confirming that reseeders have a significantly higher speciation rate than resprouters (Fig. 2A). However, overlapping credible intervals for speciation rates in the Australian clade indicate similar rates of speciation in resprouters

and reseeders (Fig. 2A). Extinction rates on both continents do not differ between fire response trait states (Fig. 2B). We find that reseeders diversify four times faster than resprouters in South Africa (Fig. 2C). The net diversification rate for resprouters is close to zero, which is included in the 95% credible interval of the posterior distribution. Diversification rates do not differ significantly between reseeders and resprouters in the Australian clade (Fig. 2C). Moreover, there is no diversification rate difference between Australian species and South African resprouters. The inferred transition rates between trait states are high and similar on the two continents (Fig. 2D).

The sensitivity analysis (Figs. S1, S2) shows that the results are robust to a potential sampling bias in the data. Indeed, in the South African clade, the speciation rate of reseeders is still significantly higher than that of resprouters even if 6% of the species have been swapped to the other group. The speciation rate difference disappears only when 14% or more of the species are reassigned to the other strategy. In the Australian clade, the reseeders and resprouters never differ in their diversification rates, suggesting that it is unlikely that a random assignment of the fire-strategy trait could create the pattern we find in South Africa. Moreover, computer simulations confirm that the patterns we find can be accurately recovered on simulated data (Fig. S3).

CLIMATIC PREFERENCE AND EVOLUTIONARY PROCESSES
The first two axes of the OMI ordination explain 45% and 27% of the total variance, respectively, and are used in subsequent analyses. The first axis (OMI1) is mainly driven by precipitation variables, with low values indicating wet conditions with low seasonality (temperature and precipitation) and high values indicating highly seasonal, low-precipitation conditions. The second axis (OMI2) displays a temperature gradient ranging from hot at the lower end to cold conditions at the upper end. We find that South Africa is two times more heterogeneous for OMI1 and OMI2 and three times more for PET than Australia (Fig. 3). Changing the spatial scale we consider does not affect the results (Fig. 3).

