

ABSTRACT

QUERNS, ALEAH KELSEY. The Evolution of Thermal Tolerance and Clines in Native and Invasive Populations of *Mimulus guttatus* (Under the direction of Dr. Seema Sheth).

The rise of globalization has spread organisms beyond their natural range, allowing further opportunity for introduced species to outcompete native inhabitants. Many questions remain about how niche evolution contributes to the success of invasive species. Here, we use thermal performance curves (TPCs) to test the following hypotheses about thermal adaptation during the invasion process. First, in response to strong selection from novel temperature regimes, populations in the invasive range should evolve distinct TPCs relative to native populations. Second, by exhibiting a broad TPC with high maximum performance, invasive species may overcome specialist-generalist tradeoffs, whereby tolerance across a wide range of temperatures comes at the cost of lower peak performance. Third, with sufficient time, standing genetic variation, and temperature-mediated selection, native and invasive populations may exhibit parallel adaptation to thermal gradients. To test these hypotheses, we built TPCs for 18 native (United States) and 13 invasive (United Kingdom) populations of the yellow monkeyflower, *Mimulus guttatus*. We grew clones of multiple genotypes per population across a range of temperatures in growth chambers. We found that invasive populations have not evolved different thermal performance breadth, critical thermal limits, or plasticity, and there were similar specialist-generalist tradeoffs in both native and invasive populations. Native populations did not exhibit clines in TPC parameters, indicating limited thermal adaptation across latitudinal and temperature gradients across the native range. Invasive populations have evolved a higher thermal optimum and exhibited clines in TPC parameters which were absent in native populations, but these clines countered the direction expected based on environmental gradients.

Thus, generalist characteristics of source populations and the evolutionary lability of thermal optimum may have promoted the invasion of *M. guttatus* in the United Kingdom.

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The Evolution of Thermal Tolerance and Clines in Native and Invasive Populations of *Mimulus
guttatus*

by
Aleah Kelsey Querns

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APPROVED BY:

Seema N. Sheth
Committee Chair

Martha Burford Reiskind

William A. Hoffmann

DEDICATION

For my grandparents, Ronald and Theresa Bolton

“Those who contemplate the beauty of the earth find reserves of strength that will endure as long
as life lasts.”—Rachel Carson

BIOGRAPHY

Aleah K. Querns was born in Durham, CT. She received her B.S. in Biological Sciences, with a concentration in ecology, conservation, and evolution from North Carolina State University in 2017. She has worked for multiple land management organizations, including the U.S. Fish and Wildlife Service, the National Audubon Society, and the Bureau of Land Management. These experiences have inspired her to pursue research expanding upon the evolutionary mechanisms governing plant invasion and competition. In doing so, she believes we can improve how management is conducted and even prevent future invasions altogether. In 2018, Aleah began her M.S. training at North Carolina State University with Dr. Seema Sheth. Throughout her graduate career, she has had many valuable experiences which have allowed her to grow both as a scientist and a teacher. In the long term, she aspires to use evolutionary theory to solve real issues that land managers deal with while conducting research and outreach that she hopes will inspire involvement from the community.

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CHAPTER 1: The Evolution of Thermal Tolerance and Clines in Native and Invasive Populations of *Mimulus guttatus*

Introduction

Invasive species are one of the greatest threats to biodiversity in the 21st century, and while the importance of managing their spread is widely recognized, the factors that contribute to a species becoming invasive are still debated (Sala et al. 2000, Lee 2002, van Kleunen et al. 2015a). Baker's classic description of "ideal weeds" suggested that invasive species originate from "general-purpose" genotypes with high phenotypic plasticity, allowing them to easily tolerate novel environments within their introduced range (Baker 1965). However, others have proposed that invasive species can undergo rapid niche evolution through shifting and expanding the range of environments which they are able to tolerate in response to novel selective pressures in the introduced range (Harper 1965, Lee 2002, Davidson et al. 2011). These hypotheses, which are not mutually exclusive, have a variety of implications. For example, while pre-existing or evolved generalist characters such as broad environmental tolerance and phenotypic plasticity may promote invasion, these traits may come at the cost of reduced performance, as in specialist-generalist tradeoffs whereby a "jack-of-all-trades is a master of none" (Richards et al. 2006, Le Vinh Thuy et al. 2016). Yet, the ability to overcome these tradeoffs by achieving both broad tolerance and high performance could promote invasion success. Should invasive populations undergo rapid evolution in response to environmental conditions as they spread throughout their novel range, they may form phenotypic clines along environmental gradients which parallel clines found in the native range (Li et al. 2016, Hernández et al. 2019, van Boheemen et al. 2019). Although both general-purpose genotypes and rapid evolution upon introduction likely

contribute to invasion, studies rarely consider both in tandem (Whitney & Gabler 2008, Davidson et al. 2011). Our study seeks to simultaneously explore thermal niche evolution, specialist-generalist tradeoffs, and local adaptation to provide a more comprehensive view of species invasions. Examination of the ecological and evolutionary processes which may facilitate invasion can answer long-standing questions surrounding range expansion and niche shifts, as well as provide insight toward creating optimal land management practices to predict and control biological invasions.

