

The effect of range overlap on ecological niche divergence depends on spatial scale in monkeyflowers

Qin Li,^{1,2,3} Dena L. Grossenbacher,⁴ and Amy L. Angert⁵

¹Department of Botany, University of British Columbia, Vancouver, British Columbia, Canada

²Integrative Research Center, The Field Museum, Chicago, Illinois, USA

³E-mail: qin.li@biodiversity.ubc.ca

⁴Department of Biology, California Polytechnic State University, San Luis Obispo, California, USA

⁵Department of Botany and Zoology, University of British Columbia, Vancouver, British Columbia, Canada

Received January 10, 2017

Accepted July 20, 2018

Patterns of niche divergence and geographical range overlap of closely related species provide insights into the evolutionary dynamics of ecological niches. When ranges overlap, shared selective pressures may preserve niche similarity along coarse-scale macrohabitat axes (e.g., bioclimates). Alternatively, competitive interactions may drive greater divergence along local-scale microhabitat axes (e.g., micro-topographical features). We tested these hypotheses in 16 species pairs of western North American monkeyflowers (*Erythranthe* and *Diplacus*, formerly *Mimulus*) with estimations of species' niches, geographic ranges, and a robust phylogeny. We found that macrohabitat niche divergence decreased with increasing range overlap, consistent with convergent selection operating at a coarse scale. No significant relationship was detected for microhabitat niches. Additionally, niche divergence was greater for recently diverged pairs along all macrohabitat niche axes, but greater for distantly diverged pairs along one microhabitat axis related to vegetation cover. For species pairs with partially overlapping ranges, greater microhabitat divergence was detected in sympatry than in allopatry for at least one niche axis for three of four pairs, consistent with character displacement in sympatry. Thus, coarse- and local-scale niche divergence show dissimilar patterns in relation to range overlap and divergence time, perhaps because the relative importance of convergent versus divergent selection depends on spatial scale.

KEY WORDS: *Mimulus*, monkeyflower, niche divergence, range overlap, phylogenetic distance.

Complicated feedbacks between niche divergence, range overlap, and diversification play an essential role in generating patterns of biodiversity on Earth. Niche divergence among species can lead to differences in geographic range position and extent. In turn, differences in geographic range, and hence environments experienced can cause selection for niche divergence. The initial stages of niche and range divergence are intimately related to speciation, while subsequent niche and range evolution can impact which species assemble into a community (Ricklefs and Jenkins 2011; Wiens 2011). In particular, how daughter species inherit niche properties from their common ancestor is often associated with range dynamics (Schluter 2001; Coyne and Orr 2004). In theory, niche divergence could promote speciation in sympatry,

but postspeciation range shifts and niche evolution might remove the signature of initial divergence (Barraclough and Vogler 2000; Losos and Glor 2003). Likewise, species might retain high niche similarity during allopatric speciation, but divergent adaptation to distant environments and interspecific competition during secondary contact might obscure the signature of initial conservatism. Thus, patterns of niche divergence are predicted to differ depending on whether species are sympatric or allopatric and the time since their split from the ancestor.

In areas of allopatry, there are opposing predictions regarding the degree of niche divergence or similarity between close relatives. When geographic barriers of unsuitable environments lead to allopatric speciation (Barraclough and Vogler 2000;

Fitzpatrick and Turelli 2006), species may retain similar niches because of convergent selection in similar though discontinuous habitats. Such a pattern of niche conservatism (the tendency to maintain ancestral niches) is supported across many taxa and geographic regions (Peterson et al. 1999; Wiens and Graham 2005; Pearman et al. 2008; Wiens et al. 2010; and reviewed in Peterson 2011). Niche conservatism on either side of a geographic or habitat barrier ensures that populations are isolated, with no or little gene flow (Wiens 2004). Geographical separation itself could be viewed as a form of premating isolation, while intrinsic reproductive isolation might evolve via accumulated divergence by genetic drift (Coyne and Orr 2004). Alternatively, if allopatric populations experience different environmental conditions or they were genetically differentiated prior to barrier formation, they are more likely to experience divergent selection pressures promoting speciation and increased niche divergence (McCormack et al. 2010; Schemske 2010).

In areas of sympatry, the degree of niche divergence is predicted by the relative strength of convergent selection due to shared environments and divergent selection due to interspecific competition. High range overlap potentially increases encounter frequencies among individuals and hence interspecific competition, leading to selection for greater niche divergence, which is character displacement (Brown and Wilson 1956; Schluter, 2000; Silvertown 2004; Symonds and Elgar 2004; Tobias et al. 2013; Weber et al. 2016). Conversely, environmental filtering stemming from abiotic or biotic factors at a given location sorts preadapted phenotypes in and/or imposes selection for niche convergence. Given strong convergent selection pressure during sorting, species that co-occur should have similar niches (Webb et al. 2002; Kraft et al. 2008; Cavender-Bares et al. 2009; Moullot and Gaston 2009).

By examining niche divergence in multiple species pairs that vary in their degree of range overlap, we can gain insight into which of the processes described above are dominant. For example, a negative relationship between niche divergence and range overlap suggests convergent selection in sympatry and divergent selection in allopatry (i.e., abiotic factors dominate; Fig. 1A). In contrast, a positive relationship between niche divergence and range overlap suggests evolutionary stasis in allopatry and competition driving niche divergence in sympatry (i.e., biotic interactions dominate; Fig. 1D). A lack of relationship suggests that either multiple processes are at play simultaneously, or acting differently among pairs (Fig. 1B and Fig. 1C).

Furthermore, the relationship between niche divergence and range overlap could differ depending on the spatial scale of environmental variation. Macrohabitats represent the conditions that a species can tolerate and persist in at coarse spatial scales, such as range-wide macroclimate and topography. Microhabitats describe local-scale environments of an organism or population,

such as soil moisture and nutrients, micro-topographical features, and light characteristics. Environmental filtering is predicted to favor similarity in coarse-scale niche axes while competitive interactions will favor divergence in local-scale niche axes (Swenson et al. 2007; HilleRisLambers et al. 2012). For example, various ecomorphs of *Anolis* species generally co-occur in the Greater Antilles, but they are able to coexist by partitioning resources at the fine scale by specializing on structural microhabitat (e.g., tree crown/trunk/twig/ground; Losos 2009). This leads to an expectation of more divergence in allopatry for macrohabitat axes, but more divergence in sympatry for microhabitat axes to allow coexistence. Therefore, we expect a negative relationship between niche divergence and range overlap at the coarse scale, but a positive one at the fine scale. However, how biotic interactions constrain or promote niche evolution at the range-wide scale remain poorly explored (Wiens 2011), and more empirical studies are needed to determine which patterns are prevalent across spatial scales in nature.

Hypothetically, if none of the above processes occur, the null hypothesis would be that niche divergence among close relatives is unrelated to range overlap. Instead, because evolutionary changes are assumed to accumulate through time, the degree of niche divergence is only expected to positively correlate with evolutionary time (Harvey and Pagel 1991). Hence, we must account for divergence time when testing the relationship between niche divergence and range overlap. However, niche axes could exhibit different degrees of lability. To date it is difficult to generalize whether macro- or microhabitat niche variables are more conservative or labile (Losos and Glor 2003; Peterson and Holt 2003; Knouft et al. 2006). How range overlap affects the evolutionary rate and the magnitude of divergence for niche axes at various scales is still understudied.

Here, we explored the effects of range overlap and phylogenetic distance on multiple niche axes for closely related species pairs in Western North America monkeyflowers of the plant genera *Erythranthe* and *Diplacus*. Among species pairs, we asked: (1) accounting for divergence time, how does the magnitude of niche divergence change with the degree of range overlap? (2) does the relationship differ across spatial scales or among niche axes? and (3) for pairs with partial range overlap, is niche divergence in sympatry greater than that in allopatry, or vice versa? By testing such patterns in a phylogenetic context across spatial scales, we aimed to infer interactions between niche evolution and range shifts over evolutionary time.