In the Australian clade, the best description of the evolution of climatic preferences are models BM1 for OMI1, OU_M for OMI2, and OU_{MA} for PET. Akaike weights (ωi) for the evolutionary models show the relative support each receives (Table 1). In South Africa, OU_{MV} is the best model for OMI1 and PET whereas, as in the Australian clade, OU_M has the highest support for OMI2 (Table 1). The picture given by the OU models with multiple optima shows reseeders being selected towards colder and less seasonal climates with higher PET than resprouters (Tables 2,3). The pattern is consistent between the two continents. Out of the seven models, three also infer the rate of evolution (σ^2) of the characters. In all cases except one (PET in Australia), reseeders
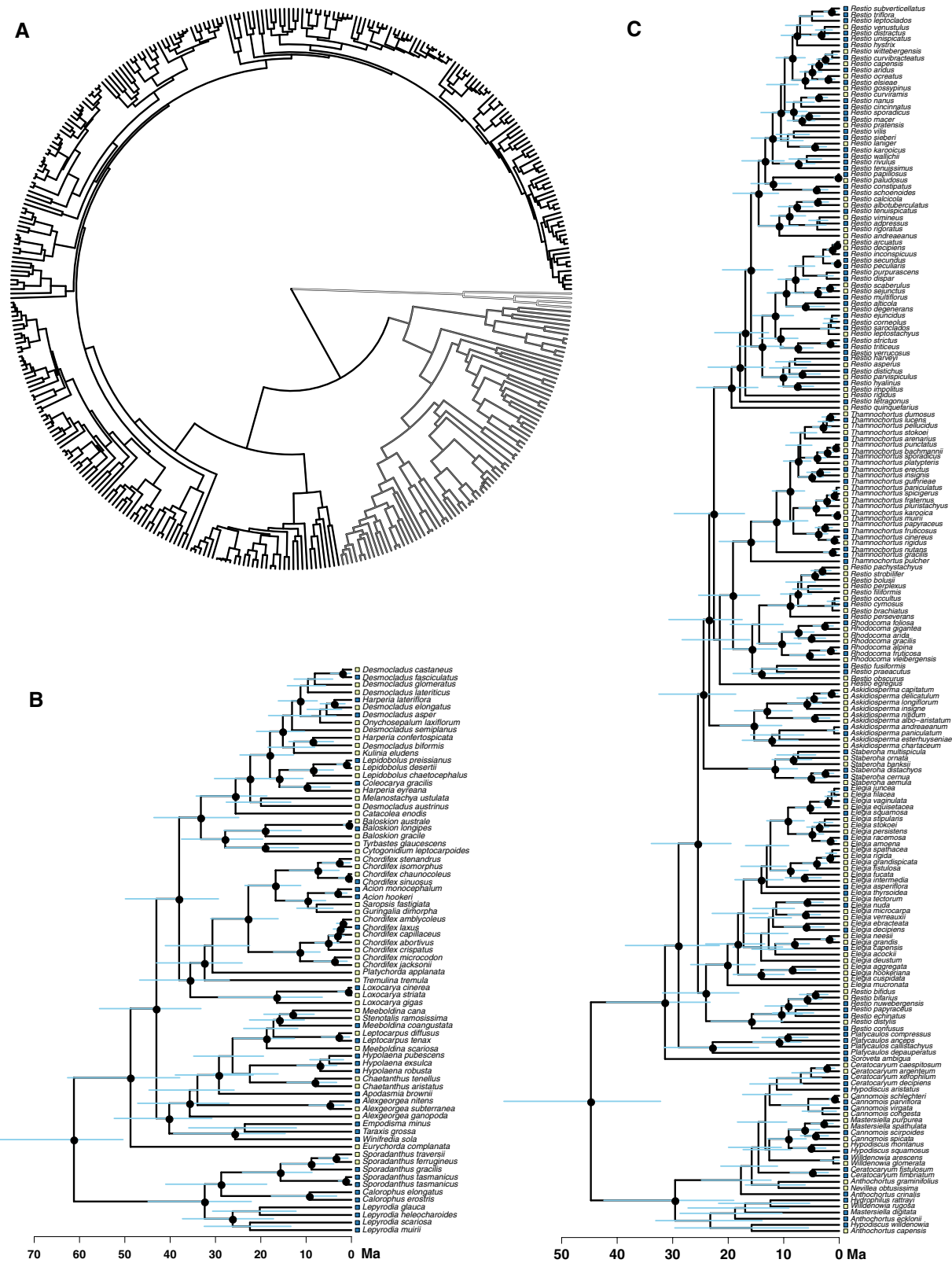
Figure 1. Maximum clade credibility tree of the Restionaceae (A). The branches belonging to the outgroups are colored in white. The Australian clade is highlighted in gray in panel A and shown in detail in panel B. The South African clade is shown in black in panel A and in detail in panel C. In panels B and C, credible intervals for the age estimates are shown and nodes with posterior probabilities above 0.95 are identified by dots. Colored boxes next to species names refer to the fire response strategies (light yellow, reseeder; dark blue, resprouter).
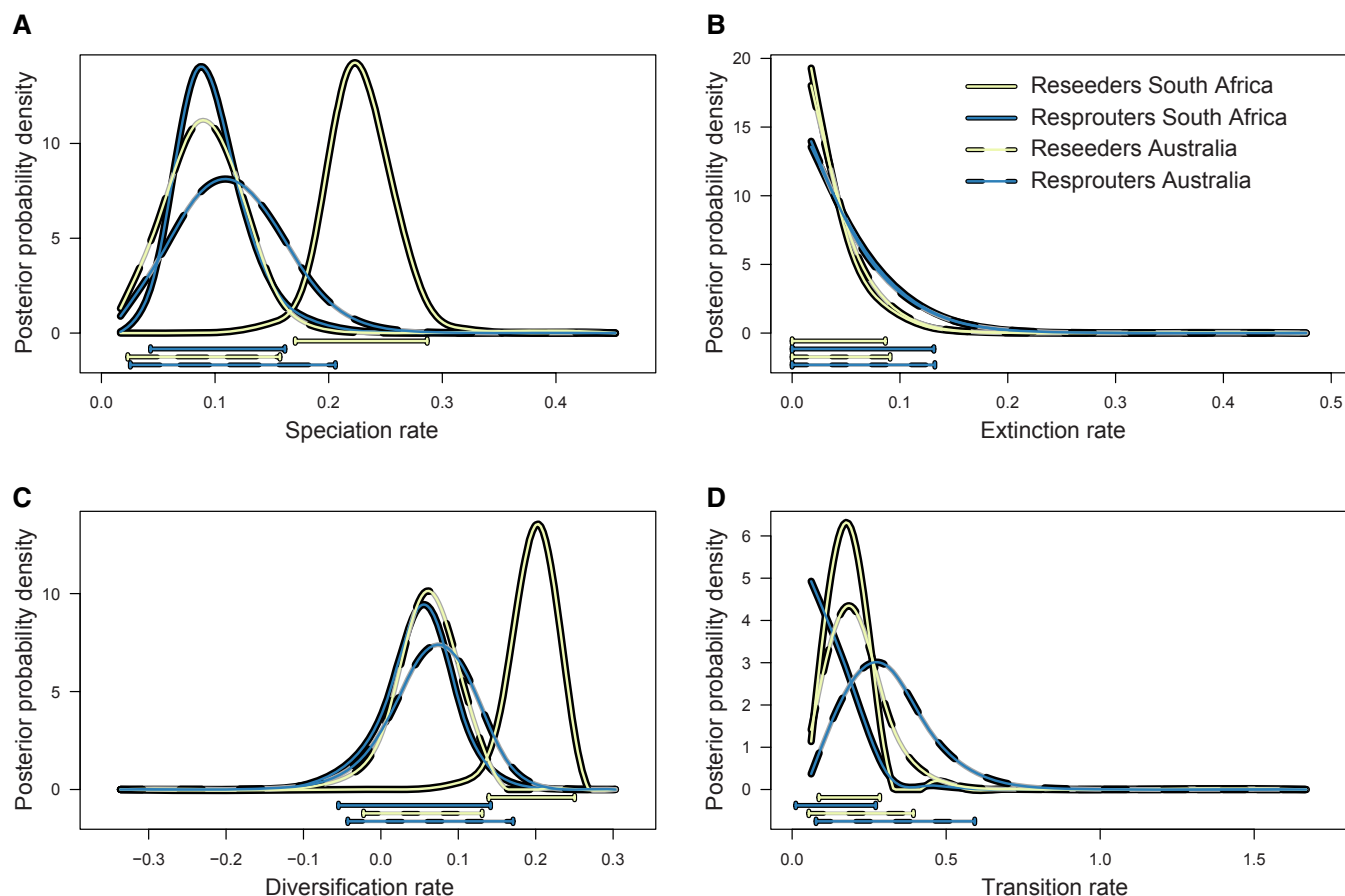
Figure 2. Posterior probability densities of the inferred parameters from the BiSSE analyses performed on the South African (solid lines) and Australian (dotted lines) clade. Diversification rate (panel C) is calculated by subtracting extinction (panel B) from speciation rates (panel A). Reseeders are shown in light yellow and resprouters in dark blue. Relevant 95% credible intervals are shown below the curves and are colored accordingly.