One dimension of a species niche space that influences its ability to invade new areas is temperature. Thermal performance curves (TPCs, Fig. 1.1a) describe the performance of a genotype, individual, population, or species across a temperature gradient (Huey & Stevenson 1979). TPC parameters that have been hypothesized to influence adaptation to temperature gradients include maximum performance, thermal optimum, thermal performance breadth, and critical upper and critical lower thermal limits (Fig. 1.1A, Huey & Stevenson 1979, Sheth & Angert 2014, Wooliver et al. 2020). Maximum performance is the highest level of performance achievable, corresponding to the peak of the TPC. Thermal optimum details the temperature at which maximum performance is achieved (Huey & Stevenson 1979). Representing heat and cold tolerance, the critical upper and lower limits correspond to the respective maximum and minimum temperature at which performance reaches 0. Thermal performance breadth describes the span of temperatures across which a specified percentage of the maximum performance is achieved (Huey & Stevenson 1979). This value is related to thermal niche width, with specialists having narrow breadth, and generalists having wide breadth (Huey & Stevenson 1979). Finally, the area under the curve refers to the total amount of area between a TPC and the temperature axis, analogous to total thermal niche space. Evolutionary divergence of TPC parameters

between invasive and native populations of the same species may explain the success of invasive species in their introduced range. However, the realization of these changes depends on standing genetic variation for TPC parameters, which provides the evolutionary fuel for selection (Prentis et al. 2008). Further, if invasive populations either are generalists that can tolerate many temperatures, or experience little to no temperature-mediated selection in the novel range, evolutionary change may be slowed or prevented altogether (Prentis et al. 2008, van Boheemen et al. 2019).

Evolutionary change in thermal performance breadth may contribute towards the success of invasive species. On one hand, invasive populations could evolve a broader TPC upon introduction in response to novel conditions, which could increase the probability of a species becoming established in new thermal regimes and taking advantage of the disturbed conditions that are unfavorable for native species (Zerebecki & Sorte 2011, Bates et al. 2013, van Kleunen et al. 2015b). One way that populations can achieve broad TPCs through high standing genetic variation, in which a greater diversity of adaptively differentiated genotypes increases population-level performance breadth (Sheth & Angert 2014). Thus, increases in thermal performance breadth are especially achievable in instances of introduction from multiple differentiated source populations to the non-native range, where admixture may produce invasive populations with higher genetic variation than native populations (Kolbe et al. 2004, Lavergne & Molofsky 2007). However, genetic bottlenecks that occurred during founding events may constrain the ability of invasive species to occupy conditions beyond those which they are already adapted to survive, or even cause reductions in breadth due to genetic drift (Kitayama & Mueller-Dombois 1995, Daehler 2003). Invasive species, which initially experience significant reductions of population size upon introduction, may therefore experience niche unfilling, which

can reduce the range of temperatures that they occupy (González-Moreno et al. 2015). Given these differing processes, invasive populations of a species may exhibit a broader thermal tolerance (due to selection for increased plasticity and/or admixture) or narrower tolerance (due to bottlenecks and/or niche unfilling) than their native counterparts (Fig. 1.1B). Alternatively, if source populations represent general-purpose genotypes with broad TPCs, they may be predisposed to tolerating a wide range of temperatures in the invasive range, resulting in similar thermal performance breadths in the native and invasive ranges. Further studies on the role of thermal tolerance in invasion will improve our understanding of the evolutionary mechanisms governing range expansions, as well as predict how invasive species may fare under changing climates.

In addition to genetic variation, another important driver of thermal performance breadth is phenotypic plasticity, which determines the ability of a genotype to undergo phenotypic changes in response to environmental conditions (Donohue 2013). If a species experiences temperature fluctuations, plasticity can be adaptive as genotypes may consistently express the optimum phenotype in each environment (Donohue 2013). Genotypes with greater plasticity in functional traits may persist over a wider range of temperatures and be more successful upon introduction to novel environments within the invasive range, allowing established populations opportunity to undergo subsequent adaptation (Richards et al. 2006, Lande 2009, Donohue 2013, Valladares et al. 2014, Lande 2015). As a result, species which have become invasive may either possess high levels of plasticity pre-introduction, or evolve increased plasticity upon introduction to the invasive range, which can contribute toward greater thermal performance breadth and, ultimately, broader population-level TPCs. However, genetic drift coupled with declines in temperature seasonality could result in reduced plasticity in invasive populations. Although

reduced plasticity could limit a species ability to tolerate rapid temperature changes, it could also allow increased specialization and resource acquisition under optimal temperatures (Davidson et al. 2011).

Additional TPC parameters that could exhibit evolutionary shifts in invasive populations due to differential selective pressures are thermal optimum, critical upper thermal limit, and critical lower thermal limit. Just as fitness tradeoffs are a ubiquitous result of local adaptation in many taxa (Hereford 2009), there are tradeoffs associated with thermal performance in contrasting environments. One such tradeoff exists for thermal optima and critical upper and lower thermal limits (Fig. 1.1C) because the ability to perform well under hot temperatures comes at a cost to performance under cold temperatures, and vice versa (Angilletta et al. 2010). Further, invasive species are often able to occupy disturbed habitats. Traits that may contribute to their success in disturbed habitats, for example those with low vegetative cover and high light, include high thermal optimum and heat tolerance (i.e., high critical upper thermal limit), which could result in lower cold tolerance (i.e., high critical lower thermal limit). Nonetheless, if invasive populations have broader TPCs than native populations, selection for other TPC parameters may be relaxed, preventing evolutionary shifts in optima, critical upper thermal limits, and critical lower thermal limits in the invasive range (Murren et al. 2015). To date, there are few empirical studies which compare TPCs of native and invasive populations of a single species (but see Comeault et al. 2020), particularly in plants.

