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ORIGINAL ARTICLE

Scale-dependent adaptive evolution and morphological convergence to climatic niche in Californian eriogonoids (Polygonaceae)

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ABSTRACT

Aim Macroevolutionary patterns and processes change substantially depending on levels of taxonomic and ecological organization, and the resolution of environmental and spatial variability. In comparative methods, the resolution of environmental and spatial variability often defines the number of selective regimes used to test whether phenotypic characteristics are adaptively correlated with the environment. Here, we examine how investigator choice of the number of selective regimes, determined by varying the resolution of among-species variability in the species climatic niche (hereafter called 'ecological scale'), influences trait morphological diversification among Eriogonoideae species. We assess whether adaptive or neutral processes drive the evolution of several morphological traits in these species.

Location South-western North America.

Methods We applied a phylogenetic framework of three evolutionary models to four morphological traits and the climatic niches of Eriogonoideae (in the buckwheat family, Polygonaceae). We tested whether morphological traits evolve in relation to climate by adaptive or neutral process, and whether the resulting patterns of morphological variability are conserved or convergent across the clade. We inspected adaptive models of evolution under different levels of resolution of among-species variability of the climatic niche.

Results We show that morphological traits and climate niches of Eriogonoideae species are not phylogenetically conserved. Further, adaptive evolution of phenotypic traits is specific to climatic niche occupancy across this clade. Finally, the likely evolutionary process and the level of detectable niche conservatism change depending on the resolution of environmental variability of the climatic niche.

Main conclusions Our study demonstrates the need to consider both the resolution of environmental variability and alternative evolutionary models to understand the morphological diversification that accompanies divergent adaptive evolution of lineages to climatic conditions.

Keywords

Adaptive evolution, climatic niche, convergent evolution, Eriogonoideae, morphological evolution, niche conservatism, phylogeny, scale, south-western North America.

INTRODUCTION

Discerning the evolutionary processes responsible for patterns of morphological diversity and species diversification is a major research question in evolutionary biology and ecology. This is a challenge that is complicated by three problems. First, both adaptive and neutral evolutionary processes can have either diversifying or conservative effects on the

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evolution of species' traits (Losos & Ricklefs, 2009; Wiens *et al.*, 2010). Second, these evolutionary processes can produce nearly identical macroevolutionary patterns, such as trait convergence or niche conservatism, making it difficult to infer any evolutionary process solely from observed macroevolutionary patterns (Revell *et al.*, 2008). Third, macroevolutionary patterns and processes change depending on the chosen levels of taxonomic and ecological organization, the resolution of environmental and spatial variability, and other effects of scale (Levin, 1992; Losos, 2008). This triptych of problems suggests the need for closer examination of the relationship between mechanisms of evolution, environmental variability and associated patterns of trait diversification.

Recent advances in macroevolutionary modelling allow adaptive and neutral modes of evolution to be disentangled (Beaulieu *et al.*, 2012; O'Meara, 2012). Furthermore, these developments enable the assessment of the diversifying or conservative effects of these two processes on species morphological, behavioural and ecological traits (see Appendix S1 in Supporting Information). For example, inflorescence and leaf size in *Acer* evolve adaptively in response to different selective regimes imposed by specific breeding systems (Verdú & Gleiser, 2006). Similarly, in Neotropical tanagers (Thraupidae), the adaptive evolution of plumage brightness is governed by the different selective regimes represented by open versus closed habitats and foraging strata, and permits rapid divergence among closely related taxa (Shultz & Burns, 2013). However, adaptive evolution does not always drive species diversification (Wiens *et al.*, 2010). For example, in evergreen sclerophyllous vegetation in the mediterranean climate of California, the lack of substantial evolutionary change is also maintained by stabilizing selection and adaptive evolution results in phylogenetic conservation of leaf traits (Ackerly, 2004). While the coupling of molecular phylogenetics and ecological data with adequate evolutionary models allows discrimination among alternative evolutionary hypotheses, the potential effects of scale on adaptive evolution and trait diversification have not been thoroughly investigated.

When trait evolution is driven by diversifying selection, the number of possible optimal trait states is defined by the number of adaptive zones on a fitness landscape (Lande, 1976). In comparative studies, it is often necessary to define adaptive zones, or so-called selective regimes, prior to performing a comparative analysis (Martins & Hansen, 1997; Beaulieu *et al.*, 2012). The choice of selective regimes reflects a hypothesis on the possible interactions between species traits and environment. For instance, foraging regime (arboreal versus terrestrial) in pigeons and doves is associated with the optimal length of tarsi and tail (Lapiedra *et al.*, 2013). Similarly, in *Acer* (Sapindaceae), the type of breeding system influences the size of inflorescences and leaves (Verdú & Gleiser, 2006). In addition, indirect evidence shows that the detection of macroevolutionary processes, such as diversifying selection, is affected by the number of selective regimes and this number is often determined by the resolution of environmental variability. For example, in chelonians (green sea turtles), body size correlates with habitat types only when terrestrial and freshwater conditions are condensed into one category of habitat (Jaffe *et al.*, 2011). Further, the hierarchical organization of plant diversity with regard to 'niche levels' helps to distinguish evolutionary lability from conservatism in the niche traits of species in mesotrophic grassland communities (Silvertown *et al.*, 2006). While these examples evince that the resolution of environmental variability can impact inferences on species' morphological evolution, macroevolutionary comparative studies have never considered explicitly the effect of different numbers of selective optima on macroevolutionary inference, leaving unknown the effects of these decisions on the interpretation of evolutionary processes.

The North American Eriogonoideae (the buckwheat family, Polygonaceae) is an ideal group in which to address this question in detail. This clade of vascular plants comprises 20 genera and *c.* 325 species, 315 of which are distributed in western North America (Kempton, 2012). Most species are ascribed to two large genera, *Eriogonum* and *Chorizanthe*, where the latter is distinguished from the former based on the presence of awned involucres and reduction in the number of flowers per involucre (Reveal, 1978). The other 18 genera within Eriogonoideae are small, with one to three species each (Kempton, 2012). The life forms in the group are diverse and range from annual, biennial and perennial herbs to subshrubs and shrubs. The occurrence of species on coastal bluffs to alpine tundra provides a unique opportunity to study the influence of climate on the evolution of plant morphology, to test for an association between morphological traits and distinct climates, and to investigate how the choice of number of climatic selective regimes affects the interpretation of evolutionary models.