have a higher relative rate of evolution of climate preference than resprouters (Tables 2,3).

Discussion

Fire response traits are often mentioned to explain the high species richness found in the Cape Floristic Region, but concrete analyses testing this hypothesis are scarce (Linder 2003; Barraclough 2006; Schnitzler et al. 2011). Shifts in the states of fire response trait between closely related species have the potential to simultaneously contribute to a reduction in gene flow while allowing for divergent response to selection (Servedio et al. 2011). Ecological divergence may emerge because of differences in the environmental conditions associated with different fire regimes (Ojeda et al. 2005). Our results reveal a strong link between fire response traits and diversification patterns in the Restionaceae, but only in the South African clade (Fig. 2). We show that reseeders and resprouters occupy different climatic optima along both OMI axes and PET in South Africa (Table 2), whereas in Aus-

tralia this is only the case along the second OMI axis and PET gradient (Tables 1,3). The different selective optima linked with the fire response trait is a pattern consistent with diversification happening through ecological speciation (Schluter 2000; Rundle and Nosil 2005) in the Cape Floristic Region. In contrast, we do not observe the same trend in the evolution of the Australian Restionaceae. Moreover, we show that South-African climate is more heterogeneous, regardless of the spatial scale we consider (Fig. 3). The discrepancy among continents in the effect of the fire response trait on diversification shows the importance of the ecological context (e.g., climatic heterogeneity) in which lineages diversify.

