

THE EVOLUTION OF ENVIRONMENTAL TOLERANCE AND RANGE SIZE: A COMPARISON OF GEOGRAPHICALLY RESTRICTED AND WIDESPREAD *MIMULUS*

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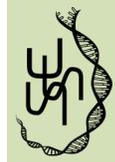
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The geographic ranges of closely related species can vary dramatically, yet we do not fully grasp the mechanisms underlying such variation. The niche breadth hypothesis posits that species that have evolved broad environmental tolerances can achieve larger geographic ranges than species with narrow environmental tolerances. In turn, plasticity and genetic variation in ecologically important traits and adaptation to environmentally variable areas can facilitate the evolution of broad environmental tolerance. We used five pairs of western North American monkeyflowers to experimentally test these ideas by quantifying performance across eight temperature regimes. In four species pairs, species with broader thermal tolerances had larger geographic ranges, supporting the niche breadth hypothesis. As predicted, species with broader thermal tolerances also had more within-population genetic variation in thermal reaction norms and experienced greater thermal variation across their geographic ranges than species with narrow thermal tolerances. Species with narrow thermal tolerance may be particularly vulnerable to changing climatic conditions due to lack of plasticity and insufficient genetic variation to respond to novel selection pressures. Conversely, species experiencing high variation in temperature across their ranges may be buffered against extinction due to climatic changes because they have evolved tolerance to a broad range of temperatures.

KEY WORDS: Climatic variability hypothesis, geographic range size, genetic variation, niche breadth, specialist–generalist trade-offs, thermal performance curve.

Geographic range size can vary by orders of magnitude among species in the same clade (Darwin 1859), among clades, and predictably across geography (e.g., Rapoport's rule; Stevens 1989), yet we do not fully grasp the mechanisms underlying such variation. Numerous hypotheses have been invoked to explain variation in range size (reviewed in Gaston 2003), but in particular explanations for variation in range size among closely related species and across space have focused on the evolution of niche breadth (Pither 2003; Slatyer et al. 2013). Some have regarded a species' geographic range as a projection of the ecological niche onto

geography (Pulliam 2000). The ecological niche can be viewed as the set of environments across which a species can maintain viable populations (Hutchinson 1957). The niche breadth hypothesis posits that, all else being equal, species that are able to maintain viable populations across a greater set of environments can achieve larger geographic ranges than species with narrow ecological niches (Fig. 1A, B; Brown 1984). This hypothesis has garnered consistent support, suggesting that a positive relationship between niche breadth and geographic range size is a general pattern (Slatyer et al. 2013). This relationship is particularly strong



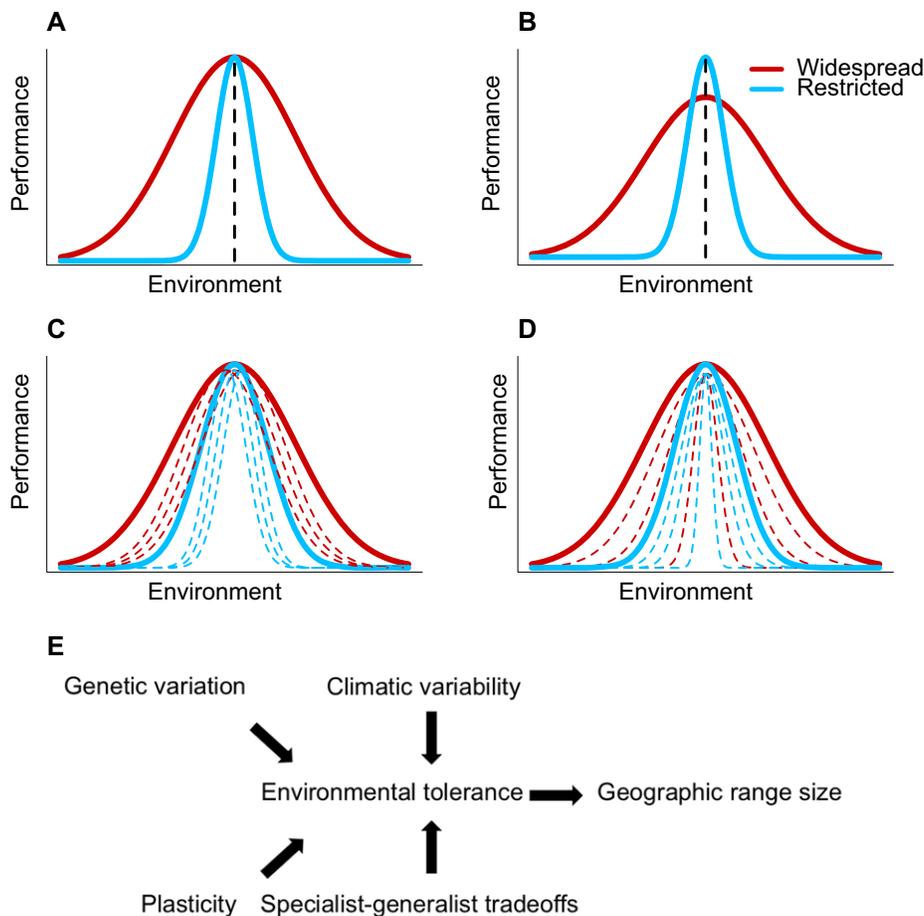


Figure 1. Hypothesized relationship between environmental tolerance and geographic range size for two closely related species in the absence (A) and presence (B) of a specialist–generalist trade-off between width of performance curve and maximum performance. Dashed lines in panels A and B indicate optimum environment for maximum performance. (C) Illustration of how phenotypically plastic genotypes or families (i.e., genotypes or families that are able to maintain high performance across a broad range of environments; represented by dashed curves) can lead to a broad species-level environmental tolerance (solid curves). (D) Illustration of how genetic variation in environmental tolerance among genotypes or families (dashed curves) can result in broad species-level environmental tolerance (solid curves). In panels A–D, the geographically widespread species has a broader environmental tolerance than the geographically restricted species. (E) Conceptual diagram illustrating how climatic variability, plasticity, genetic variation in environmental tolerance, and specialist–generalist trade-offs are hypothesized to affect geographic range size via their effects on environmental tolerance. Although there are other potential relationships among the variables depicted (e.g., climatic variability may increase genetic variation and/or lead to specialist–generalist trade-offs), only paths that represent predictions tested in this study are depicted here. Arrows represent positive effects. In Tables 1 and 2, B_{50} corresponds to environmental tolerance, SD_{tw} corresponds to climatic variability, specialist–generalist trade-offs occur if the species in each pair with a greater B_{50} has a lower RGR_{max} , \overline{WSD} refers to within-family plasticity, and V_{cold} and V_{hot} are estimates of genetic variation at the cold and hot extremes of the thermal reaction norm, respectively.

when quantifying niche breadth as environmental tolerance, defined as the range of abiotic conditions (e.g., temperature) across which performance is high (Slatyer et al. 2013).

A species can accrue environmental tolerance in a number of ways. First, a species with broad environmental tolerance may be composed of phenotypically plastic genotypes (Baker 1965) that perform well across a broad range of environmental conditions (Fig. 1C). For example, phenotypic plasticity, rather than local adaptation, has allowed the weed *Verbascum thapsus* to invade

high elevations in California (Parker et al. 2003). Second, adaptively differentiated individuals within a population may shape a species' environmental tolerance, such that populations of species with broad environmental tolerances consist of many divergently specialized individuals differing in environmental optima (Bolnick et al. 2003). In fact, there is evidence that individual specialization can explain a large fraction of a population's total niche breadth across a variety of taxa (Bolnick et al. 2003). Third, a species may achieve broad environmental tolerance via local

adaptation of divergent populations to a range of environments (Ackerly 2003). For example, each population of lodgepole pine (*Pinus contorta*) is locally adapted to a subset of climates occupied by the species as a whole, such that the broad climatic tolerance exhibited by the species can be partitioned among populations (Rehfeldt et al. 1999). Thus, variation in environmental performance within and among genotypes, families, or populations may play an important role in shaping species-level niche breadth (Slatyer et al. 2013), and these alternative means for achieving broad environmental tolerance have important implications for understanding variation in evolutionary potential of populations and species (Etterson 2008).