In this study, we (1) investigated how the number of selective regimes, determined by choosing different levels of resolution of among-species variation in species climatic niches (hereafter, 'ecological scale'), affects the detection and interpretation of macroevolutionary processes underlying species morphological evolution; and (2) determined the mechanisms of morphological trait evolution in plants under different selective regimes. To address these questions, we applied three evolutionary models to four morphological traits and three principal components that describe the climatic niches of the species in the Eriogonoideae. We tested in a phylogenetic framework whether morphological traits evolve by adaptive or neutral process in relation to climate at four ecological scales and whether the resulting patterns of morphological variability are conserved or convergent across the clade.

MATERIALS AND METHODS

Species sampling and DNA sequencing

We collected samples of 40 species of Californian Eriogonoideae for sequencing (Appendix S1) and supplemented them with sequences from 16 additional species from GenBank.

These 56 species were taxonomically unbiased (*c.* 20% of species from each subgenus) and constituted a representative sample of Eriogonoideae morphological and niche diversity across each major subgenus of *Eriogonum* (*Eriogonum*, *Eucycla*, *Ganysma*, *Oligogonum*, *Oregonium*, *Pterogonum*) and *Chorizanthe* (Appendix S1). The specimen vouchers were deposited at the Herbarium of Rancho Santa Ana Botanical Garden (Appendix S1). We sequenced the plastid *trn*K–*mat*K and the nuclear internal transcribed spacer (ITS) region for the 40 species using standard procedures (Appendix S2; Sanchez & Kron, 2008).

Phylogenetic analyses

To the sequences from a total of 56 Eriogonoideae species we added sequences from GenBank for an additional 98 species from the Polygonaceae. The addition of these 98 species was necessary for divergence-time analysis (see below), because fossil records were not available for the Eriogonoideae. Sequences from three outgroup species from the Plumbaginaceae (*Plumbago auriculata*, *Ceratostigma minus* and *Limonium dufourii*) were also added to the DNA matrix (Sanchez & Kron, 2008). We aligned the DNA matrix with MAFFT 6 (Katoh & Toh, 2008) using the default settings and adjusted the alignment by hand to maintain the amino acid reading frame within the exons. Any site with an alignment probability of less than 50% was excluded from the alignment. We selected the GTR+Γ model of sequence evolution based on the Akaike information criterion (AIC) for each DNA region, using the phymltest function in the APE package in R (Paradis *et al.*, 2004).

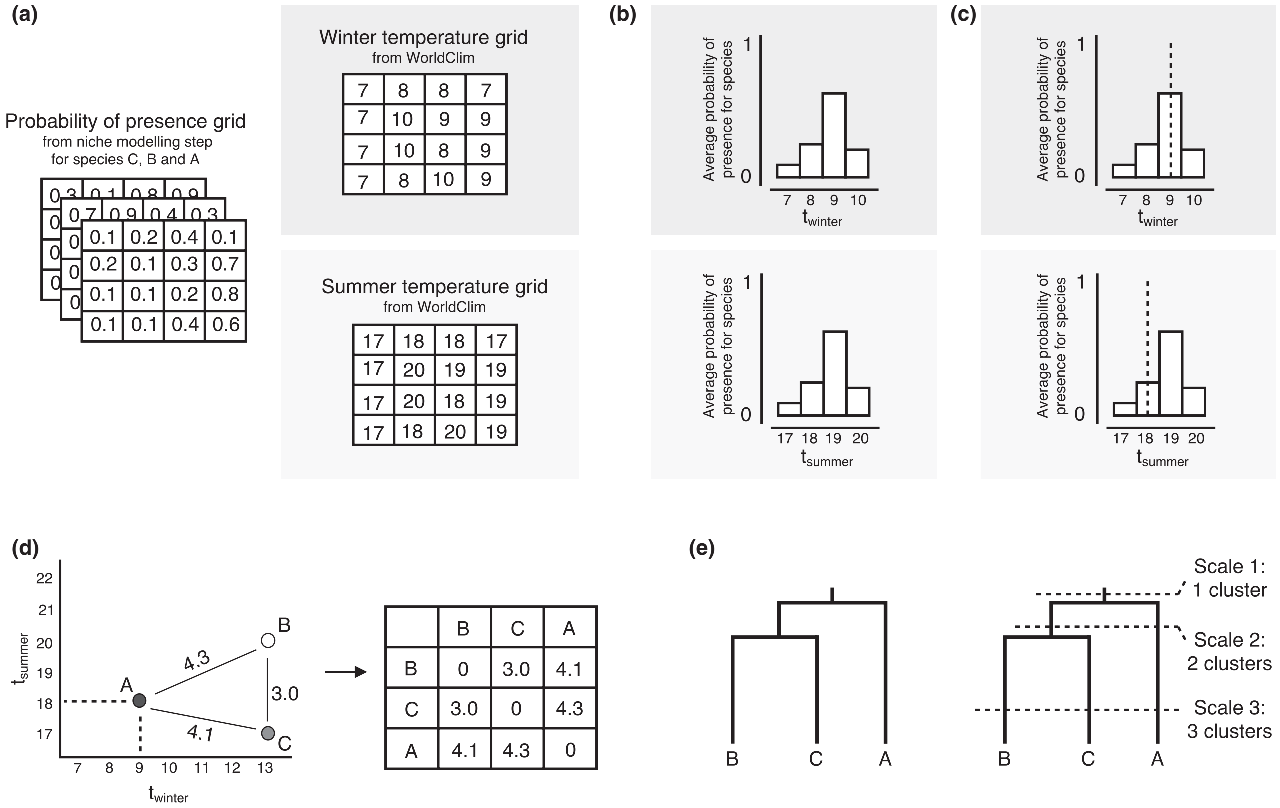
We performed divergence-time analysis in BEAST 1.4.7 (Drummond & Rambaut, 2007). The root of the Polygonaceae was constrained by setting a lognormal prior distribution with a mean of 94.15 Ma and a standard deviation of 15.9 Myr (Magallón & Castillo, 2009). We ran BEAST analysis for 5×10^6 generations sampling every 1000 generations under the uncorrelated lognormal relaxed-clock model, a Yule tree prior and a separate GTR+Γ model of substitution for each DNA region. We repeated the analyses four times and verified convergence by examining the posterior distribution of parameters in TRACER 1.4 (Drummond & Rambaut, 2007). All subsequent analyses (see below) were performed on a sample of 200 trees randomly drawn from the posterior distribution of dated trees after removing a burn-in of 2000 trees and with non-Eriogonoideae species removed from the tree.