Another tradeoff that may emerge across invasive and native populations is the cost of lower maximum performance with the ability to persist over a wider range of temperatures. This hypothesis is commonly referred to as the “jack-of-all-temperatures is a master of-none” scenario or a specialist-generalist tradeoff (Huey & Hertz 1984, Richards et al. 2006, Le Vinh Thuy et al.

2016). Populations exhibiting such a tradeoff will maintain high performance across a broad range of temperatures, but will not perform as well at the thermal optimum as populations specialized to a narrower range of temperatures due to additional energetic costs (Dewitt et al. 1998, Richards et al. 2006, Fig. 1.1D). Phenotypic plasticity, which evolves based on the degree of environmental variability, may pose similar tradeoffs where greater plasticity can incur costs to maximum performance (Murren et al. 2015, Kingsolver & Buckley 2017). In contrast, populations that have a narrower TPC and lower plasticity may avoid these costs and perform higher at their thermal optima. This tradeoff operates under the assumption that the area under the TPC remains constant (Angert et al. 2011), but some species do not meet this assumption due to physiological or biochemical alterations that allow high performance across temperatures (Angilletta et al. 2003, Richards et al. 2006). This phenomenon, which has been referred to as “jack-and-master”, or “master of all” (Richards et al. 2006, Sheth & Angert 2014), may be one mechanism that stimulates the invasibility of species.

Given a temperature or latitudinal gradient, populations with sufficient time and genetic variation may exhibit adaptive clines in TPC parameters in response to temperature-mediated selection, and rapid local adaptation may facilitate invasion success (Prentis et al. 2008, Oduor et al. 2016). Adaptive phenotypic clines across geographic, latitudinal, or climatic gradients are commonly detected in both native and invasive ranges (Fig. 1.1E-G, Li et al. 2016, Hernández et al. 2019, Thawley et al. 2018, van Boheemen et al. 2019). For example, thermal optimum decreased with increasing latitude in populations of the scarlet monkeyflower, *Mimulus cardinalis* (Angert et al. 2011). Consistent with an adaptive phenotypic cline, performance tradeoffs between low and high temperatures should result in higher thermal optima, critical upper thermal limits, and critical lower thermal limits at lower latitudes (Fig. 1.1E) and/or higher

mean annual temperatures (Fig. 1.1F, Angert et al. 2011). Further, as temperature seasonality typically increases with latitude, populations across a species range should show clines of increasing thermal performance breadth and phenotypic plasticity across both latitude and seasonality (often referred to as the climate variability hypothesis, CVH; Gutiérrez-Pesquera et al. 2016, Fig. 1.1G). Thus, with sufficient time since introduction, ample standing genetic variation, and strong temperature-mediated selection, clines in these TPC parameters should be repeated and parallel across the native and invasive ranges (Fig. 1.1E-G, Hernández et al. 2019). However, if invasive populations have not had sufficient time or standing genetic variation for adaptation to novel temperature gradients, or if temperature-mediated selection in the introduced range is weak, then phenotypic clines may be shallower in the invasive range than in the native range, or even absent altogether (Bhattarai et al. 2017, Fig. 1.1E-G). In addition, if invasive populations have broader TPCs overall relative to native populations, selection for thermal optimum and critical upper and lower limits may be relaxed due to the ability to tolerate a wide range of temperatures. The timescale and circumstances which facilitate rapid local adaptation remain unclear. Understanding the ability and rate at which invasive species adapt to local conditions may further our ability to predict niche and range expansion in invasive species.

In this study, we compare TPCs of invasive and native populations of the yellow monkeyflower, *Mimulus guttatus*, to improve our understanding of the processes underlying species abilities to colonize and invade new environments. This species spans a broad climatic and latitudinal gradient in its native range in western North America, and has become invasive in Europe and New Zealand. Examination of thermal performance across geographic and climatic gradients provides valuable information about adaptive evolution in response to the environment, and to our knowledge, this is the first study to compare clinal variation in TPC parameters

between a species native and invasive range. Here, we assess three hypotheses about whether thermal niche evolution and the ability to overcome specialist-generalist tradeoffs contribute to the invasive success of *M. guttatus*. First, we hypothesized that if the species experiences altered thermal regimes in its invasive range, there would be shifts in TPC parameters and phenotypic plasticity between the native and invasive ranges (Fig. 1.1B,C). Second, we evaluated the hypothesis that the ability to overcome specialist-generalist tradeoffs (consistent with a “master-of-all”) has fostered the invasibility of *M. guttatus* (Fig. 1.1D). This hypothesis predicts that native populations possess “master-of-all” characteristics (i.e., broad TPCs with high maximum performance) which have increased their potential success as an invader and are maintained in invasive populations. Third, given sufficient time, standing genetic variation, and temperature-mediated selection, we hypothesized parallel adaptation to thermal gradients in the invasive range (Fig. 1.1 E-G).