FIRE RESPONSE TRAITS AND DIVERSIFICATION RATES

The hypothesis that reseeders have a higher speciation rate than resprouters has been proposed some time ago (Wells 1969). We test this hypothesis by comparing the difference in rates of speciation of reseeders versus resprouters using the BiSSE model
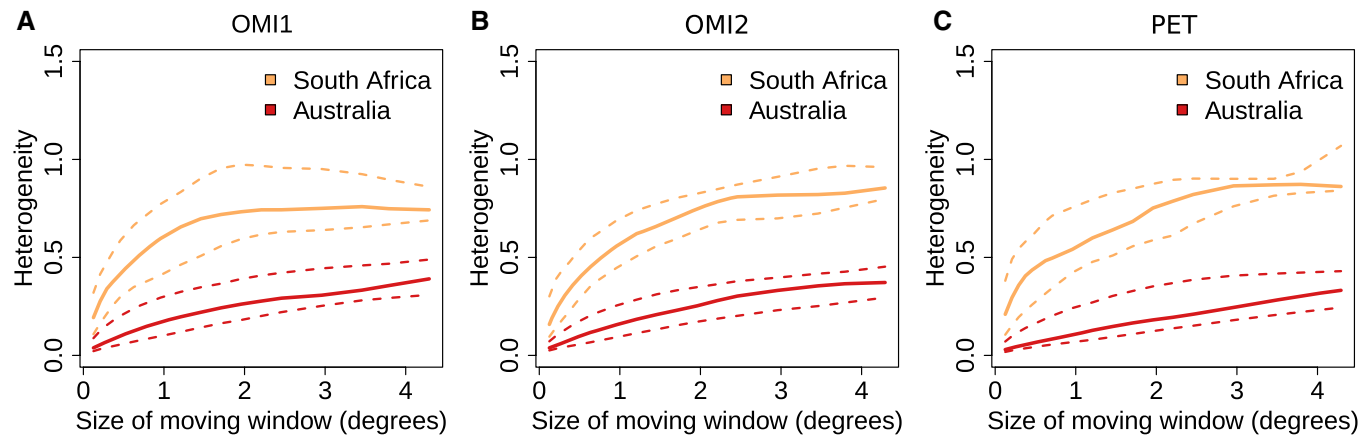
Figure 3. The spatial heterogeneity of the first (panel A) and second (panel B) OMI axis and PET (panel C). Mean heterogeneity is shown with a solid line and dashed lines represent the first and third quantiles. Heterogeneity of Southern Africa is shown in black and Australia is shown in gray. Spatial scale is shown on the x-axis which gives in degree the size of the moving window used in the analysis.

(Maddison et al. 2007). We find that these reproductive strategies differ significantly in speciation rates in the South African clade, where the estimated diversification rate is higher for reseeders than resprouters, but the same relationship does not hold for the Australian Restionaceae (Fig. 2A). The other parameters of the model (rate of extinction and character transition) do

not differ between states of the fire response trait or continents (Fig. 2B,D). The posterior distribution of resprouter diversification rates (whether South African or Australian) included zero (Fig. 2C). This could be interpreted as meaning that diversification mostly occurs in reseeder lineages. Indeed, likely due to their shorter generation times, reseeders present a more dynamic

Table 1. Comparison of the fit of two Brownian motion models (BM) and five Orstein–Uhlenbeck models (OU) of climatic niche evolution.

