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Climate, Niche Evolution, and Diversification of the "Bird-Cage" Evening Primroses (*Oenothera,* Sections *Anogra* and *Kleinia*)

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abstract: We integrate climatic niche models and dated phylogenies to characterize the evolution of climatic niches in *Oenothera* sections *Anogra* and *Kleinia* (Onagraceae), and from that we make inferences on diversification in relation to climate. The evolution of climatic tolerances in *Anogra* + *Kleinia* has been heterogeneous, across phylogenetic groups and across different dimensions of climate. All the extant taxa occur in semiarid to arid conditions (annual precipitation of 10.1–49.1 cm and high temperatures in the warmest month of 28.5°–40.1°C), but there is striking variation among taxa in their climatic tolerances, especially temperature (minimum temperatures in the coldest month of −14.0° to 5.3°C) and summer versus winter precipitation (precipitation in the warmest quarter of 0.6–19.4 cm). Climatic disparity is especially pronounced in two subclades (*californica*, *deltoides*) that radiated in the southwestern United States and California, apparently including both divergent and convergent evolution of climatic tolerances. This niche evolution is remarkable, given the probable timescale of the radiation (∼1 million years). We suggest that the spatiotemporal climatic heterogeneity of western North America has served as a driver of diversification. Our data are also consistent with Axelrod's hypothesis that

the spread of arid conditions in western North America stimulated diversification of arid-adapted lineages.

Introduction

Determining what processes have generated biodiversity is a major goal of evolutionary biologists, ecologists, and conservation biologists. In the face of anthropogenic climate change, studies of speciation and diversification in relation to climate, in particular, have taken on new importance. The past 15 years have also seen new opportunities emerge for studying the evolution of climatic tolerances and understanding how past climate changes have shaped extant species diversity (e.g., Graham et al. 2006). Georeferenced occurrence data from natural history collections and high-resolution climate data can be combined to predict species' ranges and characterize climatic dimensions of a species' niche (predictive distribution modeling or ecological niche modeling; Peterson et al. 2003; Graham et al. 2004b; Soberón and Peterson 2004; Guralnick et al. 2006). Species-level phylogenies, estimated from DNA sequence data, can be associated with a timescale via relaxed molecular clock methods (Sanderson 2002). Here we use these ingredients in novel ways to characterize the evolution of climatic niches in a particular plant clade, and from that, we make inferences on diversification in relation to climate.

We focus on evening primroses (*Oenothera*) in sections *Anogra* and *Kleinia* (Onagraceae). Recent phylogenetic studies give us confidence that the 19 herbaceous perennials and annuals of *Anogra* and *Kleinia* together form a monophyletic group (Levin et al. 2004; Evans et al. 2005). Further, the diversity of habitats they occupy, their relatively homogeneous morphology, and their similar biotic interactions makes *Anogra* + *Kleinia* a good group in which to focus on abiotic forces as potential drivers of speciation and diversification (as opposed to "key inno-

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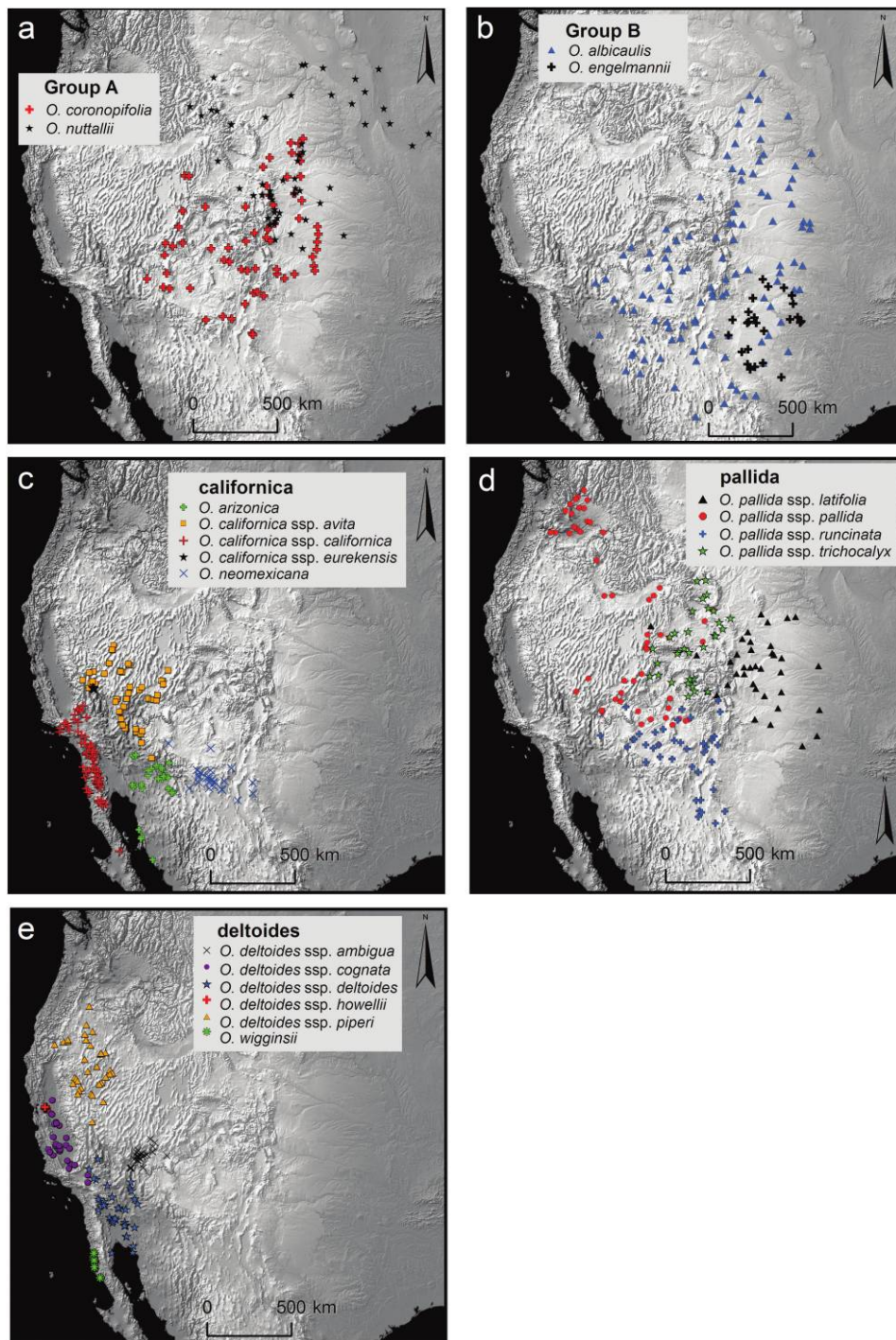
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Figure 1: Locality data for the 19 taxa of sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae) in western North America. These points were used for species distribution modeling. Taxa are arranged in according to five phylogenetically defined groups (see fig. 2*A*). Background shading illustrates the complex topography of western North America.

vations" or coevolution). They occur throughout western North America on loose, coarse-grained soils in a wide range of habitats, from low-elevation deserts of the southwestern United States to semiarid grasslands, meadows, and open sites in forests above 2,000 m in the Rocky Mountain region (Evans et al. 2005; Wagner et al. 2007; fig. 1). All 19 taxa have large white flowers that are visited by widely distributed hawkmoths (particularly *Hyles lineata*) during crepuscular hours and by bees in the morning (Linsley et al. 1963*a*, 1963*b*, 1964; Gregory 1964; Klein 1970). Herbivory by the larvae of *Hyles lineata* and by leaf beetles (Chrysomelidae) is common in all 19 taxa (R. Raguso, M. E. K. Evans, personal observation). This group includes two microendemics that are listed as endangered species (*Oenothera californica* ssp. *eurekensis* and *Oenothera deltoides* ssp. *howellii*; USFWS 1978).

