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SPECIAL ISSUE

Climatic niche evolution and species diversification in the Cape flora, South Africa

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ABSTRACT

Aim To evaluate the evolutionary dynamics of the ecological niche by quantifying the modes and rates of ecological niche evolution (with a particular focus on climatic parameters) and species diversification.

Location Greater Cape Floristic Region, southern Africa.

Methods Using the genus *Babiana* (Iridaceae) from the Cape flora, South Africa, we study the evolutionary dynamics of the ecological niche, which includes a characterization of the ecological niche, an assessment of phylogenetic signal, comparisons of different macroevolutionary models, and the estimation of rates of niche evolution (and their variation within and between clades) and lineage diversification, while accounting for phylogenetic uncertainty.

Results A principal components analysis (PCA) identified mean annual precipitation and mean annual temperature as the most important climatic determinants differentiating species within *Babiana*. All parameters show significant phylogenetic signal, and the best-fit model of evolution is the Ornstein–Uhlenbeck process with two distinct precipitation optima for two neighbouring biomes: the Fynbos and the Succulent Karoo. Evolutionary rates of climatic niches vary by more than an order of magnitude over the phylogeny, and rates of niche evolution and lineage diversification are both higher in the Fynbos biome than in the Succulent Karoo.

Main conclusions Our results show a possible link between rates of climatic niche evolution and rates of species diversification, indicating that rates of niche evolution might be driving diversification rates.

Keywords

***Babiana*, Cape flora, diversification, ecological niche, Fynbos, macroevolution, niche evolution, Ornstein–Uhlenbeck, phylogenetics, Succulent Karoo.**

INTRODUCTION

The ecological niche has long been a central concept in ecology (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). Despite variation in the precise definition, the niche of a species is commonly defined as the set of conditions – both biotic and abiotic – that allow a species to maintain a viable population (Hutchinson, 1957; Chase & Leibold, 2003; Holt, 2009). Species' ecological niches can be quantified in several ways. Generally, niches are defined via dimension-reducing techniques such as ordination or species distribution modelling (e.g. Phillips *et al.*, 2006; Thuiller *et al.*, 2009) from inferred environmental parameters. More rarely used, but possibly as important, are direct measures of putatively relevant morphological or ecophysiological traits (Dawideit *et al.*, 2009). Species distribution modelling explicitly relates broad environmental parameters of the niche to species' actual or potential distributions (Soberón & Nakamura, 2009), and has been widely applied to understand spatial patterns of species diversity (Wiens *et al.*, 2006; Svenning *et al.*, 2010), and to predict species distributions under past (Hugall *et al.*, 2002; Nogués-Bravo *et al.*, 2008) or future (Pearman *et al.*, 2010; Engler *et al.*, 2011) environmental conditions. Less frequently addressed, however, are the temporal dynamics of the niche (Linder & Hardy, 2005; Pearman *et al.*, 2008; Evans *et al.*, 2009; Vieites *et al.*, 2009). Yet, these dynamics

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are central for the evaluation and prediction of rapid evolution of species under novel environmental conditions such as those resulting from climate change (Visser, 2008; Ozgul *et al.*, 2010; Hoffmann & Sgro, 2011) or in new areas encountered by invasive species (Broennimann *et al.*, 2007; Gallagher *et al.*, 2010). Likewise, some of the best-known examples of adaptive radiations have been associated with substantial ecological niche differentiation (Fryer & Iles, 1972; Baldwin & Sanderson, 1998; Lovette *et al.*, 2002). Niche evolution may be studied at different organizational levels: within a single species adapting to novel or changing environmental conditions (Broennimann et al., 2007; Nogués-Bravo, 2009 and references therein; Soberón & Nakamura, 2009), and/or throughout the evolutionary history of a clade as species diverge (Evans *et al.*, 2009; Vieites *et al.*, 2009; Dormann *et al.*, 2010; Wiens *et al.*, 2010). Nevertheless, niche evolution remains a complex and little understood concept.

Tracing and quantifying niche dynamics has more recently received considerable attention due to the increasing availability of well-sampled molecular phylogenies and the development and improvement of ecological niche modelling approaches (e.g. Evans *et al.*, 2009; Vieites *et al.*, 2009; Smith & Donoghue, 2010). In addition, various models of trait evolution, rooted in phylogenetic comparative methods, are available to assess the mode and tempo of niche evolution (Butler & King, 2004; O'Meara *et al.*, 2006; Harmon *et al.*, 2010; Revell *et al.*, 2011; Beaulieu *et al.*, 2012). Studying evolutionary dynamics of the ecological niche across clades (instead of within a single species), and thus tracing niche dynamics across multiple time-scales, offers several advantages. Comparative analyses can be used to assess niche differentiation among clades (including the frequency of major shifts, e.g. Crisp *et al.*, 2009), or to study the temporal dynamics of niche evolution and test correlations with rates of species diversification (Kozak & Wiens, 2010). Finally, deeper clades are likely to have experienced substantial variation in environmental conditions throughout their history, which could offer insights into the potential impact of the current climatic changes on species diversity. Moreover, it is likely that niche differentiation is not uniform across all dimensions of the ecological niche, and thus evaluation of the evolutionary rates of different niche parameters may illuminate mechanisms that have allowed lineages to persist and diversify in a given region (Ackerly, 2003). Several approaches have been developed that allow us to understand the temporal dynamics of species' ecological niches (Evans *et al.*, 2009; Vieites *et al.*, 2009; Harmon *et al.*, 2010; Kozak & Wiens, 2010; Revell *et al.*, 2011). However, none of these currently implement the estimation of evolutionary rates and their variation within a clade while accounting for phylogenetic uncertainty.