Variation in environmental tolerance among species may arise due to constraints on the evolution of broad environmental tolerances. One constraint may arise due to a lack of genetic variation in traits that would permit range expansion via adaptation to novel environments (Kellermann et al. 2009). If so, species with narrower environmental tolerances may have less genetic variation for environmental tolerance and thus have smaller geographic ranges than species with broader environmental tolerances (Fig. 1D). Another explanation for constraints to evolving a broader environmental tolerance deals with fitness trade-offs (Futuyma and Moreno 1988). Theory predicts trade-offs between environmental tolerance and maximum fitness, such that there is a cost in maximum fitness to having a broad environmental tolerance (Huey and Hertz 1984). If a specialist–generalist trade-off is present among species and “a jack-of-all-trades is a master-of-none” (MacArthur 1972), then on average, species with broad environmental tolerances should have a lower maximum fitness or performance metric than species with narrow niches (Huey and Slatkin 1976; Fig. 1B, E).

In addition to intrinsic constraints within species, extrinsic factors such as geographically variable selection pressures may also shape environmental tolerance. In particular, the climatic variability hypothesis invokes variation in natural selection across space to posit that species that have adapted to climatically variable environments such as temperate zones have evolved broader climatic tolerances and should thus be able to occupy larger geographic ranges than species occurring in climatically stable environments such as the tropics (Janzen 1967; Stevens 1989). Although in its original form, this hypothesis focused on temporal climatic variability within a site, this hypothesis also predicts that species with ranges encompassing greater variation in climate should have broader environmental tolerances and larger geographic ranges than species experiencing less variation in climate across their ranges (Quintero and Wiens 2013; Fig. 1E). The climatic variability hypothesis has been invoked to explain Rapoport’s rule, the pattern of average range size in a clade decreasing from temperate to tropical areas (Stevens 1989), as well as latitudinal gradients in biodiversity (Ghalambor et al. 2006),

but it can be applied more generally to species that differ in the climatic variability experienced across their ranges. Depending on the relationship between selection and gene flow (Lenormand 2002), climatic variability across species’ ranges could favor locally adapted populations, phenotypic plasticity (Fig. 1C), within-population genetic variation in climatic tolerance (Fig. 1D), or a combination of strategies leading to an overall broad species-level environmental tolerance.

In this study, we examine the ideas outlined above (Fig. 1E) in western North American monkeyflowers (genus *Mimulus*, renamed *Erythranthe* in Barker et al. 2012). We focus on one niche axis, temperature, which affects a number of physiological processes in living organisms (Angilletta 2009). Specifically, we experimentally quantified thermal performance breadth for five pairs of closely related species that differ in geographic range size. First, we evaluated the hypothesis that geographically widespread species have wider thermal performance breadths than geographically restricted species (Fig. 1A). Second, we determined whether species achieve broad thermal tolerance via phenotypically plastic genotypes (Fig. 1C). Third, we tested whether genetic variation in thermal reaction norms increases thermal tolerance (Fig. 1D), and examined whether specialist–generalist trade-offs (Fig. 1B) shape patterns of thermal tolerance. Finally, we assessed the prediction of the climatic variability hypothesis that species with broader thermal tolerance experience greater variation in temperature across their geographic ranges than species with narrow thermal tolerance (Fig. 1E).

Methods

STUDY SYSTEM

The objectives of this research were addressed with the monkeyflower genus *Mimulus* (Phrymaceae), a group of wildflowers with ~90 species in western North America (Beardsley and Olmstead 2002). Western North American *Mimulus* is in the process of taxonomic revision (Barker et al. 2012), but the anticipated modifications are predominantly nomenclatural and should not affect the species identity of the populations in our study. *Mimulus* species occur in several habitats, including wetlands, alpine environments, and deserts, and some species are edaphic specialists (Wu et al. 2008). Further, *Mimulus* species encompass herbaceous and woody habits, annuals and perennials, and mating systems ranging from complete outcrossing to obligate selfing (Wu et al. 2008). Due to its short generation times (6–12 weeks), ease of propagation, high seed production, and genomic resources, *Mimulus* has become an emerging model system in evolutionary ecology (Wu et al. 2008). The geographic ranges of *Mimulus* species are well known, occur primarily within protected areas in western North America, and exhibit strong variation in size

(Beardsley et al. 2004), thus constituting an appropriate study system for testing hypotheses about relationships between range size and thermal tolerance. Previous work suggests that *Mimulus* species exhibit substantial variation in climatic niche breadth (Sheth et al. 2014), with some species possessing significant genetic variation for climatic tolerance (Vickery 1972).

FIELD SAMPLING AND CROSSES

To test hypotheses about relationships among geographic range size, environmental tolerance, and processes shaping environmental tolerance (Fig. 1E), we focused on five species pairs that broadly sample the western North American *Mimulus* phylogeny and consist either of putative sister species or of species within a single subclade of *Mimulus* (Beardsley et al. 2004; Table 1). We selected pairs in which species differ markedly in range size (Sheth et al. 2014) and are amenable to greenhouse study (Hiesey et al. 1971; Sobel 2010). Comparison of close relatives allows for comparisons of traits among widely and narrowly distributed species pairs and prevents drivers of variation of range size from being masked by differences that have accumulated over long periods of independent evolution. For each species, we collected seeds from 20 to 50 individuals at a single site, collecting where species in a given pair either co-occur at a site (Fig. 2A, E) or are at least regionally sympatric (Fig. 2B–D). This sampling scheme of one population per species yields a conservative test of the niche breadth hypothesis by assuming that there are innate species-level differences in niche breadth, and avoids potential confounding of local adaptation and spatial distance among multiple populations of widespread versus rare species. We planted field-collected seeds from each species in the Colorado State University Greenhouse. For the species with focal populations that are predominantly outcrossing (*M. cardinalis*, *M. verbenaceus*, *M. eastwoodiae*, *M. bicolor*, *M. filicaulis*, and *M. guttatus*; Sheth, unpubl. data), we randomly crossed individuals within each species to produce outcrossed seeds with which to conduct controlled experiments. For the species with focal populations that are predominantly selfing (*M. parishii*, *M. floribundus*, *M. norrisii*, and *M. laciniatus*; Sheth, unpubl. data), we allowed individuals to self for one generation and used the resulting seeds in subsequent experiments. We used this crossing scheme because it best mimics what is occurring in natural populations. If we had created outcrossed seeds from predominantly selfing species, the resulting estimates of thermal performance breadth and genetic variation in thermal reaction norms could have been inflated, failing to correspond to what actually occurs in the wild. A single *Mimulus* fruit typically contains hundreds of seeds, so we used the outcrossed or selfed seeds from the same full-sibling seed families in all experiments described below (see Table 2 for number of families per species).

PLANT PROPAGATION

We established seedlings of all study species in 72-cell plug trays (4 × 4 × 5.5 cm). For *M. cardinalis*, *M. parishii*, *M. verbenaceus*, *M. eastwoodiae*, *M. guttatus*, and *M. laciniatus*, we filled plug trays with Farfard 4P Mix potting soil with a thin layer of Farfard Superfine Germinating mix on top (Conrad Farfard, Inc., Agawam, MA). *Mimulus guttatus* and *M. laciniatus* were first placed in a refrigerator at 4°C for 10 days to improve germination success prior to being moved to the Colorado State University Greenhouse. For *M. floribundus*, *M. norrisii*, *M. bicolor*, and *M. filicaulis*, we treated seed with gibberellic acid (Acros Organics) to improve germination success. In particular, we soaked seeds in 0.2 mM gibberellic acid solution in 1.5 mL microcentrifuge tubes for ~8 h and then rinsed seeds thoroughly with dH₂O to minimize potential downstream effects of gibberellic acid on growth (Bachelard 1968). Subsequently, we planted seeds into a mix of three parts potting soil and two parts perlite with a thin layer of germination mix on top. Prior to being placed in growth chambers for thermal performance experiments, plug trays were kept in the Colorado State University Greenhouse with a 16 h day/8 h night photoperiod with day temperature programmed to ~25°C and night temperature at ~20°C.