Methods

Study Species

We used *Mimulus guttatus* (Phrymaceae), also known as *Erythranthe guttata* (Fraga 2018, Lowry et al. 2019), as a model system to test the hypotheses outlined above about the role of thermal adaptation and phenotypic plasticity in facilitating biological invasions. Due to ease of clonal propagation, short generation times, and previous documentation of effects of temperature on growth within a short time frame (Sheth & Angert 2014), this species is a superior candidate for use in growth studies quantifying TPCs. *Mimulus guttatus* is an herbaceous wildflower native to western North America, occupying wet habitats from sea level to ~2500 m from Alaska to Northern Mexico (Fraga 2018). In 1812, *M. guttatus* was brought to the United Kingdom for

horticultural use and has subsequently become widespread across the British Isles and Europe (Preston et al. 2002, Newman 2015). In recent years, *M. guttatus* has expanded its invasive range due to climate change and altered flooding regimes (Truscott et al. 2006, Newman 2015). As a result, *M. guttatus* is now considered invasive in many countries, including New Zealand and eastern North America (Vallejo-Marín & Lye 2013, van Kleunen et al 2015, Fraga 2018). Genomic data suggest that invasive genotypes of *M. guttatus* in the UK originated from perennial populations in Alaska (Puzey & Vallejo-Marín 2014, Pantoja et al. 2017). *Mimulus guttatus* exhibits remarkable diversity in terms of genetics, life history, and habitat occupancy within its native range, and has thus become a model system in evolution, ecology, and genetics (Wu et al. 2008). Although there are both annual and perennial populations within the native range of *M. guttatus* (Hall & Willis 2006), we focused exclusively on perennial populations in the native range, as they likely gave rise to invasive populations in the UK (Puzey & Vallejo-Marín 2014, Pantoja et al. 2017).

Population Selection Criteria

To compare TPCs of native and invasive populations of *M. guttatus*, we propagated field-collected seeds from 1-15 families in each of 32 perennial populations from the native North American range and 20 perennial populations from the invasive United Kingdom range (Appendix A), totaling 346 seed families (see “Propagation of Mother Plants” below). For this study, we selected focal populations that spanned the greatest amount of temperature variability within the native and invasive ranges. To select focal populations among the populations that successfully germinated (26 native and 13 invasive populations), we conducted a principal component analysis (PCA). We used the geospatial coordinates of these populations to extract

data on 11 temperature variables (1970-2000, ~1km resolution) from WorldClim v. 2 (Fick & Hijmans 2017) for all populations in which at least one seed family germinated (Appendix A). We used these variables to conduct a PCA to understand how climate varies within and between the native and invasive ranges (Appendix B).

The PCA indicated two principal components explaining the majority of variance across populations (Appendix B). The first principal component, which explained 53.94% of variance, was characterized primarily by differences in mean temperature of the warmest quarter, mean temperature of the driest quarter, and mean annual temperature. The second principal component, which explained 32.74% of variance, was characterized by differences in maximum temperature of the warmest month, minimum temperature of the coldest month, and annual temperature range. The first two principal components showed moderate separation between native and invasive populations (Appendix B). Invasive populations encompassed a subset of temperature conditions occupied by native populations.

Using PCA coordinates generated for each population, we selected native populations for our experiment which were distributed throughout the full range of temperatures in the native range without over-representation of specific climates. Specifically, over-representation was indicated by a population being within 0.2 units of another population on either PC axis. Some exceptions were made to include a higher number of Alaskan populations, which may be the source of UK invasive populations (Pantoja et al. 2017). From this analysis, we identified 18 populations that represented a wide breadth of temperatures within the native range (Fig. 2.1A). Due to lower germination success of genotypes from the invasive range in the UK, we used all 13 available populations (Fig. 2.1B). Within each population, we randomly selected 1-5 seed families to represent in our experiment.

Propagation of Mother Plants

In June 2019, we grew seed families from each population (32 native and 20 invasive populations) in the North Carolina State University Phytotron. 3-5 seeds of each seed family were sown in 72-cell plug trays filled with Fafard 4P soil and topped with Sunshine germination mix, placed in a Percival LT-105X chamber, and subjected to a 4°C cold treatment for one week. During this time, seeds received no light and were misted daily. After one week, as seeds began to germinate, we transferred them to a growth room, with a 16-hour day and 8-hour night photoperiod and a 20/15°C day/night temperature regime. We bottom-watered trays daily with a nutrient solution, and their location within the growth room was randomized along with stagnant water being dumped on a bi-weekly basis. The same cold treatment methods were repeated for seed families with poor initial germination. After cold treatments, these replanted families remained in the Percival chamber with 20°C days and colder (5°C) nights for two weeks before being moved to the growth room. Three weeks after planting, seedlings were thinned to one, central-most individual per cell.

Six weeks after planting, individuals were repotted into 8-inch pots with Fafard 4P. Within each population of both ranges, we randomly selected 1-5 plants for inclusion in the full experiment, representing a total of 95 unique genotypes from 31 populations (Appendix A). These large “mother” plants served as the source of replicate cuttings for thermal performance experiments and remained in the growth room for the remainder of the experiment. We randomized the pots into new trays, each of which held 2 plants. Then, we allowed plants to continue growing on a schedule of daily watering with nutrient solution with bi-weekly dumping of stagnant water and tray randomization to reduce location effects. During this time, plants exhibiting annual characteristics (diminutive size, lack of side branches, small flowers; Hall &

Willis 2006) were excluded in favor of perennial plants. Eight weeks after planting, we cut the primary stem of each plant to its base to encourage branching, which is ideal for taking replicate cuttings.