Evidence for large-scale ecological conservatism (Prinzing, 2001; Qian & Ricklefs, 2004; Crisp *et al.*, 2009) suggests that ecological tolerances have remained relatively stable over long periods of time. A scenario under which such a pattern is likely to occur is the inability of species to adapt to novel abiotic conditions, driven, at least partly, by stabilizing selection for an ecological optimum (Ackerly, 2003; Wiens & Graham, 2005). If such a process governs the evolution of ecological tolerances, we would expect these ecological differences to be recognizable as distinct adaptive optima. Likewise, different degrees of environmental heterogeneity between regions might in turn result in different rates of evolution of ecological tolerances.

Here we test the hypotheses that (1) niche evolution is phylogenetically constrained, and (2) that the rates of niche evolution are correlated with species diversification rates. The genus *Babiana* (Iridaceae), from the Greater Cape Floristic Region (GCFR) of southern Africa, is an ideal group for such an investigation. A near complete species level phylogeny of the genus has recently been published (Fig. 1a; Schnitzler *et al.*, 2011) which includes 89 of the 95 described taxa (94%, including three subspecies). A relaxed molecular clock analysis provided a crown node age of 8.66 Ma (95% highest posterior density, HPD: 5.42–12.37 Ma), placing the onset of the radiation of the genus in the late Miocene (Schnitzler *et al.*, 2011). The genus occurs almost exclusively in the CGFR, which is dominated by two vegetation types: the Fynbos and the Succulent Karoo (Born *et al.*, 2007; Fig. 1b). Fynbos covers much of the south-western tip of South Africa and includes widespread coastal lowlands and mountain ranges reaching up to around 2300 m a.s.l. Most of the region receives between 300 and 800 mm annual rainfall, mean annual temperatures range from below 12 °C in the mountains to up to 19 °C in lowland areas (Mucina & Rutherford, 2006). The Succulent Karoo borders the Fynbos in the north and extends along the coast into southern Namibia. Rainfall is concentrated in the winter months with an annual average of 170 mm (between 100 and 200 mm throughout most of the region), annual temperatures are around 17 °C (Mucina & Rutherford, 2006). We combine recent developments in phylogenetics and comparative methods, employing a series of tests that involve: (1) the evaluation of phylogenetic signal, (2) fitting different macroevolutionary models, and (3) estimation of the rates of niche disparification and lineage diversification. Together, these analyses allow us to make inferences about the evolutionary dynamics of species' ecological niches and explore the links between environmental conditions, niche evolution, and species diversification.

MATERIALS AND METHODS

Niche quantification

Distribution data for all species of *Babiana* were compiled from herbarium vouchers (K, MO, NBG, PRE) and the literature (Lewis, 1959; Goldblatt & Manning, 2007, 2010; Goldblatt *et al.*, 2008). Subsequent to georeferencing (with a spatial precision of 5 km), all localities were carefully checked and spatial outliers were excluded. The resulting data set contained a total of 1774 localities, with an average of 19 data points per species (ranging from 1 to 133). Many