		South Africa				Australia			
	Model	lnL	AIC	ΔAIC	ωi	lnL	AIC	ΔAIC	ωi
OMI axis 1	BM1	−281.92	567.91	83.09	0	**−150.13**	**304.45**	**0**	**0.36**
	BMS	−281.31	568.74	83.92	0	−149.42	305.19	0.75	0.25
	OU1	−240.71	489.62	4.8	0.04	−148.96	306.52	2.07	0.13
	OU$_M$	−240.45	489.11	4.29	0.05	−149.41	307.43	2.98	0.08
	OU$_{MA}$	−238.47	487.24	2.42	0.12	−148.34	307.6	3.15	0.07
	OU$_{MV}$	**−237.26**	**484.82**	**0**	**0.41**	−148.26	307.43	2.99	0.08
	OU$_{MVA}$	−236.29	485.01	0.19	0.38	−147.91	309.13	4.69	0.03
OMI axis 2	BM1	−317.37	638.81	45.64	0	−141.18	286.54	40.44	0
	BMS	−316.59	639.3	46.13	0	−140.13	286.62	40.52	0
	OU1	−293.13	594.46	1.29	0.16	−118.81	246.22	0.12	0.29
	OU$_M$	**−292.48**	**593.17**	**0**	**0.3**	**−118.75**	**246.1**	**0**	**0.31**
	OU$_{MA}$	−291.81	593.93	0.76	0.2	−118.14	247.2	1.1	0.18
	OU$_{MV}$	−291.57	593.44	0.27	0.26	−118.27	247.46	1.36	0.15
	OU$_{MVA}$	−291.63	595.69	2.52	0.08	−117.8	248.91	2.8	0.08
PET	BM1	−116.32	236.7	58.94	0	−92.22	188.62	18.38	0
	BMS	−115.71	237.55	59.8	0	−89.67	185.7	15.45	0
	OU1	−85.93	180.07	2.31	0.11	−82.05	172.72	2.47	0.1
	OU$_M$	−85.7	179.61	1.86	0.14	−81.65	171.91	1.67	0.14
	OU$_{MA}$	−84.61	179.53	1.77	0.14	−80.01	170.94	0.7	0.23
	OU$_{MV}$	**−83.72**	**177.76**	**0**	**0.35**	−80.19	171.31	1.07	0.19
	OU$_{MVA}$	−82.97	178.39	0.63	0.26	**−78.46**	**170.24**	**0**	**0.33**

Models with the better fit are shown in bold and are identified as having the lowest AIC. ΔAIC shows the difference in AIC value compared to the best model and the Akaike weights (ωi) give the relative likelihood of the model. The table shows results from the two replicate analyses done on the South African and Australian clade and three ecological variables (two first axes of the OMI and PET). Reported values are medians of all replicated analyses.

Table 2. Estimates of the rate of climatic niche evolution (σ^2), strength of selection (α), and selective optimum (θ) with credible interval of the South African data set for all models and stochastic mappings replicates. Models with the higher support (ωi; Table 1) are shown in bold.

	Model	σ^2 reseeder	σ^2 resprouter	α reseeder	α resprouter	θ reseeder	θ resprouter
OMI axis 1	BM1	0.116±0.012					
	BMS	0.124±0.015	0.094±0.02				
	OU1	0.305±0.072		0.205±0.052			
	OU$_M$	0.304±0.07		0.205±0.051		0.115±0.147	0.171±0.097
	OU$_{MA}$	0.282±0.054		0.184±0.035	0.176±0.034	0.089±0.147	0.155±0.114
	OU$_{MV}$	**0.382±0.093**	**0.188±0.056**	**0.209±0.048**		**0.112±0.115**	**0.165±0.102**
	OU$_{MVA}$	0.395±0.136	0.076±0.076	0.195±0.048	0.208±0.046	0.086±0.106	0.129±0.103
OMI axis 2	BM1	0.166±0.017					
	BMS	0.182±0.022	0.124±0.032				
	OU1	0.355±0.065		0.127±0.027			
	OU$_M$	**0.355±0.065**		**0.129±0.027**		**0.948±0.158**	**0.904±0.259**
	OU$_{MA}$	0.349±0.063		0.122±0.025	0.117±0.025	0.934±0.225	0.889±0.276
	OU$_{MV}$	0.395±0.082	0.27±0.08	0.128±0.027		0.945±0.166	0.9±0.236
	OU$_{MVA}$	0.39±0.099	0.29±0.246	0.129±0.028	0.127±0.027	0.941±0.173	0.857±0.222
PET	BM1	0.022±0.002					
	BMS	0.024±0.003	0.018±0.004				
	OU1	0.049±0.009		0.146±0.032			
	OU$_M$	0.049±0.01		0.147±0.032		5.508±0.085	5.485±0.051
	OU$_{MA}$	0.055±0.012		0.164±0.037	0.158±0.037	5.495±0.06	5.492±0.051
	OU$_{MV}$	0.059±0.013	0.035±0.009	0.152±0.033		5.494±0.07	5.489±0.053
	OU$_{MVA}$	**0.067±0.021**	**0.014±0.012**	**0.139±0.033**	**0.152±0.031**	**5.493±0.059**	**5.483±0.058**