Niche models combined with phylogenetic information can shed light on a variety of important questions about diversification and disparification (Kozak et al. 2008; Pearman et al. 2008; Swenson 2008; "disparification" is a term we use to refer to the evolution of interspecific disparity in morphology, life history, or niche dimensions). Two recent papers that pioneered the integration of niche modeling and phylogenies inferred contrasting roles for niche evolution and climate in speciation. Graham et al. (2004*a*) argued that clear differences between the climatic niches of closely related dendrobatid frogs suggest that adaptation in response to climatic gradients played a role in their speciation. Kozak and Weins (2006) argued that niche conservatism (evidenced by niche overlap) within species pairs of North American salamanders caused them to track particular climates during periods of climate fluctuation, leading to vicariance and lineage isolation and thus speciation. Niche models have not been used to evaluate the tempo of ecological radiation, that is, whether disparity emerged early versus late in a radiation and what that implies about the processes shaping the radiation (sensu Harmon et al. 2003; Kozak et al. 2005; but see the approach of Ackerly et al. 2006). The use of niche models to address paleoclimatic explanations for diversification has only begun (Yesson and Culham 2006*a*) Two such hypotheses are relevant for our study group: (1) the development and spread of arid conditions in western North America is hypothesized to have stimulated diversification of arid-adapted lineages (Axelrod 1958, 1979*a*, 1979*b*), and (2) a second hypothesis is that climatic fluctuations of the Pleistocene might have stimulated diversification (Hewitt 1996, 2000).

In order to address these questions about climate and diversification, we developed tools to integrate niche models with phylogenies and to quantify and visualize niche evolution. First, we used niche models to predict species' occupancy of climatic niche dimensions. From that we quantified climatic disparity among taxa and, hence, the degree to which niches have evolved. Further, we inferred the evolutionary history of climatic tolerances, using methods that account for both intraspecific variability and phylogenetic uncertainty. We considered the temporal development of climatic disparity by evaluating whether the evolution of climatic tolerances was continuous or concentrated at an early versus a later stage of the radiation. Finally, we used the combination of dated phylogenies, predicted geographical ranges, and climatic data extracted from the predicted ranges to address paleoclimatic causes of diversification. Together, these approaches reveal the probable impacts of climate change on the tempo and mode of diversification in *Anogra* + *Kleinia*.

Methods

Phylogeny, Chronology

A previous study showed that the taxa in *Anogra* and *Kleinia* form a monophyletic group (Evans et al. 2005), but the study left much uncertainty about relationships within the group. We sequenced an additional three chloroplast gene spacer regions (*rpoB-trnC, trnD-trnT,* and *trnS-trnG*), using the DNA samples described by Evans et al. (2005; table A1 in the appendix in the online edition of the *American Naturalist*) and the primers and polymerase chain reaction (PCR) protocols of Shaw et al. (2005). All delimited taxa in *Anogra* and *Kleinia* were included (species and subspecies listed in Wagner et al. 2007). Amplified products were cleaned with the QIAquick PCR Purification Kit (Qiagen, Valencia, CA). Cycle sequencing reactions used ABI BigDye Terminator, version 3.1 (Applied Biosystems, Foster City, CA), and all reactions were run on an ABI 3730xl. GenBank accession numbers for all sequences are listed in table A1.

Sequences for six gene regions (*rpoB-trnC, trnD-trnT,* and *trnS-trnG* from this study, plus *ITS, trnH-trnK,* and *trnL-trnF* from Evans et al. 2005) were aligned using Muscle (Edgar 2004) and then adjusted manually. A partition homogeneity test contrasting the six gene regions did not reject the null hypothesis of homogeneity ($P = .05$), justifying analysis of a combined data set. Partition-specific substitution models for the new sequence data were chosen on the basis of Akaike scores using Modeltest (ver. 3.7; Posada and Crandall 1998); *ITS, trnH-trnK,* and *trnL-trnF* were analyzed using the GTR $+ \Gamma$ model, as in Evans et al. (2005). The posterior distribution of trees was explored using the Metropolis-coupled Markov chain Monte Carlo algorithm implemented in MrBayes (ver. 3.1.2; Ronquist and Huelsenbeck 2003). We replicated the MrBayes analysis ($N = 2$) to verify convergence to the same topology. In each analysis, we ran four chains for 10^7 generations, sampling every 10^3 steps.

Assigning a timescale to phylogenies typically involves using dated ingroup fossils to temporally constrain interior nodes. Fossil or pollen data specific to our study group are not available, so we rely on fossil-based dating of the larger clade in which our study group is known to be nested (tribe Onagreae; Levin et al. 2004; Wagner et al. 2007) for calibration. This was the approach of Moore and Jansen (2006) and Goldblatt et al. (2002), who also lacked fossils. A dating analysis for 69 members of tribe Onagreae (including four samples from *Anogra* + *Kleinia*) based on fixed-age nodes from Sytsma et al. (2004) and penalized likelihood rate smoothing (Sanderson 2002) resulted in a stem date of 9.4 million years for *Anogra* + *Kleinia* and a crown date of <1 million years (K. Sytsma, unpublished manuscript). This suggests that the *Anogra* + *Kleinia* lineage has been isolated for on the order of 9 million years but that the extant diversity is quite recent.

Given this temporal information, we performed a Bayesian dating analysis, which allowed us to specify a prior distribution for a chosen node in the phylogeny, reflecting uncertainty about the date of that node. We assigned a standard lognormal prior distribution (mean of 0.0, standard deviation of 1.0) for the root node of *Anogra* + *Kleinia*, offset by 0.01 million years, reflecting the increasingly small probability that the extant diversity is much older than 1 million years (*inset*, fig. 2*B*). Without additional data, the posterior probabilities of divergence times will reflect this prior information. Each individual partition and the combined data set rejected a molecular clock; therefore, divergence times were estimated under a relaxed molecular clock, using the uncorrelated lognormal model (as implemented in BEAST, ver. 1.6; Drummond and Rambaut 2007). In BEAST, we found it necessary to constrain the topology at three nodes for which MrBayes found very strong support (posterior probability $\geq$ 0.98; fig. 2*A*). Convergence to the same joint posterior distribution was confirmed by replicating the BEAST analysis ($N = 2$). In each analysis, we ran one chain for 10^8 generations, sampling every 10^4 steps.

Climatic Niche Modeling

We used ecological niche modeling, also known as predictive distribution modeling (see discussion of these terms in Soberón and Peterson 2005; Peterson 2006), to summarize the climatic tolerances of the extant taxa in *Anogra* and *Kleinia*. Two types of data are required to predict species' ranges: environmental data and information on where species occur. We used current (~1950–2000) data on 19 "Bioclim" variables developed by Hijmans et al. (2005; http://www.worldclim.org), which summarize temperature and precipitation dimensions of the environment (see table 1). We used all 19 of these variables because our study species occur in a wide range of climates
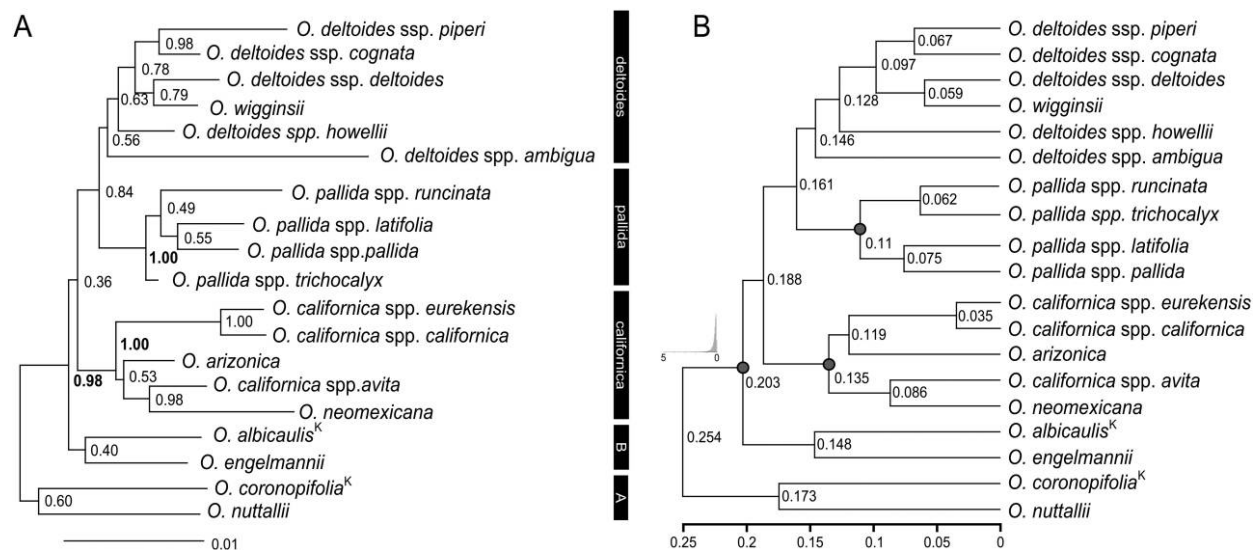

