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Linking Life-History Traits, Ecology, and Niche Breadth Evolution in North American Eriogonoids (Polygonaceae)

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ABSTRACT: Macroevolutionary and microevolutionary studies provide complementary explanations of the processes shaping the evolution of niche breadth. Macroevolutionary approaches scrutinize factors such as the temporal and spatial environmental heterogeneities that drive differentiation among species. Microevolutionary studies, in contrast, focus on the processes that affect intraspecific variability. We combine these perspectives by using macroevolutionary models in a comparative study of intraspecific variability. We address potential differences in rates of evolution of niche breadth and position in annual and perennial plants of the Eriogonoideae subfamily of the Polygonaceae. We anticipated higher rates of evolution in annuals than in perennials owing to differences in generation time that are paralleled by rates of molecular evolution. Instead, we found that perennial eriogonoid species present greater environmental tolerance (wider climate niche) than annual species. Niche breadth of perennial species has evolved two to four times faster than in annuals, while niche optimum has diversified more rapidly among annual species than among perennials. Niche breadth and average elevation of species are correlated. Moreover, niche breadth increases more rapidly with mean species elevation in perennials than in annuals. Our results suggest that both environmental gradients and life-history strategy influence rates and patterns of niche breadth evolution.

Keywords: niche breadth, intraspecific variability, latitudinal niche breadth hypothesis, elevation, phylogeny, Eriogonoideae, climatic niche evolution.

Introduction

The evolution of the ecological niche (Hutchinson 1957) is a fundamental research topic for ecologists and evolutionary biologists. The mode and tempo of niche evolution play important roles in adaptation of species to novel environments (Losos and Ricklefs 2009), influence diversification patterns through speciation and extinction rates (Kozak and Wiens 2010), and contribute to diversity in species communities (Cavender-Bares et al. 2009). At least two niche components contribute differentially to species evolution. On the one hand, each species can occupy a unique fitness optimum along an environmental gradient (Wright 1932). On the other hand, species differ considerably in the degree of niche specialization, with a wider niche signifying greater dispersion of resource use or broader environmental tolerance (Futuyma and Moreno 1988). Understanding the evolutionary dynamics of the niche as an empirical multivariate distribution along diverse types of gradients and variables requires investigation of both niche components.

The evolution of niche breadth, expressed as intraspecific variation in niche occupancy (Colwell and Futuyma 1971), has received less attention in comparison with that focused on niche position. Despite the extensive literature examining niche breadth through the prism of adaptive evolutionary dynamics in in vitro systems (Brown and Pavlovic 1992; Holt 1992; Kassen 2002), only rarely has the evolution of intraspecific niche variation been considered in natural systems, at least ones with more than a handful of species (Ingram et al. 2009; Caitlin Fisher-Reid et al. 2012). Exclusive focus on the evolution of niche position is problematic when species have complex lineage structure, and these lineages differ in their niche characteristics (Pearman et al. 2010). Further, evolution of niche breadth in communities impacts community composition and ecosystem structure and function (Pianka 1974). For instance, the identification of intraspecific niche variation is particularly relevant in examination of groups experiencing ongoing speciation (Kocher 2004), in understanding the ecological diversification of phylogenetically younger clades (Evans et al. 2009), and in discerning mechanisms underlying species range expansion and/or rapid (local) adaptation (Urbanski et al. 2012). Immense variation in niche breadth among species suggests that increased focus on the evolution of niche breadth can

provide insight regarding the evolutionary origins of ecological variation. Moreover, because niche breadth is a character that expresses intraspecific variability, understanding the evolutionary dynamics of niche breadth likely requires integrating both intraspecific (microevolutionary) and interspecific (macroevolutionary) perspectives.

From a microevolutionary perspective, the contributions of distinct genetic mechanisms to the evolution of niche breadth are not entirely clear (Kassen 2002). For example, in experimental populations of *Escherichia coli* grown under distinct thermal conditions, antagonistic pleiotropy drives negative genetic correlations in fitness across environments, limiting the evolution of niche breadth (Futuyma and Moreno 1988; Bennett and Lenski 2007). Further, accumulation of deleterious mutations with habitat-specific expression can impair the competitive ability of generalist species against specialists (Kawecki 2000). Rates of molecular evolution also provide an additional level of complexity but have been considered only rarely in existing theories of niche breadth evolution (e.g., for allelic fixation rates; Whitlock 1996; Kassen 2002). Rates of molecular and niche breadth evolution are likely connected because higher rates of molecular evolution increase the fixation rates of alleles with environment-specific effects, thus influencing the rates at which species adapt and specialize (Whitlock 1996). In addition, among-species variability in rates of molecular evolution is partly associated with species life-history traits, such as age at first reproduction, number and size of offspring, and reproductive life span and generation time (Tsantes and Steiper 2009; Lanfear et al. 2010). For example, adding a long-lived stage in two-stage populations leads in theory to lower rates of adaptive evolution (Barfield et al. 2011). Thus, these life-history properties should be explicitly accounted for when testing hypotheses on the relationships between macroecological variation and rates of molecular and niche evolution. Finally, while rates of evolution of niche optima are negatively correlated with species generation time and positively with molecular rates (Smith and Beaulieu 2009), the extent to which these two characteristics shape evolution of niche breadth remains unaddressed.

From a macroevolutionary perspective, theory predicts that niche breadth evolution is associated with existing latitudinal variation in environmental stability, and in general, generalization should increase toward the poles, where populations experience the highest environmental instability (MacArthur 1965, 1972). For instance, empirical research shows that host specificity, with the number of hosts being equated to niche breadth, decreases with latitude in Palearctic flea species (Krasnov et al. 2008). Further, the existence of latitudinal gradients in the diversity of avian lineages leads temperate species to have larger

ranges and span broader ecological gradients than do tropical species (Salisbury et al. 2012). In contrast, metastudy of 12 major taxa of mammals, birds, and insects (Vázquez and Stevens 2004) shows that niche breadth has evolved to increase with latitude in only two species groups, while five groups display the reverse relationship and five reveal no significant pattern. Similarly, the niche breadth of species may increase with the mean elevation of their distribution (Rasmann et al. 2014). For example, generalism in feeding habits of two groups of herbivorous and nectivorous insects (Buprestidae and Apiformes, respectively) increases with elevation (Pellissier et al. 2012; Rasmann et al. 2014). In contrast, ant communities of the Mojave Desert have relatively constant trophic niche breadths, regardless of elevation (Bernstein and Gobbel 1979). These results suggest that environmental variation that is associated with latitude or elevation may be mechanistically associated with evolved patterns of niche breadth but that the relationship appears group specific.

The Eriogonoideae subfamily (Polygonaceae), which constitutes ~325 species (Kempton 2012), is an excellent group to investigate questions regarding niche evolution. Growth forms of eriogonoids include tiny, fragile annuals; herbaceous perennials; low shrubs; and large, arborescent shrubs (Reveal 1978). The members of the Eriogonoideae are restricted to xeric regions of the New World, with most species confined to the western half of central North America, from the Tropic of Cancer northward to the fiftieth parallel. Ecologically, eriogonoids span broad latitudinal and altitudinal gradients, occur from the seashore to alpine environments, and reach the vegetation limit in low-elevation deserts. About one-third of the species are uncommon to rare in their distribution (Reveal 1978).