THERMAL PERFORMANCE EXPERIMENTS

Temperature is one niche dimension that affects fitness components in *Mimulus*. For example, temperature affects whole-plant performance of *M. cardinalis* and *M. lewisii* (Angert 2006), and the species pairs we chose differ in latitudinal distributions and in the range of temperatures experienced within these distributions (Table 1). We measured survival and relative growth rate (*RGR*) of individuals of each species across eight temperature regimes simulated in growth chambers with 14 h of daylight and 10 h of darkness per 24-h period according to these day/night temperatures (°C): 15/0, 20/5, 25/10, 30/15, 35/20, 40/25, 45/30, and 50/35 (based on the range of temperatures experienced by western North American *Mimulus*). *RGR* constitutes one of many possible measures of performance, and we chose it because it was the most feasible performance metric to estimate for thousands of plants. Although *RGR* need not be correlated with lifetime fitness, there is evidence for many of our study species that as *RGR* increases, flower number increases (Weimer and Sheth, unpubl. data). Further, rapid growth at early life stages during which plants are smaller and more vulnerable should increase the chances of juvenile survival and thus should influence the probability that a plant will reproduce.

Experiments were conducted from September 2012 through January 2013. During any given week, 5–10 seeds from each family (11–50 families per species; Table 2) of all or a subset of species pairs were sown as described above. Each tray was composed of both species in a species pair, with families and

Table 1. Widespread and restricted species pairs (denoted by species with the same letter superscript) used in this study.

Species	Range size ¹ (km ²)	LM ¹ (°)	LR ¹ (°)	Mean _{ts} (°C)	SD _{ts} (°C)	Mean _{tw} ¹ (°C)	SD _{tw} ¹ (°C)
<i>M. cardinalis</i> ^a	470,772	36.1	15.8	26.80	0.78	20.28	2.87
<i>M. parishii</i> ^a	95,116	33.7	4.4	27.41	0.78	22.49	3.46
<i>M. verbenaceus</i> ^b	514,264	29.9	14.8	22.30	0.87	23.38	3.84
<i>M. eastwoodiae</i> ^b	43,862	37.4	2.6	21.91	0.78	22.66	2.06
<i>M. floribundus</i> ^c	4,423,834	36.7	34.6	24.05	0.86	20.99	4.33
<i>M. norrisii</i> ^c	275	36.4	0.24	25.58	0.78	22.33	1.85
<i>M. bicolor</i> ^d	56,551	38.5	4.8	18.81	0.95	19.99	2.43
<i>M. filicaulis</i> ^d	436	37.8	0.40	20.89	1.05	18.99	1.28
<i>M. guttatus</i> ^e	12,053,145	41.1	47.7	20.89	1.05	19.85	5.20
<i>M. laciniatus</i> ^e	25,048	38.2	3.3	20.89	1.05	17.35	4.22

Range size = area of minimum convex polygon encompassing primary occurrence data; LM = latitudinal midpoint of primary occurrence data; LR = latitudinal range: difference between maximum and minimum latitudes encompassed by primary occurrence data; Mean_{ts} and SD_{ts} = mean and standard deviation in mean summer temperature (from 1970 to 2012; Wang et al. 2012) of sampled populations included in study (Fig. 2); Mean_{tw} and SD_{tw} = mean and standard deviation in mean temperature of warmest quarter (www.worldclim.org) across primary occurrence data.

¹See Sheth et al. (2014) for details.

Table 2. Widespread (w) and restricted (r) species pairs (denoted by species with the same letter subscript) used in this study.

Species	B_{50} (°C)	B_{80} (°C)	T_{opt} (°C)	RGR_{max}	\overline{WSD} (SE)	V_{cold}	V_{hot}	N
<i>M. cardinalis</i> ^a (w)	25.916	14.712	41.416	0.052	9.17 (0.25)	0.000017	0.000021	22
<i>M. parishii</i> ^a (r)	26.632	15.881	38.813	0.085	9.02 (0.16)	0.000080	0.000082	50
<i>M. verbenaceus</i> ^b (w)	32.474	23.638	32.082	0.029	8.98 (0.25)	0.000021	0.000015	24
<i>M. eastwoodiae</i> ^b (r)	23.142	13.197	31.823	0.048	7.74 (0.16)	0.000017	0.000010	42
<i>M. floribundus</i> ^c (w)	26.982	17.064	31.601	0.120	8.55 (0.27)	0.000153	0.000175	18
<i>M. norrisii</i> ^c (r)	25.956	16.416	31.996	0.077	7.58 (0.46)	0.000064	0.000026	18
<i>M. bicolor</i> ^d (w)	20.185	11.453	34.834	0.225	7.81 (0.23)	0.000100	0.000769	23
<i>M. filicaulis</i> ^d (r)	19.086	10.829	35.910	0.128	7.65 (0.32)	0.000015	0.000113	13
<i>M. guttatus</i> ^e (w)	14.230	8.073	39.723	0.442	8.19 (0.47)	0.000045	0.003926	11
<i>M. laciniatus</i> ^e (r)	12.830	7.28	37.841	0.350	7.18 (0.16)	0.000027	0.000302	14

B_{50} = thermal performance breadth based on relative growth rate (RGR); T_{opt} = optimum daytime temperature for RGR; RGR_{max} = maximum relative growth rate; \overline{WSD} = standard deviation in temperature weighted by relative performance, representing an estimate of family-level thermal performance breadth; V_{cold} = among-family variance in the slope of RGR from 15°C to 20°C; V_{hot} = among-family variance in the slope of RGR from 45°C to 50°C; N = number of families planted per temperature. For the first three species pairs above, the units of RGR are based on leaf counts (number number⁻¹ day⁻¹), and for the remaining two species pairs the units of RGR are based on stem length (cm cm⁻¹ day⁻¹).

species completely randomized. Within each growth chamber run, there were two replicate trays per species pair for *M. cardinalis*, *M. parishii*, *M. verbenaceus*, and *M. eastwoodiae*, such that each tray contained one replicate set of families for each species. For *M. floribundus*, *M. norrisii*, *M. bicolor*, *M. filicaulis*, *M. guttatus*, and *M. laciniatus*, there was one tray per species pair, but each tray contained two replicates of each family for each species within each growth chamber run. Thus, each family of each species was replicated twice within each growth chamber run. Once seeds were sown, trays were subirrigated daily and rotated three times weekly to reduce positional effects. Two weeks after sowing *M. floribundus*, *M. norrisii*, *M. bicolor*, and *M. filicaulis* and three weeks after sowing *M. cardinalis*, *M. parishii*, *M. verbenaceus*, *M. eastwoodiae*, *M. guttatus*, and *M. laciniatus* seeds, each cell

in each plug tray was thinned down to one central-most seedling. Three weeks after sowing *M. floribundus*, *M. norrisii*, *M. bicolor*, and *M. filicaulis* and four weeks after sowing *M. cardinalis*, *M. parishii*, *M. verbenaceus*, *M. eastwoodiae*, *M. guttatus*, and *M. laciniatus* seeds, we measured stem length and leaf number and placed plants into one of two Percival LT-105 growth chambers (Percival Scientific, Inc., Perry, IA) programmed at one of the eight temperature regimes described above for seven days. Upon being placed into a particular temperature regime, plants ranged from having two to 12 leaves, with stem length ranging from 0.1 to 3.5 cm, depending on species. While plants were in growth chambers, we subirrigated trays daily and rotated trays within each chamber three times to reduce positional effects. Seven days later, we removed plants from chambers and measured them again