Methods

STUDY SYSTEM AND PHYLOGENY RECONSTRUCTION

Monkeyflowers in the genera *Erythranthe* and *Diplacus* (Phrymaceae, formerly *Mimulus*) are a model system in evolutionary

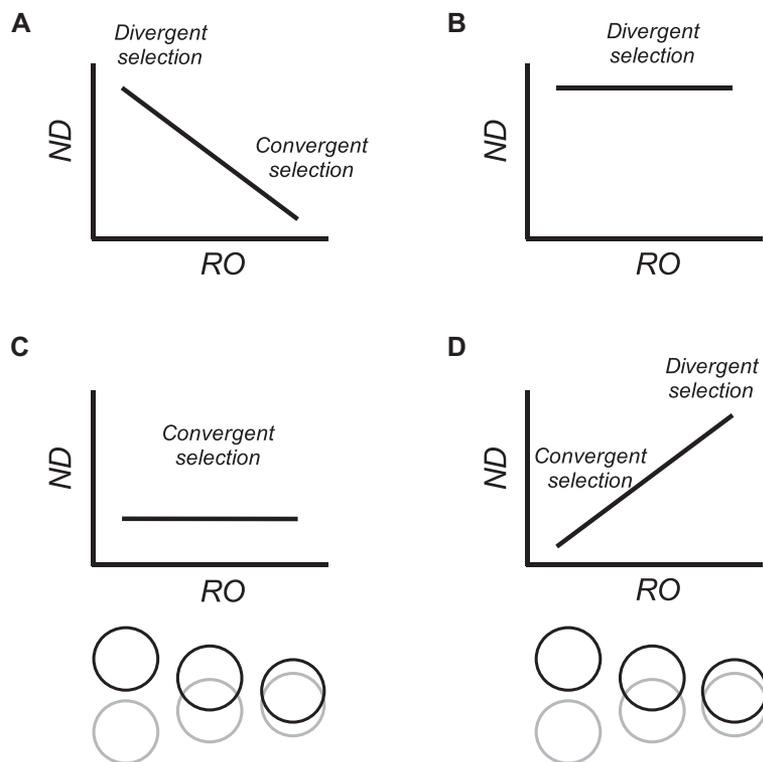


Figure 1. Illustrations of four possible patterns between niche divergence (*ND*) and range overlap (*RO*), predicted under combinations of contrasting processes in high level of range overlapping areas (sympatry) and in low level of range overlapping areas (allopatry), respectively: (A) convergent selection in sympatry and divergent selection in allopatry result in a negative relationship; (B) divergent selection in both sympatry and allopatry result in a nonsignificant relationship with relatively high niche divergence; (C) convergent selection in both sympatry and allopatry result in a nonsignificant relationship with relatively low niche divergence; (D) divergent selection in sympatry and convergent selection in allopatry result in a positive relationship. Range overlap is treated as a continuous variable, with complete sympatry and complete allopatry at its two extremes. Circles below the above four panels, with black and grey depicting two species' ranges, presented three scenarios of range overlap from left to right: no range overlap, partial range overlap, substantial range overlap.

ecology (Wu et al. 2008). Western North American monkeyflowers contain about 90 species (about 75% of described species worldwide, Beardsley et al. 2004), or about 140 species in revised classification (Barker et al. 2012), with great variation in range size, habitat preference, and climatic niche breadth (Sheth et al. 2014). We note that a recent taxonomic revision in these genera (Barker et al. 2012) resulted in some nomenclatural modifications that do not affect our major results (Supplementary Materials). We aimed to choose evolutionarily independent species pairs in western North America and quantified their divergence times (phylogenetic distances), degrees of niche divergence, and range overlap.

To identify species pairs, we used the consensus phylogeny in Grossenbacher and Whittall (2011), selecting pairs that were closest relatives and with native range restricted to western North America. We excluded one pair (*M. nelsonii*–*M. rupestris*) due to limited occurrence data, and added one pair, (*E. guttata*–*E. laciniata*) which was not included in Grossenbacher and Whittall,

but are closely related (Vickery 1964). This resulted in a total of 16 evolutionarily independent species pairs (Table 1).

To estimate phylogenetic distance of species pairs, we used BEAST v1.8.2 (Drummond et al. 2012) on CIPRES (<http://www.phylo.org>) following Grossenbacher et al. (2014; $N = 120$ accessions, including three outgroup species; for 16 species there were multiple samples). We applied the GTR+G substitution model for three DNA regions (*ITS*, *ETS*, and *trnL-F*) of Beardsley et al. (2004) and Whittall et al. (2006), a Bayesian uncorrelated log-normal relaxed clock models, and a birth-death speciation model for phylogenetic reconstruction. We conducted three runs, each for 100 million generations with sampling every 2000 generations. Posterior samples were summarized by Tracer v1.6 (Rambaut et al. 2014) to check the stationary status of converged chains and effective sampling sizes. Using LogCombiner v1.8.2 and TreeAnnotator v1.8.2 (Drummond et al. 2012), we combined posterior samples with 40% burn-in, and after randomly dropping duplicate tips we computed a maximum clade

Table 1. Summary of monkeyflower species pairs and revised taxonomic names (Baker et al. 2012), with information on number of occurrence records (given as species 1/species 2), number of surveyed populations (field site) for each, and range overlap (RO_{sum}) and phylogenetic distance (PD_{mctt}) and phylogenetic distance (PD_{mctt}) between them.

Pair id	species 1 (old name)	species 1 (new name)	species 2 (old name)	species 2 (new name)	# occurrence records	# field site	RO_{sum}	PD_{mctt}
p1	<i>M. guttatus</i>	<i>Erythranthe guttata</i>	<i>M. laciniatus</i>	<i>E. laciniata</i>	2834/59	13/4	0.011	0.042 [‡]
p2	<i>M. floribundus</i>	<i>E. floribunda</i>	<i>M. norrisii</i>	<i>E. norrisii</i>	624/10	3/2	0.006	0.048
p3	<i>M. fremontii</i>	<i>Diplacus fremontii</i>	<i>M. johnstonii</i>	<i>D. johnstonii</i>	296/70	4/3	0.126	0.077
p4	<i>M. androsaceus</i>	<i>E. androsacea</i>	<i>M. shevockii</i>	<i>E. shevockii</i>	66/14	4/3	0.063	0.007
p5	<i>M. lewisii_n</i>	<i>E. lewisii</i> [†]	<i>M. lewisii_s</i>	<i>E. erubescens</i> [†]	272/108	5/7	0.000	0.040
p6	<i>M. bigelovii</i>	<i>D. bigelovii</i>	<i>M. bolanderi</i>	<i>D. bolanderi</i>	471/119	4/6	0.003	0.072
p7	<i>M. angustatus</i>	<i>D. angustatus</i>	<i>M. pulchellus</i>	<i>D. pulchellus</i>	47/30	4/3	0.002	0.085
p8	<i>M. verbenaceus</i>	<i>E. verbenacea</i>	<i>M. eastwoodiae</i>	<i>E. eastwoodiae</i>	45/14	3/3	0.000	0.036
p9	<i>M. washingtonensis</i>	<i>E. washingtonensis</i>	<i>M. jungermanniioides</i>	<i>E. jungermanniioides</i>	25/7	3/3	0.000	0.024
p10	<i>M. parryi</i>	<i>D. parryi</i>	<i>M. rupicola</i>	<i>D. rupicola</i>	23/23	0/0	0.000	0.074
p11	<i>M. breweri</i>	<i>E. breweri</i>	<i>M. bicolor</i>	<i>E. bicolor</i>	622/148	10/11	0.088	0.047
p12	<i>M. douglasii</i>	<i>D. douglasii</i>	<i>M. congonii</i>	<i>D. congonii</i>	124/61	4/4	0.130	0.105
p13	<i>M. cardinalis</i>	<i>E. cardinalis</i> [†]	<i>M. parishii</i>	<i>E. parishii</i>	436/77	5/0	0.074	0.024
p14	<i>M. suksdorfii</i>	<i>E. suksdorfii</i>	<i>M. montioides</i>	<i>E. montioides</i> [†]	192/85	3/3	0.050	0.132
p15	<i>M. constrictus</i>	<i>D. constrictus</i>	<i>M. whitneyi</i>	<i>D. whitneyi</i>	88/81	3/3	0.228	0.071
p16	<i>M. palmeri</i>	<i>E. palmeri</i> [†]	<i>M. gracilipes</i>	<i>E. gracilipes</i>	141/10	1/2	0.030	0.023