Thermal Performance Experiment

Ten weeks after planting, mother plants possessed sufficient vegetative growth to support many cuttings. To generate thermal performance data for each genotype within each population, we took cuttings from these mother plants and grew them in 2.5 inch pots within 32-pot trays in one of three identical Percival LT-105X chambers. Each set of cuttings contained two replicates (clones) of each of the 95 genotypes which were randomized within six trays to reduce tray effects. We subjected replicate clones to one of six day/night temperature regimes (10°C/0°C, 20°C/10°C, 25°C/15°C, 30°C/20°C, 40°C/30°C, and 45°C/35°C), with 16 hour days and 8 hour nights, according to procedures which have been previously implemented by Paul et al. (2011), Sheth & Angert (2014), and Wooliver et al. (2020).

Prior to temperature treatments, we allowed each set of cuttings two weeks to establish roots. During this period, cuttings were kept within chambers set to 20°C day/15°C night and watered with a nutrient solution. We randomized cuttings both within and among chambers on a bi-weekly basis to reduce location effects. After the two-week establishment period, clones were moved into an alternate chamber programmed to one of the six temperature treatments. Within each chamber, we exposed these clones to a given temperature treatment for one week. During this period, trays were sub-irrigated daily with water (rather than nutrient solution) to prevent confounding effects of different rates of nutrient uptake at different temperatures.

We collected data on relative change in stem length over the course of the 7-day temperature treatment. We opted for this short treatment period due to time and space constraints. Although longer treatment times are ideal for gauging plant growth, previous work with *Mimulus spp.* has documented significant growth in one week across a range of temperatures (Sheth & Angert 2014). Before and after each temperature treatment, we took measurements of the length of the primary stem and the total length of branches (including stolons and side branches; $stem_{in}$ and $stem_{out}$, respectively). Total length of branches was estimated as the number of branches multiplied by the length of an average branch located at the midpoint of each clone. We then calculated relative growth rate (RGR), as a proxy for fitness as the change in total stem length per initial stem length per day (Eq. 1). Negative RGR values in cases where clones lost stem length or branches due to vegetation die-off at temperature extremes were set to zero, and negative RGR values in cases where clones lost stem length due to accidental severance were excluded. Although RGR is not a measure of total reproductive output, we used this metric as a proxy for fitness, and size has been related to reproductive output in other *Mimulus* species (Sheth & Angert 2018).

$$RGR = \frac{(Stem_{out} - Stem_{in})}{(Stem_{in} * \text{number of days})} \quad (\text{Eq. 1})$$

Temperature treatments were replicated twice, resulting in 12 total chamber runs, plus an additional chamber run of the 10°C/0°C temperature treatment. We included this additional chamber run due to failure to collect branch length measurements during our initial runs. In total, we took 2,418 cuttings. However, 115 of these cuttings were eliminated due to failed establishment, resulting in a final dataset of 2,303 individual clones from 18 and 13 invasive populations, each comprising 54 and 41 genotypes, respectively. Additionally, as we had not originally anticipated needing the length of average branches in our calculations of RGR, we

only took this measurement for one replicate of each temperature treatment (1,252 plants). We found that using genotype-level average, population-level average, and multiple linear models to predict this measure for the remainder of our dataset provided an inaccurate estimate of RGR (Appendix C). Therefore, we included the subset of 1,252 plants for which we measured average branch length in our final dataset.

SLA Plasticity

To compare overall phenotypic plasticity as well as latitudinal and thermal clines of plasticity among native and invasive genotypes, we measured specific leaf area (SLA) at temperature extremes. We chose to use SLA because of its demonstrated importance in determining photosynthetic productivity in a wide range of systems (Reich et al. 1999), and because *M. guttatus* has shown considerable plasticity of SLA in response to the environment (Wu et al. 2010, Kooyers et al. 2015). A drought experiment showed that *M. guttatus* had lower SLA in drier treatments, possibly because slow growth and thick, expensive leaves allow plants to avoid desiccation (Wu et al. 2010). However, because we maintained consistently wet soil, we expected that clones would instead have higher SLA at higher temperatures to increase rates of transpiration and leaf cooling. After chamber runs were carried out, we collected one of the newest fully expanded leaves from each clone within the 10°C/0°C and 40°C/30°C day/night temperature regimes. We opted to use the 40°C/30°C temperature regime, rather than 45°C/35°C, as our upper extreme due to higher mortality at 45°C. Leaf area measurements were calculated to the nearest 0.01 cm² using a LI-3100C leaf area meter prior to dehydration. Then, each leaf was stored in a coin envelope and oven-dried at 70°C for 1-2 weeks until all moisture was removed. Subsequently, we used a balance to weigh each leaf to the nearest 0.1 mg. Specific

leaf area for each clone was calculated as the area of the leaf divided by its dry mass (cm^2/mg). Plasticity is defined as the amount of phenotypic change that an individual genotype expresses across different environments (Bradshaw, 1965). We calculated plasticity in SLA as the absolute value of the slope of the reaction norm between $10^\circ\text{C}/0^\circ\text{C}$ and $40^\circ\text{C}/30^\circ\text{C}$ temperature treatments for each genotype. This gauge of plasticity is considered adequate in the context of two environments, but ignores variance in plastic responses that may occur across intermediate temperatures (Valladares et al. 2006).