In this article, we examine the evolution of climatic niche position and niche breadth in the Eriogonoideae in relation to generation time and macroecological correlates such as latitude and elevation. First, we test whether rates, optima, and selection strength on climatic niche evolution differ between annual and perennial species. We regard niche breadth as intraspecific variation in niche occupancy and do not discuss the role of between-individual niche breadth variation in niche evolution (Bolnick et al. 2003), owing to the lack of experimental data. We focus on climate tolerance as a measure of the breadth of the species environmental niche, because this measure accounts simultaneously for multiple phenotypic traits (Smith and Beaulieu 2009). We use annual and perennial classes as a proxy for generation time. The assumption that annuals and perennials have different generation times is supported by many empirical studies (Hamrick et al. 1979; Andreasen and Baldwin 2001; Whittle and Johnston 2003; Soria-Hernanz et al. 2008; Duminil et al. 2009). With few exceptions and unlike annual species, perennial Eriogo-

noideae species do not flower in their first year (Reveal 1978; Freeman 2005), which is a basic prerequisite for the differences in generation time. Second, we investigate whether differences in rates of climatic niche breadth evolution can be explained by the latitudinal or elevational positions of species. To address these questions, we use phylogeny-based evolutionary modeling and reconstructions of climate niche and geographical range. Our results suggest that rates of climatic niche breadth evolution are at least three times higher in species with longer generation times (i.e., in perennials compared with annuals) and such differences cannot be explained as anticipated by differences in species relative latitudinal position. In contrast, the evolution of climatic niche breadth is associated with elevational differences between annual and perennial species. Our results suggest that both environmental gradients and life-history strategies influence the rates and patterns of niche breadth evolution.

Methods

Climatic Niche Modeling, Niche Breadth, and Geographical Range Estimations

We obtained locality data (SI 1a [SI 1–13 available online]; average of 342 localities per species, ranging from 18 for *Eriogonum contorum* to >2,900 for *Eriogonum fasciculatum*) from Calflora, the Consortium of California Herbaria, and the Global Biodiversity Information Facility databases for 68 species (underlying data and SI are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.46kv1; Kostikova et al. 2013). While we analyze only a quarter of the Erigonoideae species, these species cover most of the geographic distribution of all Eriogonoideae species and are representative of Eriogonoideae taxonomic (25% of species from each subgenus), life history (approximately two-thirds of annuals and approximately one-third of perennials), and niche diversity (SI 1b, SI 1c). We obtained climatic layers at a resolution of 30 arcseconds from the WorldClim database (Hijmans et al. 2005). We generated pseudo-absence points (2,500 points per species) with nonstratified random sampling over the entire study area (SI 1d) using ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA). Because we used observational data, we conducted climatic niche modeling of the species realized niche and not the fundamental niche, which would have required experimental methods on a large number of species (Hutchinson 1957). We conducted ensemble niche modeling using regression trees (CART) and random forests (RF) algorithms. Because CART/RF are insensitive to correlated predictors (Breiman 2001; Strobl et al. 2008; Nicodemus et al. 2010), we kept all 19 bioclimatic variables at the niche

modeling stage but summarized them as principle components for evolutionary modeling (see below). The models were estimated in R (R Development Core Team 2011) using the trees (Ripley 2012), randomForest (Breiman and Cutler 2012), raster (Hijmans and van Etten 2012), and rgdal (Keitt et al. 2012) packages. We followed a published procedure (Cutler et al. 2007) for RF involving 500 trees and 20% of the training data set held out for the model performance assessment. We used a bagging approach (Breiman 2001) for CART to create more generalized and stable classification models. Training data were sampled 500 times, each time extracting 50% of the training data set with replacement. We estimated the probability of species presence by averaging the 500 classification results. Model performance was tested against the remaining 50% of the data set.

We integrated the probability grids from climatic niche modeling with respect to each original climatic variable to estimate species-specific distributions for each variable (Evans et al. 2009). We then sampled randomly with replacement from these distributions 2,000 values from between the 2.5% and 97.5% quantiles and summarized these values on the first three principal component (PC) axes (Ade4 package; Dray and Dufour 2007). We then extracted from each PC species-specific niche position and niche breadth values, where niche positions were the weighted average values for a given species and niche breadths were the variances of species PC scores. These weighted values were calculated using OMI analysis (Doledec et al. 2000; Thuiller et al. 2004). We used Pearson χ^2 (1 and 3 df) and the Lilliefors (Kolmogorov-Smirnov) statistics (Thode 2002) to test the species-specific PC scores for normality and appropriateness for subsequent comparative analysis. We examined the distributions visually to confirm unimodality.

To assess the relationship between the life-history trait and latitude or elevation, we extracted coordinates and elevation values from the WorldClim elevation data set for all species occurrence records. We then calculated mean latitude for annual and perennial life-history classes in two ways. First, we extracted latitude coordinates for each occurrence record, pooled them for each class, and averaged. Second, we computed a centroid for each polygon of species range maps and then pooled data by life-history class to obtain averaged values using ArcGIS 10. Because we had extensive occurrence records for all species, we estimated species ranges directly from these data instead of using modeled species distributions. We minimized uncertainty by calculating species range maps in terms of area of occupancy and extent of occurrence (Gaston 1994). We manually digitized distribution polygons comprising all the occurrence records for a given species to obtain the area of occupancy of the species. We kept multiple poly-

gons when isolated populations or discontinuous spatial ranges were observed. A convex hull was created for each species to obtain the extent of occurrence records. The same approaches were used to calculate species elevational positions for the two life-history classes.

Phylogenetic Reconstruction and Molecular Dating

We reconstructed a phylogeny based on two plastid genes (*matK*, *ndhF*), two plastid intergenic regions (*rbcL-accD*, *trnL-trnF*), and two nuclear genes (*5.8-ITS-18S* block, *LFY*) to assess phylogenetic relationships among the 68 taxa of Eriogonoideae. The data were compiled from sequences available in GenBank (mean sequence length of the concatenated sequence, 2,200 base pairs; range, 419–6,904; median, 1,694.5) and supplemented by our own sequences (Dryad data: http://dx.doi.org/10.5061/dryad .b9m853tp). Four outgroup species—*Oxyria dygina, Fagopyrum esculentum, Fagopyrum gracilipes*, and *Fagopyrum tataricum*—were further added to the DNA matrix (Sanchez and Kron 2008). The DNA matrix was aligned with Mafft (ver. 6; Katoh and Toh 2008) using the default settings and then adjusted by hand to maintain the amino acid reading frame in *matK* and *ndhF* exons. We ran Gblocks (Talavera and Castresana 2007) with default settings to eliminate poorly aligned positions and divergent regions of the DNA alignment. The GTR + Γ model of sequence evolution was selected on the basis of the Akaike information criterion (AIC) for all DNA regions. Maximum likelihood analysis was done with PhyML (ver. 3.0; Guindon et al. 2009) using the SPR branch swapping algorithm and 10^3 bootstrap replicates to assess node support. We determined the tree topology by Bayesian inference with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) before conducting the divergence time analysis. We obtained the posterior distribution of phylogenetic trees with GTR + Γ parameters being unlinked for the plastid genes, plastid intergenetic regions, and nuclear genes (three GTR + Γ estimates in total). We repeated the MrBayes analyses four times and determined convergence by examining trace plots of each parameter in Tracer (ver. 1.4). Each analysis consisted of four chains of 10^8 generations, sampling every 10^3 steps.