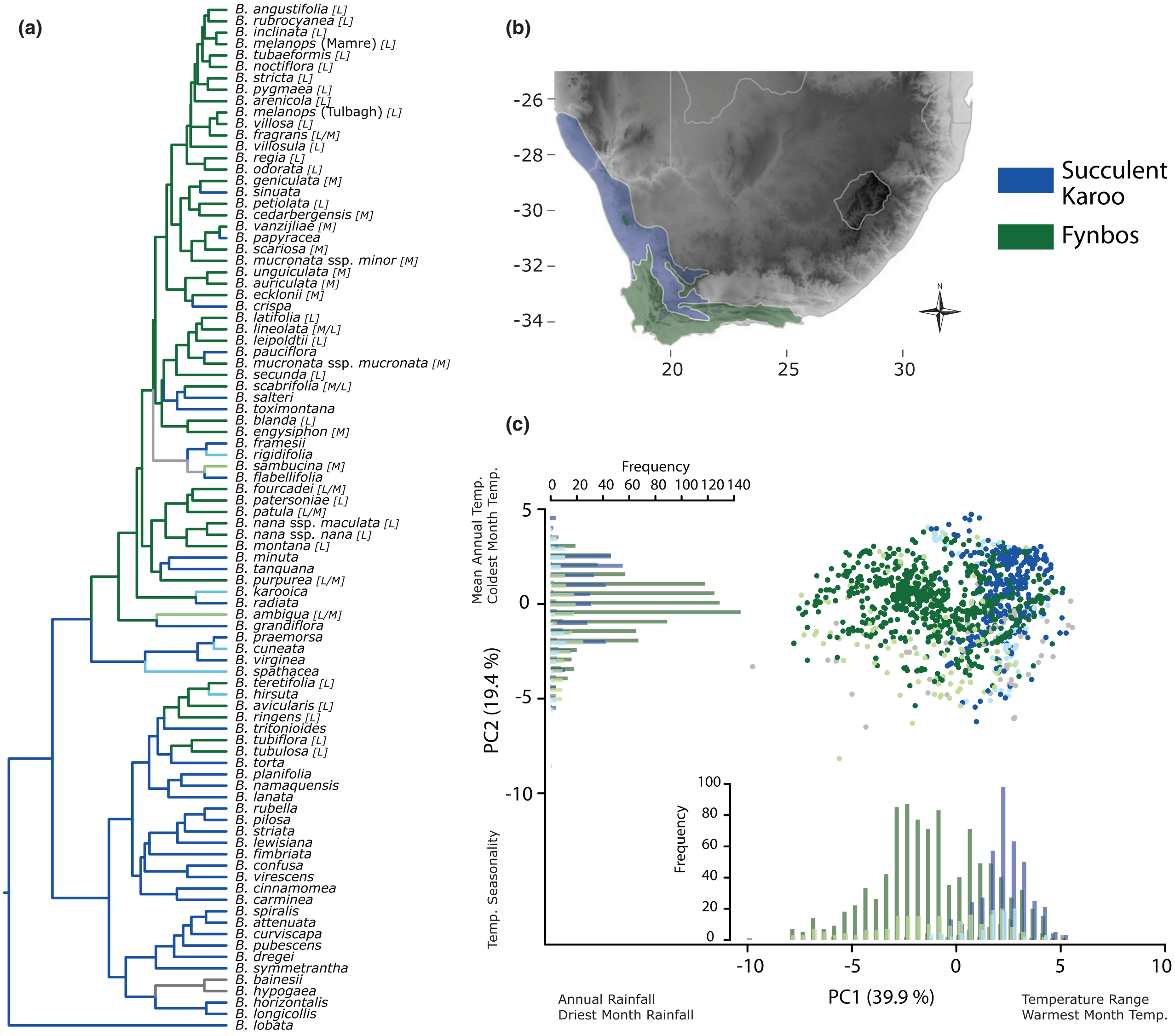

Figure 1 Phylogeny, geographical distribution, and principal components analysis (PCA) of the genus *Babiana* in southern Africa. (a) Phylogenetic tree of *Babiana* with colours indicating the geographical distribution shown in panel (b); most species are endemic to a single biome: Fynbos (green) or the Succulent Karoo (blue). Species in light green or light blue are near endemics, but extend their range into the neighbouring biome (Succulent Karroo or Fynbos, respectively). The only two species with a wider geographical distribution (throughout southern Africa) are highlighted in grey. Letters next to species names indicate whether they occur in lowland (L) or montane (M) habitats (Fynbos only). (c) Plot of the first two axes of the PCA using 19 climatic variables based on the localities of all species of *Babiana*. The ordination shows dry, warm regions with lower annual temperature variability in the top right, while areas with wet, cool conditions and a higher variability in temperatures are located at the bottom left.

taxa are narrow endemics and are thus represented by few localities (20 species had fewer than five localities); however, these localities were spread across their known distributions. Here, we used a dimension-reducing operation (principal components analysis), based on species occurrences to quantify the realized climatic niche and assess species' divergence in climatic space. Climatic information was extracted for all collection localities from 19 variables of the WorldClim data set (Hijmans *et al*., 2005). Additionally, species' mean values (based on all occurrences) were calculated for each climatic variable. While other environmental factors (e.g. soil) are also likely to influence species distributions, we here focus on climatic parameters because these can be obtained relatively easily from public databases, and given the sometimes steep climatic gradients in the Cape are likely to have a strong impact on species distributions and evolutionary dynamics (Linder, 1985).

Phylogenetic signal

As a first step in understanding the evolutionary patterns of climatic niches, we evaluated the phylogenetic signal using Pagel's λ (Pagel, 1999), which is a branch length scaling parameter that indicates the degree to which the pattern observed in the data can be explained by the shared evolutionary history. A λ value of 1 indicates phylogenetic pattern as expected under Brownian motion, while 0 indicates no phylogenetic pattern. Pagel's λ was calculated for 1000 randomly selected trees from the posterior distribution of a BEAST analysis (v.1.4.7; Drummond & Rambaut, 2007) using the first and second principal components (PC1 and PC2), as well as annual precipitation (Bio12) and mean annual temperature (Bio1). We evaluated annual precipitation and mean annual temperature individually because they represent the major environmental gradients in the Cape across which plant species are likely to differentiate. For each tree, significance of the phylogenetic signal was assessed by estimating the likelihood under $\lambda = 0$ and performing a likelihood ratio test (assuming a χ^2 distribution with one degree of freedom).

Comparison of macroevolutionary models and estimation of rates of niche evolution

In order to estimate the rate of niche evolution accurately, an appropriate macroevolutionary model should be considered. Three models are currently available that allow exploration of different evolutionary trajectories of species' climatic niches: the Brownian motion (BM), the Ornstein–Uhlenbeck (OU) model (Hansen, 1997; Butler & King, 2004; Beaulieu *et al.*, 2012), and the 'early burst' (EB) model (Harmon *et al.*, 2010). These models mainly differ in how trait variances in a phylogeny are distributed among subclades and through time. The Brownian motion model describes the evolution of a continuous trait as a random walk process where the change at each time step is drawn from a normal distribution centred on 0 with variance = σ^2 (the rate parameter of the Brownian process). A model of adaptive evolution can be approximated by the Ornstein–Uhlenbeck process, which incorporates additional parameters that describe one or several optima in trait space (θ) and a selection strength parameter (α), which constrains the drift of a trait away from its optimum. This selection parameter reflects an evolutionary process that might be stabilizing where the ancestral trait value of a clade is equal to the trait optimum, or divergent when several optima force clades to evolve away from each other and their common ancestors. Finally, the 'early burst' model describes a process of adaptive radiation whereby character evolution is rapid early in the history of a clade but slows down through time (as constraints on evolutionary change increase). Thus, this model includes a scaling parameter (r) that describes the pattern of rate decrease through time.