Morphological data and climatic niche modelling

Morphological data were obtained from the *Flora of North America*, Vol. 5 (FNA; Flora of North America Editorial Committee, 2005) for all 56 Eriogonoideae species present in the phylogenetic tree. We recorded four trait values (leaf width, leaf length, rosette diameter, stem height) for each species and log-transformed them before analysis. We took trait means from the range reported in the FNA, excluding rare values. These traits are highly variable within Eriogonoideae species and may be adaptively correlated with different climatic zones (Raven & Axelrod, 1978; Ackerly, 2004). The correlations between these four traits lay between 35 and 47 (Pearson's $r_{2,56}$ = 0.35–47, P = 0.0123–0.002) and, therefore, we analysed each trait independently.

We obtained climatic variables at a resolution of 30 arc-seconds from the WorldClim database for niche modelling (Hijmans *et al.*, 2005), and collected occurrence records for Eriogonoideae species from the databases CalFlora (http://www.calflora.org/, accessed 1 October 2010), Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/, accessed 1 October 2010), and GBIF (http://www.gbif.org/, accessed 1 October 2010). We manually checked all species occurrences and excluded samples coming from botanical gardens and from regular-grid surveys with a precision of less than 30 arc-seconds. The final number of points per species ranged from 23 (*Eriogonum breedlovei*) to > 2900 (*Eriogonum fasciculatum*), with an average of 432 localities per species. We generated 2500 randomly distributed pseudo-absence points (ARCGIS/ARCINFO 9.2; ESRI, Redlands, CA, USA) for each species over the entire study area, defined as the total extent of all occurrences available for the 56 species. We performed ensemble projection based on classification and regression trees (CART; Breiman, 2001) and random forests (RF; Cutler *et al.*, 2007) methods for climatic niche modelling. As CART/RF are insensitive to correlated predictors (Breiman, 2001; Cutler *et al.*, 2007), we kept all climatic variables for niche modelling, but calculated and used principal components for the phylogenetic analyses (see below). The niche models were estimated in R using the TREE (Ripley, 2012), RANDOMFOREST (Breiman & Cutler, 2012) and RGDAL (Keitt *et al.*, 2012) packages. For RF we followed the procedure described in Cutler *et al.* (2007) with 500 trees and 20% hold-out dataset for the model performance assessment. For CART, we used a bagging approach (Breiman, 2001) to create more generalized and stable classification models. We used 80% of the dataset for model training and repeated sampling 500 times to achieve stable classification results. Model performance was tested on hold-out datasets, which were 20% of the initial dataset. Finally, we obtained species-specific grid layers with probabilities of species presence (values between 0 and 1 inclusive for each grid cell) by averaging results of RF and CART.

We combined the grids of probabilities of species presence with grids of the original climatic variables from the WorldClim database (Fig. 1a) to calculate the average probability of species occurrence under the range of climatic conditions. For example, in Fig. 1a,b, five grid cells from the summer temperature grid correspond to the temperature of 17 °C. The average probability of species A to live at 17 °C is a simple average of five probabilities from the corresponding cells of the probability of presence grid [(0.1 + 0.1 + 0.2 + 0.1 + 0.1)/5 = 0.12]. We thus obtained, for each species, a distribution of averaged probabilities



0.1	0.2	0.4	0.1
0.2	0.1	0.3	0.7
0.1	0.1	0.2	0.8
0.1	0.1	0.4	0.6

7	8	8	7
7	10	9	9
7	10	8	9
7	8	10	9

17	18	18	17
17	20	19	19
17	20	18	19
17	18	20	19

	B	C	A
B	0	3.0	4.1
C	3.0	0	4.3
A	4.1	4.3	0

Figure 1 A figure explaining the niche modelling process and hierarchical cluster analysis (HCA) for a hypothetical species. (a) Two types of source grids are shown: probability of presence grids from the niche modelling step for each species and climatic grids from the WorldClim database. (b) Average probability densities over unique values of a given climatic variable. (c) Sampling (random with replacement) of climatic values given the probability densities; vertical dashed line represents a first sample. Steps (b) and (c) are repeated for species A, B and C. (d) Calculating pairwise Euclidean distances among species in a multivariate climatic niche space that is defined by species scores on principal components analysis (PCA) axes. (e) Hierarchical clustering of species based on pairwise distances and grouping to define three different scales. Note: in the actual analysis steps (d) and (e) were done with PCA scores instead of climatic variables themselves. A small t denotes temperature in all panels.

describing the propensity of a species to occur, conditioned on values of the climate variables (Fig. 1b). These probability densities can be viewed as an analogue of the species fitness curve along an environmental gradient: the highest probabilities are associated with the climatic conditions where the species is most likely to be observed (Fig. 1b). We summarized these probability densities using a principal components analysis (PCA; Dray & Dufour, 2007). To calculate the PCA, we sampled randomly with replacement 500 points from the densities (Fig. 1c) and extracted PCA scores for each species for the analysis of phylogenetic signal, several phylogenetic generalized least squares analyses (PGLS, see below), and a hierarchical cluster analysis (HCA, see below). Use of a distribution of PCA scores for each species incorporated intraspecific variation into these analyses.

Phylogenetic signal and evolutionary models

We conducted all phylogenetic analyses on a sample of 200 trees randomly drawn from the posterior distribution of dated trees, with non-Eriogonoideae species omitted. We examined the lability of the morphological traits and climatic PCA scores using Pagel's λ and Blomberg's K as measures of phylogenetic signal, implemented in the R package PHYTOOLS (Revell, 2012). Phylogenetic signal represents the level of dependency among species trait values owing to their phylogenetic relatedness (Revell *et al.*, 2008). For both indices (Blomberg's K and Pagel's λ), a value close to 0 is diagnostic of weak or non-existent phylogenetic structure, while values indistinguishable from one (1) are expected if the data follow a Brownian motion (BM) model of character evolution (Pagel, 1999; Blomberg *et al.*, 2003). These indices were calculated for scores from each of the three PCA axes. We applied PGLS as implemented in the R package CAPER (Orme *et al.*, 2011), to investigate the relationships between climate and morphology, where the morphological traits served as dependent variables and climatic PCA scores as independent ones. We used the λ transformation in PGLS, with λ being estimated by maximum likelihood (Pagel, 1999).