Figure 2: Phylogenetic hypotheses for the "bird-cage" evening primroses (sections *Anogra* and *Kleinia*, *Oenothera*, Onagraceae). *A*, Consensus tree from a Bayesian analysis of DNA sequence data. Posterior probabilities indicate the support for each node; branch lengths are proportional to sequence change. *B*, Consensus chronogram resulting from the dating analysis. Numbers indicate the mean age of each node in millions of years. The two species in section *Kleinia* are indicated with a superscript K. Three strongly supported nodes in *A* that were fixed in the dating analysis are indicated in *B* with gray dots. The lognormal prior distribution assigned for the age of the root node is shown in a small histogram (in millions of years).

Table 1: Trait data for the 19 taxa in sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae)

| | Rocky Mountains and Great Plains | | | | | | | | Southwestern United States and California | | | | | | | | | | | |
| | Group A | | Group B | | *pallida* clade | | | | | *californica* clade | | | | *deltoides* group | | | | | |
Bioclim variable	nut	cor	alb	eng	tri	lat	pal	runc	neo	av	eur	cal	ariz	pip	amb	how	cog	wig	delt
1. Mean annual T	6.6	8.1	11.6	15.7	6.9	9.0	9.9	11.9	10.3	12.3	14.5	15.2	21.1	9.2	15.0	15.6	16.7	17.9	21.2
2. Mean diurnal range[a]	14.9	16.4	16.3	16.3	16.1	16.1	15.1	17.4	17.4	16.0	16.9	14.9	16.3	16.7	15.7	14.4	15.8	16.2	16.1
3. Isothermality[b]	3.5	4.0	4.1	4.2	3.7	3.8	3.8	4.4	5.0	4.1	4.1	4.9	4.7	4.3	3.9	4.6	4.6	6.0	4.5
4. T seasonality[c]	9.7	8.5	8.4	8.0	9.3	9.2	8.5	7.8	6.5	7.9	8.4	5.5	7.0	7.4	8.4	5.9	6.4	3.9	7.2
5. Maximum T, warmest month	29.0	29.6	32.1	34.4	30.2	31.0	31.7	32.2	28.5	33.5	36.5	31.9	39.0	31.1	36.3	33.1	35.6	32.4	40.1
6. Minimum T, coldest month	−14.0	−11.2	−7.8	−4.0	−13.3	−11.5	−7.9	−6.9	−6.7	−5.1	−4.4	1.6	4.1	−7.1	−3.1	2.3	1.7	5.3	4.1
7. Annual range T[d]	43.0	40.7	39.9	38.4	43.5	42.5	39.6	39.1	35.2	38.6	40.8	30.3	34.9	38.1	39.3	30.8	33.9	27.1	36.0
8. Mean T, wettest quarter	16.0	15.9	19.8	24.2	12.1	17.7	9.3	20.2	16.8	9.0	6.3	9.7	28.2	3.7	8.8	8.2	9.7	13.7	20.9
9. Mean T, driest quarter	−5.5	2.3	5.2	6.2	−2.5	−1.4	13.8	10.8	10.9	14.6	18.6	20.2	23.8	17.9	18.6	22.8	24.3	20.4	24.7
10. Mean T, warmest quarter	19.1	19.1	22.3	25.8	18.9	20.9	21.0	22.0	18.7	22.7	25.5	22.5	30.1	19.0	26.0	23.0	24.9	23.4	30.6
11. Mean T, coldest quarter	−5.9	−2.6	.8	5.2	−5.0	−2.7	−.8	2.0	2.1	2.5	4.0	8.6	12.5	.2	4.5	8.1	8.6	13.3	12.2
12. Annual P	42.1	40.0	40.9	43.4	26.5	42.8	28.2	30.8	49.1	23.2	12.3	35.0	20.9	28.7	20.6	35.1	25.9	18.4	10.1
13. P, wettest month	7.1	6.6	7.4	7.3	3.8	7.3	3.8	5.4	9.4	3.0	1.6	6.5	3.8	4.1	2.6	7.1	5.0	3.6	1.7
14. P, driest month	1.2	1.3	1.0	1.1	1.2	1.1	1.1	.9	1.2	.8	.5	.2	.3	.8	.6	.1	.0	.0	.1
15. P seasonality[e]	5.5	5.0	6.0	5.8	3.6	5.8	3.5	5.5	6.5	3.2	3.2	7.5	6.0	3.8	3.2	8.4	8.0	8.0	5.6
16. P, wettest quarter	18.8	17.3	19.1	18.7	9.8	19.6	10.3	13.9	24.2	8.0	4.2	17.9	9.0	11.3	6.9	18.5	13.7	10.0	4.2
17. P, driest quarter	4.1	4.6	3.7	4.1	4.2	3.9	4.2	3.4	4.5	3.5	2.1	1.3	1.3	3.4	3.0	.5	.4	.2	.6
18. P, warmest quarter	16.8	14.8	16.5	17.0	7.5	17.2	6.3	11.6	19.4	5.2	2.7	3.1	7.4	4.2	4.7	.7	.6	1.2	2.4
19. P, coldest quarter	4.1	5.9	5.3	4.2	4.6	4.1	7.5	5.7	9.6	6.6	4.0	16.7	5.9	10.4	5.9	18.4	13.2	9.7	3.8
Life history	P	P	A	A	A/P	P	P	P	P	P	P	P	A	A	A	P	A/P	A	A
Chromosomes	7, 14	7, 14	7	7	7	7	7	7	7	7	7	14	7	7	7	7	7	7	7

Note: We list the weighted mean for each of 19 Bioclim variables (Hijmans et al. 2005) predicted by species distribution modeling (T is temperature in degrees C, P is precipitation in cm), life history (perennial vs. annual [P vs. A, respectively]), and the haploid number of chromosomes. The taxa are grouped according to the phylogeny shown in figure 2a and according to their predominant geographic area (fig. 1). Within phylogenetic groups, the taxa are ordered by mean annual temperature from cooler to warmer. Key to *Oenothera* species abbreviations: alb = O. albicaulis, amb = O. deltoides ssp. ambigua, ariz = O. arizonica, av = O. californica ssp. avita, cal = O. californica ssp. californica, cog = O. deltoides ssp. cognata, cor = O. coronopifolia, delt = O. deltoides ssp. deltoides, eng = O. engelmannii, eur = O. californica ssp. eurekensis, how = O. deltoides ssp. howellii, lat = O. latifolia, neo = O. neomexicana, nut = O. nuttallii, pal = O. pallida ssp. pallida, pip = O. deltoides ssp. piperi, runc = O. pallida ssp. runcinata, tri = O. pallida ssp. trichocalyx, and wig = O. wigginsii.