[†]associated with changes in range; otherwise recent taxonomic revision solely a nomenclatural change.[‡]used PD between *E. guttata* and *E. nudata* instead due to no genetic sequence of *E. laciniata* for phylogeney reconstruction.

credibility tree (MCCT, Fig. S1). We scaled the pruned phylogeny to a root depth of 1.0 and expressed branch lengths in relative units. In the MCCT, monophyly was supported for 11 out of 16 pairs. We note that the most closely related pairs might not be true sister pairs due to incomplete taxon sampling or intervening extinction. Phylogenetic distance (PD_{mcct}) of each pair was calculated as the sum of their branch lengths divided by two.

OCCURRENCE DATA

Occurrence records were collected mainly from the Global Biodiversity Information Facility (<http://www.gbif.org>, accessed 6 March 2014) using R package *rgbif* (v0.5.0, Chamberlain et al. 2014). Additional data were collected from several local herbarium databases: Consortium of California Herbaria (<http://ucjeps.berkeley.edu/consortium>), Consortium of Pacific Northwest Herbaria (<http://www.pnwherbaria.org>), Southwest Environmental Information Network (<http://swbiodiversity.org>), and Canadensys (<http://www.canadensys.net>) (all accessed March 2014). After removing duplicate records and observations, we filtered specimen data by excluding records without georeferences, or with mismatches between location descriptions and coordinates, or in gardens rather than native habitats. After Albers equal area projection, we further restricted occurrences to one per grid cell (1-km-resolution) by deleting records at random for each species. The number of final records per species ranged from 7 to 2834 (mean: 226; Table 1).

NICHE AXES

The niche concept employed here includes the essential features of Hutchinson's fundamental niche in multidimensional environmental space (Hutchinson 1957), and the availability of niche space relative to the background environment. Therefore, it describes both the conditions within which a species persists across spatial scales, and the species' usages, which can be quantified as frequency distributions along various component axes (Broennimann et al. 2012). We separated niche variables into macrohabitat and microhabitat axes according to the hierarchical scale at which the variables were measured.

Three macrohabitat axes were estimated based on range-wide occurrences at the coarse scale: bioclimatic, edaphic, and topographic. Five contemporary bioclimatic variables were derived from monthly temperature and precipitation data of the time period 1950–2000 at 30-second resolution from WorldClim (<http://www.worldclim.org>, Hijmans et al. 2005; for methods see Kou et al. 2011). These included the average temperature of the coldest month, growing degree days above 0°C degree, precipitation seasonality, the synchronicity of temperature and precipitation (TP_{sym}), and growing season aridity. TP_{sym} , calculated as the Pearson correlation coefficient between monthly temperatures and precipitation, is an effective index for distinguishing between

two major climatic classes, the Mediterranean-type climate (low TP_{sym}) and the monsoon-type climate (high TP_{sym}) (Kou et al. 2011). Eight edaphic variables describing soil textures and chemistry at 1-km resolution were downloaded from SoilGrids (mean values at the depth of 5–15 cm, <http://soilgrids1km.isric.org>), including bulk density, coarse fragments volumetric, fraction sand, fraction silt, fraction clay, soil organic carbon content (log-transformed), soil pH, and cation exchange capacity. Four topographical variables derived from 90 m-resolution digital elevation models (DEMs, <http://srtm.csi.cgiar.org>) included elevation, slope, roughness, and hillshade (a relative solar radiation index based on aspect and slope), all being log-transformed except hillshade.

The microhabitat axes captured habitat attributes at the local scale of individuals within populations. For each pair, we sampled populations from areas of range overlap (i.e. regional sympatry) and/or nonoverlap (allopatry; hereafter called *site type*) along a latitudinal gradient (Fig. S2), based on buffered polygon ranges (see below). For each species, 3–5 populations were chosen to encompass latitudinal variation within site types. Within each population, we surveyed 5–10 square plots that were scaled with edge length being three times the focal plant height, since the size of the surrounding area that impacts an individual plant is likely to depend on the size of a plant (range 1–90 cm). Plots ranged from 0.0009–7.29 m². We measured slope (by clinometer), canopy (by densiometer), the percent total vegetation cover (including overstory and understory), the percent of rocky ground (rock diameter > 0.2 cm), and the percent of bare ground (sand and soil), measured within scaled plots centered on focal individuals of each species. These microhabitat variables were tightly associated with individual life cycle at a local scale, affecting photosynthesis function, water availability, and interactions with other organisms in neighborhood. In total, we collected microhabitat data for 14 species pairs during the growing season of 2008, 2009, 2013, and 2014. The number of populations and total plots for each population site type per species ranged 1–7 and 10–68, respectively (Table 1). We conducted principal components analysis (PCA) on both macro- and microhabitat niche axes before quantifying niche divergence (see below).

RANGE OVERLAP

The range area for each species was estimated from a buffered polygon (Fig. S2), formed by merging circles of 50-km radius around each occurrence point and then reducing it from the edge by 40 km. The 50-km radius was chosen to avoid gaps among regionally adjacent circles. The perimeter was reduced from 50 km to 10 km to avoid overestimating range extent. The range overlap (RO_{sum}) was a ratio, known as Jaccard similarity coefficient (Phillimore et al. 2008), with the area of overlap between two species' ranges as the numerator and the area of the

union of two species' ranges as the denominator. We conducted a sensitivity analysis by evaluating results using alternative methods for estimating range (e.g., minimum convex polygon) and range overlap (e.g., nestedness) (Supplementary Materials).

NICHE DIVERGENCE

We quantified niche divergence (ND) between species pairs for all niche axes separately. For each macrohabitat axis (bioclimatic, edaphic, and topographic), ND was calculated as $1 - D$, where D is a metric of niche overlap (Schoener 1970; Warren et al. 2008), and ND ranges between 0 (no divergence) and 1 (complete divergence). We used an ordination technique (*PCA-env*, Broennimann et al. 2012), which makes comparisons directly in environmental space, independent of resolution and sampling effort. Additionally, a species' preference is weighted by the availability of environmental conditions within its distribution, which avoids systematic underestimation of niche overlap due simply to differences in range placement. We created a joint monkeyflower range by merging all 32 species' ranges, and sampled 10,000 random points from it. Then we conducted PCA on niche variables associated with background points, and created a two-dimensional environmental space as a grid of 100×100 cells. Kernel smoothing was applied to project the occurrence density for each species across all gridded cells. Similarly, kernel smoothing was used to estimate environmental availability across random background points sampled within each species' geographical range ($N = 429\text{--}9910$). The ratio of the density of species to the density of the environment in each cell was then standardized by dividing by the maximum ratio across all cells. The standardized ratio (z) represents corrected species' occupancy of a given environment. We calculated D as 1 minus half of summed absolute differences in z between two species across the environmental space. To estimate uncertainty in the degree of niche overlap, we used bootstrapping to resample occurrences and background points (75% of original dataset) 200 times, or, when the number of occurrence records was smaller than 10 (for one species), we used jackknife resampling. Then, we calculated the mean ND value and its bootstrapped standard deviation.