We fitted three alternative evolutionary models to investigate different hypotheses for the evolution of plant morphology in response to climate. First, we used a Brownian motion model to represent a neutral evolutionary process with constant rates (BM; Felsenstein, 1985). Second, we applied an Ornstein–Uhlenbeck model that assumed lineages evolved under a single selective regime (OU1 model; Kozak & Wiens, 2010b; Smith *et al.*, 2011), but were constrained by stabilizing selection (Smith *et al.*, 2011). Third, we constructed an Ornstein–Uhlenbeck model with multiple climatic selective regimes (OUM; Butler & King, 2004) to assess the possibility that trait evolution was driven by diversifying selection towards multiple trait optima.

As climate was represented by continuous variables (PCA scores) in our study, we used hierarchical cluster analysis (HCA) to define discrete selective regimes for the OUM model (Fig. 1d,e). The HCA algorithm clustered species together based on the pairwise distances between species centroids in the multidimensional climatic space (Fig. 1d). This space mimicked the plant perspective on climate because it represented a multivariate fitness landscape, across which the pairwise distances between the empirically derived species optima were calculated (Fig. 1d). We assumed that the smaller the distance between species in the climatic (i.e. PCA) niche space, the more similar were the climatic selective regimes they experienced. Thus, in HCA the species clustered according to the similarity of the climatic conditions in which they occurred in the data and this clustering was used to define distinct selective regimes (Levin, 1992; Turner, 2005). The HCA produced a tree-like representation of species positions relative to each other in a niche space (Fig. 1e). The resolution with which this was converted into nominal selective regimes determined the different 'ecological scales' (i.e. number of selective regimes) of our study (Fig. 1e, dashed lines).

The HCA was estimated using the Ward method (Euclidean distances) as implemented in the R package PVCLUST (Suzuki & Shimodaira, 2006). We performed hierarchical clustering 500 times, each time sampling for each of the species a value from their distribution on PC1, PC2 and PC3 at random. We calculated a consensus HCA from these 500 trees. We ensured that this consensus HCA was reliable by constructing HCA from 50, 100, 200, 300, 500, 1000 and 5000 samples and identifying the threshold above which the resulting HCA topologies were invariant (here, 300 samples). We used approximate and unbiased *P*-values (AU) and bootstrap probabilities (Suzuki & Shimodaira, 2006) to identify well-supported clusters in the consensus HCA. We also applied a phylogenetic ANOVA (PHYTOOLS package in R; Revell, 2012) to assess the statistical significance of PCA scores in the discrimination of the selective regimes (clusters).

Finally, we expanded the OUM model into two submodels (Butler & King, 2004; Kozak & Wiens, 2010a). In OUM(A), selective regimes of terminal branches were specified, but all internal branches were left in a single and additional, unspecified ancestral regime. In OUM(ML), selective regimes were specified for terminal branches based on HCA results and regimes of internal branches were reconstructed with a maximum likelihood method (Pagel, 1994). The ancestral state reconstruction was performed in the APE package in R (Paradis *et al.*, 2004) and the best supported model of selective regime evolution was chosen by comparing AIC values. We constructed and tested the OUM(A) and OUM(ML) models at differing ecological scales (number of selective regimes) derived previously from the HCA. We assigned branches of the phylogenetic tree to either two, three, four or five selective regimes when constructing the OUM(ML) models. Each of these possibilities for the number of regimes was highly supported with AU values and bootstrap probabilities. We compared all alternative models using their corresponding AIC weights. This was then repeated on a sample of 200 phylogenetic trees. We also applied a randomization procedure by shuffling selective regimes on the phylogeny to ensure that fit of the OUM models was not due to chance alone.

RESULTS

Phylogenetic analyses and divergence-time estimation

We deposited sequences of the *trn*K–*mat*K and ITS region in the Dryad database (doi:10.5061/dryad.b9m853tp) and in GenBank (Appendix S2). The topologies recovered during the divergence-time analysis had good or moderate support (> 0.8 posterior probabilities) for most of the nodes (Fig. 2). The outgroup lineage to the rest of Eriogonoideae is *Pterostegia drymarioides*, originating 18–31 Ma (95% HPD). The *Eriogonum* sect. *Ganysma* is the oldest section in *Eriogonum* and diversified between 9 and 18 Ma. We find that the *Eriogonum* sect. *Eucycla* clade has a younger origin. Its crown node diverged from sect. *Ganysma* between 8 and 15 Ma (95% highest probability density, HPD), while most of the speciation events become evident only from 0.5 to 6 Ma. The majority of the *Chorizanthe* species have diversified between 0.1 and 4 Ma (95% HPD), yet *Chorizanthe spinosa* and *Chorizanthe rigida* lineages found outside of the main *Chorizanthe* clade, are older and originated *c.* 7–12 Ma.

Climatic niche modelling, climatic scales and regimes

Values of the area under the receiver operating characteristic curve (AUC) for climatic niche models range from 0.92 to 0.99, confirming their high predictive accuracy (Swets, 1988). Overall, the variables wettest quarter precipitation and mean temperature had the highest relative importance in the models fitted by CART/RF. The first (PC1: temperature seasonality, isothermality and mean annual temperature), second (PC2: precipitation and temperatures during the wettest and warmest seasons) and third (PC3: precipitation and isothermality gradient) PCA scores from the niche modelling step explained 53.12%, 22.24% and 9.81% of the variation, respectively. We identified four clustering levels (ecological scales) in HCA (all AU *P*-values > 95%, supporting existence of clusters at a $P < 0.05$; Appendix S3). These four scales