Table 3. Estimates of the rate of climatic niche evolution (σ^2), strength of selection (α) and selective optimum (θ) with credible interval of the Australian dataset for all models and stochastic mappings replicates. Models with the higher support (ωi; see Table 1) are shown in bold.

	Model	σ reseeder	σ resprouter	α reseeder	α resprouter	θ reseeder	θ resprouter
OMI axis 1	**BM1**	**0.235±0.04**					
	BMS	0.376 ±0.308	0.086±0.329				
	OU1	0.296±0.078		0.012±0.011			
	OU$_M$	0.295±0.079		0.013±0.011		−1.375±1.283	−1.402±1.372
	OU$_{MA}$	0.2±0.101		0.014±0.012	0.005±0.014	−1.452±1.209	−1.31±1.285
	OU$_{MV}$	0.452±0.444	0.09±0.48	0.011±0.012		−1.424±1.358	−1.334±1.393
	OU$_{MVA}$	0.026±0.354	0.312±0.604	0.015±0.017	0.011±0.017	−1.382±1.286	−1.352±1.321
OMI axis 2	BM1	0.183±0.031					
	BMS	0.32±0.148	0.004±0.15				
	OU1	1.053±0.77		0.305±0.229			
	OU$_M$	**0.979±0.741**		**0.282±0.221**		**−1.16±0.274**	**−1.178±0.209**
	OU$_{MA}$	0.019±0.083		0.206±0.135	0.178±0.121	−1.282±0.225	−1.068±0.222
	OU$_{MV}$	1.035±1.043	0.541±1.1	0.269±0.207		−1.18±0.256	−1.187±0.214
	OU$_{MVA}$	0.035±0.141	0.036±0.693	0.2±0.112	0.18±0.109	−1.209±0.224	−1.167±0.213
PET	BM1	0.046±0.008					
	BMS	0.078±0.045	0±0.053				
	OU1	0.093±0.027		0.06±0.02			
	OU$_M$	0.096±0.032		0.064±0.026		5.852±0.234	5.842±0.227
	OU$_{MA}$	0.027±0.035		0.07±0.029	0.052±0.039	5.831±0.19	5.835±0.183
	OU$_{MV}$	0.135±0.107	0±0.122	0.057±0.025		5.796±0.237	5.863±0.23
	OU$_{MVA}$	**0±0.002**	**0.876±2.14**	**0.102±0.023**	**0.056±0.027**	**5.757±0.275**	**5.865±0.23**

system than resprouters, and thus experience more diversification. It is only because of transitions between fire response traits that resprouters happen to be so numerous. Schnitzler et al. (2011) found no difference in rate of speciation between fire response trait states in *Protea* (Proteaceae) or the legume tribe Podalyriae. Statistical power issues due to a smaller number of species in phylogenies, as well as unknown clade-specific factors, such as differing pollination systems or more complex types of seed storage, release, and germination, may explain why no speciation rate difference is found between reseeders and resprouters in these two plant groups. Nevertheless, mode of regeneration after fire is the most variable factor among Podalyriae sister species (Schnitzler et al. 2011), and shows that even if diversification rates do not differ between fire responses, fire is still an important factor promoting speciation in the Mediterranean climate regions.