For microhabitat ND , we used a different method because background data were not available. We conducted PCA across all species' microhabitat data (after log-transformation) to collapse them to the first three PC axes. For each axis, we calculated the average of each site based on plot-level measurements, and then calculated the average of each species based on site means. We then calculated ND as the absolute value of species differences within one pair. To account for the uncertainty due to our limited site measurements and to avoid false positives, we used a simulation method to estimate variation in ND . For each pair along each PC axis, we applied mixed effect models to fit the relationship between PC scores and species using R package *lme4* (v1.1–10,

Bates et al. 2015), with species as the fixed effect and sites as the random effect. The model returned means and variances for both fixed and random effects for all sites, which were used to simulate normal distributions for each site separately. We then sampled 30 values per site to calculate the site mean. Then the species mean was calculated as the mean of the site means. ND was estimated as the absolute difference between species means. We repeated this procedure 200 times, and calculated the averages of ND and the standard deviation.

RELATIONSHIPS AMONG RANGE OVERLAP, PHYLOGENETIC DISTANCE, AND NICHE DIVERGENCE

For each niche axis, we used multiple linear regression models to test for any significant association between ND and RO , with PD as a covariate. We built a full model including an interaction term between RO and PD , and three reduced models with one or two explanatory factors. Models were ranked by AICc and the one with the lowest AICc value was treated as the best model. We also tested whether range overlap was significantly associated with phylogenetic distance or not. We note that range overlap is not the same as the percentage of range overlap over the smaller range (i.e., nestedness, but see Supplementary Materials for alternative analysis), and hence the result cannot be interpreted as an age-range correlation for the geography of speciation.

Spatial autocorrelation might confound the association between ND and RO at the coarse scale, leading to an appearance that closely distributed species pairs share more similar niche properties. Though this problem is alleviated to some extent by accounting for the background availability of environments when estimating species' corrected occupancy z , we further explored its potential influence on our results by testing for correlation between ND and geographic distance between species pairs' ranges. The geographic distance was calculated as the distance between the centroids of the two range polygons.

NICHE DIVERGENCE IN SYMPATRY VERSUS IN ALLOPATRY

Five species pairs have partial range overlap, which means both species have allopatric and sympatric portions of their ranges. Tests for differences in niche divergence between sympatry and allopatry were conducted for these pairs. Due to insufficient microhabitat data, one pair was excluded for microhabitat niche comparison. For macrohabitat axes, we estimated ND (with the same method above) in allopatry and sympatry separately using occurrences and random background data falling into each site type. We also applied bootstrapping to estimate mean ND and 95% confidence intervals (CIs). For estimates of microhabitat ND , we calculated species means in allopatry or sympatry separately, using sites falling into the corresponding site types. We added site type as the second fixed effect in mixed effect models, everything else being

kept the same, and returned mean *ND* and 95% CIs based on 200 simulations. For each pair along each niche axis, we tested if mean *ND* in sympatry was larger than mean *ND* in allopatry and if 95% CI of *ND* in sympatry was not overlapping with that in allopatry. If both criteria were met, we concluded that there was significantly greater *ND* in sympatry than in allopatry, which is the prediction of character displacement. We further conducted sensitivity tests for macrohabitat divergence with the species pair-specific range as *PCA-env* background choice, and for microhabitat divergence with *PCA* conducted within each pair (Supplementary Materials).

Results

EFFECTS OF RANGE OVERLAP AND PHYLOGENETIC DISTANCE ON NICHE DIVERGENCE

The first three components from *PCA* captured 77.84–84.60% of the total variation for three macrohabitat axes, and 84.16% of the total variation in microhabitat (Fig. S3, Supplementary Materials). In particular, for three two-dimensional macrohabitat niches, the first two *PC* axes explained 54.2% and 30.4% variation for bioclimate, 47.33% and 30.51% for soil, 58.77% and 24.59% for topography, respectively. For microhabitat niche, the variations explained by the first three *PC* axes were 38.94, 24.63, and 16.06%, mainly related to bare ground cover, vegetation cover, and slope, respectively. Multiple linear regression returned contrasting patterns between macrohabitat and microhabitat axes, for both relationships with *RO* and *PD* (Fig. 2). The full model including an interaction between *RO* and *PD* was never the best model to explain the variance in niche divergence (Table S1). Rather, for three macrohabitat axes, bioclimatic, edaphic, and topographic, *ND* was better explained by a reduced linear model with only main effects of *RO* and *PD* (adjusted $R^2 = 0.45, 0.57,$ and 0.76 , respectively; Table 2). Overall, *ND* decreased significantly as *RO* increased for macrohabitat axes (Table 2), implying species pairs share more coarse-scale niche properties when they have more sympatric areas (Fig. 2A). *ND* also decreased with increased *PD* for macrohabitat axes, meaning recently diverged species pairs had larger coarse-scale niche divergence (Fig. 2C). This is opposite to the expectation that divergence accumulates over time after speciation. For each microhabitat axis, a single-factor model was better supported, with *PD* favored in the models for *PC1* (related to bare ground cover) and for *PC2* (related to total vegetation cover), and with *RO* favored in the model for *PC3* (related to slope) (adjusted $R^2 = 0.13, 0.26,$ and 0.00 , respectively; Table 2). For *PC3*, the other single-factor model with *PD* as the explanatory variable was within one *AICc* unit in comparison with the best model. However, there was no significant association between microhabitat *ND* and *RO* in any model (Fig. 2B, Table S1). Among the above models, only a significantly

Table 2. Best linear models and regression estimates of the effects of range overlap (RO_{sum}) and phylogenetic distance (PD_{mcc}) on niche divergence (*ND*) for each of three coarse-scale macrohabitat axes and three fine-scale microhabitat axes.

Niche axes	Model	df	Adjusted R^2	AICc	Slope (RO)	Slope SE (RO)	t-statistic (RO)	P (RO)	Slope (PD)	Slope SE (PD)	t-statistic (PD)	P (PD)
<i>Macrohabitat</i>												
Bioclimatic	$ND \sim RO + PD$	4	0.45	-16.13	-1.00	0.46	-2.18	0.05	-2.20	0.90	-2.44	0.03
Edaphic	$ND \sim RO + PD$	4	0.57	-24.46	-1.17	0.35	-3.30	0.01	-1.65	0.70	-2.37	0.03
Topographic	$ND \sim RO + PD$	4	0.76	-42.79	-0.88	0.20	-4.38	0.00	-1.67	0.39	-4.27	0.00
<i>Microhabitat</i>												
Micro_PC1 (bare ground) †	$ND \sim PD$	3	0.13	36.53					-9.97	5.76	-1.73	0.11
Micro_PC2 (total vegetation) †	$ND \sim PD$	3	0.26	32.77					11.87	5.04	2.36	0.04
Micro_PC3 (slope) †	$ND \sim RO$	3	0.00	24.75	-0.83	1.90	-0.44	0.67				

†Named according to which microhabitat variable loaded most strongly.

The significant *P* values (<0.05) and estimates of corresponding explanatory variables are in bold.