Bayesian TPC Models

We performed all models and analyses in R v. 3.6.2 (R Core Team, 2019). To generate TPCs for native and invasive populations of *M. guttatus*, we used a hierarchical Bayesian model (R package `performr` v0.2; Tittes et al. 2019). As this model does not allow inclusion of random effects, we first averaged total RGR across clones of each genotype at each temperature. This model required that we scale values of RGR using the overall mean RGR across all data points and center daytime temperature around zero. However, after we ran the model, we rescaled outputs to reflect actual RGR values and temperatures. To improve the effectiveness of posterior sampling, we altered the default settings of the model to include a total of 4,000 iterations per chain and a maximum tree depth of 15 (Gelman et al. 2014). This model utilizes a derivation of Kumaraswamy's probability density function to fit performance curves across a continuous environmental gradient. We used this model to simultaneously fit curves predicting RGR across temperature for all populations. These curves generated estimates of critical upper and lower thermal limits (temperatures at which RGR decreases to zero). However, these estimates extended beyond our temperature treatments and should thus be interpreted with caution. We

assessed the fit of Bayesian models using a posterior predictive p-value, which uses a test variable to give the probability that values drawn from the simulated posterior predictive distribution will exceed the observed values. P-values closest to 0.5 are indicative of adequate fit between the modeled and observed data (Gelman et al. 2014). The Bayesian p-value for the overall model was 0.53, and p-values for each population ranged from 0.2-0.82 (Appendix D). From these Bayesian models, we obtained estimates of thermal optimum (T_{opt}), critical upper thermal limit (T_{max}), critical lower thermal limit (T_{min}), maximum performance (P_{max}), performance breadth ($T_{breadth}$), and area under the curve for each population. In our study, we selected critical values for thermal performance breadth from 100 equally spaced points along the temperature axis closest to the temperature values corresponding to 50% of a TPC's P_{max} .

Statistical Analyses for Hypothesis Testing

We tested for divergence in overall TPC parameters between native and invasive populations of *M. guttatus* independent of latitude by conducting post-hoc comparisons of TPC model iterations. For each model iteration, we calculated range-level mean TPC parameter estimates. We used these range-level means to determine the mean pairwise difference in each parameter between the native and invasive range, and for each comparison we included a 90% credible interval. For all pairwise differences, we interpreted a difference to be statistically significant if its 90% credible interval did not include zero. Positive mean differences indicated higher parameter estimates within the native range, whereas negative mean differences indicated higher parameter estimates within the invasive range. We also conducted a two-tailed t-test to examine differences in SLA plasticity between native and invasive genotypes.

We examined the potential for specialist-generalist tradeoffs between P_{max} and $T_{breadth}$ within either range using a general linear model with $T_{breadth}$, range (native or invasive), and their interaction as predictors and P_{max} as the response. Although this relationship is typically determined through correlation, we used a regression with P_{max} arbitrarily chosen as the response variable to test whether the tradeoff is stronger in either range. For all linear models, we evaluated statistical significance using $\alpha=0.1$. A significant negative effect of $T_{breadth}$ on P_{max} would indicate a specialist-generalist tradeoff wherein increased breadth comes at the cost of lower maximum performance, whereas a significant $T_{breadth}$ *range interaction would indicate that the strength of the tradeoff varies between the native and invasive range. When there was a significant interaction term, we ran separate general linear models for each range with $T_{breadth}$ as the predictor and P_{max} as the response variable to understand the differing relationships within each range. Otherwise, a lack of a significant interaction term would indicate similar tradeoffs across both ranges. To determine if the modeled TPCs fulfilled the expectation that the area under TPCs remained constant, we used Bayesian model iterations to conduct pairwise comparisons of population-level mean values of area under the curve. Using a 90% credible interval, we determined if significant differences existed both within populations within each range and between populations of different ranges. Because phenotypic plasticity may also incur performance costs, we repeated these analyses replacing $T_{breadth}$ with genotype-level SLA plasticity as a predictor of population-level P_{max} .

To determine whether invasive populations could rapidly adapt to temperature and latitudinal gradients in the novel range, we compared latitudinal and thermal clines of TPC parameters in the native and invasive range using general linear models. Full linear models of T_{opt} , T_{min} , and T_{max} included predictors of either latitude or mean annual temperature, range, and

their interaction. If a model included a significant interaction term, we conducted additional range-specific models with only latitude or mean annual temperature as predictors. Inclusion of a significant interaction term within the full models, as well as shallower or nonsignificant slopes within the invasive range in comparison to the native range, would suggest that lack of repeated, rapid local adaptation in invasive range. In contrast, a significant effect of latitude or mean annual temperature, in conjunction with a nonsignificant interaction term would indicate parallel evolution of clines across ranges. Similarly, to test whether $T_{breadth}$ and SLA plasticity increase with temperature seasonality, we modeled $T_{breadth}$ and SLA plasticity as functions of latitude or temperature seasonality, range, and their interaction. Given a significant interaction term, we also conducted range-specific models with latitude or temperature seasonality as predictors.