[a] The mean of the difference between monthly maximum temperature and minimum temperature.

[b] Mean diurnal range as a percentage of annual range of temperature ([Bioclim 2/Bioclim 7] × 100).

[c] The standard deviation of monthly mean temperature multiplied by 100.

[d] The difference between the maximum temperature in the warmest month and the minimum temperature in the coldest month.

[e] The coefficient of variation of monthly mean precipitation.

and elevations in North America. The landscape of western North America is topographically heterogeneous, so we used high-resolution data: a grid size of 30″, which corresponds to ~1 km² at the equator. Because we did not include information on biotic interactions or soils, we refer to our niche modeling effort as "climatic niche modeling."

The 19 taxa in *Anogra* and *Kleinia* are charismatic, well studied, and well collected (Spach 1835; Munz 1931; Klein 1962, 1964, 1970; Wagner 1998; Wagner et al. 2007), providing a wealth of high-quality locality data. Descriptions of collection localities, derived from the labels on herbarium specimens, were used to build a database of occurrences of the study taxa. Such locality descriptions were compiled from specimens loaned by six herbaria (Rancho Santa Ana Botanic Garden; University of Nevada, Las Vegas; University of California, San Diego; University of New Mexico; University of California, Berkeley; and University of Arizona). To this, we added localities identified by Warren Wagner (Smithsonian Institution) based on specimens at the U.S. National Herbarium. We used Biogeomancer (Guralnick et al. 2006) to generate georeferenced coordinates from as many of these localities as possible. A small number of points were removed because they were well outside the expected range of a taxon and were not collected by known experts. We removed duplicate localities. The number of localities available for the two endangered species was limited, since each occurs on a unique dune system (*Oenothera californica* ssp. *eurekensis* on the Eureka Dunes, CA, and *Oenothera deltoides* ssp. *howellii* on the Antioch Dunes, CA). We added extra points within the spatial extent of these dune systems to reach a minimum number of points (10–20; Hernandez et al. 2006) for climatic niche modeling. The final number of points per species ranged from 10 (*Oenothera wigginsii*) to 111 (*Oenothera albicaulis*; table A2).

To predict species' climatic niches, we used Maxent (ver. 2.3.0; Phillips et al. 2006), which performed well in a recent comparison of methods (Araujo and Rahbek 2006; Elith et al. 2006). It has the advantage of requiring only presence data and performs relatively well with small samples (as few as 10 points), which are inevitable in the case of microendemics (Hernandez et al. 2006; Pearson et al. 2007). Maxent uses a maximum entropy method to predict habitat suitability as a function of environmental variables (here, the 19 Bioclim variables). This prediction takes the form of a two-dimensional probability distribution; that is, predicted suitability per landscape unit (s_{ij}) summed across the study landscape is equal to 1.0 (known in Maxent as "raw probabilities"). This probability distribution has maximum entropy (i.e., is closest to a uniform distribution), subject to the constraint that the expectation for each environmental variable closely matches its empirical average across the presence localities. We parti-

tioned the locality data into training and testing data (75% and 25%, respectively) for model evaluation but used all points to build the models used for subsequent analyses. Model performance was evaluated using AUC, the area under the receiving operating characteristic (ROC) curve (table A2). AUC ranges from 0.5 for a model that performs no better than random to 1.0 for perfect ability to predict presence versus absence. Maxent uses randomly selected pseudo-absences instead of observed absences, thus, AUC (as implemented in Maxent) quantifies the degree to which the model identifies presences more accurately than a random prediction (Phillips et al. 2006).

Niche Occupancy, Disparity

While ecological niche modeling and phylogenetic analysis are well-trodden methodological paths, integrating output from these two is still an area of development. Maxent is a preferred method for niche modeling (Elith et al. 2006), but it has not been clear how its output could be linked to the original climate variables and used in a phylogenetic context (Yesson and Culham 2006*b*). Approaches thus far have been to use other niche modeling methods that make predictions with respect to climate (predictions about maximum and minimum tolerances; e.g., Graham et al. 2004*a*; Yesson and Culham 2006*a*, 2006*b*) or extract climate data from localities (Evans et al. 2005; Ackerly et al. 2006; Knouft et al. 2006; Stockman and Bond 2007); these data are then used to reconstruct ancestral climatic tolerances. Our goal was to use Maxent predictions about the suitability of the landscape to quantify species' tolerance or occupancy of climatic niche dimensions, for use in subsequent analyses of niche evolution. We did this by integrating Maxent probability distributions with respect to each original climate variable. In the cartoon example in figure 3*f*, the total suitability of those units in the landscape where mean annual temperature is 5°, 6°, 7°, 8°, 9°, and 10°C is 0.08, 0.18, 0.34, 0.18, 0.12, and 0.07 (which sums to 1.0), respectively. A script is available on request (from S. A. Smith) to bin Maxent "raw probabilities" according to climate data in this manner. The result is unit area histograms of suitability that illustrate a species' (predicted) occupancy of each climate variable.

Niche overlap can be quantified by comparing predicted climate occupancy profiles. If two taxa occupy entirely different niches (with respect to a particular climate variable), the absolute value of the difference between the two unit area histograms is 2.0; thus, we divide the difference by 2 and subtract from 1.0 to create an index of niche overlap (θ) that ranges from 0 to 1.0:
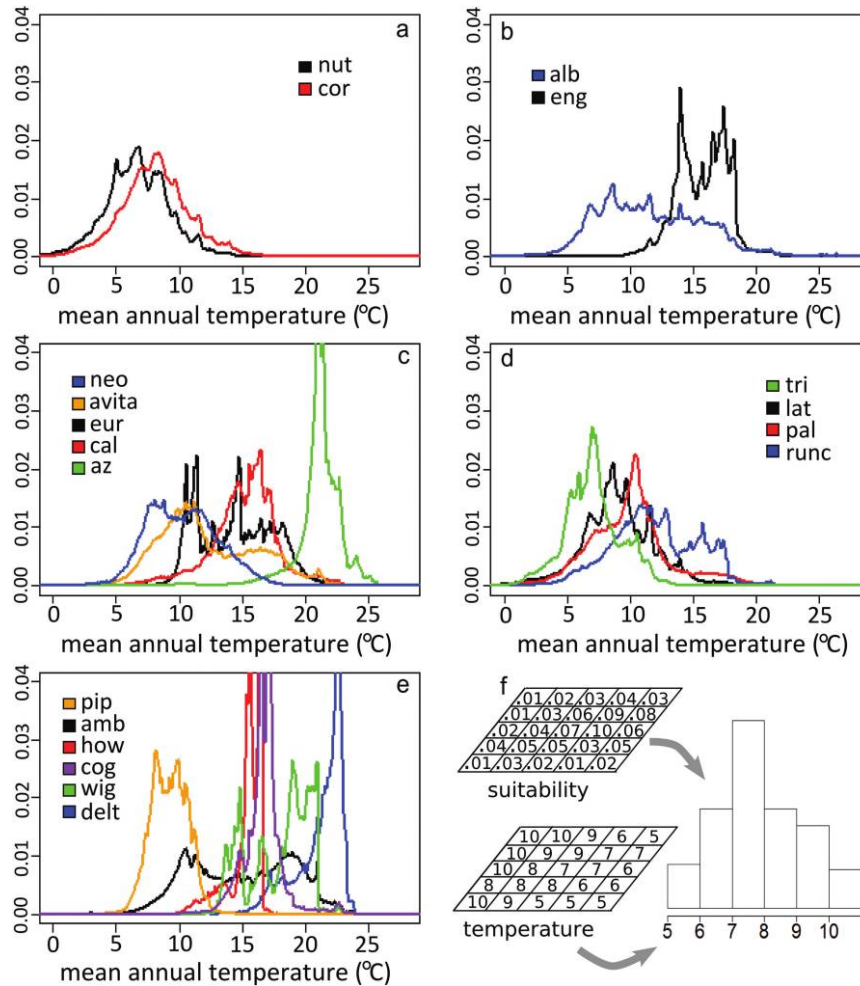
Figure 3: Predicted niche occupancy, with respect to mean annual temperature, of the 19 taxa in sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae). The taxa are grouped in *a–e* with their closest relatives (see fig. 2); *f* illustrates the process of generating such histograms from climate data and predicted suitability (Maxent "raw probabilities"). Suitability is summed according to the temperature data with which it is associated (see "Methods"). Species abbreviations are defined in the table 1 note.

$$\theta = 1 - \left[\frac{\sum \mathrm{abs}(p_{iA} - p_{iB})}{2}\right],$$

where p_{iA} and p_{iB} are total predicted suitability at a given value (i) of a climate variable for species A and B, respectively. Supposing that the example in figure 3*f* comes from species A: $p_{5A} = 0.08$. This kind of index of niche overlap was first introduced by Feinsinger et al. (1981; see Gotelli and Graves 1996). We calculated this index using only extant taxa, grouped according to the phylogenetic results (fig. 3).