Divergence time analysis was performed in BEAST (ver. 1.4.7; Drummond and Rambaut 2007). The root of the group was constrained by setting a normally distributed prior with a mean of 23.5 million years and a standard deviation of 4.5 million years (SI 2). One more internal node (root of *Chorizanthe* clade) was constrained with a fossil age obtained from the Paleobiology database (http: //paleodb.org; SI 2). We placed this fossil on the root of the *Chorizanthe* clade according to the topology retrieved from the MrBayes analysis (e.g., the *Chorizanthe* clade ex-

cluding *Chorizanthe spinosa* and *Chorizanthe rigida* species). The BEAST analysis was run using a random starting tree for 10^8 generations sampling every 10^3 generations under the uncorrelated lognormal relaxed clock model, the Yule tree prior, and the GTR + Γ model of substitution (same partitioning as for the MrBayes analysis). The analyses were repeated four times to verify convergence by examining the posterior distribution of parameters in Tracer. All subsequent analyses (see below) were done on a sample of 100 trees randomly drawn from the posterior distribution of dated trees after removing a burn-in of 3,000 trees. A consensus tree for graphical purposes was calculated after the removal of a burn-in period (30% or 3,000 samples), which was determined by examining trace plots in Tracer. In addition, the tree log files with branch lengths in nucleotide substitutions were recorded for subsequent calculation of rates of molecular evolution per branch.

Evolutionary Modeling

We conducted an evolutionary analysis with respect to the life-history trait (annuals and perennials), used as a proxy for generation time. This trait was determined for all eriogonoid species using the Flora of North America (SI 3; Freeman 2005). We performed a phylogenetic ANOVA (Revell 2012) to determine whether latitudinal, elevational, and niche positions—as well as niche breadth and species geographical ranges—differed between annuals and perennials. We tested the relationship between niche breadths and mean latitudinal or elevational positions using a phylogenetic GLM model (Orme et al. 2011), with niche breadth serving as the dependent variable, latitude or elevation as the independent ones, and the life-history trait as a covariate.

We compared the fit of the following models to determine the necessary level of model complexity to describe niche evolution using the OUwie package (Beaulieu et al. 2012): (1) a Brownian motion model of evolution with a single rate parameter σ (BM1; Felsenstein 1985); (2) a Brownian motion model with two rate parameters σ_a and σ_p, estimated independently for annuals and perennials (BMS; O'Meara et al. 2006); (3) an Ornstein-Uhlenbeck model with a single trait optimum parameter θ (OU1; Hansen 1997); (4) an Ornstein-Uhlenbeck model in which trait optimum parameters θ_a and θ_p were estimated separately between the annuals and perennials (OUM; Butler and King 2004); (5) an expanded Ornstein-Uhlenbeck model in which both the rate parameters σ_a and σ_p and the trait optima parameters θ_a and θ_p could differ between the annuals and perennials (OUMV; Beaulieu et al. 2012); (6) Ornstein-Uhlenbeck models that assume different strength of selection α_a and α_p between annual and pe-

rennial species (OUMA; Beaulieu et al. 2012); and (7) an expanded Ornstein-Uhlenbeck model in which both the rate parameters σ_a and σ_p and the strength of selection parameters α_a and α_p could vary between annuals and perennials (OUMVA; Beaulieu et al. 2012). We applied the same set of seven models to analyze separately the evolution of niche position and niche breadth.

Five models (BMS, OUM, OUMV, OUMA, OUMVA) in the analysis required ancestral state reconstructions of a categorical trait (i.e., whether a particular branch belongs to the annual or perennial state). We obtained these ancestral states estimates using stochastic mapping (Revell 2012). Two models of discrete trait evolution (symmetrical and asymmetrical) were assessed with the ace function (Paradis et al. 2004), and the best-performing model was used in subsequent analysis. Stochastic mapping was run 10 times for each of the 100 trees to further account for possible uncertainty in the estimated values. Finally, we calculated an average AIC weight and lower (2.5%) and upper (97.5%) quantiles of the distributions of AIC weights for each evolutionary model. We used stochastically mapped ancestral reconstructions of the life-history trait to calculate the mean molecular rate for each life-history class because the rates of molecular evolution obtained from BEAST analysis are branch specific. The estimated ancestral reconstructions were rescaled to branch-wise proportions and then summarized for each life-history class.

Results

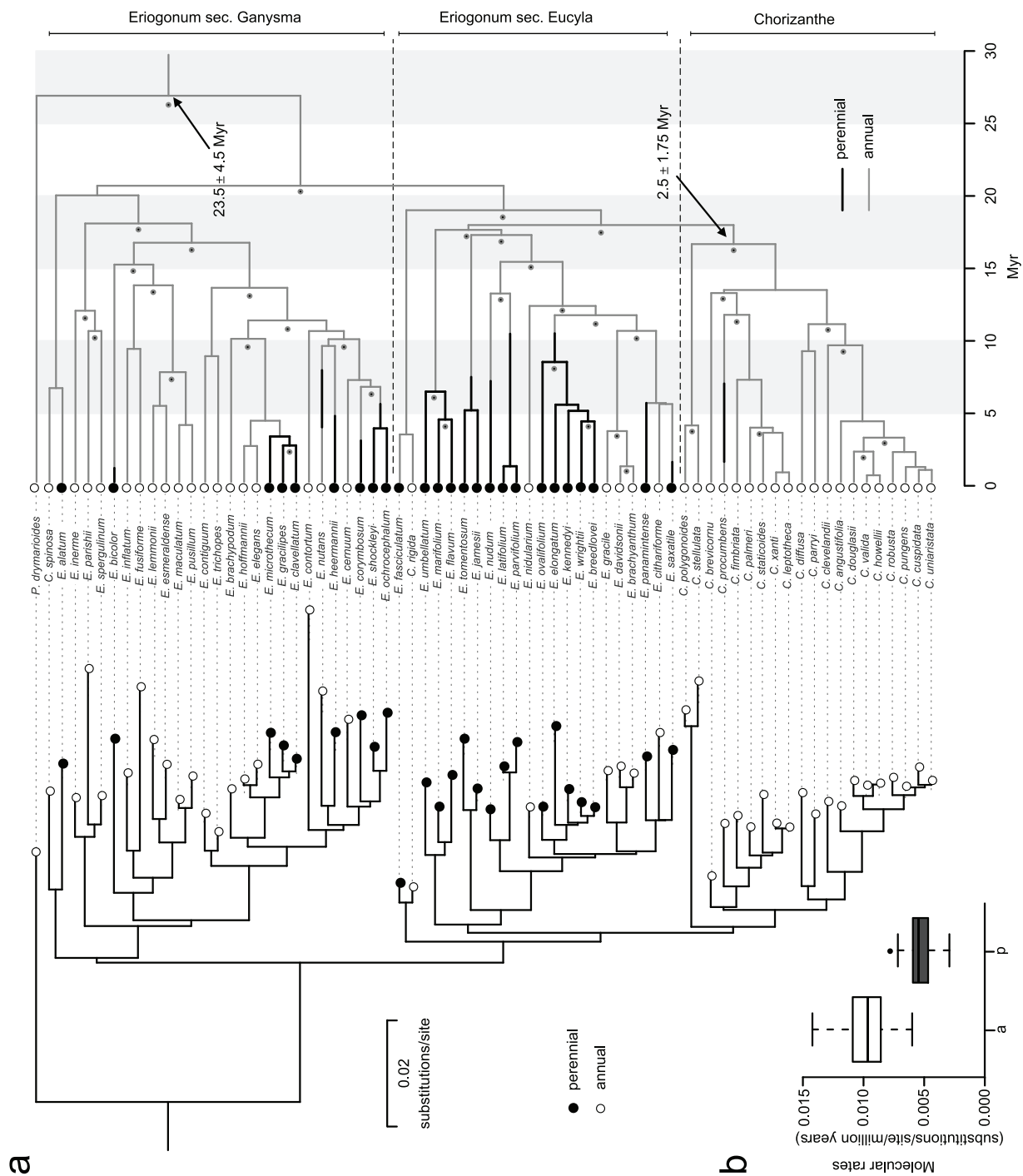### Climatic Niche Modeling, Niche Breadth, and Geographical Range Estimations