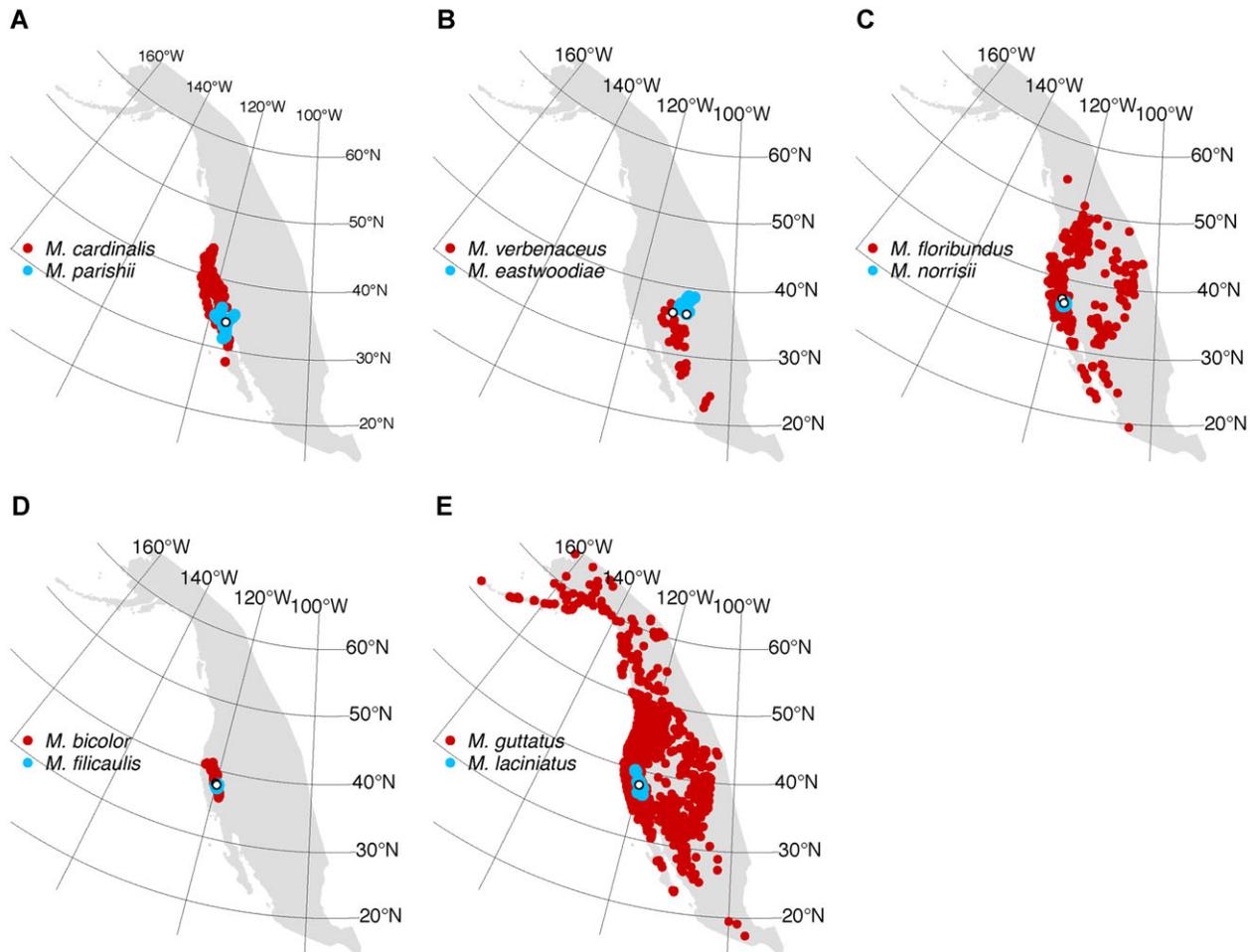


Figure 2. Herbarium specimen localities with red corresponding to the widespread species and blue corresponding to the restricted species in each pair, and sampling localities for each species are shown with white circles. In panels C and D, we sampled seed for species within each pair from different sites, but sampling localities are so close together that they overlap at the scale shown.

to estimate *RGR* in stem length and leaf number as the change in size per initial size per day. For *M. cardinalis*, *M. parishii*, *M. verbenaceus*, *M. eastwoodiae*, *M. floribundus*, and *M. norrisii*, *RGR* in leaf number varied more predictably with temperature and was thus considered a more relevant estimate of performance, and similarly, *RGR* in stem length was more appropriate for *M. bicolor*, *M. filicaulis*, *M. guttatus*, and *M. laciniatus*. Before going into chambers, *M. filicaulis* and *M. laciniatus* were the only species that ever had floral buds or flowers. In addition, *M. bicolor*, *M. floribundus*, *M. norrisii*, and *M. guttatus* plants sometimes had floral buds or flowers when coming out of the growth chambers.

We replicated these temperature regimes twice for *M. cardinalis*, *M. parishii*, *M. verbenaceus*, and *M. eastwoodiae*, with each temperature replicated in each growth chamber once, except for the 50/35°C temperature regime, which we replicated twice in the same chamber. Due to logistical constraints, we replicated these temperature regimes once (randomly assigning each temperature regime to one of the two growth chambers) for the

remaining species. We randomized the order in which we conducted the eight temperature regimes. During the course of the experiment, we planted a total of 5960 individuals but 307 individuals did not germinate, resulting in a total of 5653 individuals that we measured prior to going into a particular temperature treatment. Of these individuals, we excluded 202 individuals that did not have any leaves at least 1 mm long prior to exposure to a particular temperature treatment, resulting in a total of 5451 plants used for estimating thermal performance curves. For 364 individuals that did not survive after exposure to a particular temperature treatment (most often 50°C), we set *RGR* equal to zero. During the course of the experiment, there was a growth chamber malfunction, and so we had to perform experiments with *M. floribundus*, *M. norrisii*, *M. bicolor*, *M. filicaulis*, *M. guttatus*, and *M. laciniatus* at the 35/20°C and the 30/15°C temperature regimes in a third growth chamber (Percival model PGC-15WC) with the same lighting and identical setup as the original chambers. When using this third chamber, *M. floribundus*, *M. norrisii*, *M. bicolor*,

and *M. filicaulis* were much smaller and looked very unhealthy overall compared to all other growth chamber experiments. Thus, we repeated growth chamber experiments at 35/20°C and the 30/15°C temperature regimes for these species in one of the two original growth chambers in late March through early April of 2013.

THERMAL PERFORMANCE BREADTH AND SPECIALIST–GENERALIST TRADE-OFFS

We fitted three functions that have been used to describe thermal performance curves to our data: quadratic, Gaussian (Angilletta 2006), and Kumaraswamy (M. Sears, pers. comm.) functions using the nlsLM function in the minpack.lm package (Elzhov et al. 2013) in R 3.0.2 (R Core Team 2013). Specifically, we fitted thermal performance curves to family means (mean *RGR* across replicates of each family at each temperature) to avoid pseudoreplication. We then used the Akaike information criterion to select the best-fitting function for each species pair (Angilletta 2006). We estimated maximum performance (RGR_{max}) as the peak *RGR* value based on the predicted thermal performance curve, optimum temperature for maximum performance (T_{opt}) as the temperature at which RGR_{max} was achieved, and thermal performance breadth as the range of temperatures across which each species achieved $\geq 50\%$ (B_{50}) and $\geq 80\%$ (B_{80}) of its predicted maximum performance (Huey and Stevenson 1979). Our results using B_{50} and B_{80} were qualitatively similar (Table 2), so we focus on B_{50} here. Because we fit thermal performance curves to unequal numbers of families for the two species within each pair, species may have narrower thermal performance breadth due to an artifact of having more families. Thus, we fit thermal performance curves to data obtained by randomly sampling an equal number of families per species within each pair 100 times, but results were nearly identical, so we present estimates of thermal performance curves based on all families here. Because species pair is the unit of replication in this study, we used one-tailed paired Wilcoxon signed-rank tests to evaluate the prediction that narrowly distributed species have narrower thermal performance breadths than their widespread relatives, and to detect a specialist–generalist trade-off between B_{50} and RGR_{max} .