The best-fit model of evolution was identified using the Akaike information criterion (AIC; Akaike, 1973), adjusted for small sample size (AIC$_c$; Hurvich & Tsai, 1989), again using the first and second principal components (PC1 and PC2), as well as annual precipitation (Bio12) and mean annual temperature (Bio1). In cases where the OU model was the best-fit model, we additionally tested the performance of various multi-optima OU models (for annual precipitation and mean annual temperature only), where distinct optima were allowed for each biome (Fynbos and Succulent Karoo) and for montane and lowland regions. Here, the selective optima (θ) were not estimated, but set to the mean values of the region's climatic conditions (see Appendix S1 in Supporting Information). The fit of each of the different models was evaluated using the AIC$_c$ values. Specifically, this approach compares the fit of models where the adaptive optimum is forced to correspond to the regions' mean values to test the *a priori* hypothesis that these geographical regions represent distinct selective optima. States at internal nodes, which define the selective optima present, were based on a maximum likelihood ancestral character reconstruction. The two widespread species (*Babiana hypogaea* and *B. bainesii*) were excluded in this analysis, as we were mainly interested in the evolutionary dynamics within the GCFR and because they occur under a different rainfall regime.

To further evaluate the magnitude of change in climatic tolerances within and between biomes we calculated independent contrasts for annual precipitation and mean annual temperature. Contrasts were calculated on 1000 trees, using both the original trees as well as after applying a branch length transformation that corresponds to an OU model of evolution. The significance of differences in climatic niche contrasts was determined as the proportion of contrasts within a region that were greater than the mean contrast between regions.

To assess variation in the rate of evolution of climatic tolerances (annual precipitation and mean annual temperature) within and among clades, we estimated σ^2 (and other model parameters where appropriate) across all internal nodes of the phylogeny under the best-fit model of evolution. To account for phylogenetic uncertainty, evolutionary rates were calculated on a distribution of trees ($n = 1000$), randomly selected from the posterior distribution of the BEAST analysis and summarized as the modal value of the frequency distribution on the consensus tree. Tests of macroevolutionary models and estimations of model parameters were conducted using the R packages GEIGER (Harmon *et al.*, 2008), OUCH (Butler & King, 2004), and OUWIE (Beaulieu *et al.*, 2012); ancestral character reconstructions were performed using the R package APE (Paradis *et al.*, 2004).

Estimation of species diversification rates

To assess the rate of species diversification and its temporal and spatial variation, we used a Bayesian Markov chain Monte Carlo (MCMC) approach implemented in BAYESRATE (v.1.3.43; Silvestro *et al.*, 2011), which estimates the relevant parameters on a posterior distribution of trees generated in a Bayesian molecular clock analysis, thus taking into account the sometimes considerable uncertainty on divergence times (Graur & Martin, 2004). The approach further allows evaluation of differential rates of diversification among clades while accounting for non-random, incomplete taxon sampling. Differences in the rate of lineage diversification were assessed between the Fynbos and Succulent Karoo clades. From the six species not included in the phylogeny (including one subspecies), three occur in the Fynbos and three are found in the Succulent Karoo. Accordingly, the clade-specific sampling proportion (ρ) was set to 0.937 and 0.933 for the Fynbos and Succulent Karoo clade, respectively. Applying the best-fit model of lineage diversification (pure-birth or birth–death; identified using Bayes factors) we evaluated differences in diversification rates between the two clades using 1000 randomly selected trees from the post-burn-in distribution of trees generated in BEAST.

RESULTS

Niche parameters

The first two axes of the PCA together explained 59.3% of the variance (the first five components explained 94%; Appendix S1). PC1 (which explains 39.9% of the variation, Fig. 1c) corresponds to a gradient in precipitation and temperature range, with annual precipitation (Bio12), precipitation of the driest month (Bio14), and annual temperature range (Bio7) showing the strongest correlations. Environments with higher temperature ranges load positively, while wetter sites load negatively. Factor loadings for PC2 (which explains 19.4% of the variation, Fig. 1c) mainly correspond to variation in temperature, being strongly correlated with mean annual temperature (Bio1), minimum temperature of the coldest month (Bio6), and temperature seasonality (Bio4). Warmer sites load positively, whereas environments with higher annual variability in temperatures (calculated as the standard deviation of mean monthly temperatures) load negatively.