History of Niche Occupancy

Comparing the niches of extant taxa avoids the problems associated with reconstructing the character states of hypothesized ancestors (Cunningham et al. 1998; Graham et al. 2004*a*) but forgoes information on the directionality of niche evolution (Knouft et al. 2006). In order to make inferences on convergent versus divergent niche evolution in the *Anogra* + *Kleinia* radiation, we calculated the maximum likelihood estimate for each climate variable at each interior node under the assumption of Brownian motion evolution (as described by Schluter et al. 1997). We repeated this process using 100 random samples from the niche occupancy profiles for the extant taxa. This method

reconstructs the distribution of climatic tolerance rather than reconstructing the maximum, minimum, or mean tolerance (in contrast to Graham et al. 2004*a*; Evans et al. 2005; Ackerly et al. 2006; Yesson and Culham 2006*a*, 2006*b*; Stockman and Bond 2007; and others). We were motivated both by the desire to take into account intraspecific variability (as discussed in Hardy and Linder 2005 and Hardy 2006) and by the observation that species' tolerances of climate do not always follow a normal distribution (see *O. deltoides* ssp. *ambigua* [*amb*] in fig. 3*e*) and thus may not always be well described by a mean and variance. Our method differs from those of Ives et al. (2007) and Felsenstein (2008) in that it is nonparametric. Further, our method was developed explicitly to reconstruct a probability distribution that captures intraspecific variability (the histograms of fig. 3), whereas the methods of Ives et al. (2007) and Felsenstein (2008) aim at accounting for measurement error (with respect to the mean value of a trait). We repeated this process on a thinned sample ($N = 1{,}000$) from the posterior distribution of ultrametric trees to take into account phylogenetic uncertainty (as discussed by Donoghue and Ackerly [1996]). This code is open source and available on request from S. A. Smith.

Accumulation of Disparity

Relative disparity plots (Harmon et al. 2003) are a useful way to quantify the distribution of disparity within versus among subclades (thus measuring niche evolution vs. conservatism) and evaluate the temporal development of disparity. Here, disparity is the mean of squared pairwise differences between extant taxa with respect to mean predicted climate occupancy. This measure of disparity does not take into account intrataxon variability in niche occupancy, but it does capture the increasing disparity of nonoverlapping climate profiles that are increasingly distant from one another (in contrast to the index above). Disparity is calculated for each subclade defined by the $n - 1$ interior nodes in the phylogeny (where n is the number of extant taxa) and then standardized relative to the disparity of the entire clade. At the depth of each interior node, mean relative disparity is calculated among all subclades whose lineages were either present or originated then. Thus, relative disparity declines from 1.0 (at the stem) to 0 (at the tips). We then calculated the morphological disparity index (MDI; Harmon et al. 2003; Kozak et al. 2005), which compares observed disparity to that expected under an unconstrained, Brownian motion model of evolution. Negative values of MDI indicate that disparity tends to be distributed among subclades (because of niche evolution among subclades and conservatism within subclades), whereas positive values of MDI indicate that disparity tends to be distributed within subclades (because of niche evolution within subclades). This analysis

was implemented using the GEIGER library in R (Harmon et al. 2008). Because there is still uncertainty about the phylogeny for our group, we repeated this exercise using a sample ($N = 300$) of posterior trees (Donoghue and Ackerly 1996).

Results

Phylogeny, Chronology

The *rpoB-trnC*, *trnD-trnT*, and *trnS-trnG* sequences (1,270, 877, and 1,655 aligned characters, respectively) increased our total sample to 6,491 characters. We identified (and discarded) a burn-in phase, the first 10^6 generations of MrBayes output, by plotting time series of parameters and checking for consistency across replicate analyses. Examination of the two posterior samples revealed that they converged on the same topology, thus, the two post-burn-in samples were combined and summarized into a majority-rule consensus (fig. 2*A*). The data matrices and post-burn-in trees resulting from the MrBayes analysis are available from TreeBASE (http://www.treebase.org). In the consensus tree, geographically overlapping *Oenothera nuttallii* and *Oenothera coronopifolia* form a group that is sister to the remaining taxa (group A; fig. 2*A*). Both have diploid and tetraploid populations, whereas the remaining taxa (except *Oenothera californica* ssp. *californica*) are diploid (table 1; Wagner et al. 2007). Geographically overlapping *Oenothera albicaulis* and *Oenothera engelmannii* form a second group (group B), which is sister to the remaining taxa (fig. 2*A*). *Oenothera coronopifolia* and *O. albicaulis* were previously placed in section *Kleinia* (Munz 1935); however, our results indicate they do not form a clade (fig. 2*A*; as in Evans et al. 2005).

We recovered a very well-supported clade that groups *Oenothera neomexicana* with the three subspecies of *O. californica* (*avita*, *californica*, and *eurekensis*) and *Oenothera arizonica* (formerly *O. californica* ssp. *arizonica*; fig. 2*A*). Among the remaining taxa, the four subspecies of *Oenothera pallida* (*latifolia*, *pallida*, *runcinata*, and *trichocalyx*) clearly form a clade (fig. 2*A*). This leaves the five subspecies of *Oenothera deltoides* plus *Oenothera wigginsii*, which may or may not form a clade (posterior probability = .56).

We removed the first 10^7 generations of BEAST output as burn-in, based on examination of the trace plots of parameters. Examination of the two posterior samples revealed that they converged on the same topology, thus, the two post-burn-in samples were combined and summarized into a majority rule consensus chronogram (using TreeAnnotator, ver. 1.4.1; fig. 2*B*). The mean date for the most recent common ancestor of the extant *Anogra* and *Kleinia* taxa is 0.254 million years, reflecting the prior

distribution for this node. Many of the interior divergences are dated to 200,000–100,000 years ago, and most of the sister relationships between extant taxa are inferred to be less than 100,000 years old. Because this dating analysis relies on unpublished results, we present all analyses that use dated trees on a relative timescale. That is, we make no quantitative inferences based on an absolute timescale.

Climatic Niche Modeling

AUC values for our models range from 0.934 to 1.000 (table A2), which compares well with AUC values reported by Hernandez et al. (2006) and Elith et al. (2006). Maxent uses L-1 regularization to avoid overfitting. We included all 19 Bioclim variables in Maxent modeling, with few points for some taxa, so we report Maxent weights for each climate variable in table A3.