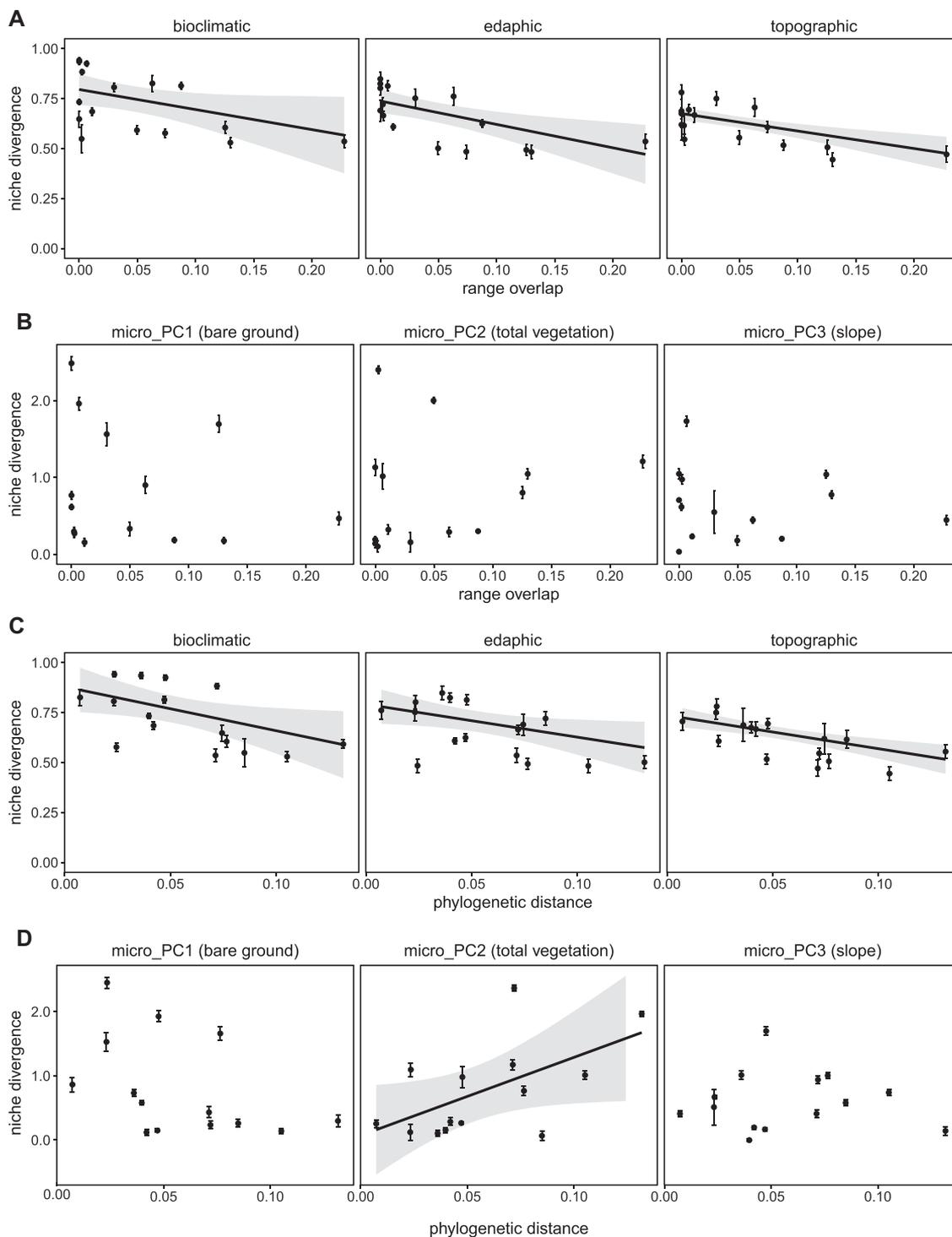


Figure 2. Linear regression plots show the relationships between niche divergence and two individual variables, range overlap (*RO*), and phylogenetic distance (*PD*) in monkeyflowers. Best-fitted models included both *RO* and *PD* as explanatory variables for three coarse-scale macrohabitat axes (A, C), and included only *PD* for microhabitat PC1 and PC2 and only *RO* for PC3 (B, D). Error bars are estimations of standard deviation from bootstrap (A, C) and mixed-effect model-based simulation (B, D). Best-fit lines are from significant linear regressions ($P < 0.05$; same slopes as in Table 2). Gray shading denotes 95% confidence intervals.

positive relationship was detected between microhabitat *ND* and *PD* for PC2, indicating greater fine-scale niche divergence over time along this axis (Fig. 2D, Table 2).

No significant relationship was found between *RO* and *PD* nor when using range nestedness (both adjusted $R^2 = 0$; Fig. S4), implying no clear pattern regarding the change of range overlap between close relatives over evolutionary time with these data. Furthermore, for all niche axes we found no association between *ND* and range distance (all adjusted $R^2 = 0$; Fig. S5). This suggests that spatial autocorrelation was not the major driver of niche divergence patterns with range overlap.

NICHE DIVERGENCE IN SYMPATRY VERSUS IN ALLOPATRY

For species pairs with partial range overlap, the pattern of *ND* in sympatry compared to *ND* in allopatry differed between macrohabitat and microhabitat axes (Fig. 3A). For five pairs, macrohabitat *ND* in sympatry was significantly smaller than or similar to that in allopatry across niche axes, supporting convergent selection in sympatry. There was only one case where mean *ND* was larger in sympatry (*D. congdonii* and *D. douglasii* on topographic axis), but 95% CIs were overlapping. Results were similar when *ND* was calculated based on pair-specific ranges, showing it was not sensitive to the choice of environmental background (Fig. S6).

In contrast, three species pairs had greater microhabitat *ND* in sympatry than in allopatry (Fig. 3B), one pair for each microhabitat axis (*D. douglasii* and *D. congdonii* on PC1 related to bare ground cover, *E. suksdorfii* and *E. montioides* on PC2 related to total vegetation cover, *E. breweri* and *E. bicolor* on PC3 related to slope). These results were consistent with character displacement in sympatry. Two more pairs showed larger mean *ND* on PC3, but their 95% CIs were overlapping. This suggests that species within pairs might interact with each other differently and diverge idiosyncratically with respect to microhabitat partitioning. When *ND* was calculated based on pair-specific PCA, results were similar, where pairs showed greater *ND* in sympatry mainly for PC1 and PC2 (Fig. S7).

Discussion

Among studies exploring the association between niche divergence and range overlap, quantitative inferences are still rare in a phylogenetic context. Thus, it remains unclear whether the predominant effect of range overlap is to select for convergent niche evolution in shared environments or divergent niche evolution to minimize competitive interactions, and whether the relative balance of these forces changes across spatial scales or with time since speciation. Here we quantified how niche evolution at coarse and fine scales was driven by shared abiotic environ-

ments, the potential for species interactions (mediated by range overlap), and time (indexed by phylogenetic distance). Our results suggest that convergent selection plays a role at the coarse scale, leading to similar macrohabitat preference between co-occurring monkeyflower species. At the fine scale, we did not find a single overall signal of microhabitat divergence across all species pairs. However, we detected more microhabitat divergence in sympatry than in allopatry when focusing on species pairs with partial range overlap. This is consistent with potential competitive interactions driving closely related species to diverge locally through ecological character displacement, but the specific niche axis that showed divergence was idiosyncratic to each pair. When testing the relationship between niche divergence and phylogenetic distance, we also found opposite patterns for niche axes across spatial scales. Greater coarse-scale niche divergence was found for recently diverged pairs, consistent with allopatric speciation in different regions. In contrast, fine-scale niche divergence increased with divergence time, consistent with competitive interactions driving fine-scale niche divergence after species come into secondary contact. Though the pattern-based approach should be used with caution to interpret underlying processes, our results here imply that the association between niche evolution and range overlap changes across spatial scales and over time for close relatives.

ASSOCIATION BETWEEN NICHE DIVERGENCE AND RANGE OVERLAP AT A COARSE SCALE

The contrasting relationships between niche divergence and range overlap for macrohabitat and microhabitat imply that the processes underlying niche dynamics depend on spatial scale. At a coarse scale, negative patterns between niche divergence and range overlap suggest that species share ecological conditions in sympatry and adapt to divergent environments in allopatry (Fig. 1A). Though our analysis cannot precisely distinguish whether the above pattern was due to environmental filtering, which sorts preadapted species with similar niche properties, or convergent evolution, which means *in situ* evolution of similar niche properties specifically, these results suggest the degree of niche divergence is tightly linked to the status of range overlap among close relatives. Similarly, Steinbauer et al. (2016) found climatic niche differentiation in allopatry was either stronger than or similar to that in sympatry for six plant clades in the Canary Islands. Kozak and Wiens (2010) suggested range overlap, representing local biotic interactions, had a negative effect on the rate of climatic niche evolution for 16 clades of plethodontid salamanders, because dispersal of one clade was restricted by the presence of others.