Mode of climatic niche evolution

Estimates of Pagel's λ indicated that all four parameters (PC1, PC1, Bio12 and Bio1) show a significant amount of phylogenetic signal ($\lambda > 0$) over the entire distribution of trees (PC1: mean $\lambda = 0.862$, all P values < 0.007; PC2: $\lambda = 0.88$, $P < 0.001$; Bio12: $\lambda = 0.882$, $P < 0.001$; Bio1: $\lambda = 0.742$, $P < 0.047$; Appendix S1), indicating a high degree of phylogenetic dependency in species' climatic niches. Intermediate values of λ (i.e. $0 < \lambda < 1$) could result from a measurement error in the traits, but also from non-Brownian motion evolution (e.g. OU process; Freckleton *et al.*, 2002).

Akaike weights (Burnham & Anderson, 2002) show that the best-fit model of evolution for all parameters is the Ornstein–Uhlenbeck model (Table 1), except for PC2 where the Brownian motion model provided a marginally better fit (Table 1). The comparison of different OU models shows that for mean annual temperature (Bio1), a single-optimum OU model (with single adaptive optimum for the entire GCFR) provided the best fit ($\text{AIC}_c = 246.38$; Table 2). For annual precipitation (Bio12) on the other hand, a two-optima OU model (with different optima for the Fynbos and Succulent Karoo) performed significantly better than the single-optimum model ($\Delta\text{AIC}_c = 28.34$) or the alternative two-optima model ($\Delta\text{AIC}_c = 33.37$; Table 2). The model with three optima yielded only a marginal improvement ($\Delta\text{AIC}_c = 0.56$).

The analysis of independent contrasts shows that transitions in climatic tolerances that span the two biomes are significantly higher than differences within biomes (Appendix S1). For montane and lowland Fynbos on the other hand, no significant differences were found for rainfall tolerances when comparing contrasts within each region to those that are associated with a transition (Appendix S1).

Rates of niche evolution and diversification

Estimated rates of niche evolution (σ^2) for the entire clade are 1.72 (variance: 0.802) and 0.99 (variance: 0.194) for annual precipitation (Bio12) and mean annual temperature (Bio1), respectively, and in both cases vary by more than an order of magnitude across the tree (more than two orders of magnitude in the case of annual precipitation; Fig. 2, Appendix S1). While direct comparisons of the evolutionary rates among different traits are of limited value (Ackerly, 2009), the higher variance indicates higher overall rate heterogeneity across the phylogeny for annual precipitation than for mean annual temperature. For annual precipitation, the highest rate of niche evolution was found in the *B. stricta–B. melanops* clade ($\sigma^2 = 4.45$; Fig. 2), which comprises species that occur in a range of habitats extending from the lowland areas of the western Cape coastal plain (e.g. *B. angustifolia*) to the lower slopes of the Cape fold belt mountains (*B. stricta*). Low evolutionary rates can be found for example

Table 1 Results of fitting three different macroevolutionary models in the genus *Babiana* in southern Africa using the following variables: the first two axes of the principal components analysis (PC1 and PC2) using all 19 climatic variables, annual precipitation (Bio12), and mean annual temperature (Bio1). Lower AIC_c scores indicate a better fit (higher Akaike weights indicate better support); AIC_c values of the best-fit model are in bold.

	Brownian motion (BM)				Ornstein–Uhlenbeck (OU)					Early burst (EB)			
	σ^2	θ	AIC_c	w_i	σ^2	α	θ	AIC_c	w_i	σ^2	r	AIC_c	w_i
PC1	1.500	1.479	372.48	0.111	2.462	0.259	1.404	**368.4**	0.852	1.500	0	374.62	0.038
PC2	0.703	0.469	**304.32**	0.437	0.903	0.117	0.307	304.44	0.413	0.703	0	306.46	0.150
Bio12	0.924	2.195	328.92	0.145	1.421	0.222	2.604	**325.5**	0.805	0.924	0	331.07	0.050
Bio1	0.398	16.81	253.25	0.080	0.670	0.276	16.90	**248.44**	0.892	0.398	0	255.4	0.027

σ^2, rate parameter; θ, inferred optimum (Bio12: * 100); α, strength of stabilizing selection; r, rate change parameter; w_i, Akaike weights.

Table 2 Results of fitting the Ornstein–Uhlenbeck model with different numbers of optima for annual precipitation (Bio12), and mean annual temperature (Bio1) in the genus *Babiana* in southern Africa. Lower AIC$_c$ scores indicate a better fit. Optima (θ) were set to the mean values of the region's climatic conditions as specified under the different models. Note that in OUwie (Beaulieu et al., 2012), phylogenetic trees are rescaled; therefore, model parameters (σ^2, α) are not reported.

No. of optima	Model fit AIC$_c$	Optima θ_1	θ_2	θ_3	Models
Bio12					
1	315.01	3.218	–	–	All regions
2	286.67	4.835	1.790	–	Fynbos (θ_1); Succulent Karoo (θ_2)
2	320.04	4.652	2.630	–	Montane Fynbos (θ_1); Lowland Fynbos & Succulent Karoo (θ_2)
3	286.11	4.652	5.068	1.790	Montane Fynbos (θ_1); Lowland Fynbos (θ_2); Succulent Karoo (θ_3)
Bio1					
1	246.38	16.302	–	–	All regions
2	247.37	15.691	16.679	–	Fynbos (θ_1); Succulent Karoo (θ_2)
2	246.41	14.973	16.855	–	Montane Fynbos (θ_1); Lowland Fynbos & Succulent Karoo (θ_2)
3	247.2	14.973	17.05	16.679	Montane Fynbos (θ_1); Lowland Fynbos (θ_2); Succulent Karoo (θ_3)

Optima (θ) for annual precipitation (Bio12: * 100).

for *B. confusa* and *B. virescens* ($\sigma^2 = 0.008$) and a clade comprising the *B. lewisiana–B. pilosa* clade ($\sigma^2 = 0.017$; Fig. 2). Despite being distributed throughout the Succulent Karoo (from the Orange River to the Richtersveld), these species are mainly found in coastal lowlands and show little overall divergence in rainfall tolerances.