Results

Shifts in TPC Parameters and Plasticity

We found mixed support for the hypothesis that *M. guttatus* has adapted to novel thermal regimes within its invasive range via TPC shifts. In support of this hypothesis, invasive populations had a higher T_{opt} than native populations, with an average difference of 0.654 °C (Table 1.1, Fig. 3.1, Appendix I, CI=[-1.296, -0.014]). Contrary to the hypothesized shifts in TPC parameters in the invasive range, T_{max} , T_{min} , and $T_{breadth}$ did not differ significantly between ranges (Table 1.1, Appendix I, Fig. 3.1). Additionally, plasticity in SLA did not differ between native and invasive populations ($t = -1.0126$, $df = 83.309$, $p = 0.3142$; Appendix E).

Specialist-Generalist Tradeoffs

Consistent with specialist-generalist tradeoffs, P_{max} decreased with $T_{breadth}$ ($\beta=-0.140$, $p=0.00817$, Adj. $R^2=0.219$, Appendix F, Fig. 4.1A). A lack of interaction between $T_{breadth}$ and range indicated that the direction and strength of this relationship did not differ between the native and invasive ranges ($p=0.159$, Appendix F). Further supporting specialist-generalist tradeoffs, P_{max} decreased with SLA plasticity ($\beta=-2.278$, $p=0.0848$, Adj. $R^2=0.062$, Appendix F, Fig. 4.1B), and this relationship did not differ between ranges ($p=0.345$). However, SLA plasticity explained much less variation in P_{max} relative to $T_{breadth}$ (6.2% vs. 21.9% respectively). Pairwise comparisons indicated that population-level means of area under TPCs significantly differed both within populations of the same range and between populations of different ranges (Appendix H), failing to meet the assumption that area is constant when there are specialist-generalist tradeoffs (Angert et al. 2011).

Clines of TPC Parameters and Plasticity

Overall, latitudinal and thermal clines varied in strength depending on the TPC parameter and/or the geographic range, and there was no support for the hypothesis of adaptive clines in either range. Failing to support our hypotheses, T_{opt} did not decrease with latitude ($p=0.712$, Table 2.1, Fig. 5.1A) or increase with mean annual temperature (MAT; $p=0.899$, Table 3.1, Fig. 5.1B). Similarly, T_{max} did not decrease with latitude ($p=0.139$, Table 2.1, Fig. 5.1C) or increase with MAT ($p=0.111$, Table 3.1, Fig. 5.1D). Although the main effect of MAT on T_{max} was not significant, there was an interaction between MAT and range ($p=0.0891$, Table 3.1). According to range-specific models, T_{max} did not vary with MAT in the native range ($\beta=0.0159$, $p=0.544$, Adj. $R^2=-0.0375$, Appendix G), but decreased with MAT in the invasive range, which countered

predicted relationships ($\beta=-0.168$, $p=0.0529$, Adj. $R^2=0.236$, Appendix G, Fig. 5.1D). Opposing the hypothesis that T_{min} should decrease with increasing latitude and decreasing MAT, T_{min} increased with latitude ($p<0.001$, Table 2.1, Fig. 5.1E) and decreased with MAT ($p=0.0233$, Table 3.1, Fig. 5.1F). The relationship between T_{min} and latitude differed between ranges ($p<0.001$, Table 2.1). T_{min} increased with latitude in the invasive range ($\beta=0.0642$, $p<0.001$, Adj. $R^2=0.645$, Appendix G, Fig. 5.1E), but showed no trend in the native range ($\beta=-0.00620$, $p=0.282$, Adj. $R^2=0.0139$, Appendix G). Similarly, the relationship between T_{min} and MAT differed between ranges ($p=0.0146$, Table 3.1). T_{min} decreased with MAT in the invasive range ($\beta=-0.112$, $p=0.0549$, Adj. $R^2=0.231$, Appendix G, Fig. 5.1F), and did not vary with MAT in the native range ($\beta=0.0125$, $p=0.204$, Adj. $R^2=0.0424$, Appendix G).

Contrary to the prediction that $T_{breadth}$ should increase with latitude, $T_{breadth}$ decreased with latitude overall ($p=0.0689$, Table 2.1), and clines differed between ranges ($p=0.0790$, Table 2.1). While $T_{breadth}$ did not vary with latitude in the native range ($\beta=0.00364$, $p=0.929$, Adj. $R^2=-0.0620$, Appendix G, Fig. 5.1G), $T_{breadth}$ decreased with latitude in the invasive range ($\beta=-0.201$, $p=0.0369$, Adj. $R^2=0.279$, Appendix G, Fig. 5.1G). We found no clines of $T_{breadth}$ with temperature seasonality ($\beta=0.0581$, $p=0.407$, Adj. $R^2=-0.0076$, Appendix F, Fig. 5.1H), failing to support the climatic variability hypothesis that $T_{breadth}$ should increase with temperature seasonality.

Phenotypic plasticity decreased with latitude overall ($p=0.096$, Table 2.1, Fig. 5.1I), opposing the prediction of greater plasticity at higher latitudes. This relationship differed between ranges ($\beta=0.00296$, $p=0.0171$, Table 2.1), increasing with latitude within the native range ($\beta=0.00104$, $p=0.013$, Adj. $R^2=0.102$, Appendix G, Fig. 5.1I), and showing no trend within the invasive range ($\beta=-0.00192$, $p=0.118$, Adj. $R^2=0.0373$). However, plasticity did not vary with

temperature seasonality ($\beta=4.713e-04$, $p=0.499$, Appendix F, Fig. 5.1J), providing no support for the climate variability hypothesis.