Spatial autocorrelation could potentially lead to higher niche divergence estimates with greater geographic distance even if niches are not diverged. For example, organisms occurring at different locations might prefer microhabitats that maintain similar

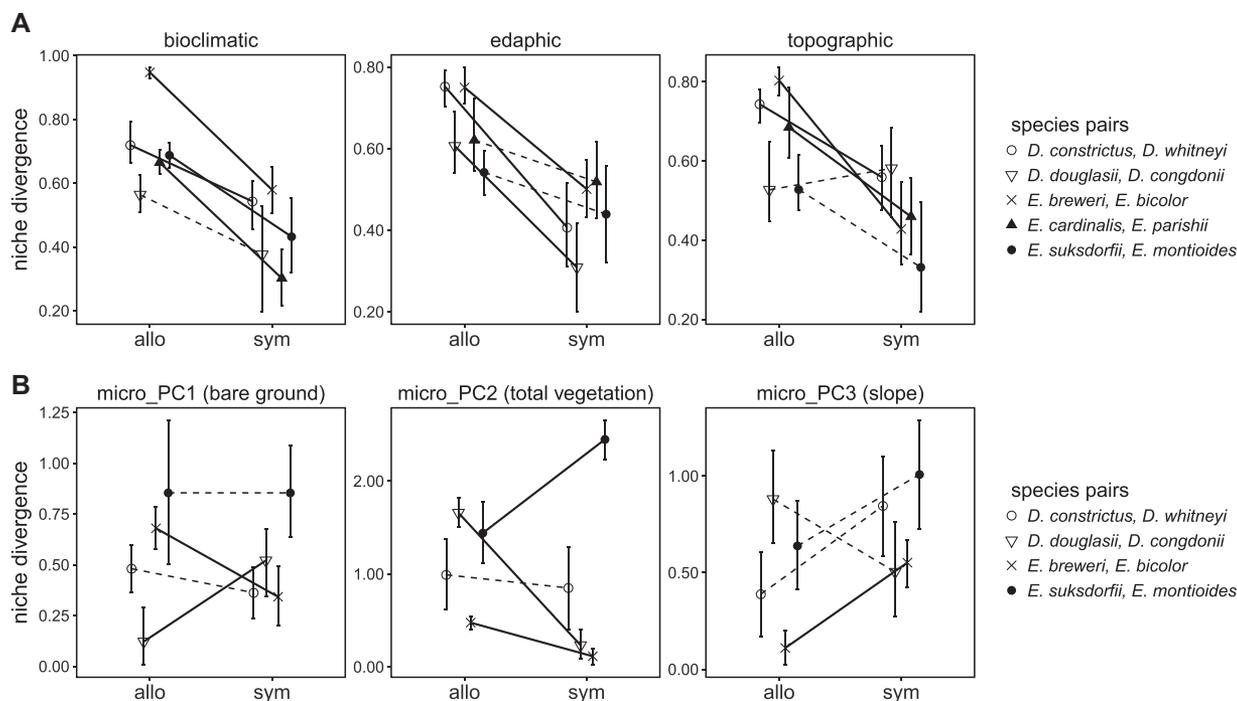


Figure 3. Niche divergence in sympatry (sym) versus niche divergence in allopatry (allo) for monkeyflower species pairs with partial range overlap, for five pairs along three coarse-scale macrohabitat axes (A) and for four pairs along three fine-scale microhabitat axes (B). Error bars are estimations of 95% confidence intervals from bootstrap (A) and mixed-effect model-based simulation (B). Various symbols connected by lines depicted different species pairs. Solid lines denote significant comparison results with more niche divergence in allopatry or in sympatry.

abiotic conditions despite overall macroclimatic differences. The way we estimated niche divergence by the *PCA-env* technique accounted for the availability of background environments and spatial resolution, and therefore corrected biases in geographic space to some degree (Broennimann et al. 2012). Additionally, we found niche divergence was not significantly associated with geographic distance between species' range centroids. Furthermore, dissimilar environmental conditions in different locations are indeed potential agents of divergent selection on isolated populations.

ASSOCIATION BETWEEN NICHE DIVERGENCE AND RANGE OVERLAP AT A LOCAL SCALE

At the local scale, though microhabitat axes are more conserved than macrohabitat axes in some plant groups (Ackerly et al. 2006; Emery et al. 2012), character displacement is generally expected to cause niche divergence for closely related species in sympatry (Beans 2014). Our analyses failed to detect global patterns in the relationship between niche divergence and range overlap for any microhabitat axis. There are several possible reasons. Firstly, divergence might occur along one or more niche axes that vary depending on species pairs. More generally, pairs could differ in various aspects, such as which traits are labile, show preexisting differences, or mutate first to facilitate niche divergence

and hence facilitate coexistence. The results for niche divergence in sympatry versus allopatry for partially overlapping pairs were consistent with this idea. For example, *E. bicolor* occurs on steep slopes in sympatry while *E. breweri* occurs in flatter areas (pers. obs., also supported by more divergence on microhabitat PC3 related to slope in sympatry); in contrast, both *E. bicolor* and *E. breweri* occur in flatter areas in allopatry. Analogously, *D. congdonii* generally occurs at disturbed or sloped runoff areas, while *D. douglasii* occurs on bare clay, serpentine or granitic soils (Baldwin et al. 2012); more niche divergence was found in sympatry on microhabitat PC1 related to bare ground and slope. Together, these could possibly explain why there was no overall pattern when testing across all 16 species pairs. Secondly, increasing sampling effort of local populations and examining more niche axes could potentially increase the power to detect divergence at the local scale. The microhabitat data we collected might not capture relevant factors reflecting niche partitioning. For example, shifts between soil types (e.g., serpentine and non-serpentine) was suggested to be common for angiosperms in the California Floristic Province (Anacker and Strauss 2014; Baldwin 2014). Thirdly, modern coexistence theory suggests that competitive outcomes among species are determined by both stabilizing niche differences and relative fitness differences, such that species can coexist by weak stabilization when they have small fitness

inequalities (Chesson 2000; Adler et al. 2007). Close relatives often have similar fitness (Godoy et al. 2014), implying that slight niche differentiation (perhaps less than what we could detect here) would allow coexistence. Lastly, here we used range overlap as a surrogate for biotic interactions, but it was not a direct metric of interaction intensity. Regionally sympatric species might not co-occur locally or compete directly, by spatial or temporal partitioning (e.g. different substrate patches or flowering times).

We applied different methods to quantify niche divergence for macrohabitat and microhabitat axes. It would be ideal to use the same analytical framework across the two scales. The method we used for macrohabitat variables relies on estimates of background environmental availability, which were not available for microhabitat variables. Adjusting niche estimates based on the background environment is meant to correct potential differences in sampling intensity and niche availability across spatially varying environments. For example, if allopatric species occupy different positions along a niche axis, it could be merely because the two regions differ in the ranges of this variable. This is likely to be a more severe problem for climatic variables at a coarse scale, which are more likely to be spatially autocorrelated, than locally varying and highly heterogeneous microhabitat variables. We conducted an additional analysis treating macrohabitat niches in the same way as we treated microhabitat (i.e., by ignoring the background), and it yielded similar inferences (data not shown). Future studies would benefit by collecting background microhabitat data at field sites across species ranges and quantifying microhabitat niche divergence relative to a common background niche space.