Differences between the Fynbos and Succulent Karoo were further assessed under the two-optima OU model for annual precipitation. Model parameters were compared for all clades that evolved under one of the two optima (based on the consensus tree), i.e. comparing nodes where all descendant lineages evolved under the same regime (thus excluding nodes that give rise to clades with mixed selective regimes). Mean evolutionary rates in the Fynbos ($\sigma^2 = 1.41$; Fig. 3) show a fivefold increase compared to the Succulent Karoo ($\sigma^2 = 0.28$; *F*-test: $F = 17.75$, $P < 0.001$), while the selection strength were found to be slightly higher in the Succulent Karoo ($\alpha = 3.71$, Fynbos: $\alpha = 2.85$; *F*-test: $F = 0.337$, $P = 0.011$; Fig. 3). Bayes factors (BFs) provide strong support for the pure-birth model over a birth–death model of species diversification for both clades (BF = 15.07). Furthermore, a clade-specific analysis of diversification rates reveals slightly (1.5-fold) higher speciation rates in the Fynbos than in the Succulent Karoo (Fig. 4; Fynbos = 0.58 species Myr^{-1}, Succulent Karoo = 0.378 species Myr^{-1}).

DISCUSSION

In the southern African genus *Babiana*, the high degree of biome-specific endemism might be the result of an adaptation to divergent rainfall regimes. The evolution of climatic niches is best explained by a model that includes stabilizing selection towards an ecological optimum (OU process), which incorporates two distinct rainfall optima for the Fynbos and Succulent Karoo biomes, and moderate selection strength against evolutionary drift away from these. Nonetheless, there are several instances where lineages have shifted between the two biomes (in both directions), highlighting the dynamic nature of climatic niche evolution in this group. The fact that the evolution of temperature preferences is best approximated by a single-optimum OU process – despite differences between lowland and montane habitats – suggests that temperature tolerances might be evolutionary labile (within the constraints afforded by the OU process), or that the mean temperature of the montane Fynbos might not represent an adaptive optimum for *Babiana*. Species might, for example, predominantly inhabit lower slopes in mountainous regions, but be absent from mid- to high elevations. The relatively small observed contrasts in temperature tolerances associated with shifts between lowland and montane habitats suggest that the latter is more likely.

The Fynbos and Succulent Karoo differ most dramatically in rainfall regimes and this environmental parameter also varies substantially across the phylogenetic tree. However, precipitation tolerance shows a fivefold higher rate of evolution and slightly weaker selection in the Fynbos (where both wet and dry adapted species occur) than in the Succulent Karoo, where species are more consistently adapted to drier conditions (Fig. 3). It should be noted that both estimates of evolutionary rates (σ^2) and selection strength (α) show considerable degrees of uncertainty (Appendix S1). This is partly due to the uncertainty on the node ages, but might also result from potential difficulties in the optimization of parameters under the OU model, where small changes in both σ^2 and α might result in nearly equal likelihood values (Beaulieu *et al*., 2012).

Rates of lineage diversification parallel rates of climatic niche evolution and were also greater in the Fynbos. While this correlation supports the notion that high rates of niche evolution might drive increased diversification rates (Kozak & Wiens, 2010), attribution remains difficult. By quantitatively assessing the variation of niche evolution and species diversification in *Babiana*, we can begin to understand how species evolved to fill climatic niche space across the Greater Cape Floristic Region, thus illuminating the evolutionary factors that govern differences in richness across the two major biomes. Even though ecological divergence in *Babiana* has