PLASTICITY

Ideally, to test the hypothesis that broad thermal tolerance is achieved via phenotypic plasticity, we would fit a thermal performance curve to each family mean and test whether families of species with broad thermal tolerance have greater mean thermal performance breadth than families of species with narrow thermal tolerance. Due to lack of sufficient within-family replication, however, we were unable to fit curves to family means. Instead, using family means, we calculated standard deviation in temperature weighted by relative performance, analogous to estimates of

niche breadth that weight standard deviation in an environmental axis by relative abundance (Pither and Aarssen 2005), resulting in 9–48 estimates of family-level thermal performance breadth (in units of °C) per species. Specifically, we used the formula:

$$\sqrt{\sum_{i=1}^8 p_i (T_i - \bar{T}_w)^2},$$

where p_i corresponds to relative performance (*RGR* at temperature i divided by the sum of *RGR* across all eight temperature regimes, such that the sum of p_i across all temperatures should equal 1); T_i corresponds to the i th temperature; and \bar{T}_w corresponds to mean temperature weighted by relative performance (p_i). Because we estimated family-level thermal performance breadth for unequal numbers of families for the two species within each pair, species with more families may have lower average family-level breadth due to an artifact. Thus, we repeated the procedure above by randomly sampling an equal number of families per species within each pair 100 times, but results were nearly identical, so we present estimates of family-level thermal performance breadth based on all families here. To test the prediction that on average, species with broad thermal tolerance have families with broader thermal tolerance when compared to species narrow thermal tolerance, we used a one-tailed t -test for each species pair.

GENETIC VARIATION IN THERMAL REACTION NORMS

To test whether widespread species have greater genetic variation in thermal reaction norms than restricted species, we examined the change in performance at extreme temperatures. We focused exclusively on thermal extremes because species did not differ substantially in thermal optima (Table 2; Fig. 3), suggesting that overall variation in thermal performance breadth between species in each pair resulted primarily from differences in performance at the lowest and highest temperatures. Specifically, using family means for each temperature, we estimated the slope in *RGR* for each family between 15°C and 20°C and between 45°C and 50°C (Fig. 4). As an estimate of genetic variation in thermal reaction norms for each species, we calculated among-family variance across slopes at both temperature extremes: between 15°C and 20°C and between 45°C and 50°C. Because we estimated among-family variance for unequal numbers of families for the two species within each pair, species with more families may have lower among-family variance due to an artifact. Thus, we repeated estimates of among-family variance by randomly sampling an equal number of families per species within each pair 100 times, but results were nearly identical, so we present estimates of among-family variance based on all families here. We performed one-tailed paired Wilcoxon signed-rank tests to assess the hypothesis that species with narrow thermal performance breadth have lower among-family variance in the slope of *RGR* between

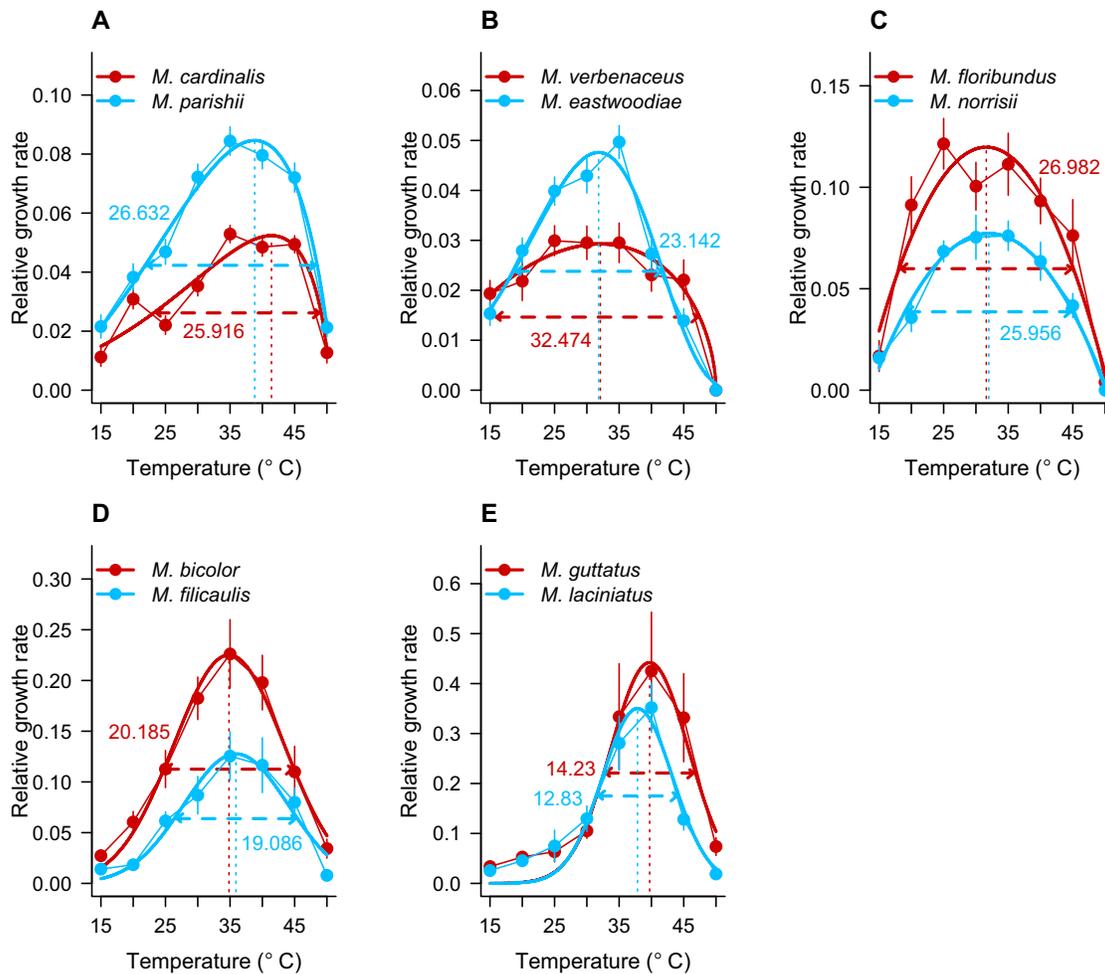


Figure 3. Observed (± 1 SE) and fitted thermal performance curves for each species, with red corresponding to the widespread species and blue corresponding to the restricted species in each pair. Horizontal arrows and numerical values represent thermal performance breadth ($^{\circ}\text{C}$), and vertical lines represent optimum temperature for maximum performance ($^{\circ}\text{C}$). In panels A and B, Kumaraswamy functions were fit to relative growth rate in leaf number; in panel C, quadratic functions were fit to relative growth rate in leaf number (with units as number number $^{-1}$ day $^{-1}$); and in panels D and E, Gaussian functions were fit to relative growth rate in stem length (with units as cm cm $^{-1}$ day $^{-1}$). X-axes represent diurnal temperatures used in experiments.

15 $^{\circ}\text{C}$ and 20 $^{\circ}\text{C}$ and the slope of *RGR* between 45 $^{\circ}\text{C}$ and 50 $^{\circ}\text{C}$ than species with broad thermal performance breadth.

CLIMATIC VARIABILITY

To test whether species with ranges encompassing greater variation in temperature should have broader thermal tolerances and larger geographic ranges than species with ranges encompassing less climatic variation, we used standard deviation of mean temperature of warmest quarter (www.worldclim.org) across primary occurrence data of each species to estimate variation in temperature across each species' range. Because our sampling design focused on regionally sympatric populations of species in each species pair, we did not examine temperature seasonality or other measures of thermal variation within each species' sampling site to estimate climatic variability, but we provide such

estimates (Wang et al. 2012) to assist in interpretation of results. We used a one-tailed paired Wilcoxon signed-rank test to assess support for the prediction that species with broader thermal performance curves should have higher standard deviation in temperature across their known occurrences than species with narrow thermal performance curves.