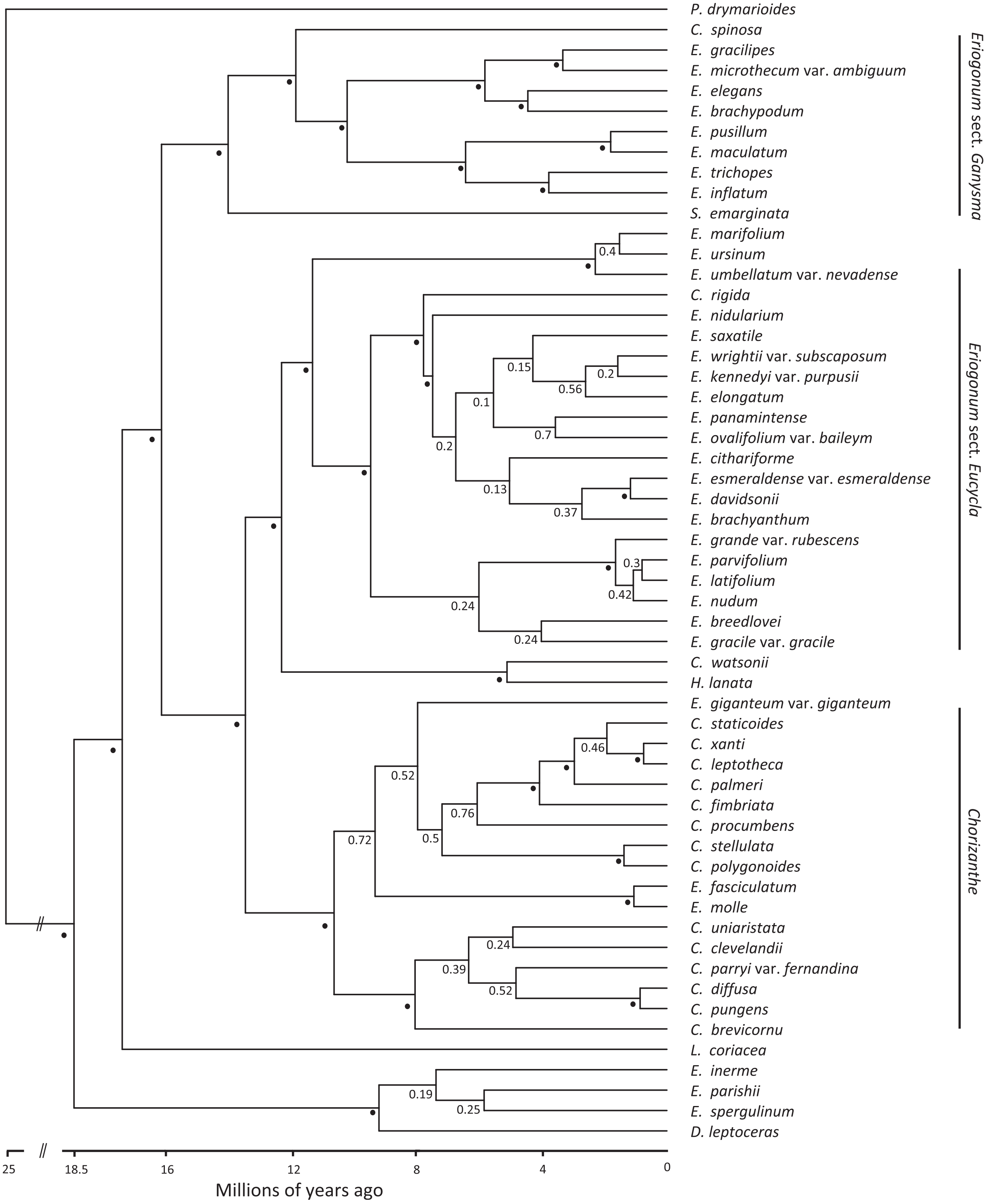


Figure 2 Time-calibrated phylogeny of Eriogonoideae recovered during the divergence-time analysis. Nodes highlighted with a dot have bootstrap support > 90% and posterior probabilities > 0.98. Genera names are coded as follow: *C.*, *Chorizanthe*; *D.*, *Dodecahema*; *E.*, *Eriogonum*; *H.*, *Hollisteria*; *L.*, *Lastarriaea*; *P.*, *Pterostegia*; *S.*, *Sidotheca*.

divided the climatic space into two to five selective regimes and at each scale the differences between the selective regimes were highly significant.

Climatic niche modelling and HCA confirm the diversity of habitats occupied by Eriogonoideae and produce a biologically plausible approximation to the climatically distinct biogeographical regions of south-western North America (Fig. 3a–d). Each scale characterized a different level of climatic specialization among the species. For example, the selective regime of the species commonly found in creosote/saltbush/sagebrush communities of Sonora and Mojave deserts (e.g. *Eriogonum inflatum, Eriogonum trichopes, Chorizanthe spinosa*; light pink dots in Fig. 3a–d) is characterized by mean temperatures of 40.5 °C (range: 35–43 °C) during the warmest period (BIO5), down to −1.5 °C during the coldest months (BIO6). Mean annual precipitation is extremely low (380 mm, BIO13), which is expected for this type of habitat, while the precipitation of the driest quarter (BIO17) shows extreme values of 8–50 mm (mean 32 mm per month). In contrast to these species of arid climates, the species of coastal selective regimes (e.g. *Eriogonum latifolium, Eriogonum parvifolium, Chorizanthe pungens, Chorizanthe diffusa*; blue dots in Fig. 3b–d) are characterized by significantly milder climate, with an annual temperature range half as great as that in desert-like environments (16.5 °C vs. 32.6 °C). These species encounter the wettest type of climate among those inhabited by the North American Eriogonoideae, with an average annual precipitation of 1060 mm, which corresponds to scrub and grasslands communities along the Pacific coast. Up to three additional selective regimes are detected at the more-detailed ecological scales (Fig. 3c,d), and the climatic variation among these regimes is also high.

Phylogenetic signal and PGLS

We do not consistently detect the presence of phylogenetic signal in axes PC2 and PC3 (*P*-values for both *K* and $\lambda > 0.5$; Table 1). Low phylogenetic signal in PC1 under the