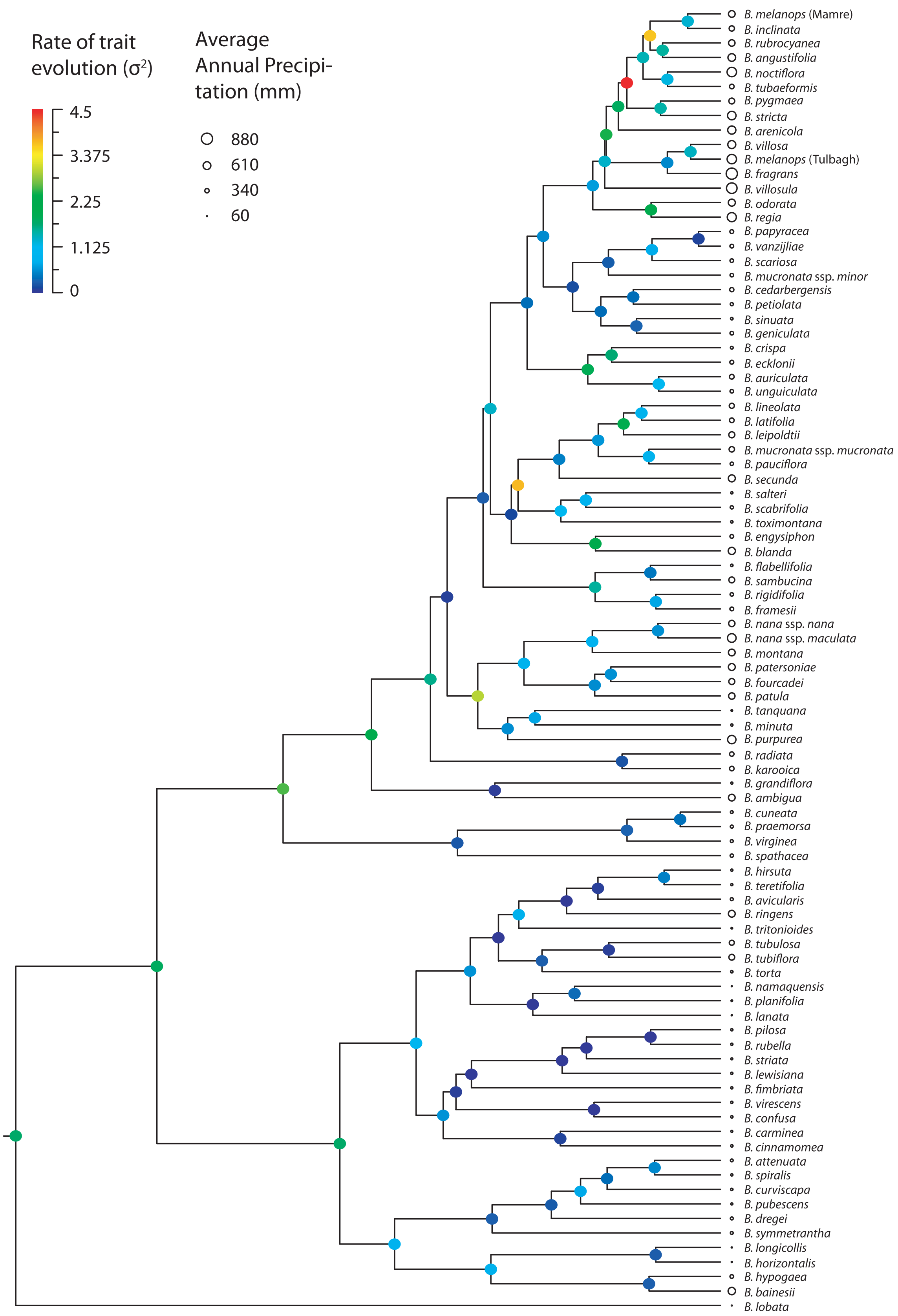

Figure 2 Rates of evolution of climatic tolerances in the genus *Babiana* in southern Africa. Open circles at the tips represent the mean value for each species (here: annual precipitation, Bio12) derived from their geographical distribution. Filled circles at internal nodes represent the evolutionary rate (σ^2), calculated on a distribution of 1000 trees.

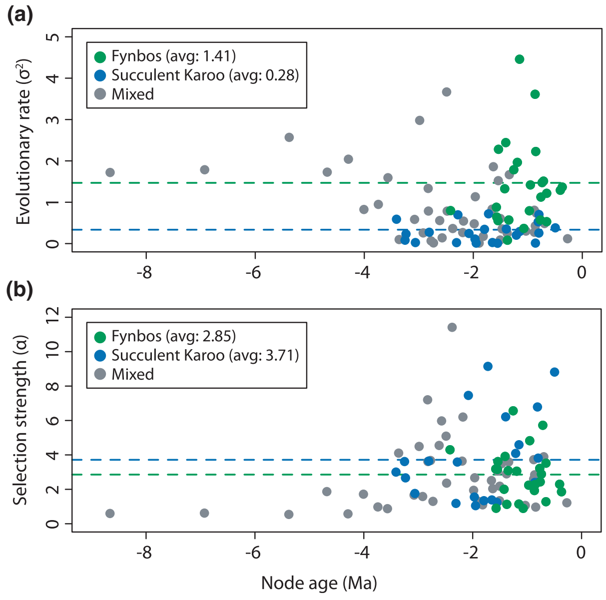

Figure 3 Temporal and geographical variation in the rate and selection strength in the evolution of rainfall tolerances in *Babiana* in southern Africa. The estimated evolutionary rate (a) and selection strength (b) for each node are plotted against node ages. Nodes where all descendant lineages evolved under the same regime (i.e. the same optimum) are coloured in green (Fynbos) or blue (Succulent Karoo). Nodes that were found to give rise to clades where selective regimes differ are coloured in grey.

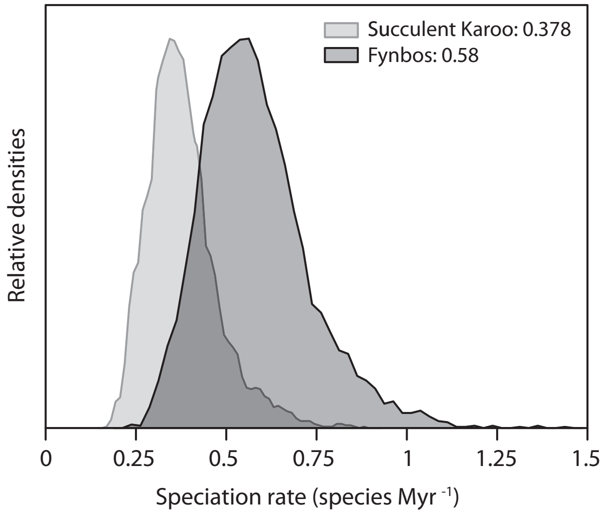

Figure 4 Rates of species diversification in *Babiana* in southern Africa calculated on a distribution of 1000 trees under a pure-birth model. Posterior rate estimates (relative densities) show a higher speciation rate (λ) in the Fynbos (λ = 0.58) than in the Succulent Karoo (λ = 0. 378).

been found to be particularly strong along a rainfall gradient, other environmental factors not included here might be key determinants of the diversification of the clade, and additional niche dimensions (other than climate) should ideally be incorporated in future studies.