Results

THERMAL PERFORMANCE BREADTH

A Kumaraswamy function provided the best fit to the thermal performance data of *M. cardinalis*, *M. parishii*, *M. verbenaceus*, and *M. eastwoodiae*; a quadratic function provided the best fit to data of *M. floribundus* and *M. norrisii*; and a Gaussian function provided the best fit to thermal performance data of *M. bicolor*, *M.*

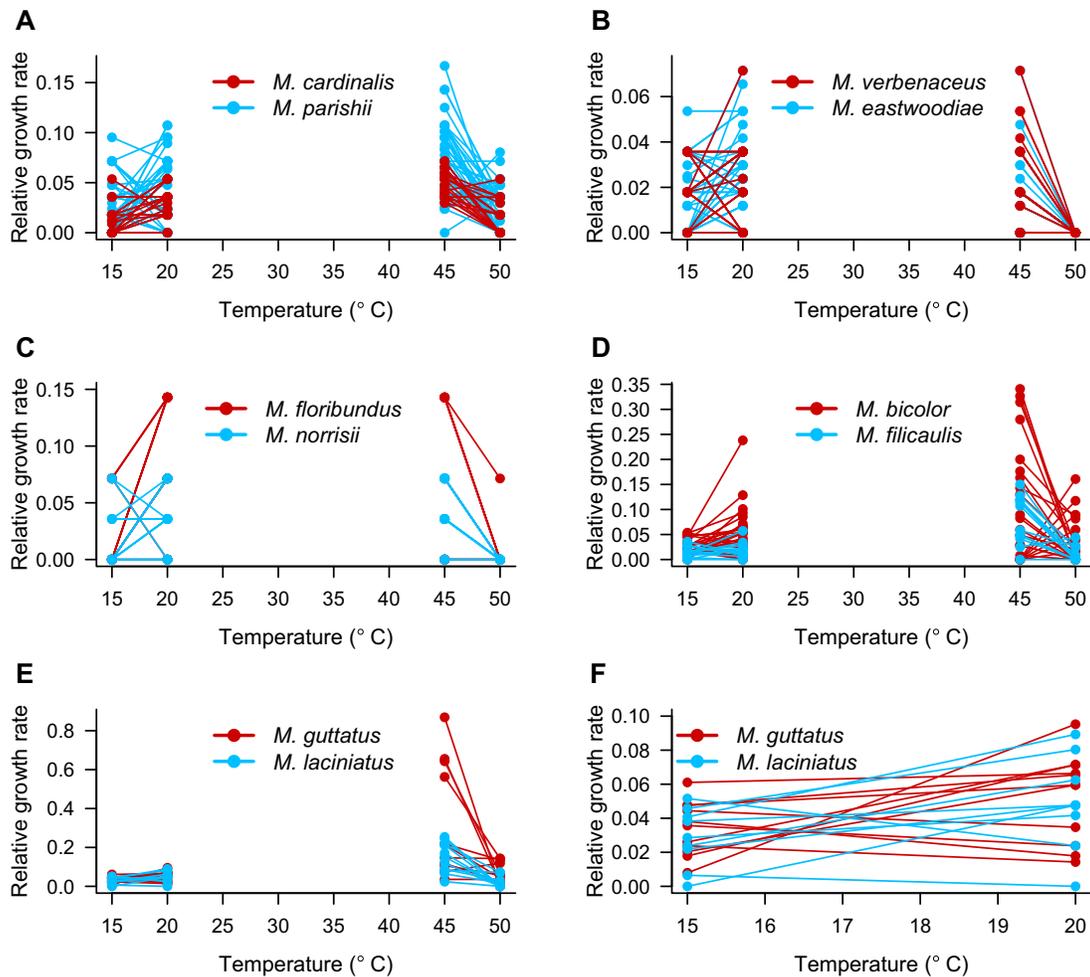


Figure 4. Slopes connecting family means of relative growth rate between 15°C and 20°C and between 45°C and 50°C for each species, with red corresponding to the widespread species and blue corresponding to the restricted species in each pair. To estimate genetic variation in thermal performance at low and high temperatures, we calculated among-family variance across slopes of each species at each temperature extreme. Panel F shows slopes in relative growth rate between 15°C and 20°C for *M. guttatus* and *M. laciniatus* in more detail. In panels A–C, relative growth rate in leaf number is in units of number number⁻¹ day⁻¹, and in panels D–F, relative growth rate in stem length has units of cm cm⁻¹ day⁻¹. Species that appear to have a small number of families actually have multiple families with overlapping values of relative growth rate at each temperature.

filicaulis, *M. guttatus*, and *M. laciniatus* (Tables S1, S2). Thermal performance breadth (B_{50}) ranged from 12.830°C (*M. laciniatus*) to 32.474°C (*M. verbenaceus*; Table 2). Optimum daytime temperature for maximum performance ranged from 31.601°C (*M. floribundus*) to 41.416°C (*M. cardinalis*; Table 2).

In four of the five species pairs, the widespread species had a broader thermal performance than the restricted species (Table 2; Fig. 3), but the magnitude of difference in thermal performance breadth between widespread and restricted species varied among species pairs. Widespread species had marginally significantly larger thermal performance breadths than their narrowly distributed relatives ($W = 14$, $P = 0.0625$), with mean thermal performance breadth of widespread species 2.43°C greater than that of restricted species.

PLASTICITY

On average, families of *M. verbenaceus*, *M. floribundus*, and *M. guttatus* (species with broader thermal tolerance) exhibited a higher standard deviation in temperature weighted by relative performance than families of *M. eastwoodiae*, *M. norrisii*, and *M. laciniatus* (species with narrower thermal tolerance), respectively, supporting the prediction that thermal tolerance is achieved via phenotypically plastic families ($t = 4.2181$, $df = 41.279$, $P < 0.001$; $t = 1.8223$, $df = 21.708$, $P = 0.04$; $t = 2.02$, $df = 12.382$, $P = 0.03$, respectively; Table 2). Failing to support this prediction, families of *M. parishii* and *M. bicolor* (species with broader thermal tolerance) did not have a higher standard deviation in temperature weighted by relative performance than families of *M. cardinalis* and *M. filicaulis* (species with narrower thermal

tolerance), respectively ($t = -0.4843$, $df = 39.018$, $P = 0.68$; $t = 4.4136$, $df = 17.765$, $P = 0.34$, respectively; Table 2).

GENETIC VARIATION IN THERMAL REACTION NORMS

For all species pairs, the species with a broader thermal performance also had significantly greater among-family variance in the slopes of *RGR* between both 15°C and 20°C ($W = 15$, $P = 0.03125$) and 45°C and 50°C ($W = 15$, $P = 0.03125$; Table 2, Fig. 4).

SPECIALIST–GENERALIST TRADE-OFFS

Mimulus verbanaceus had a broader thermal performance and a lower maximum *RGR* than its geographically restricted counterpart, *M. eastwoodiae*, thereby supporting the prediction of a specialist–generalist trade-off between performance breadth and maximum performance (Table 2, Fig. 3). Within every remaining species pair, however, the species with the broader thermal performance also had a higher maximum *RGR* (Table 2, Fig. 3). Altogether, species with broader thermal performance curves did not have significantly lower maximum *RGR* than species with narrow thermal performance curves ($W = 14$, $P = 0.9688$; Table 2), failing to support the prediction of a specialist–generalist trade-off between thermal performance breadth and maximum performance.

CLIMATIC VARIABILITY HYPOTHESIS

As predicted, within each species pair, the species whose range encompasses more variation in mean temperature of the warmest quarter also had a significantly broader thermal performance curve ($W = 15$, $P = 0.03125$; Table 1). Despite the expectation that widely distributed species may encompass more variation in temperature across their ranges than their narrowly distributed relatives purely by chance (Davies et al. 2009), geographically restricted *M. parishii* had a broader thermal tolerance and experienced more variation in temperature across its range than *M. cardinalis*, its widely distributed counterpart (Tables 1, 2).