Niche Occupancy, Disparity

Niche modeling of the extant members of sections *Anogra* and *Kleinia* predicts these taxa to occur in semiarid to arid conditions, with relatively little annual precipitation (10.1–49.1 cm) and high temperatures in the warmest month (28.5°–40.1°C; table 1). Beyond this general similarity lies striking variation in a number of climatic niche dimensions (table 1). The three phylogenetic groups found primarily in the Rocky Mountain region (group A, group B, and the *pallida* clade; fig. 1) fall at the cool end of the spectrum for a number of temperature variables (Bioclim 1, 5, 6, 10, and 11 in table 1). Predicted mean annual temperature among these taxa ranges from 6.6° to 15.7°C (table 1; fig. 3*a*, 3*b*, 3*d*). The two groups found primarily in the southwestern United States and California (*californica*, *deltoides*) have temperature profiles ranging from cool to warm (fig. 3*c*, 3*e*). At the extremes in the *californica* clade are *O. neomexicana* (1,800–2,700 m in the sky islands linking the southern Rocky Mountains and the Sierra Madre Occidental) and *O. arizonica* (of the Sonoran Desert; fig. 3*c*). At the extremes in the *deltoides* group are *O. deltoides* ssp. *piperi* (of the Great Basin Desert) and *O. deltoides* ssp. *deltoides* (of the Sonoran Desert; fig. 3*e*). Among these taxa, predicted mean annual temperature ranges from 9.2° to 21.2°C (table 1).

The taxa found in the Rocky Mountain region (group A, group B, the *pallida* clade, and *O. neomexicana*) tend to experience summer rain (Bioclim 18, table 1), though within the *pallida* clade there is a trend from mostly summer precipitation (*O. pallida* ssp. *latifolia* and *O. pallida* ssp. *runcinata* in the Great Plains and southern Rocky Mountains) to mostly winter precipitation (*O. pallida* ssp. *pallida* and *O. pallida* ssp. *trichocalyx* in the Pacific Northwest and northern Rocky Mountains; Bioclim 8, 18, table

1). The taxa in the extreme West and Southwest experience little summer precipitation, including those in the Mediterranean climate of California or in deserts of the southwestern United States (i.e., most of the *californica* clade and the *deltoides* group; Bioclim 18, table 1). Precipitation in the warmest quarter ranges from 0.6 to 19.4 cm (Bioclim 18, table 1), spanning extreme summer drought in California's San Joaquin Valley (*O. deltoides* ssp. *cognata*) to summer thunderstorms at higher elevations in the southern Rocky Mountains (*O. neomexicana*). Modifying this is the signal of summer monsoon rains in taxa of the Sonoran Desert region (*O. arizonica*, *O. deltoides* ssp. *deltoides*; see Bioclim 8, table 1). That is, the taxa of the Sonoran Desert experience little summer precipitation in absolute terms, but a substantial fraction of their total rain arrives in the summer. A few taxa experience quite a bit of winter rain (*O. californica* ssp. *californica*, *O. deltoides* ssp. *cognata*, *O. deltoides* ssp. *howellii*; Bioclim 19, table 1); the latter two are (or can be) perennial in an otherwise annual clade, perhaps in response to this winter rain (Evans et al. 2005).

Pairwise niche overlap is variable among the five phylogenetically defined groups (fig. A1 in the appendix in the online edition of the *American Naturalist*). Niche overlap is greatest in group A and group B, particularly with respect to precipitation variables (Bioclim 12–19; fig. A1). Niche overlap among the *pallida* taxa is mixed: high for some variables (Bioclim 5, 10, 14, 17, and 19) and lower for others (Bioclim 9, 13, 16, and 18; fig. A1). Niche overlap is generally low among the taxa in the *californica* and *deltoides* groups (fig. A1).

History of Niche Occupancy

The evolution of climatic tolerances becomes explicit when we reconstruct the history of niche occupancy. Divergent evolution (within clades) and convergent evolution (among clades) with respect to mean annual temperature and summer versus winter precipitation is apparent (fig. 4*a*, 4*b*; fig. A2), causing the lines connecting putative ancestors with their descendants to cross.

Accumulation of Disparity

The relative disparity plots are constrained to start at 1.0 and end at 0. In between, they are consistent with niche conservatism early in the *Anogra* + *Kleinia* radiation, followed by the development of disparity equal to or greater than that expected under a Brownian motion (unconstrained) model of evolution (fig. 5). This corresponds with the lack of disparity in group A and group B described above and the subsequent radiation into a variety of climates, particularly in the *californica* and *deltoides* groups.
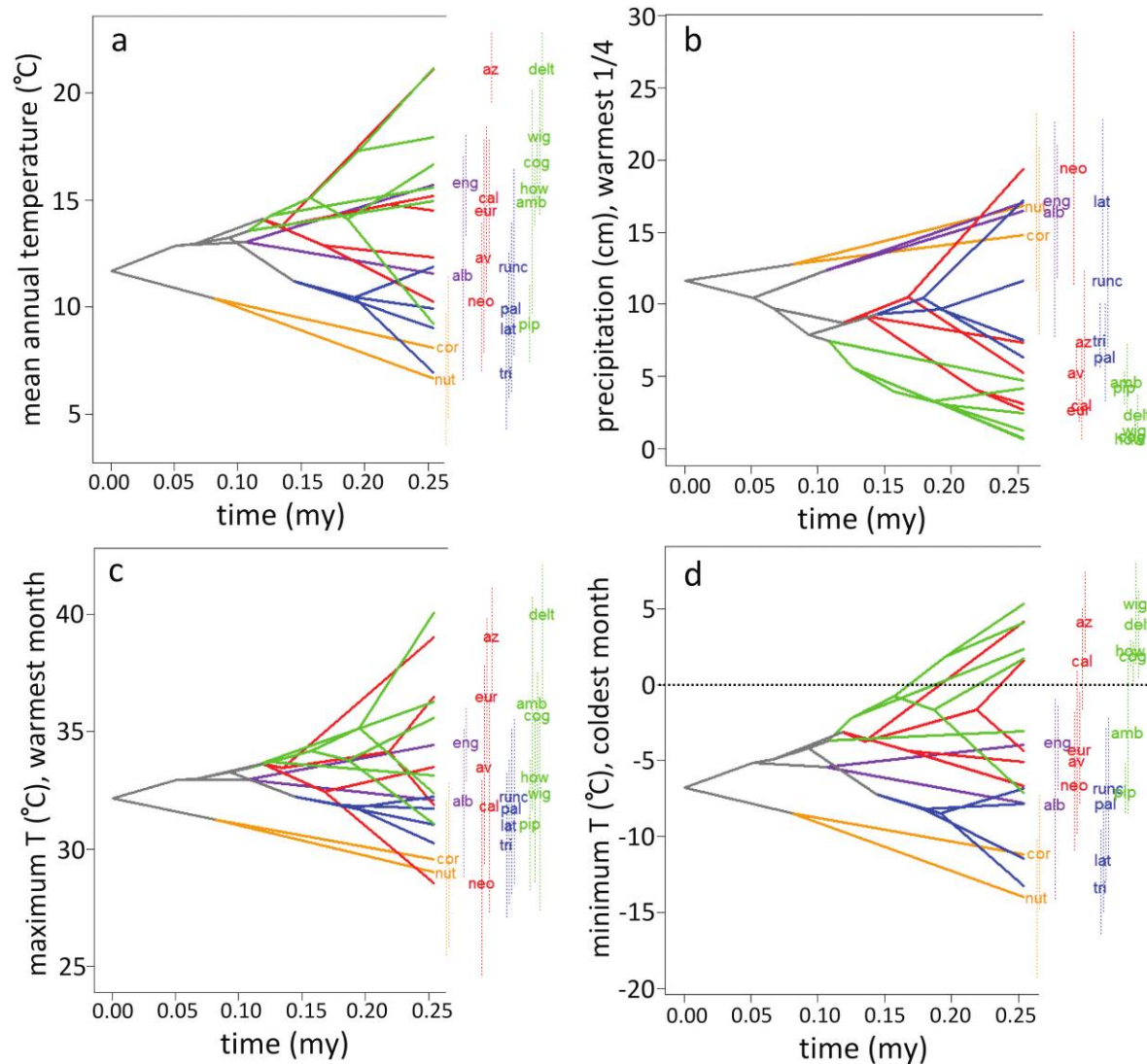
Figure 4: Inferred history of the evolution of climatic tolerances in sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae). We show the maximum a posteriori topology produced by the BEAST analysis. Interior nodes represent the mean of climatic tolerances inferred for the most recent common ancestor of the extant taxa defined by that node (allowing a summary of ancestral states across a posterior distribution of trees with different topologies, as in BayesTRAITS). Solid lines connect ancestors with their descendants. The 80% central density of climatic tolerance for each extant taxon is indicated by a vertical dashed line, and the mean is indicated by the taxon label, to the right of each graph. Lines and labels are colored to identify phylogenetic groups according to figure 2*a*. *a*, Mean annual temperature (Bioclim 1); *b*, precipitation in the warmest three consecutive months (Bioclim 18); *c*, maximum temperature in the warmest month (Bioclim 5); and *d*, minimum temperature in the coldest month (Bioclim 6), with a horizontal line at freezing. Species abbreviations are defined in the table 1 note.