Values of the area under the receiver operating characteristic curve for climatic niche models range from 0.92 to 0.99 (SI 4), confirming very good model performance (Swets 1988). Overall, the precipitation and maximum temperature of the wettest quarter have the highest relative importance in the models fitted by CART/RF (SI 5). The first (PC1), second (PC2), and third (PC3) components—extracted from the probability grids—explain 43.42%, 30.82%, and 8.48% of the variation, respectively. PC1 is most strongly correlated with temperature seasonality, isothermality, and mean annual temperature (BIO3, BIO4, and BIO1 WorldClim variables), while PC2 represents precipitation and temperatures during the wettest and warmest seasons (BIO16, BIO8, BIO5, and BIO10), and PC3 represents a precipitation and isothermality gradient (BIO17, BIO18, BIO19, and BIO3). All PC scores of species, except for *Chorizanthe spinosa* and *Chorizanthe rigida*, are unimodal and, in the majority of cases (86%), not different from a normal distribution (SI 6). Thus, the mean

and variance values are adequate for phylogenetic comparative analysis as proxies for niche positions and niche breadths (SI 7). In the remaining 14% of cases, we reject the normality hypothesis but find that the kurtosis and skewness of the distributions are not significantly different from the normal expectation (SI 8). The distributions of PC scores for *C. spinosa* and *C. rigida* are not unimodal, and these two species are excluded from further analyses.

The area of occupancy and the extent of occurrence of species express correlated estimates of species geographical ranges (SI 9; $r_{2,66} = 0.76$, $P < .001$), suggesting that either estimate could be used for modeling. We consider only area of occupancy in further analysis. Mean latitudinal
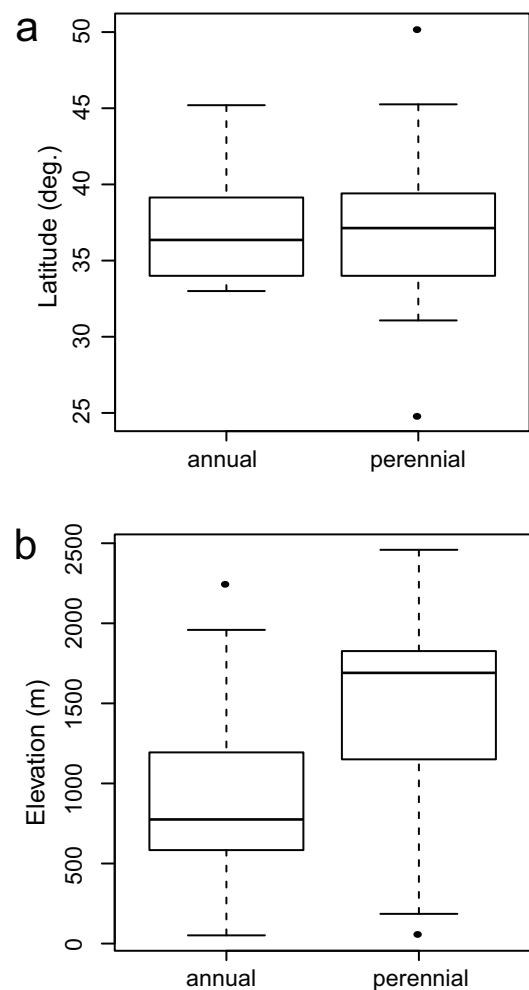
Figure 1: Box and whisker plots showing the latitudinal (*a*) and elevational (*b*) differences between annual and perennial species (medians, upper/lower quartiles, and whiskers of × 1.5 interquartile range are shown). Latitudinal and elevational position have been measured for each occurrence record and then averaged for each species.

Eriogonum sec. Ganysma

Eriogonum sec. Eucyla

Chorizanthe

23.5 ± 4.5 Myr

2.5 ± 1.75 Myr

perennial
annual

Myr

30 25 20 15 10 5 0

P. drymarioides
C. spinosa
E. alatum
E. inerme
E. parishii
E. spergulinum
E. bicolor
E. inflatum
E. fusiforme
E. lemmonii
E. esmeraldense
E. maculatum
E. pusillum
E. contiguum
E. trichopes
E. brachypodum
E. hoffmannii
E. elegans
E. microthecum
E. gracilipes
E. clavellatum
E. contortum
E. nutans
E. heermannii
E. cernuum
E. corymbosum
E. shockleyi
E. ochrocephalum
E. fasciculatum
C. rigida
E. umbellatum
E. marifolium
E. flavum
E. tomentosum
E. jamesii
E. nudum
E. latifolium
E. parvifolium
E. nidularium
E. ovalifolium
E. elongatum
E. kennedyi
E. wrightii
E. breedlovei
E. gracile
E. davidsonii
E. brachyanthum
E. panamintense
E. cithariforme
E. saxatile
C. polygonoides
C. stellulata
C. brevicornu
C. procumbens
C. fimbriata
C. palmeri
C. staticoides
C. xanti
C. leptotheca
C. diffusa
C. parryi
C. clevelandii
C. angustifolia
C. douglasii
C. valida
C. howellii
C. robusta
C. pungens
C. cuspidata
C. uniaristata

a

0.02
substitutions/site

● perennial
○ annual

b

Molecular rates
(substitutions/site/million years)

0.015

0.010

0.005

0.000

a   p

position, calculated either as a centroid from range polygons or as an estimate of latitudinal position from the occurrence records (SI 10), does not differ between annual and perennial species ($F_{2,66} = 3.12$, $P = .92$; fig. 1a). In contrast, the mean elevation of perennial species is significantly greater than that of annual species ($F_{2,66} = 13.44$, $P < .05$; fig. 1b). We find no evidence for range size differences between perennial and annual species ($F_{2,66} = 9.26$, $P = .071$).