ASSOCIATION BETWEEN NICHE DIVERGENCE AND PHYLOGENETIC DISTANCE

Associations between range overlap and niche divergence do not imply unidirectional causality, since complex feedbacks can occur through evolutionary time (Donoghue and Moore 2003; Warren et al. 2014). Although the pattern of niche conservatism is common (Prinzing et al. 2001), studies have also shown evidence of rapid niche evolution in multiple taxa, either for climatic variables (Broennimann et al. 2007; Kozak and Wiens 2010) or microhabitat preferences (Losos et al. 2003; Silvertown et al. 2006; Wiens et al. 2010). Moreover, estimates of niche evolution depend on the phylogenetic scale of investigation, as niche conservatism is more apparent when including greater phylogenetic diversity (Cavender-Bares et al. 2006; Evans et al. 2009; Peterson 2011). Here, we found contrasting relationships between niche divergence and phylogenetic distance, which depended on spatial scale. Macrohabitat niche divergence was highest between the most recently diverged species pairs. Opposite to the null hypothesis that evolutionary changes accumulate over time, this implies that macrohabitat traits are highly evolutionarily labile and perhaps that diver-

gence is concentrated near speciation events. In support of niche lability in monkeyflowers, others have found no detectable phylogenetic signal for other bioclimatic variables (Grossenbacher et al. 2014; Sheth et al. 2014). In contrast, microhabitat divergence increased with phylogenetic distance, though only along one axis, which is consistent with the idea of more divergence over time. Together with increased divergence in sympatry, this suggests that biotic interactions at a local scale might drive increasing niche divergence, perhaps in conjunction with more intense interactions happening during increasing secondary contact over time.

CAVEATS ABOUT INTERACTIONS BETWEEN RANGE AND NICHE DYNAMICS

The lack of a significant relationship between range overlap and phylogenetic distance implies either no single dominant geographical mode of speciation or rapid postspeciation range shifts that obscure the geography of speciation (Losos and Glor, 2003). However, without quantifying reproductive isolation between species, our measurements of niche divergence and range overlap cannot make explicit inference about their relationship with the geography of speciation and postspeciation changes. Additional information on the timing and the frequency of secondary contact would be important for understanding the effect of range overlap on niche dynamics during and after speciation. Furthermore, incomplete taxon sampling and relatively low phylogenetic support for some species pairs mean that species pairs in the present analysis may not true sister species and instead simply represent evolutionarily independent close relatives. Nevertheless, range overlap was generally low (maximum 0.23 km² of overlap per km² of unioned range), indicating that a high likelihood of ecogeographic isolation. Recent analyses of the geography of speciation in the Californian flora (Anacker and Strauss 2014) and monkeyflowers in particular (Grossenbacher et al. 2014) showed that younger species pairs had higher asymmetry in niche breadth and range size, suggesting a dominance of “budding” speciation. Such niche breadth asymmetry could also contribute substantially to niche divergence, though we did not consider it here. Furthermore, we applied different methods of calculating range (instead of minimum convex polygon) and range overlap (instead of nestedness), which likely are less prone to overestimating range size and overlap, but more prone to concluding low range overlap even for fully nested species with asymmetric range sizes (Supplementary Materials).

Conclusion

Contrasting patterns across spatial scales are consistent with multiple evolutionary forces acting simultaneously and at different spatial scales in shaping niche differentiation. In western North

American monkeyflowers, niches are labile and the degree of range overlap and interactions between close relatives can contribute to niche dynamics across space, and thus to the diversification in this group. Further analyses of evolutionary rates of different niche axes and niche breadths across all species in this plant group will advance our understanding at deeper phylogenetic and temporal scales. For the species pairs for which we detected greater microhabitat niche divergence in sympatry than allopatry, further work to characterize selection on niche properties, competitive interactions, and reproductive isolation would help test links between niche divergence and speciation. Furthermore, probabilistic modeling of phylogeographic range evolution to reconstruct ancestral areas can supply direct inference of biogeographic processes (Donoghue and Moore 2003), for example via the Dispersal-Extinction-Cladogenesis model (Ree and Smith 2008). Moreover, modeling of diversification processes while incorporating ecological traits can explicitly test the effect of ecology on diversification, such as high speciation rate with certain traits or the evolutionary mode of trait transition (e.g. Binary-State Speciation and Extinction model and its extensions; Maddison et al. 2007; FitzJohn 2010). Future studies can harness these types of analyses to better understand feedbacks between niche and range dynamics.

AUTHOR CONTRIBUTIONS

The initial idea for the study was conceived and developed by QL and ALA. QL and DG collected data. QL conducted the analyses with critical input from ALA and DG. QL led manuscript writing; ALA and DG contributed to manuscript revisions.

ACKNOWLEDGMENTS

We thank B. Gass, M. Bayly, B. Green and J. Smith for helping with field data collection. We thank M. Bontrager, X. Kou, J. Lee-Yaw, S. Sheth, D. Schluter, J. Whitton, and J. Jankowski for discussions and feedback on this study and manuscript. Four anonymous reviewers and two editors, Dr. Ortiz-Barrientos and Dr. Mohamed Noor, provided valuable comments on the manuscript. Both QL and ALA were supported by department of Botany and a Discovery Grant from the National Science and Engineering Research Council of Canada. DG was supported by a graduate fellowship from the Center for Population Biology at UC Davis and NSF-DDIG DEB0910038.

DATA ARCHIVING

Data deposited in the Dryad repository: <https://doi.org/10.5061/dryad.9q2v7c4>.

LITERATURE CITED

- Ackerly, D. D., D. W. Schwilk, and C. O. Webb. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* 87:S50–S61.
- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecol. Lett.* 10:95–104.
- Anacker, B. L., and S. Y. Strauss. 2014. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proc. R. Soc. Lond. B Biol. Sci.* 281:20132980.
- Baldwin, B. G. 2014. Origins of plant diversity in the California Floristic Province. *Ann. Rev. Ecol. Evol. Syst.* 45:347–369.
- Baldwin, B. G., D. H. Goldman, K. J. David, R. Patterson, T. J. Rosatti, and D. Wilken. 2012. *The Jepson manual: vascular plants of California*. California Univ. Press, California.
- Barker, W. R., G. L. Nesom, P. M. Beardsley, and N. S. Fraga. 2012. A taxonomic conspectus of Phrymaceae: a narrowed circumscription for *Mimulus*, new and resurrected genera, and new names and combinations. *Phytoneuron* 39:1–60.
- Barracough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *Am. Nat.* 155:419–434.
- Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, G. Grothendieck, and P. Green. 2015. lme4: linear mixed-effects models using ‘Eigen’ and S4. R package version 1.1–13.
- Beans, C. M. 2014. The case for character displacement in plants. *Ecol. Evol.* 4:852–865.
- Beardsley, P. M., S. E. Schoenig, J. B. Whittall, and R. G. Olmstead. 2004. Patterns of evolution in western North American *Mimulus* (Phrymaceae). *Am. J. Bot.* 91:474–489.
- Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, B. Petitpierre, L. Pellissier, N. G. Yoccoz, W. Thuiller, M.-J. Fortin, C. Randin, N. E. Zimmermann, et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecol. Biogeogr.* 21:481–497.
- Broennimann, O., U. A. Treier, H. Mueller-Schaerer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* 10:701–709.
- Brown, W. L., and E. O. Wilson. 1956. Character displacement. *Syst. Zool.* 5:49.
- Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:S109–S122.
- Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12:693–715.
- Chamberlain, S., C. Boettiger, K. Ram, V. Barve, and D. Mcglinn. 2014. rgbif: Interface to the Global Biodiversity Information Facility API. R package version 0.5.0.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.* 31:343–366.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Sunderland, MA.
- Donoghue, M. J., and B. R. Moore. 2003. Toward an integrative historical biogeography. *Integr. Comp. Biol.* 43:261–270.
- Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* 29:1969–1973.
- Emery, N. C., E. J. Forrester, G. Jui, M. S. Park, B. G. Baldwin, and D. D. Ackerly. 2012. Niche evolution across spatial scales: climate and habitat specialization in California *Lasthenia* (Asteraceae). *Ecology* 93:S151–S166.
- Evans, M. E. K., S. A. Smith, R. S. Flynn, and M. J. Donoghue. 2009. Climate, niche evolution, and diversification of the “bird-cage” evening primroses (Oenothera, sections *Anogra* and *Kleinia*). *Am. Nat.* 173:225–240.
- FitzJohn, R. G. 2010. Quantitative traits and diversification. *Syst. Biol.* 59:619–633.
- Fitzpatrick, B. M. B., and M. M. Turelli. 2006. The geography of mammalian speciation: mixed signals from phylogenies and range maps. *Evolution* 60:601–615.