For a number of climate variables, mean subclade disparity is much greater than expected at the last few nodes (e.g., fig. 5*b*, 5*c*), because of exceptional divergences inferred by niche reconstruction involving *O. californica* ssp. *californica* and *O. californica* ssp. *eurekensis* (see fig. 3*c*). The MDI is positive for most climate variables, indicating that overall disparity tends to be distributed within subclades rather than among (fig. A3).

Discussion

Climatic niche modeling of the extant members of *Oenothera* sections *Anogra* and *Kleinia*, combined with phylogenetic information on the relationships among these taxa (fig. 2*A*), reveals both conservatism and evolution of climatic niche dimensions. All members of *Anogra* and *Kleinia* are associated with semiarid to arid conditions, but
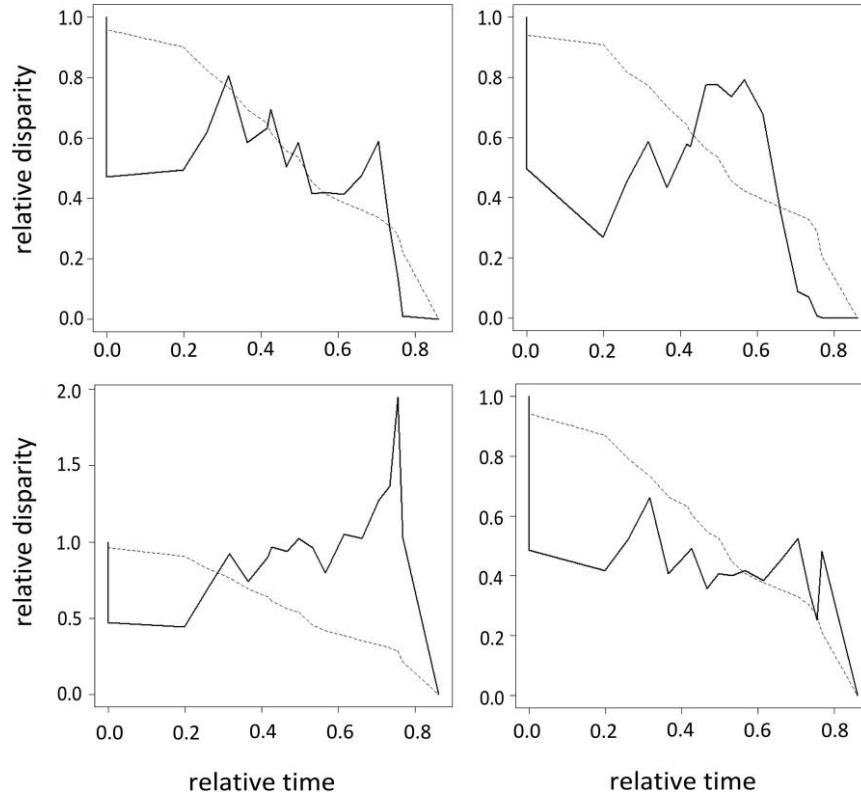
Figure 5: Relative disparity as a function of time for sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae; solid line), compared with mean disparity from 1,000 simulations of Brownian motion evolution of that trait (*dashed line*). Disparity is the mean of the squared pairwise differences between all terminal taxa defined by each node (see "Methods"). *a*, Mean annual temperature (Bioclim 1); *b*, precipitation in the warmest three consecutive months (Bioclim 18); *c*, maximum temperature in the warmest month (Bioclim 5); *d*, minimum temperature in the coldest month (Bioclim 6).

there is considerable variation in their climatic niches, particularly with respect to temperature and summer versus winter precipitation (table 1). Precipitation in the warmest quarter ranges from 0.6 to 19.4 cm, and minimum temperatures in the coldest month are from −14.0° to 5.3°C (table 1). Thus, some taxa experience summer drought and freezing temperatures; others do not. Group A, group B, and the *pallida* clade, which are found in the Rocky Mountains and Great Plains, are generally predicted to experience cooler temperatures and summer rain, whereas the *californica* and *deltoides* groups, which are found in the southwestern United States and California, are predicted to experience a range of temperatures and summer rain to summer drought. Climatic niche reconstruction illustrates that there has been considerable evolution of climatic tolerances, including both divergence (within subclades) and convergence (among subclades; fig. 4), particularly in the *californica* and *deltoides* groups: one representative from each of these groups has converged on a cool niche, and one from each has converged on a warm niche (fig. 4*a*). In the case of *Oenothera deltoides* ssp. *del-*

toides and *Oenothera arizonica*, this convergence reflects the fact that both are found in the Sonoran Desert (though they occupy different parts of the Sonoran Desert; fig. 1*c* vs. 1*e*). In the case of *O. deltoides* ssp. *piperi* and *Oenothera neomexicana*, convergent evolution with respect to mean annual temperature has occurred in spite of the fact that they are found in very different geographic and climatic regions (fig. 1; thus, they show divergent evolution with respect to other climatic niche dimensions). The niche overlap index (fig. A1) confirms that the greatest niche evolution is associated with these two groups. Thus, the evolution of climatic tolerances has been heterogeneous across phylogenetic groups and across different dimensions of climate.

This heterogeneity of niche evolution, particularly the phylogenetic heterogeneity, is reflected in the temporal development of climatic disparity, as inferred from relative disparity plots. The development of disparity appears to have been initially slow (fig. 5), owing to apparent climatic conservatism in groups A and B. Subsequently, average subclade disparity reached or exceeded the level expected

under unconstrained evolution of niches. Overall, climatic disparity tends to be found within rather than among subclades (positive MDI; fig. A3), which is primarily due to the evolution of climatic tolerances in the *californica* and *deltoides* groups. This contrasts with the decelerating pattern of disparification found in some other radiations. Kozak et al. (2005) found deep time shifts in larval microhabitat, followed by niche conservatism, in the radiation of *Desmognathus* salamanders. Ackerly et al. (2006) detected a deep time split in fire recovery strategy in *Ceanothus*, which was subsequently conserved. These patterns suggest a niche-filling process associated with the early phase of radiation, with subsequent diversification involving within-site coexistence of species from different subclades. Harmon et al. (2003) found a similar pattern of decelerating disparity in the radiation of Australian agamid lizards but disparity equal to or slightly greater than that expected under Brownian motion evolution in three other lizard clades.