Phylogenetic Reconstruction and Molecular Dating

Both maximum likelihood and Bayesian inference analyses result in congruent topologies with good or moderate node support, with most of the nodes having a posterior probability >0.9 and bootstrap values >80% (fig. 2a, nodes with black dots). The *Eriogonum* and *Chorizanthe* genera are not monophyletic in both maximum likelihood and Bayesian inference analyses, which is consistent with previous studies (Sanchez and Kron 2008; Kempton 2012). *Pterostegia drymarioides* is an outgroup lineage relative to Eriogonoideae, originating 18–31 million years ago (95% highest probability density). Most cladogenesis events in Eriogonoideae occurred during the past 15 million years (fig. 2a). Molecular rates estimated from the phylogeny are 1.5 higher in annuals than in perennials (fig. 2b).

Evolutionary Analysis

The phylogenetic ANOVA of the relationship between niche breadth and the life-history trait reveals wider niche breadth in perennials than in annuals consistently on all ordination axes (table 1; SI 11). On average, the niche positions of annuals and perennials do not differ along the temperature seasonality/isothermality (PC1) or the precipitation/isothermality (PC3) gradients (table 1). In contrast, the perennials occupy colder niches than do annual species (PC2; table 1). The phylogenetic GLM model confirms that perennial species have wider climatic niches than do annuals (fig. 3). The slope of the regression of niche breadth on mean elevation is positive along all three PC axes (fig. 3; PC1: $F_{1,68} = 30.14$, $P < .001$; PC2: $F_{1,68} = 26.81$, $P < .001$; PC3: $F_{1,68} = 7.66$, $P < .001$) and differs between annuals and perennials (table 2). We do

Table 1: Phylogenetic ANOVA table for niche position and niche breadth differences between annual and perennial Eriogonoideae species

	F	SS	MS	df_{effect}	$df_{residuals}$
Niche position:					
PC1	2.855	7.879	182.151	2	66
PC2	19.487**	31.253	105.851	2	66
PC3	.405	.247	40.219	2	66
Niche breadth:					
PC1	21.178**	1.345	4.191	2	66
PC2	20.359**	1.681	5.447	2	66
PC3	22.889*	2.912	10.646	2	66

Note: Results from phylogenetic ANOVA showing the significance of differences in niche position and niche breadth between annual and perennial species. The niche breadth of perennial species differs significantly from the niche breadth of annual species across all principal component (PC) axes. For niche position, only PC2 is significantly different between these two classes.

* $P < .05$.
** $P < .01$.

not detect any effects of latitudinal position on niche breadth (SI 12).

The asymmetrical model of character change used to model the evolution of annuals and perennials does not differ significantly from the symmetrical model (AIC 25.21 and 23.46, respectively; ΔAIC <2); therefore, the simpler model (symmetrical) is used in all subsequent analyses. For the niche breadth analysis, the best-performing model allows different variances in niche breadth values (σ) and optimum niche breadth (θ) for annuals and perennials (OUMV; SI 13; average AIC weights = 0.79, 0.72, and 0.58 for PC1, PC2, and PC3, respectively). Two models compete as second-best model: (1) the OUM model that allows only optimum niche breadth (θ_a and θ_p) to differ between annuals and perennials and estimates a single common variance (σ) in breadth values (average AIC weights = 0.034, 0.17, and 0.13 for PC1, PC2, and PC3, respectively) and (2) the OUMA model permits different strength of selection α_a and α_p between annual and perennial species (average AIC weights = 0.13, 0.12, and 0.21 for PC1, PC2, and PC3, respectively). The OUMV model confirms the presence of two distinct niche breadth optima for annual and perennial species, where niche breadth of perennials exceeds niche breadth of annuals by factors of 1.36, 1.33, and 1.43 for PC1, PC2, and PC3, respectively (fig. 4a). Further, this model reveals consid-

Figure 2: *a*, Phylogenetic trees for Eriogonoideae species (E., *Eriogonum*; C., *Chorizanthe*; P., *Pterostegia*), with molecular branch lengths (*left*) and branches proportional to time (*right*). Nodes with dots have bootstrap support >80% and posterior probabilities >0.9. Nodes marked with arrows were calibrated with fossils during the dating analysis with BEAST, and dates indicated are the upper bounds of the calibration prior. Specific clades of *Eriogonum* and *Chorizanthe* genera are separated with dashed lines and labeled on the dated phylogeny. *b*, Molecular rates estimated separately for annual and perennial species. Branches of the phylogenetic tree are proportional to substitutions per site. Molecular rates are approximately 1.5 times higher in annuals than in perennials. Myr, million years.
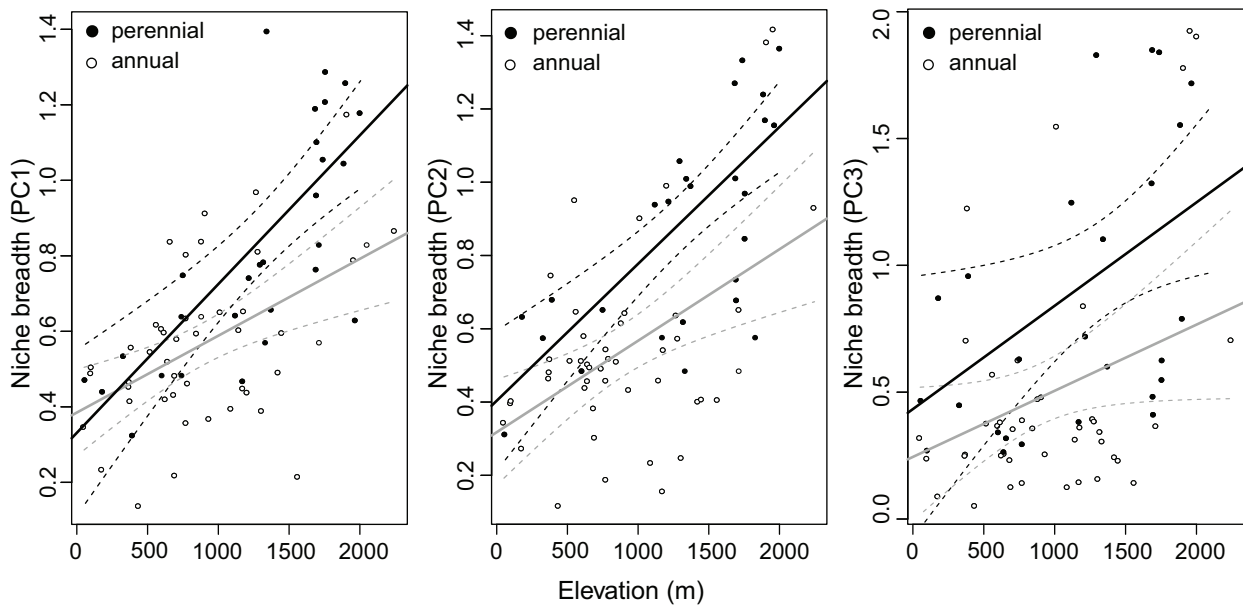
Figure 3: Phylogenetic generalized least squares results that estimate the linear relationship between niche breadth and elevation for scores on the three principal component (PC) axes. The fitted linear regression lines (solid lines) and confidence intervals (dashed lines) are presented independently for annuals (gray) and perennials (black). Scores on axis PC1 express niche breadth along the seasonality, isothermality, and mean annual temperature gradients; scores on PC2 represent niche breadth along the temperature and precipitation gradients; and scores on PC3 represent niche breadth along the precipitation and isothermality gradients.

erably higher rates of niche breadth evolution in perennial than in annual species by a factor of between 2 and 4 ($\chi^2 = 360.3$, 365.4, and 281.8 for PC1, PC2, and PC3, respectively; df $= 1$; all $P < .001$). For niche position analysis, the best-performing model differs depending on the ordination axes (SI 13), but across PC1 and PC2, niche position evolves faster in annual than in perennial species (fig. 4b). For PC1 and PC2, we find that models allowing different rate parameters σ_a and σ_p (BMS) and different rate and optimum parameters (OUMV), respectively, have the highest average AIC weights, while for PC3, the OU1 model with single niche position optimum θ shows the best fit (SI 13).