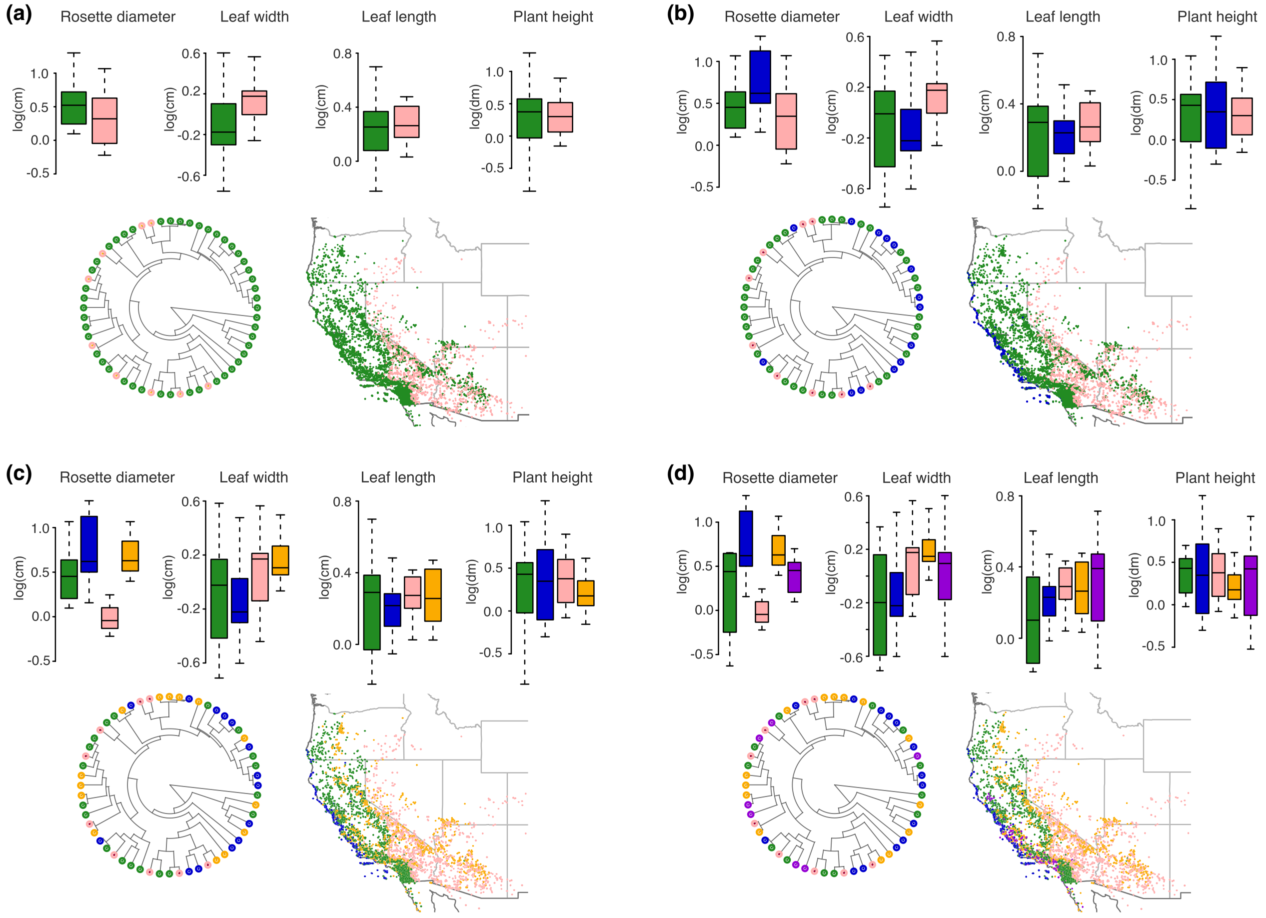


Figure 3 Phylogenetic trees of Eriogonoideae (south-western North America) with regimes indicated by colours (shown as dots next to tips of phylogeny). The corresponding maps show the distribution of species occurrence points, coloured according to the selective regimes and boxplots of log-transformed morphological trait values associated with species occupying each selective regimes. Throughout the plots green boxplot represents ‘all-remaining-species’ class. (a) Only two selective regimes are painted on the tree, the corresponding map and boxplots. The distinction is between desert climate (light pink) and the rest of the climatic niche space; mean leaf width of desert plants is greater than that of other species; (b) adding a third selective regime (blue) reveals the coastal climate and large differences in leaf width, length and rosette diameter between desert and coastal species; (c) a fourth selective regime (yellow) corresponds to climates at high elevations and is associated with mountain ranges; the leaf length and rosette diameters of these high-elevation species is larger than those of desert species, but not as big as in coastal species; (d) the fifth selective regime (violet) separates species inhabiting coastal mountains from the rest of the species.

null hypothesis of $K = 0$ is detected with K ($K = 0.28$, $P = 0.026$), but not with λ ($\lambda = 0.6175$, $P = 0.0502$). Weak phylogenetic signal in PC1 is primarily explained by the values of the two climatic variables that are phylogenetically conserved (BIO7, temperature annual range and BIO13, precipitation of the wettest month). None of the morphological traits reveals significant phylogenetic signal (all $\lambda < 0.0001$, $P = 1$; K values vary between 0.23 and 0.04, $P > 0.2$). Finally, PGLS analyses show significant ($P < 0.0001$) and strong linear trends ($R^2 = 0.67–0.89$) between morphological traits and species PCA scores (Table 2).

Evolutionary models

The OUM(ML) and OUM(A) models provide similar fit ($< 0.01\ \Delta\mathrm{AIC_c}$) and we only present the comparisons done with OUM(A), hereafter referred to as OUM (Table 3). The BM model of evolution is clearly rejected for the four morphological traits at each scale tested (Table 3). The relative performance of the OU1 versus OUM differs depending on the particular trait and the scale. For instance, OU1 outperforms OUM at all scales when tested on plant height (AIC weight = 0.412; Table 3). However, OUM has much higher support than OU1 on scales with three and four selective regimes for leaf length, leaf width and rosette diameter (AIC weights 0.584, 0.237, 0.609, respectively; Table 3). For leaf length, leaf width and rosette diameter, the strength of selection (α parameter) estimated by OUM is higher on three selective regimes than on four. Both levels of classification depict strong selection ($\alpha = 1.6–5.1$ for three regimes; $\alpha = 1.2–4.4$ for four regimes) with moderate drift ($\sigma = 0.47–1.99$ for three regimes; $\sigma = 0.61–1.81$ for four regimes). The randomization procedure confirms that the fit of OUM models is not due to chance ($P < 0.01$).

Table 1 Phylogenetic signal for morphological traits of Eriogonoideae (south-western North America) and principal components (PC) extracted from the climatic niche variables. All values represent results averaged over 200 tree topologies sampled randomly from the Bayesian posterior distribution. The variables with significant phylogenetic signal are shown in bold.

	Pagel's λ	*P*-value	Blomberg's *K*	*P*-value
Morphological traits				
Leaf length	0.000047	1.000	0.128	0.695
Leaf width	0.000066	1.000	0.232	0.217
Plant height	0.000066	1.000	0.178	0.446
Rosette diameter	0.000066	1.000	0.044	1.000
Bioclim variables PC				
PC I	0.617556	0.050	**0.285**	**0.026**
PC II	0.000066	1.000	0.126	0.606
PC III	0.000066	1.000	0.095	0.845

Table 2 Phylogenetic generalized linear model (PGLS) between morphological traits of Eriogonoideae (south-western North America) and climatic principal components analysis (PCA) scores.