Overall, our results are most similar to those of Ackerly et al. (2006), who inferred climatic tolerances to be highly labile. However, representatives in our study group of different subclades do not co-occur—unlike in *Ceanothus*—and there are no obvious "α niche" traits relevant to coexistence within communities. Life history does vary in our study group (perennial vs. annual life histories), but this trait is labile, and its evolution is correlated with (the evolution of) climatic conditions (Evans et al. 2005). Rather than being differences that might permit coexistence, perennial versus annual life histories are thought to be competing strategies. Evolutionary lability of climatic tolerances and possible bounds on the attainable climatic "states" may yield homoplasy (Donoghue and Ree 2000), which, combined with the use of a Brownian motion model to infer ancestral states, could compromise our ability to detect the true tempo of climatic niche evolution in *Anogra + Kleinia* (Ackerly et al. 2006). Better integration of emerging alternatives to Brownian motion should improve our ability to understand niche dynamics in evolutionary radiations (e.g., Blomberg et al. 2003; Hunt 2006; Estes and Arnold 2007; Pearman et al. 2008). In addition, an analysis of ecological radiation in the entire Onagreae would provide a better basis for inferring initial conditions and the earliest ecological shifts in *Anogra + Kleinia*. In the meantime, we note that biogeographic analyses of tribe Onagreae (Raven and Axelrod 1978; Katinas et al. 2004) have suggested that occupancy of the Rocky Mountain region (and thus the associated climate) is probably ancestral for *Anogra + Kleinia*, lending support for the idea that this was maintained in the early branching lineages (groups A and B; fig. 1).

Our results indicate that climatic tolerances can evolve over relatively short timescales (10,000–100,000 years) in some organisms, in contrast to the results of Peterson et al. (1999), Prinzig et al. (2001), Martínez-Meyer et al. (2004), and Martínez-Meyer and Peterson (2006), adding to other evidence of rapid trait evolution (Hendry and Kinnison 1999; Hairston et al. 2005; Smith and Betancourt 2006; Herrel et al. 2008; Losos 2008). This should inspire caution about the use of niche modeling to infer past distributions, as discussed by Kozak et al. (2008) and Pearman et al. (2008). We suggest that future research should be directed at understanding why some climatic niche variables are more labile than others and why climatic tolerances are conserved in some groups but not in others.

Moore and Donoghue (2007) recently suggested that biogeographic shifts can stimulate diversification and evolution of disparity (disparification). The *Anogra + Kleinia* clade might provide an example of this pattern. If occupancy of the southern Rocky Mountains and Sierra Madre Occidental is ancestral for the *Anogra + Kleinia* clade (Raven and Axelrod 1978; Katinas et al. 2004), occupation of the more extreme western and southwestern parts of the continent represents movement into a new geographic area. There, both niche evolution and taxonomic proliferation (10 of 19 taxa) have been striking. What mechanism might cause a shift in geography to stimulate diversification and disparification? The geographical, climatic, and phylogenetic data from the *Anogra + Kleinia* taxa suggest that the landscape of western North America has served as a template for their evolution. Indeed, our description of the variety of climatic niches that they occupy reads very much like a description of the climatic diversity of western North America. The extreme western and southwestern part of North America is especially heterogeneous, both topographically and climatically (Brown 1994). Movement into this heterogeneous landscape might have stimulated diversification. Alternatively, it might be that a large ancestral geographic range was subsequently split as climatic change played itself out on the landscape of western North America. These alternative interpretations may be difficult to distinguish, though more certain inferences of the timing of climatic and phylogenetic events would be helpful.

What role can we infer for climate in the speciation process? Like Rice et al. (2003), Graham et al. (2004a), Knouft et al. (2006), and Eaton et al. (2008), we found striking variation in the climatic tolerances of close relatives. However, demonstrating that niche evolution has occurred in a clade does not prove that niche evolution drove speciation, nor does it eliminate a role for niche conservatism in speciation. Considering that speciation can be a multistage process (de Queiroz 2005), it is possible both for vicariance to have arisen through spatiotemporal climatic heterogeneity combined with niche conservatism (as suggested by Kozak and Weins 2006) and for repro-

ductive isolation to have been hastened by adaptation to new environments (as suggested by Graham et al. 2004*a*; see also Lewis 1962; Axelrod 1967; Vanzolini and Williams 1981; Ackerly 2003; and Levin 2005). As a speculative example, *O. arizonica*, *Oenothera californica* ssp. *californica*, and *O. californica* ssp. *eurekensis* may well have been "left behind" during climate-induced migrations of an ancestor similar to *O. californica* ssp. *avita*. *Oenothera arizonica* is the only annual in the *californica* clade, *O. californica* ssp. *californica* is the only tetraploid, and *O. californica* ssp. *eurekensis* is a microendemic (table 1, fig. 1), suggesting an ancestor like *O. californica* ssp. *avita*, a diploid perennial that currently has a distribution abutting or surrounding those of the other three. A more detailed understanding of speciation in the *Anogra* + *Kleinia* clade awaits higher-resolution geographic sampling. Among close relatives that overlap geographically (e.g., the *pallida* subspecies, *Oenothera albicaulis* vs. *Oenothera engelmannii*), we do not know the degree to which lineage sorting is complete, particularly relative to niche overlap versus evolution. The combination of niche modeling and phylogeography holds promise for a better understanding of speciation in response to climatic fluctuations (Carstens and Knowles 2007; Knowles et al. 2007; Stockman and Bond 2007).

The phylogenetic, temporal, and ecological information for the *Anogra* + *Kleinia* clade also allows us to comment on paleoclimatic explanations for biodiversity in western North America. Axelrod (1958, 1979*a*, 1979*b*) proposed that plant lineages already adapted to edaphically arid outcroppings subsequently diversified with the development of more widespread arid conditions in western North America (beginning at 37–33.5 Ma). This hypothesis predicts that the lineages from which the endemic flora of the warm deserts of North America are drawn are much older than the climates that they inhabit. Our study group occupies semiarid to arid climates and has a strong affinity for edaphically arid substrates (Klein 1970; Evans et al. 2005; Wagner et al. 2007). Dating based on fixed-age nodes from fossils suggests a stem date of ∼9.4 Ma for the *Anogra* + *Kleinia* lineage (Sytsma et al., unpublished), predating the development of a seasonally dry (Mediterranean) climate in California (5 Ma; Graham 1999) or the Sonoran Desert (8–9,000 years ago; Van Devender and Spaulding 1979; Bowers 2005), to which extant members of the lineage are endemic. Thus, the data from *Anogra* + *Kleinia* are consistent with Axelrod's hypothesis. The only other phylogenetic analysis of Axelrod's hypothesis also found support for it (Moore and Jansen 2006).

The probable age of the *Anogra* + *Kleinia* radiation (∼1 million years) is at odds with the view that the Pleistocene did not witness the birth of new diversity (Bennett 2004). Instead, this time frame is consistent with the idea that

Pleistocene fluctuations played a role in speciation (Hewitt 2000; Comes and Kadereit 2003). Data from other organisms in the southwestern United States and southern Rocky Mountains have implicated complex topography and climate fluctuations in speciation or genetic structuring (Orange et al. 1999; Knowles 2000; Ayoub and Riechert 2004; Smith and Farrell 2005; Haenel 2007). In these areas, high-elevation features in the landscape may have served as "biodiversity pumps," as described by Rull (2005), since glaciers did not create a tabula rasa at each cycle.

The methods that we have demonstrated here, combining niche modeling and phylogenies, will facilitate a more integrative approach to studying diversification. Linder (2005) recently reviewed the utility of dated phylogenies and climate data for understanding the origins of plant species diversity in the Cape flora of South Africa. He and others (Hardy and Linder 2005; Hardy 2006) have highlighted the need for better methods for inferring the evolution of niches, particularly methods that take into account intraspecific variability in climatic tolerances. Here we have provided a method, beginning with climate and locality data, via ecological niche modeling, for reconstructing ancestral climatic tolerances that takes into account both the intraspecific variability of extant taxa and phylogenetic uncertainty. Our understanding of species-rich regions where complex topography and dynamic paleoecology may have played a role in generating diversity (e.g., the Cape Floristic Region, the Mediterranean, Amazonia, Guyana) will probably benefit from the combination of this method and absolute time (dating) information. An accumulation of such studies should shed light on the general processes shaping radiations, especially when complemented by phylogeographic studies and more detailed paleoecological information.

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