Discussion

In this study, we experimentally quantified thermal performance across eight temperature regimes for 5451 plants belonging to 10 species and compared thermal performance breadth, plasticity, quantitative genetic variation, and climatic variability between widespread and restricted species pairs of monkeyflower (Fig. 1E). Although four of five species pairs supported the hypothesis that species with larger geographic ranges have broader thermal performance than species with small geographic ranges, widespread species as a group only had marginally significantly broader thermal performance than restricted species, suggesting that other niche axes besides temperature may also explain

variation in range size among *Mimulus* species. However, the present study builds on our mechanistic understanding of how species acquire broad niches and/or large ranges by demonstrating that both plasticity and genetic variation in thermal performance contribute to broad environmental tolerance. Further, we show that species experiencing greater thermal variation across their ranges have evolved broader thermal tolerances than species with less variation in temperature across their ranges, supporting the climatic variability hypothesis. Below, we discuss these results in light of the natural history of each species and with regard to results from previous studies. In addition, we consider the implications of our results for gaining a better understanding of the relationships between climatic tolerance, geographic range size, extinction risk, and vulnerability to changing climate.

RELATIONSHIP BETWEEN THERMAL PERFORMANCE BREADTH AND GEOGRAPHIC RANGE SIZE

In a previous study, we used correlative climatic niche modeling to show that climatic niche breadth is a strong predictor of geographic range size across 72 species of western North American monkeyflower (Sheth et al. 2014). Although we controlled for spurious correlations between range size and niche breadth by simulating null geographic distributions (Sheth et al. 2014), the present study provides a strong experimental test of the inferences derived from occurrence data and correlative modeling. The present study complements our previous conclusions by showing that in four of five of the focal species pairs, the widespread species had a broader thermal performance than the geographically restricted species, providing additional support for the niche breadth hypothesis. With the exception of *M. cardinalis* and *M. parishii*, estimates of thermal performance breadth derived from one population per species (in the present study) for widespread versus restricted species are consistent with estimates of multivariate climatic niche breadth from correlative modeling (Sheth et al. 2014).

In the present study, we focused on the thermal niche of *Mimulus* species, based on previous work demonstrating that temperature influences growth and other performance traits in *Mimulus* (Vickery 1967, 1972; Angert 2006). Apart from differences in thermal tolerance, species in each pair also differ along other abiotic niche dimensions, including habitat and edaphic characteristics. *Mimulus cardinalis* occurs in a variety of moist habitats along seeps, streams, and rivers, whereas *M. parishii* is restricted to sandy stream edges below 2100 m (Hickman 1993). *Mimulus verbanaceus* occupies desert seeps and creeksides across a broad elevational range, whereas *M. eastwoodiae* occurs in moist, shaded hanging gardens in otherwise arid canyon country (Hiesey et al. 1971; Beardsley et al. 2003). *Mimulus floribundus* inhabits crevices, seeps around granite outcrops, and stream banks, whereas *M. norrisii* grows only in marble crevices (Hickman

1993). *Mimulus bicolor* typically occurs on clay soils, whereas *M. filicaulis* grows on loamy soils, and *M. guttatus* inhabits a diversity of wet places, whereas *M. laciniatus* grows in quick-drying seeps on granite outcrops (Hickman 1993). Despite these and other differences in niche characteristics among species, our current and past work shows that climatic niche properties play an important role in shaping patterns of geographic range size in *Mimulus*. Previous studies of invertebrates (e.g., Calosi et al. 2008; Kellermann et al. 2009; Calosi et al. 2010) and vertebrates (e.g., Cruz et al. 2005) have documented relationships between thermal tolerance and geographic range size, but there have been few tests in plants (but see Luna et al. 2012).

It would be interesting to know whether species with narrow thermal tolerance also specialize along other niche axes such as soil moisture. Similar experiments quantifying performance breadth across a range of soil moistures are currently underway. If species specialize simultaneously along multiple niche axes, then specialization along one niche axis may predict specialization along other niche axes, making specialists particularly vulnerable to extinction risks. Alternatively, specialization along different niche axes may not be correlated (Emery et al. 2012), indicating that different sets of species are predicted to have high extinction risk depending on the niche axis used to assess specialization and the type of environmental perturbation.

Support for the niche breadth hypothesis may be equivocal if tests are limited to a single population that does not represent the niche breadth of the entire species. Despite the many studies that have found support for the niche breadth hypothesis (Pyron 1999; Brandle et al. 2003; Hurlbert and White 2007; Köckemann et al. 2009; Verberk et al. 2010; Emery et al. 2012), few have addressed the potential for local adaptation to facilitate range expansion. Thus, a major question that remains unanswered is whether widespread species have achieved large distributions by means of local adaptation to a variety of environments, or because individuals across the species' range have general-purpose genotypes that permit broad environmental tolerances (Baker 1965). To distinguish the latter from the former, niche breadth must be quantified for multiple populations per species. Examination of niche breadth across multiple populations would allow one to assess how a species' total niche is partitioned among populations and families or individuals (in the case of clonal species). Thus, assessing the extent to which species accumulate niche breadth through populations that are locally adapted to different environments, or by having populations with broad environmental tolerances across the range would yield important insights about the evolution of niche breadth and range size (Slatyer et al. 2013). In a study quantifying thermal tolerance for multiple populations across the latitudinal range of a widespread copepod, species-level thermal tolerance was far greater than thermal tolerance for any given population (Kelly et al. 2012), highlighting the value of

quantifying thermal performance across several populations per species.

Even with our conservative approach of estimating thermal tolerance for only one population per species, we captured variation in thermal tolerance among *Mimulus* species, suggesting that innate differences in thermal tolerance may contribute to variation in geographic range size among species. Despite being more widespread, *M. cardinalis* may have a narrower thermal performance breadth than *M. parishii* because species-level niche breadth of *M. cardinalis* is achieved via locally adapted populations differing in thermal optima for performance. A study of variation in thermal performance among populations of *M. cardinalis* reveals that populations within the northern half of the species' range have overlapping but variable thermal optima for performance (Angert et al. 2011), and thermal optimum would likely vary to a greater degree if populations from the southern half of the range were also included. If more populations were considered, the magnitude of difference in thermal tolerance between widespread and restricted species would probably be even greater because widespread species by definition encompass a broader latitudinal range, and among-population variation would likely lead to even broader thermal tolerance.

The present study adds to a growing number of empirical tests of the niche breadth hypothesis involving comparisons of niche breadth between widespread and restricted congeners. For example, studies of two clades of diving beetles report a positive relationship between thermal tolerance and latitudinal extent, highlighting the benefits of experimentally and phylogenetically controlled tests of the niche breadth hypothesis (Calosi et al. 2008, 2010). Here, we expand upon such comparative studies by further examining the mechanisms that may promote or constrain the evolution of broad thermal tolerance.

PLASTICITY AND GENETIC VARIATION IN THERMAL PERFORMANCE

We document evidence that both plasticity and genetic variation in thermal performance contribute to an overall broad thermal tolerance. These findings provide additional insights to studies showing that species with broad geographic distributions have greater intraspecific variation in traits but that have not quantified the roles of plasticity and heritable variation in shaping species'-level niche breadth (e.g., Sides et al. 2014). In three species pairs, the species with broader thermal tolerance consisted of more thermally tolerant families than species with narrow thermal tolerance, highlighting the role of within-family plasticity in determining species-level thermal tolerance. Species with broader thermal tolerance had greater genetic variation in thermal performance at both low and high temperatures than those with narrower thermal tolerance, suggesting that genetic variation in ecologically relevant traits may facilitate the evolution of broad climatic

tolerances. This finding is consistent with a recent study of thermal tolerance and species' distributions of *Drosophila* (Kellermann et al. 2009). However, genetic variation for thermal performance may vary across species' ranges, and theoretical and empirical work suggests that populations at the edges of species' ranges may lack genetic variation in one or more ecologically important traits (Antonovics 1976; Pujol and Pannell 2008). Thus, it would be useful to estimate genetic variation in relevant traits across species' ranges to further understand how genetic variation may promote niche evolution and range expansion.