CLIMATIC PREFERENCE EVOLUTION

We inferred the patterns evolution of climatic preference by fitting models of increasing complexity, starting from simple BM to OU models with different optima, selective strength, and rates of evolution, for the fire response trait. We show that reseeder Restionaceae are selected toward colder and less seasonal climates than are resprouters in South Africa. This result corroborates well with studies on other plant lineages that include the same fire response syndrome (Ojeda et al. 2005; Russell-Smith et al. 2012). Reseeders are more likely to persist in regions with less intense summer drought because species with this strategy are vulnerable even to a single post-fire recruitment failure (Bond and Midgley 2001; Ojeda et al. 2005). The phylogenetic framework that we report in this study allows us to model distinct optima for each state of fire response trait, and to model the Brownian rate of evolution (σ^2) underlying the selective process (Beaulieu et al. 2012). We find that when the evolutionary models allow distinct rates of evolution between resprouters and reseeders, the latter displays faster rates of evolution of climatic preference (except for the variable PET in Australia; Tables 2,3). These results parallel the general finding that, similar to reseeders, herbaceous plants, experience higher rates of evolution of climatic preference than woody taxa (Smith and Beaulieu 2009). Although reseeders of South Africa and Australia all share higher rates of climatic preference evolution than do resprouters, intriguingly, we find a higher rate of speciation only in South African reseeders.

CONTEXT-DEPENDENT ECOLOGICAL SPECIATION

In this study, we show the variable effect of a fire response trait on Restionaceae diversification, using replicate radiations on two continents. Reseeders generally show a higher rate of evolution of climatic preference than do resprouters, which allows them to occupy more rapidly different climatic niches. Thus, ecological

diversity in the South African Restionaceae is most likely the result of ecological differentiation taking place in reseeder species. We find no difference in speciation rate or selective optima along OMI axes between the two fire response states in Australia. Linder et al. (2003) propose several explanations to elucidate the different radiation pattern between South African and Australian Restionaceae. Although these authors ruled out morphological differences and variable climatic histories that would explain the discrepancy between continents, they propose that higher speciation rates in South Africa are possibly best explained by the steeper elevational and climatic gradients found in the Cape Floristic Region compared to the Australian landscape (Cowling et al. 1996; Linder et al. 2003). Here, we compare climatic heterogeneity between South Africa and Australia and find that independent of the spatial scale, climatic heterogeneity is always higher in South Africa than in Australia (Fig. 3). We also find that only South African reseeder species have a higher rate of speciation, whereas South African resprouters share similar rates with Australian Restionaceae (Fig. 2). Assuming that extinction rates are well estimated (Rabosky 2010), our results rule out the possibility that Australian Restionaceae have lower extinction rates, as Linder et al. (2003) suggested. We propose that the climatic heterogeneity of Australia is insufficient to allow much ecological speciation in the Australian Restionaceae. The relative paucity of climatic heterogeneity and evolution toward different climatic optima in Australia could explain why reseeders do not show accelerated rates of diversification there.

Even though reseeder taxa exhibit a higher rate of diversification in South Africa, a similar number of extant reseeder and resprouter species has evolved on both continents. Although this result may seem contradictory at first, it can be explained by the high rates of transition between trait states during evolution (Fig. 4). We find that the transition rates between the two states are similar on the two continents and are nearly equal in both directions (Fig. 2D). This can explain the similar numbers of reseeder and resprouter species. Indeed, when new species appear, a shift from one strategy to the other (that may or may not be related to a speciation event) can easily occur. The greater number of reseeders that appear due to their higher diversification rate (black arrows in Fig. 4) is thus counter-balanced because a greater number of those putative species will change into resprouters than the reverse (due to their initial larger number). This will result in equal and constant proportions of reseeder and resprouter species. Although Figure 4 depicts a situation with transition rates of 0.5, simulations show that the proportions of reseeders and resprouters is stable even for smaller rates of transition (Fig. S4), and is accurately estimated despite the elevated transition rates (Fig. S5). A conceptually similar result has been found in Solanaceae, where self-fertilizing individuals have a negative diversification rate but nevertheless repeatedly appear throughout the phylogeny because
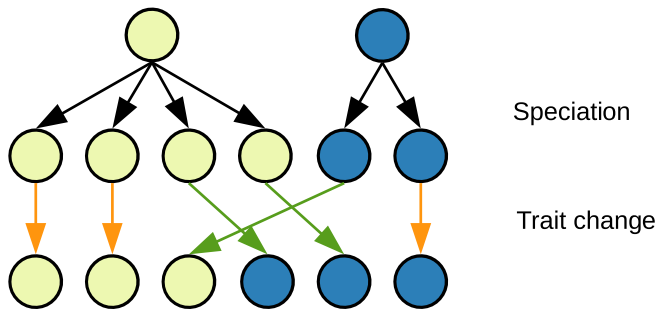
Speciation