	R^2	R^2	*F*-statistic	*P*-value
Leaf length	0.944	0.896	18.3	< 0.0001
Leaf width	0.839	0.679	5.24	< 0.0001
Plant height	0.911	0.822	10.25	< 0.0001
Rosette diameter	0.842	0.791	7.45	< 0.0001

Table 3 Comparison of small-sample-size corrected Akaike information criterion ($\mathrm{AIC_c}$) weights for models of trait evolution in Eriogonoideae (south-western North America). All values represent results averaged over 200 topologies sampled randomly from the Bayesian posterior distribution. BM, Brownian motion model; OU1, Ornstein–Uhlenbeck with a single optimum model; OUM, Ornstein–Uhlenbeck model with multiple optima. The scale represents the number of selective regimes for the OUM models. The models with the highest AIC weights are shown in bold. OU1 model is a restricted case of OUM model with a single selective regime acting on all of the species.

Models (scale)	Rosette diameter	Leaf width	Leaf length	Plant height
BM	0.000	0.000	0.000	0.000
OU1	0.209	0.153	0.127	**0.412**
OUM (2)	0.056	**0.235**	0.037	0.136
OUM (3)	**0.609**	**0.237**	**0.584**	0.187
OUM (4)	0.098	**0.250**	0.165	0.225
OUM (5)	0.027	0.124	0.088	0.040

DISCUSSION

By testing alternative evolutionary scenarios, we demonstrate that the ecological scale (i.e. the number of selective regimes) used in models of adaptive evolution has overwhelming consequences for the detection of the evolutionary mechanisms that are responsible for the diversification of plant morphological traits. We show with this approach that neither morphological evolution nor the evolution of climatic niches is phylogenetically conserved in Eriogonoideae. In contrast, adaptive evolution to different climatic niches is a likely scenario for all morphological traits we investigate, except plant height. In the absence of phylogenetic signal, such adaptive evolution may suggest morphological convergence in response to climate. In support of this proposal, we demonstrate that the presence of adaptive, labile evolution is only evident at certain ecological scales.

Morphological evolution in Eriogonoideae species

Altogether, the low phylogenetic signal we find in all morphological traits and the clear rejection of the neutral model of evolution (BM) indicate that non-neutral processes have driven morphological evolution in the Eriogonoideae (Table 3). If stabilizing or fluctuating directional selection were to drive adaptive evolution, it would result in long-term stasis in all evolutionary lineages, little morphological differentiation, and conservative niche patterns (Appendix S1; Kozak & Wiens, 2010b; Smith *et al.*, 2011). If, however, adaptive evolution acts to diversify species morphology through disruptive or directional selection (Appendix S1; Losos & Ricklefs, 2009), it would produce patterns with little or no phylogenetic signal, and morphological traits would correlate strongly with climatic niches as we observe.

The identification of the adaptive evolutionary processes varies considerably depending on the ecological scale of investigation (i.e. the varying resolution of among-species variation in the species climatic niche) and the morphological trait. Plant height is the only trait for which an evolutionary model mimicking stabilizing or fluctuating directional selection (OU1) is consistently supported at any scale. For leaf length, leaf width and rosette diameter, however, we reject the OU1 model when compared with the diversifying adaptive model of evolution (OUM) under either three, four or five selective regimes, but not at the other two ecological scales. Further, between-scale comparison confirms that OUM models with three and four selective regimes explain observed morphological patterns better than OUM models with either two or five regimes (Table 3). This supports the idea that diversifying adaptive evolution has been a dominant evolutionary force in Eriogonoideae. In addition to the better fit of the OUM models, we find a significant correlation between climatic PCA scores and morphological characters (Table 2). Given the diversity of habitat types in the North American Southwest and the substantial morphological differentiation among Eriogonoideae species (Reveal, 1978; Sanchez & Kron, 2008), the observed pattern of morphological evolution is consistent with within-lineage adaptive evolution to climate.

We find that leaf width in these North American eriogonoids is highly variable between different climatic regions (Fig. 3a–d). First, we find that the desert species have in general wider and shorter leaves than species found in wetter, coastal climates. This is consistent with previous studies that show that in the warm deserts of south-western North America, species leaves or leaflets are generally simple, entire and often relatively large (Mulroy & Rundel, 1977). In summer annuals, these relatively large leaf plates are, however, often coupled with drought-associated summer foliage (Mulroy & Rundel, 1977). We also detect more subtle variation in leaf size associated with the species of high elevations, in which leaf length increases compared with that of arid species, but still does not reach the size of long-leaved coastal species (Fig. 3c, d). Second, Eriogonoideae species of arid regions (such as the Mojave Desert) tend to have smaller rosette diameter than species occupying climates with abundant rainfall and less severe yearly seasonality. Such small basal rosettes of leaves (or sometimes their absence), most probably have evolved in response to the very high soil surface temperatures existing in mid-summer (Mulroy & Rundel, 1977). While smaller plant size is often suggestive of an adaptation to harsher conditions and shorter growing seasons, and is common in alpine ecotypes (Böcher, 1949), we do not find any general trend in plant height among these North American eriogonoids.

Scale specification is always arbitrary (Levin, 1992; Turner, 2005) and detected patterns could be pervasive at one scale but not at another (Losos, 2008; Wiens *et al.*, 2010). In this sense, a broad ecological scale (one with few selective regimes) probably encompasses a larger geographical area, and/or substantial environmental variation, by not distinguishing minor environmental differences into distinct regimes. The forces of natural selection therefore become increasingly complex with broader scale and include multiple (unresolved) environments, which results in slower observed rates of adaptive evolution (Levin, 1992). This could result in the appearance of constrained macroevolutionary patterns (Losos, 2008). On the other hand, with finer resolution of environmental variation into more numerous selective regimes, environmental heterogeneity is increasingly described by among-regime differences, revealing new ecological opportunities (Pickett & Cadenasso, 1995), while within-regime heterogeneity is reduced (Turner, 2005). Consequently, with more-highly resolved selective regimes, fewer genetic changes are required for adaptive evolution because the environments within selective regimes are increasingly homogeneous (Levin, 1992). Our analyses reveal that both such scenarios are relevant to eriogonoids. For instance, the evolution of plant height is conservative and driven by stabilizing selection towards a single optimum; there is no identifiable between-scale variation in optima for this trait. In contrast, the other traits (leaf size in particular) are under diversifying selection and an analysis that distinguishes scales is particularly important for the identification of how many selective regimes are indeed supported. The discretization of niche space could be avoided by using ‘optimal regression’ (as in Labra *et al.*, 2009), but we would have been unable to assess directly the effect of ecological scale. Moreover, it would have restricted the analysis to a linear relationship between the predictor and dependent variables, which is often inappropriate for morphology-niche comparisons (Austin, 1985).