SPECIALIST–GENERALIST TRADE-OFFS

Consistent with a growing body of literature suggesting that a “jack of all temperatures” can be a “master of all” (reviewed in Angilletta 2009), our results do not provide strong support for the notion that specialist–generalist trade-offs constrain the evolution of broad environmental tolerance. We only found evidence of a trade-off between thermal performance breadth and maximum performance for *M. verbenaceus* and *M. eastwoodiae*, the species pair with the largest difference in thermal performance breadth (Fig. 3, Table 2). Instead, within every remaining species pair, the species with the broader thermal performance also had a higher maximum *RGR* (Fig. 3, Table 2), supporting the idea that “broader is better.” *Mimulus guttatus* and *M. laciniatus* were the only species pair supporting the ideas that “hotter is better” (Hamilton 1973; Huey and Kingsolver 1989) and “hotter is broader” (Knies et al. 2009), based on *M. guttatus* having a higher T_{opt} , a broader thermal performance curve, and a higher maximum *RGR* than *M. laciniatus*. Given that the pair with the greatest difference in thermal performance breadth was the only species pair exhibiting a trade-off between breadth and maximum performance, differences in breadth among species may need to be substantial to detect a cost in maximum performance. Although we did not often detect costs in maximum *RGR* at the expense of having a broad performance curve, there could be costs in other performance metrics. For example, rapid growth may result in lower seed production, but we were unable to detect such trade-offs because we only measured *RGR*.

CLIMATE VARIABILITY HYPOTHESIS

As predicted by the climate variability hypothesis, our results are consistent with the idea that species experiencing greater variation in climate have evolved broader climatic tolerances than species originating from more climatically stable areas. In particular, our finding that thermal tolerance estimated from one population per species was related to thermal variation across a species' range for all five species pairs suggests that the climatic variability hypothesis may explain variation in climatic tolerances even at smaller spatial scales that do not encompass temperate-tropical latitudinal gradients. Although *M. cardinalis* has a much larger

geographic range than *M. parishii* (Fig. 2), *M. parishii* still had both a broader thermal tolerance and greater thermal variation across its geographic range. Consistent with our results, previous work suggests that temperate trees have broader thermal performance curves than tropical species when measuring performance as photosynthetic rate (Cunningham and Read 2002). Further, previous literature suggests that plant species are limited by reduced performance at low temperatures (Woodward et al. 1990; Cunningham and Read 2002; Pither 2003), yet we do not find clear evidence that narrow thermal tolerance results from poor performance at low (rather than high) temperatures. Specifically, *M. verbenaceus* and *M. guttatus* (species with broader thermal tolerance) were more tolerant to high temperatures than *M. eastwoodiae* and *M. laciniatus* (species with narrower thermal tolerance), respectively; *M. parishii* (species with broader thermal tolerance) was more tolerant to low temperatures than *M. cardinalis* (species with narrower thermal tolerance); and *M. floribundus* and *M. bicolor* (species with broader thermal tolerance) were more tolerant to both low and high temperatures than *M. norrisii* and *M. filicaulis* (species with narrower thermal tolerance), respectively (Fig. 3). Although we quantified thermal tolerance for small seedlings in the case of *M. cardinalis*, *M. verbenaceus*, and *M. eastwoodiae*, it is possible that survival and fecundity late in the growing season might be more important for explaining differences in distribution among perennial species with long growing seasons and the need to survive over winter.

Unlike many other tests of the climatic variability hypothesis, our work sheds light on the mechanisms by which climatic variability may lead to broad environmental tolerance. First, in all five species pairs, the species with broader environmental tolerance and greater variability in climate across its range also exhibited more quantitative genetic variation than the species with narrower thermal tolerance and less climatic variability across its range. Second, in three species pairs, the species with broader thermal tolerance and greater variability in temperature across its range also displayed a greater level of plasticity than the species with narrower thermal tolerance and less variation in temperature across its range. Together, these findings indicate that the effects of climatic variability on species-level environmental tolerance may be mediated by quantitative genetic variation and phenotypic plasticity.

CAVEATS

When interpreting results of our study, there are several caveats that should be considered. First, we only included one population per species, thereby ignoring the effects of locally adapted populations and intraspecific variation on species-level thermal performance breadth. Including only one population per species likely leads to an underestimate of species-level thermal performance breadth, but the breadths of widespread species should be

more severely underestimated than that those of restricted species. Thus, we emphasize that such a study design is conservative with respect to the niche breadth hypothesis. Further, some species were sampled at their latitudinal range centers while others were sampled near a northern or southern range edge (Fig. 2). Such idiosyncratic sampling could potentially affect the observed patterns of genetic variation and plasticity. Second, due to logistical benefits and the potential effects of early-stage performance on the probability of survival to flowering, we estimated performance as *RGR*. However, other performance metrics such as fecundity would provide further insights into understanding fitness trade-offs among species that differ in thermal tolerance. Third, we used simple thermal regimes that did not incorporate daily fluctuations in temperature that plants experience in natural settings. Finally, we caution that our conclusions are based on only five species pairs, and studies quantifying thermal performance for a greater number of populations and species are needed.

OTHER DRIVERS OF VARIATION IN THERMAL TOLERANCE AND/OR GEOGRAPHIC RANGE SIZE

Although our focal species within each pair are closely related and should be of similar age, they differ in several other characteristics aside from ecological niche dimensions that could contribute to variation in range size. For example, populations of *M. cardinalis*, *M. verbenaceus*, *M. eastwoodiae*, *M. bicolor*, *M. filicaulis*, and *M. guttatus* included in our study were predominantly outcrossing, whereas populations of *M. parishii*, *M. floribundus*, *M. norrisii*, and *M. laciniatus* were predominantly selfing (S. Sheth, unpubl. data). Mating system should affect a species' ability to colonize novel locations and environments (Baker 1955). On the one hand, selfing could facilitate range expansion when compared to outcrossing, which relies on pollinator availability, yielding the expectation that selfing species should have larger geographic ranges than closely related outcrossing species (Henslow 1879; Baker 1955). On the other hand, selfing would alter the distribution of genetic variation within and among populations, and the reduction of genetic variation associated with selfing could inhibit the evolution of broad environmental tolerance (Lowry and Lester 2006), confounding our understanding of relationships between mating system and range size. Although we did not design our study to test the role of selfing versus outcrossing in explaining variation in range size among species, our results do not support the notion that selfing affects thermal tolerance and/or range size. We had two species pairs in which one species is predominantly selfing and the other is not, and in one case the selfing species (*M. parishii*) has a broader thermal tolerance yet a smaller range than the outcrossing species (*M. cardinalis*), and in the other case the selfing species (*M. laciniatus*) has a narrower thermal tolerance and a smaller range than the outcrossing species (*M. guttatus*).

Conclusions

In this study, we demonstrate that environmental tolerance is shaped by both intrinsic factors such as plasticity and genetic variation in ecologically relevant traits, and extrinsic factors such as variation in selection pressures across geography. Inherent species-level differences in environmental tolerance, in turn, can lead to variation in geographic range size among species. We stress the need to collect more extensive physiological data on environmental tolerances of a greater number of species and populations if we are to draw broader conclusions about the mechanisms shaping patterns of environmental tolerance and geographic range size. Our results have important implications for species with narrow thermal tolerance, which may be particularly vulnerable to climatic changes, through both narrow thermal tolerance itself and because they may lack sufficient phenotypic plasticity to cope with altered temperature regimes or genetic variation to respond to novel selection pressures. In contrast, species currently experiencing high variation in temperature across their ranges may be buffered against extinction related to climatic changes because they have evolved tolerance to a broad range of temperatures. Given projected increases in temperatures of $\sim 2\text{--}5^\circ\text{C}$ by 2099 in North America according to a medium-level emissions scenario (Meehl et al. 2007), even small differences in thermal tolerance among species could translate into important differential responses to changing climate.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Akaike information criterion (AIC) values for three functions relating relative growth rate (*RGR*) to temperature (*T*).

Table S2. Widespread and restricted species pairs (denoted by species with the same letter superscript) with thermal performance curve parameter estimates and standard errors in parentheses based on the function with lowest AIC for each species pair (Table S1).