Discussion

The evolution of the ecological niche is a long-standing research topic in evolutionary biology and macroecology, with both fields offering complementary hypotheses and causal explanations. We examine the evolution of niche breadth in relation to elevation and latitude gradients while explicitly accounting for effects of life-history variation in generation time. We contrast interspecific evolutionary rates of niche evolution, which are more rapid in annuals, to rates of intraspecific niche evolution (evolution of niche breadth) that are higher in perennials, thus accommo-

dating both macro- and microevolutionary perspectives on niche variation. Our results suggest that both environmental gradients and life-history strategies influence rates and patterns of niche breadth evolution. Life-history variation, here expressed as annual and perennial habits, can be strongly associated with evolutionary patterns in niche position and niche breadth.

Testing Macroecological Hypotheses of Niche Breadth Evolution

Niche breadth of Eriogonoideae species increases with elevation (fig. 3). In plant-pollinator interactions in buprestids (Pellissier et al. 2012; Rasmann et al. 2014), a similar trend of increasing ecological generalization with elevation is associated with greater abiotic (temperature, precipitation, and wind) and biotic (vegetation cover) environmental variability. More generally, environmental stability, environmental predictability, and environmental stress can determine patterns of niche specialization (Menge and Sutherland 1976). For instance, in marine soft-sediment faunal communities arranged over gradients of decreasing environmental stress, the most ecologically stable assemblages are the most complex ones and are characterized by a large number of stenotopic species (Menge and Sutherland 1976). Similarly, in Eriogonoideae

Table 2: Relationship between niche breadth and elevation depending on life-history trait in Eriogonoideae species

Dependent variable, covariates	Estimate	SE	t	F	Adjusted R^2
PC1:					
Elevation$_a$	2.3703E−04	6.7236E−05	3.525**	30.12	.4726
Elevation$_p$	1.7290E−04	5.1432E−05	3.362**		
PC2:					
Elevation$_a$	2.6131E−04	7.7699E−05	3.363**	26.8	.4426
Elevation$_p$	1.8621E−04	5.9436E−05	3.133**		
PC3:					
Elevation$_a$	.00029446	.00016711	1.762.	7.66	.17
Elevation$_p$	.00021870	.00012783	1.711.		

Note: Statistical results from the phylogenetic GLM models of the relationship between niche breadth and elevation. Elevation$_a$ denotes a slope parameter between elevation and the niche breadth of annual species. Elevation$_p$ denotes the same but for perennial species, having accounted for annual species. The estimated t value is significant for annual species (Elevation$_a$) and confirms positive association between niche breadth and elevation across all principal component axes. Further, there is a significant difference in slope estimates between annual and perennial species, since the estimated t value is significant for perennials (Elevation$_p$) relative to annuals (Elevation$_a$).

** $P < .01$.

species, broad environmental generalists are typically found at higher elevations (figs. 1, 3), which in southwestern North America exhibit less climatic stability and predictability than found at lower elevations (Schoenherr 1995). Furthermore, high-elevation conditions of the Sierra Nevada and other mountain ranges may be favorable for climatic generalization in eriogonoid species. Conversely, as the climate becomes milder with decreasing elevation, niche specialization is a progressively more successful strategy for eriogonoids, similar to the pattern exhibited by species found along a transect of 14 flower-herbivore communities across central California (Moldenke 1975).

In contrast to niche variation over elevation, we find no evidence for increasing niche breadth with latitude (SI 12), as proposed in the latitude–niche breadth hypothesis (MacArthur 1965). For instance, Vázquez and Stevens (2004)—in their meta-analysis of 12 major taxa of mammals, birds, and insects—conclude that in its classical form, this hypothesis still lacks evidence from experimental studies. However, niche breadth in insects, measured in terms of its spatial (geographic range size) and biological (host specificity) components (Krasnov et al. 2008) and physiological tolerances (Addo-Bediako et al. 2000), increases with increasing latitude. This suggests that the latitude–niche breadth hypothesis holds for some species groups but not for others. Further, in our study, the latitudinal span of perennial species generally overlaps with the latitudinal span of annual species (fig. 1). The lack of support for the latitude–niche breadth hypothesis that we find may reflect the restricted latitudinal range of Eriogonoideae species, which in our study span from 32°N to

45°N. Furthermore, our representative sample includes a quarter of species from the Eriogonodeae subfamily; therefore, expanded analyses or focus on other taxa may be needed to fully understand the interaction between latitude, elevation, and species niche. For instance, other groups with a larger latitudinal range, perhaps spanning both the temperate zone and the tropics, might demonstrate support for the latitude–niche breadth hypothesis.

Life-History Traits Alter Interactions of Niche Breadth with Elevation

The pace at which niche breadth increases with elevation differs between annual and perennial species (fig. 3). First, perennials are generally confined to higher elevations (fig. 1) and are, in general, more frequent above 2,000 m when compared with annuals. Second, the niche breadth of perennials responds more strongly to increasing elevation than that of annuals (fig. 3). This may suggest that perennial eriogonoids are better adapted to higher elevation as a result of some morphological or physiological traits that permit them to survive short growing seasons and seasonal variability at higher elevations. Most perennial erigonoids have resistant and regenerative somatic tissue and can be classified ecologically into either hemicryptophyte or chamaephyte life forms, in which overwintering buds are at or near the soil level, respectively (Raunkiær classification; Raunkiær 1904). These two forms are usually associated with a shift into arctic and alpine tundra, where hemicryptophytes dominate florae in moist to humid temperate areas, and chamaephytes are frequent in flora of high latitudes and elevations. While we focus on the re-
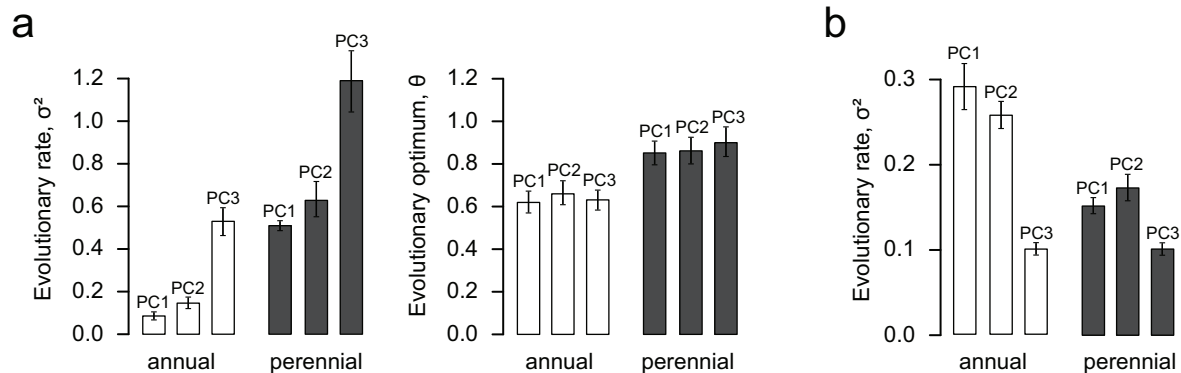
Parameter estimates of the evolutionary models for niche breadth (a) and niche position (b) of annual and perennial species