Another explanation for the different evolutionary patterns could simply be that the two regions differ in their extent of environmental change throughout the evolutionary history of the clade, and it has been suggested that such a difference might have led to different diversification histories in the Fynbos and Succulent Karoo (Verboom *et al.*, 2009). However, the winter-rainfall climate that characterizes much of the region today, is thought to have been initiated in the mid- to late Miocene (Siesser, 1980; Zachos *et al.*, 2001; Bytebier *et al.*, 2010; Dupont *et al.*, 2011), suggesting the existence of stable refugia in both biomes not only through the Quaternary (Jansson & Dynesius, 2002), but possibly since the end of the Miocene. Given that in *Babiana* only the root node age has a 95% HPD interval that extends past the late Miocene (95% HPD: 5.415–12.366 Ma; Schnitzler *et al.*, 2011), the radiation of this clade has probably been unaffected by the late Miocene climatic changes, and differential environmental histories cannot therefore explain the rate differences in *Babiana*. Kozak & Wiens (2010) further show that the climatic niche evolves faster in environments that have remained relatively stable (instead of being affected by climatic fluctuations or glaciations), possibly due to a higher degree of specialization (see also Linder, 2003). While the climate has probably remained relatively stable in both regions, the greater topographic complexity in the Fynbos could provide more opportunities for ecological divergence (Cowling *et al.*, 1996; Linder, 2003; Schnitzler *et al.*, 2011), indicating a potential link between rates of niche evolution, lineage diversification, and environmental complexity.

In the present study we focused on dynamics of the realized niche (more explicitly the climatic parameters of the realized niche). Therefore, the observed patterns might actually be due to shifts in the realized niche only (i.e. due to competitive release), while the fundamental niche might remain constant (Pearman *et al.*, 2008; Nogués-Bravo, 2009; Dormann *et al.*, 2010). However, if all species shared the same (or a very similar) fundamental niche, we would not expect to see the strong phylogenetic geographical pattern (and the associated differences in the climatic niche) observed in our data set. Conversely, an overall lower degree of biome endemism would be expected, and if the environmental conditions of both regions were part of the species' fundamental niche, those species endemic to either of the two biomes should be more randomly distributed over the phylogeny, indicating the relatively low cost of moving between biomes. We therefore conclude that climatic niches are not labile in *Babiana*, but correspond to the environmental conditions of the two biomes, and that observed differences in species climatic tolerances represent reasonable approximations of a component defining their fundamental niche. Ultimately, an experimental approach to niche characterization would be a strong test of this hypothesis.

CONCLUSIONS AND FUTURE PERSPECTIVES

Our study suggests that evolution of climatic tolerances in *Babiana* is governed by an Ornstein–Uhlenbeck process, which imposes constraints on the evolution of temperature and rainfall tolerances, the latter being associated with two distinct (biome specific) adaptive optima. Environmental variation has been appreciated as an important factor for large-scale patterns of species diversity (Dynesius & Jansson, 2000), and our results suggest that high environmental heterogeneity (a characteristic feature of the Fynbos) might be driving high rates of climatic niche evolution, resulting in high rates of lineage diversification. Comparisons across different groups and regions could indicate whether this is a general feature of the Greater Cape Floristic Region and should lead to a better understanding of how fast – and along which niche axes – ecological divergence arises to establish and maintain genetic isolation. Eventually, we need to incorporate the temporal dynamics of the niche axes (i.e. environment, but also changes in biotic interactions) to link rates of niche evolution and species diversification to rates of environmental change. Finally, it would also be desirable to incorporate fossil information in both the estimation of diversification rates and the evaluation of modes and rates of niche evolution.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary table and figures.

BIOSKETCH

Jan Schnitzler is interested in the processes that generate and maintain species diversity, with an emphasis on the evolution and ecology of the Cape flora of southern Africa.

Author contributions: J.S., C.H.G., C.F.D., K.S. and H.P.L. conceived the ideas, and designed the study; J.S. collected and analysed the data and led the writing; all authors provided comments and feedback and approved the final version of the manuscript.

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The papers in this Special Issue arose from two workshops entitled 'The ecological niche as a window to biodiversity' held on 26–30 July 2010 and 24–27 January 2011 in Arnoldshain near Frankfurt, Germany. The workshops combined recent advances in our empirical and theoretical understanding of the niche with advances in statistical modelling, with the aim of developing a more mechanistic theory of the niche. Funding for the workshops was provided by the Biodiversity and Climate Research Centre (BiK-F), which is part of the LOEWE programme 'Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz' of Hesse's Ministry of Higher Education, Research and the Arts.