Morphological convergence within climatic niches

We find evidence for the convergent evolution of morphology in the Eriogonoideae. Three patterns support this hypothesis: (1) low phylogenetic signal in both morphological traits and niche variables; (2) no phylogenetically dependent distribution of the climatic niches on the phylogenetic tree; and (3) support for adaptive evolution in relation to the climatic niches (Fig. 3, Table 3). Our results are consistent with previous studies showing adaptive response in leaf morphology towards different climatic conditions in *Eriogonum* (Cole, 1967) and in Californian plants in general (Raven & Axelrod, 1978). The lability of leaf-related traits in eriogonoids is confirmed in common garden experiments which show that physiological resemblance and specific morphological adaptation can happen quickly in this taxonomic group (Cole, 1967). Similarly, specialization of leaf shape has been linked with temperature and precipitation in *Clarkia* (Onagraceae), which is another native genus from western North America (Small, 1972).

However, labile adaptive patterns in leaf morphology are not universal in mediterranean-type climates and evolution of leaf traits may instead exhibit relative stasis as, for instance, in evergreen chaparral communities (Ackerly, 2004). Nonetheless, the plant morphological traits that we identify as associated with climate are likely to be adaptive and, thus, would qualify as functional traits in the strict sense (Ackerly, 2004). Further, direct measurements of selection in common garden experiments could exclude the possibility that the patterns we observe arise from phenotypic plasticity. Although detailed assessment of plastic response and/or exact genetic causes of convergence are beyond the scope of this study, evidence from other studies suggests that the high among-species variability in leaf traits in Eriogonoideae is adaptive (Cole, 1967; Raven & Axelrod, 1978).

Numerous morphological and physiological traits are relevant for the investigation of adaptive evolution of plants in relation to climate. For example, variation in *Teucrium chamaedrys* in response to increasingly xeric conditions includes not only reduced leaf size and smaller plant height, but also increased leaf thickness and sclerophylly (Burghardt *et al.*, 2008). In our study, we have used only a small subset of the morphological traits that are associated with climate at macroevolutionary scales (Ackerly, 2004). Examination of other traits is necessary to advance our understanding of plant adaptive processes in xeric mediterranean climates. Moreover, our current analysis is limited to climatic variables at a relatively coarse geographical resolution, and does not deal with microtopographic, soil or grazing conditions. Soil pH and microtopography could be particularly important for North American eriogonoids (Stebbins & Major, 1965; Safford *et al.*, 2005), but the lack of detailed datasets limits current efforts to analyse macroevolutionary processes to climatic variables alone.

Adaptive evolution in Eriogonoideae: possible causal factors

One possible hypothesis to explain labile adaptive evolution of morphological traits among Eriogonoideae is interspecific competition, which can cause ecological displacement of congeners into different niches (Prinzing *et al.*, 2008; Kluge & Kessler, 2011). For example, in oak communities in Florida, USA, phylogenetic overdispersion is pronounced among close relatives, where the signal of among-species competitive interactions is strongest (Cavender-Bares *et al.*, 2004). Similarly, species-rich lineages, such as Eriogonoideae, might be more likely to show overdispersion than less rich ones, as increased diversity may lead to increased competitive exclusion among closely related species. Furthermore, overdispersion might be more likely in lineages that have undergone adaptive radiations more or less *in situ*, as evolutionary processes should result in niche differentiation and, thus, high local diversity (Cavender-Bares *et al.*, 2004). Such *in situ* diversification may be the case for Eriogonoideae (Reveal, 1989), thus placing character displacement among possible causal factors for the labile adaptive evolution in this group.

The patterns of niche specialization and morphological convergence that we observe may also result from complex ecological factors, such as incidence of fire, the severity of climate change in the Miocene and Pliocene, and the environmentally heterogeneous landscape that generally characterizes species-rich regions of mediterranean climate (Raven & Axelrod, 1978). For instance, speciation could occur when disruptive selection operates on populations that are isolated by fire in habitats (usually soil types) that differ from those of the larger populations of the parent species (Cowling *et al.*, 1996). Additionally, climatic fluctuation could serve as the driving force for geographical speciation in topographically heterogeneous environments (Raven & Axelrod, 1978). The patterns that we observe could also result from a complex history of differential speciation and extinction rates during the Quaternary (Cowling *et al.*, 1996), coupled with multiple events of geographical vicariance.

In conclusion, we would like to highlight that: (1) identification of the appropriate ecological scale is essential to distinguish between candidate evolutionary mechanisms; (2) depending on the scale, both diversifying and conservative effects of adaptive evolution may be detected; and (3) even when a dominant evolutionary mechanism is clearly identified, it does not guarantee a unique explanation underlying the evolutionary history of species. This suggests that understanding which macroevolutionary mechanisms dominate during species evolution can only be fully understood when analysing evolutionary processes and patterns over multiple scales.

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SUPPORTING INFORMATION

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

Appendix S1 Table of evolutionary hypotheses and locations of sampling sites, sample representativeness and herbarium codes for collected species.

Appendix S2 Sequencing protocol and accession numbers of newly sequenced species (GenBank).

Appendix S3 Results of the hierarchical clustering analysis (HCA).

BIOSKETCH

The focus of our research group is on macroevolution, biogeography and computational phylogenetics (http://www.unil.ch/phylo/). We put a strong emphasis on computational and mathematical approaches, mixed with field sampling and molecular sequencing and work on diverse groups of animals and plants including grasses, Polygonaceae, Restionaceae and other angiosperms. We are particularly interested in understanding how patterns of biodiversity and the underlying macroevolutionary and microevolutionary processes vary across scales and environmental gradients to affect species morphological evolution.

Author contributions: A.K., P.B.P. and N.S. conceived the ideas; A.K., G.L. and S.B. collected the data; A.K., S.B. and L.M. analysed the data; and A.K., P.B.P. and N.S. led the writing.

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