Figure 4: *a*, Parameter estimates for the OUMV model (different rates σ^2 and optima θ between annual and perennial species) for the evolution of niche breadth show that perennials are characterized by higher evolutionary rates and broader optimum niche breadths compared with annuals across all principal component (PC) axes. *b*, Parameter estimates for the BMS/OUMV models (different rates σ^2) show that niche position of annuals evolves more rapidly compared with that of perennials (note that for PC3, the rate is estimated with the OU1 model).

lationship between perennial versus annual strategies and niche breadth, additional factors—such as effective population size (Kassen 2002), longevity, presence of a seed bank, seed size (Aizen and Patterson 1990), type (Edwards and Westoby 1996), and number—could be involved in evolutionary processes that influence intraspecific niche variation. Further studies may illuminate the relative adaptive performance across environmental gradients by annual and perennial Eriogonoideae species in southwestern North America.

Rates of Interspecific Evolution Are Higher in Annual Species

Recent results show that rates of interspecific evolution of climatic niche in angiosperms are two to 10 times faster in herbaceous than in woody life forms (Smith and Beaulieu 2009). Further, rates of morphological divergence in small mammals (rodents) are four to 11 times higher compared with larger mammal species with longer generation times (Martin and Palumbi 1993). This suggests that life-history attributes, such as generation time, can impose limits to the evolution of phenotypic tolerances. In Eriogonoideae, we find that rates of interspecific niche evolution are higher in annual species (fig. 4*b*). In annual eriogonoids, evolution of niche position occurs most rapidly along the temperature seasonality/isothermality gradient (PC1) and, to a lesser extent, along the temperature/precipitation gradient (PC2). On the one hand, these differences in the evolutionary rates of niche position might reflect the differences in molecular substitution rates and differential generation time, similar to the patterns of cou-

pled phenotypic and molecular evolution found in vascular plants (Davies et al. 2006) and in woody lineages (Smith and Beaulieu 2009). On the other hand, the differential patterns of interspecific evolution in Eriogonoideae may be driven by the high level of endemism that is particularly common in drought-adapted annuals in this subfamily (Reveal 1989). The evolutionary processes responsible for the greater endemism in annual species remain obscure, but complex landscape and climatic heterogeneity should promote niche specialization and speciation in the group (Raven and Axelrod 1978). Further, flowering phenology may also contribute to ecological diversification of annual eriogonoids because sympatric species typically shift pollinators during habitat diversification and speciation (Levin 2006).

Perennials Exceed Annuals in Rates of Niche Breadth Evolution

Species differ considerably in their degree of ecological specialization (Fox and Morrow 1981), and estimates of rates of niche breadth evolution should help to characterize niche evolution in general. In Eriogonoideae, estimates of rates of niche breadth evolution display the opposite pattern compared with estimates of the rate of evolution of niche position. Not only are perennial species characterized by 50% wider climatic niche than annual species (SI 11b), but also rates of niche breadth evolution are two to four times faster in perennials than in annuals (fig. 4*a*). Our analysis shows that tree branches corresponding to perenniality are on average younger than branches corresponding to annuality (fig. 2*a*, stochastic mapping, tree

on the right). The higher rate of niche breadth evolution in perennial clades is also accompanied by a shift into colder environments with abundant rainfall and, typically, higher elevation (SI 11a; PC2). Phylogenetic dating of Eriogonoideae species suggests that this pattern may be associated with species range expansion into novel climatic niches following climatic cool down (Lourens et al. 2004) during the middle and late Miocene and Plio-Pleistocene (<10 million years ago; fig. 2a). This was perhaps coupled with the acquisition of perenniality that permitted necessary physiological and morphological adaptations to shorter growing seasons and limited energy at high elevations (Raven and Axelrod 1978). Detection of complex phylogeographic patterns in perennial eriogonoids might provide evidence of ongoing speciation driven by climate cycling during the Pleistocene and Holocene, as has occurred in the *Eriogonum corymbosum* species complex (Ellis 2009). Annuals may have narrower niches because ecological variation has been partitioned among species, while in perennials this variation is partitioned among subspecific lineages in the process of ongoing speciation.

From Microevolutionary Dynamics to Macroecological Patterns

We suggest that there are at least three sets of factors that influence the evolution of niche breadth in the Eriogonoidae. First, and as discussed above, abiotic environmental factors across spatial and temporal heterogeneities, such as those associated with elevation, provide the necessary background for selective forces to act on niche expansion and contraction. Second, generation time is associated with the evolution of niche breadth across a gradient of increasing elevation. Nonetheless, the selective mechanisms that link generation time to the evolution of niche breadth remain unclear. Putatively, increased substitution rates, typical for short-generation species, could remove nearly neutral and deleterious alleles more rapidly in annuals than in perennials, thus accelerating rates of adaptation and niche specialization (Lynch 2007; Sloan et al. 2012). Consequently, rates of niche specialization should proceed faster in annual species than in perennials when the environment is homogeneous (Whitlock 1996; Kassen 2002). This is reflected in our analysis by higher rates of interspecific niche position evolution in annual than in perennial eriogonoids. In contrast, slower rates (per unit time) of removal of nearly neutral or slightly deleterious alleles in perennial species might leave extensive standing variation at the relevant loci for long periods, even though loss of allelic diversity per generation might not differ between annuals and perennials (Whitlock 1996; Baer et al. 2007). Arguably, the fitness costs of such standing variation in temporally constant environments are substantial (Kassen 2002), while in temporally heterogeneous environments this variation could be removed more slowly, increasing chances of the survival of generalists
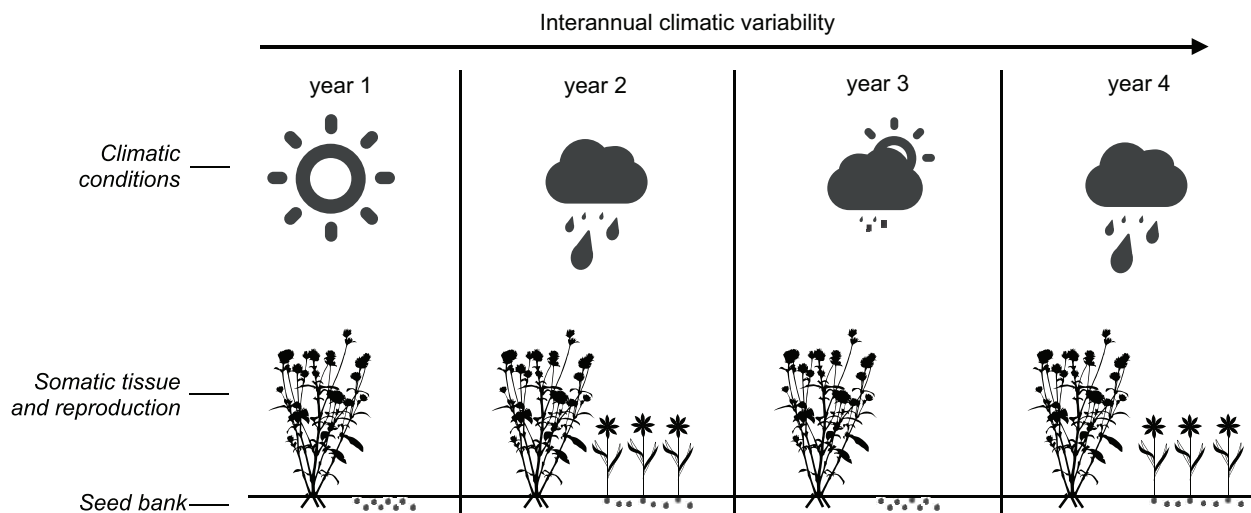
Figure 5: Schematic representation of one hypothesis for the maintenance of broader climatic niche tolerances in perennials than in annuals, in which the interannual variability experienced by perennials exposes them to more diverse regimes that may select for environmental tolerance. Annuals here have a single flowering stem, while the perennial species have several. The figure shows four consecutive years over which a perennial species is exposed to a broad range of climatic conditions. In contrast, annual species germinate only under favorable conditions for growth and reproduction during specific years, indicated here by the rainy cloud, and remain dormant in the seed bank during unfavorable years.