- Godoy, O., N. J. B. Kraft, and J. M. Levine. 2014. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* 17:836–844.
- Grossenbacher, D. L., S. D. Veloz, and J. P. Sexton. 2014. Niche and range size patterns suggest that speciation begins in small, ecologically diverged populations in North American monkeyflowers (*Mimulus* spp.). *Evolution* 68:1270–1280.
- Grossenbacher, D. L., and J. B. Whittall. 2011. Increased floral divergence in sympatric monkeyflowers. *Evolution* 65:2712–2718.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford Univ. Press, Oxford.
- Hijmans, R. J., S. E. Cameron, and J. L. Parra. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25:1965–1978.
- HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. *Ann. Rev. Ecol. Evol. Syst.* 43:227–248.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415–427.
- Knouft, J. H., J. B. Losos, R. E. Glor, and J. J. Kolbe. 2006. Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology* 87:S29–S38.
- Kou, X., Q. Li, and S. Liu. 2011. High-resolution bioclimatic dataset derived from future climate projections for plant species distribution modeling. *Ecol. Inform.* 6:196–204.
- Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecol. Lett.* 13:1378–1389.
- Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580–582.
- Losos, J. B. 2009. *Lizards in an evolutionary tree: ecology and adaptive radiation of Anoles*. California Univ. Press, California.
- Losos, J. B., and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends Ecol. Evol.* 18:220–227.
- Losos, J. B., M. Leal, R. E. Glor, K. De Queiroz, P. E. Hertz, L. R. Schettino, A. C. Lara, T. R. Jackman, and A. Larson. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* 424:542–545.
- Maddison, W. P., P. E. Midford, and S. P. Otto. 2007. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* 56:701–710.
- McCormack, J. E., A. J. Zellmer, and L. L. Knowles. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. *Evolution* 64:1231–1244.
- Moullot, D., and K. Gaston. 2009. Spatial overlap enhances geographic range size conservatism. *Ecography* 32:671–675.
- Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in space and time. *Trends Ecol. Evol.* 23:149–158.
- Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. *J. Biogeogr.* 38:817–827.
- Peterson, A. T., and R. D. Holt. 2003. Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. *Ecol. Lett.* 6:774–782.
- Peterson, A., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Phillimore, A. B., C. D. L. Orme, G. H. Thomas, T. M. Blackburn, P. M. Bennett, K. J. Gaston, and I. P. F. Owens. 2008. Sympatric speciation in birds is rare: insights from range data and simulations. *Am. Nat.* 171:646–657.
- Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. B Biol. Sci.* 268:2383–2389.
- Rambaut, A., M. A. Suchard, D. Xie, and A. J. Drummond. 2014. Tracer v1.6. Available from <http://tree.bio.ed.ac.uk/software/tracer>. Retrieved on March 10, 2015.
- Ree, R. H., and S. A. Smith. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* 57:4–14.
- Ricklefs, R. E., and D. G. Jenkins. 2011. Biogeography and ecology: towards the integration of two disciplines. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366:2438–2448.
- Schemske, D. W. 2010. Adaptation and the origin of species. *Am. Nat.* 176:S4–S25.
- Schluter, D. 2000. Ecological character displacement in adaptive radiation. *Am. Nat.* 156:S4–S16.
- . 2001. Ecology and the origin of species. *Trends Ecol. Evol.* 16:372–380.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Sheth, S. N., I. Jiménez, and A. L. Angert. 2014. Identifying the paths leading to variation in geographical range size in western North American monkeyflowers. *J. Biogeogr.* 41:2344–2356.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends Ecol. Evol.* 19:605–611.
- Silvertown, J., K. McConway, D. Gowing, M. Dodd, M. F. Fay, J. A. Joseph, and K. Dolphin. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. Lond. B Biol. Sci.* 273:39–44.
- Steinbauer, M. J., R. Field, J. M. Fernández Palacios, S. D. H. Irl, R. Otto, H. Schaefer, and C. Beierkuhnlein. 2016. Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Global Ecol. Biogeogr.* 25:792–804.
- Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88:1770–1780.
- Symonds, M. R., and M. A. Elgar. 2004. Species overlap, speciation and the evolution of aggregation pheromones in bark beetles. *Ecol. Lett.* 7:202–212.
- Tobias, J. A., C. K. Cornwallis, E. P. Derryberry, S. Claramunt, R. T. Brumfield, and N. Seddon. 2013. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature* 506:359–363.
- Vickery, R. K. 1964. Barriers to gene exchange between members of the *Mimulus guttatus* complex (*Scrophulariaceae*). *Evolution* 18:52–69.
- Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. Mistaking geography for biology: inferring processes from species distributions. *Trends Ecol. Evol.* 29:572–580.
- Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.* 33:475–505.
- Weber, M. G., L. Mitko, T. Eltz, S. R. Ramírez. 2016. Macroevolution of perfume signalling in orchid bees. *Ecol. Lett.* 19:1314–1323.
- Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* 58:193–197.
- . 2011. The niche, biogeography and species interactions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366:2336–2350.
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. Jonathan Davies, J.-A. Grytnes, S. P. Harrison, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13:1310–1324.

- Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Ann. Rev. Ecol. Evol. Syst.* 36:519–539.
- Whittall, J. B., M. L. Carlson, P. M. Beardsley, R. J. Meinke, and A. Liston. 2006. The *Mimulus moschatatus* alliance (Phrymaceae): molecular and morphological phylogenetics and their conservation implications. *Syst. Bot.* 31:380–397.
- Wu, C. A., D. B. Lowry, A. M. Cooley, K. M. Wright, Y. W. Lee, and J. H. Willis. 2008. *Mimulus* is an emerging model system for the integration of ecological and genomic studies. *Heredity* 100:220–230.

Associate Editor: D. Ortiz-Barrientos
Handling Editor: Mohamed A. F. Noor

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Multiple linear regression model comparison and regression estimates of the effects of range overlap (RO_{sum}) and phylogenetic distance (PD_{mccr}) on niche divergence for each of three coarse-scale macrohabitat axes and three fine-scale microhabitat axes.

Figure S1. 16 closely related species pairs of monkeyflowers selected from a maximum clade credibility tree (marked with asterisks).

Figure S2. The geographical distributions and range overlap of 16 monkeyflower species pairs in western North America.

Figure S3. The correlation circles of PCA for (a-c) three coarse-scale macrohabitat axes (bioclimatic, edaphic, and topographic, respectively); and (d-f) combinations of first three PCs for microhabitat axes (PC1 and PC2, PC1 and PC3, and PC2 and PC3, respectively).

Figure S4. The relationship between range overlap and phylogenetic distance for 16 monkeyflower species pairs, with two methods of quantifying range overlap: (a) RO_{sum} and (b) nestedness (RO_{min}).

Figure S5. The relationship between niche divergence and range distance for 16 monkeyflower species pairs.

Figure S6. The effect of background space choices on estimations of niche divergence of three coarse-scaled macrohabitat axes in sympatry (sym) compared to that in allopatry (allo) for monkeyflower species pairs with partial range overlap using (a) background common to all pairs and (b) background specific to each species pair.

Figure S7. The effect of background space choices on estimations of niche divergence of three microhabitat axes in sympatry (sym) compared to that in allopatry (allo) for monkeyflower species pairs pairs with partial overlap for (a) PCA conducted across all species and (b) PCA conducted separately for each species pair.