Trait change

Figure 4. Conceptual representation of the diversification and fire response trait transition in incipient species. Starting from an even number of reseeders (in light yellow) and resprouters (in dark blue), the higher diversification rate (represented by twice more black arrows) creates initially twice more reseeder than resprouter species. Nevertheless, the transition probability from one state to the other is similar in both reseeders and resprouters. Although half of the species will not change their fire response traits (orange arrows), the other half of the incipient species will experience a transition to the other trait (green arrows). The equal transition rate is illustrated by the same number of orange and green arrows. This process will keep a stable and even ration of reseeder to resprouter over time.

of frequent transitions between outcrossing and self-fertilization strategies (Goldberg et al. 2010).

The model we propose here of reseeder lineages fueling the diversification process differs from the general view presented in Keeley et al. (2012) in which the resprouting state is ancestral to reseeders and further specializes into obligate reseeder species. Given the high evolutionary liability of the trait, it is impossible to accurately reconstruct the ancestral fire response in the Restionaceae (the inferred ancestral state for the root of the Restionaceae is equivocal). The framework we use in this study allows us to better understand why the link between the fire response trait and diversification rate is not universal among plant groups (e.g., Verdú et al. 2007). Indeed, we show that the ecological context (here climatic heterogeneity) is a key component that likely impacts plant diversification patterns. However, studies on the evolution of fire response traits generally use woody taxa as focal clades. Contrary to the situation in woody species that are not basal resprouters (Bond and Midgley 2001), herbaceous resprouters loose all of their above-ground structures during fire, altering resource allocation (Clarke et al. 2013), with a potential impact on the evolutionary dynamics.

The potential confusion between adaptations and exaptations to fire could be problematic in some evolutionary studies on the evolution of fire-adaptive traits (Hopper 2009). In this study, rather than inferring adaptation, we record the relationship of fire response trait states with species diversification and environmental niche evolution. Whether the ancestor of the Restionaceae had

resprouting or reseeding capacities has thus no impact on our conclusions. Also, soil type is of primary importance in the diversification of many plant taxa in the Cape region (Schnitzler et al. 2011). The Australian Restionaceae species frequently occur in wetland areas whereas South African species usually inhabit well-drained soils (Linder et al. 2003). This difference may provide an interesting path for further studies that would encompass edaphic variables.

The resprouting trait is well known for allowing population persistence following disturbance events (Bond and Midgley 2001). As resprouting species inhabit unforeseeable environments, reseeders are more likely to specialize on particular ecological conditions. This fragile equilibrium may be disrupted under global change (Westerling et al. 2006; Wilson et al. 2010). In this case, resprouters may be privileged over reseeders in the short term because they are more likely to persist in unpredictable climates, and under reduced (anthropogenic) time to fire-return, than are reseeders (Clarke et al. 2010), which could lead to radical changes in the evolutionary trajectory of the radiation.

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Associate Editor: M. Rosenberg

Supporting Information

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

Table S1. Accession numbers of the sequences of the data set.
Table S2. Gene-specific models selected under the AICc.
Figure S1. Sensitivity analysis of the BiSSE analysis done on the South African clade.
Figure S2. Sensitivity analysis of the BiSSE analysis done on the Australian clade.
Figure S3. We performed a simulation test to asses if BiSSE could accurately recover the parameter we inferred in our study from simulated data.
Figure S4. We performed simulation using the diversitree R package to measure the effect of the transition rate on the extant ratio of reseeders/resprouters.
Figure S5. High rates of transition between binary states could create saturation in the data set leading to wrong estimates of the parameter.