(Whitlock 1996; Kassen 2002). We cannot ascribe interspecific differences in niche breadth to heritable variation in environmental tolerance within species. Consequently, a species might have a broad niche as a result of a ubiquitous genotype with broad environmental tolerance, in the absence of intraspecific variation in tolerance (Futuyma and Moreno 1988). However, the near ubiquity of local adaptation of plants to environment (e.g., Savolainen et al. 2007) suggests the existence of heritable variation in environmental optima within populations. Nonetheless, an advantage of a broader niche is evident in recent range expansions (Holt 2003), where negative genetic correlation in fitness across heterogeneous landscape patches has not yet evolved in response to selection for specialization.

Third, the differences in rates of accumulation of niche variance between annual and perennial species could also be related to the differences in strength of selection rather than mutation rates and generation times. Such differential selection strength could occur through changes in population size (Bolnick et al. 2011; Walser and Haag 2012) or as a result of the maintenance of specific ecological adaptations in one life-history class compared with the other one (Templeton and Levin 1979). For example, in xeric habitat annuals, formation of a seed bank may serve as an evolutionary filter that causes only a few years from the reproductive cycle to have any true evolutionary impact and to effectively eliminate the selective impact of other years (fig. 5). Soil seed banks greatly reduce the fitness uncertainty generated by cyclical or random environments and free the plant population from having to respond genetically to the fitness conditions realized in every year. In such case, any increase in niche breadth would be quickly wiped away as a result of strong selection on niche breadth and would promote higher rates of evolution in niche position in annual species (Templeton and Levin 1979; Baskin et al. 1993). Our results show (SI 13) that the model including differential selection strength between annuals and perennials is the second-best-supported model after the model with different rates and optima of niche breadth evolution. This suggests that in the Eriogonoideae, differential selection might compete with or complement the model with differential evolutionary rates and optima. Empirically distinguishing between the effects of generation time and selection strength is currently difficult because of the lack of experimental data on seed dormancy and seed banks of both xeric annuals and higher-elevation perennials (Marlette and Anderson 1986; Philippi 1993). In addition, generation time differences, effects of seed pools, and changes in population size are not likely independent (Venable and Brown 1988; Hartl and Clark 1997; Venable 2007) and, thus, could all influence the evolution of niche breadth and position. Field experiments would be necessary to determine the relative contribution of these mechanisms to the evolution of niche breadth.

Conclusion

Niche evolution in the eriogonoids appears to have led to partitioning of environmental tolerance among annual species, while environmental tolerance in perennial species has accumulated within species. It remains unclear whether mechanisms specific to annuals promote reproductive isolation as lineages accrue environmental tolerance or whether mechanisms specific to perennials promote species cohesion. Additional life-history traits should be considered when testing rates of niche evolution, since they may illuminate dependencies between organismal properties, breadth of environmental tolerance, and its evolutionary lability.

Acknowledgments

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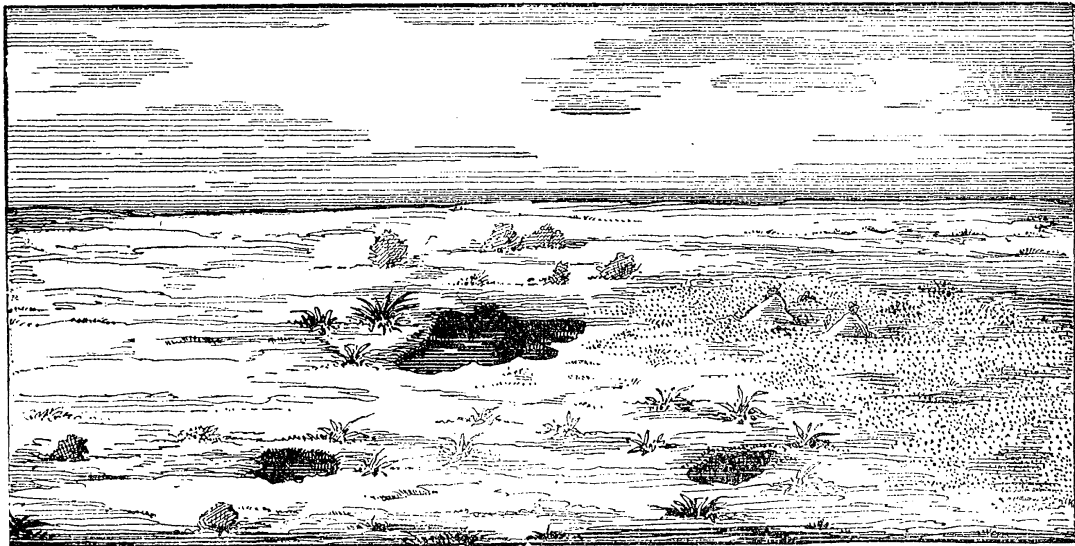
"To those who have experienced the pangs of thirst, while journeying over the desolate wastes that characterize this section, it will not be surprising that reminiscences of water should linger longest in the memory of the traveler. In fact the procurement of that necessity is a matter of such vital importance that all movements are subordinated and controlled by the answer to the question, 'Is there any water there?'" From "The Springs of Southern Nevada" by D. A. Lyle (*American Naturalist*, 1878, 12:18–27).