Discussion

In this study, we compared thermal performance curves (TPCs), phenotypic plasticity, and latitudinal and thermal clines of 18 native and 13 invasive populations of *Mimulus guttatus* to test key hypotheses about the role of climatic niche evolution in facilitating biological invasions. First, our results provided mixed support for the hypothesis that TPCs and phenotypic plasticity should vary between the native and invasive ranges. Although $T_{breadth}$, T_{max} , T_{min} , and SLA plasticity did not differ between ranges, T_{opt} was higher in the invasive range compared to the native range. Second, our findings did not support the hypothesis that *M. guttatus* overcomes specialist-generalist tradeoffs by having high $T_{breadth}$ and P_{max} . Instead, TPCs in both ranges were constrained by specialist-generalist tradeoffs, such that broad TPCs and to a lesser extent, high SLA plasticity, came at the cost of lower P_{max} . Finally, contrary to the hypothesis that native and invasive ranges show parallel phenotypic clines, there was no clinal variation of TPC parameters in native populations. The native range did show increasing phenotypic plasticity with latitude, but latitude explained only a small amount of variation in the plasticity of native populations. Invasive populations formed multiple nonadaptive or maladaptive clines across latitudinal and thermal gradients. Specifically, T_{max} and T_{min} decreased with mean annual temperature, and T_{min} increased with latitude. Additionally, $T_{breadth}$ decreased with latitude, but did not vary with temperature seasonality. Together, these results suggest that evolution of thermal optima and general-purpose genotypes have contributed to the invasibility of *M. guttatus* but that specialist-generalist tradeoffs may constrain the evolution of thermal performance. Below, we discuss the

implications of these findings in light of the evolutionary processes that could contribute to plant invasion.

Evolution of Thermal Performance Curves and Plasticity

We found mixed support for the hypothesis that invasive populations have undergone changes in mean TPC parameters or phenotypic plasticity relative to native populations (Table 1.1, Appendix I, Fig. 3.1). Although T_{opt} was higher in the invasive range, $T_{breadth}$, T_{max} , T_{min} , and SLA plasticity were similar between native and invasive ranges. Thus, while invasive populations may thrive under slightly higher temperatures, the overall range of temperatures that they can tolerate and the strength of plastic responses to temperature is ultimately the same as native populations. Recent work to model the climatic niches of native and invasive *M. guttatus* documented niche conservatism, or substantial overlap in occupied climate conditions, within invasive European populations relative to native North American populations (Da Re et al. 2020). However, while a portion of the climatic niche was conserved, the invasive range had undergone substantial niche unfilling (Da Re et al. 2020), where invasive populations were found in a comparatively small subset of the climatic conditions occupied in the native range. Our findings that invasive populations inhabited a small subset of temperature conditions occupied by the native populations (Appendix B), and that $T_{breadth}$, T_{max} , and T_{min} did not differ between ranges (Table 1.1, Appendix I), are consistent with the study modeling climatic niches. Thus, invasive *M. guttatus* populations seem poised to occupy a greater climatic niche space should it become available, but the climatic niche space in the introduced range may not currently be as wide as that of its native range. In addition, maintenance of a broad thermal tolerance may allow *M. guttatus* populations to tolerate rapid changes in temperatures, posing greater risk that

invasive populations may prosper under climate change. Collectively, lack of climate-related divergent selection may explain why evolutionary shifts in thermal performance have not differentiated invasive European *M. guttatus* populations from their native North American counterparts.

Another factor that could have contributed to evolutionary stasis of some TPC parameters in the invasive range is insufficient standing genetic variation for traits involved in niche evolution (Prentis et al. 2008, Dlugosch et al. 2015, Colautti et al. 2017). On one hand, invasive populations experiencing the introduction and recombination of multiple native genotypes, as in the case of horticultural breeding, are likely to stand a better chance of adapting to novel temperature regimes. On the other hand, genetic bottlenecks that occurred during founding events may constrain the ability of invasive species to occupy conditions beyond those which they are already adapted to survive, or even cause reductions in tolerance due to genetic drift (Kitayama & Mueller-Dombois 1995, Daehler 2003). Consistent with this latter idea, invasive UK populations of *M. guttatus* have lower neutral genetic variation than native populations, which indicates that UK populations arose from a common origin (Puzey & Vallejo-Marín 2014, Pantoja et al. 2017). Thus, low genetic variation in the introduced range could constrain the rapid evolution of T_{max} , T_{min} , and $T_{breadth}$ in this species.

Although many aspects of thermal niche space are conserved between native and invasive populations, evolutionary lability in T_{opt} could be one factor which has promoted the invasion of *M. guttatus*. While native and invasive populations did not show dramatic niche divergence at a macroclimatic scale (Da Re et al. 2020, Appendix B), invasive *M. guttatus* may occupy different microclimates, resulting in a small-scale change in the strength of selection on TPCs. For example, invasive *M. guttatus* is adapted to exposed, high-light environments created by high-

flow water events in riparian habitats (Truscott et al. 2008). Despite native *M. guttatus* also being sensitive to low light, recent increases of high-flow water events within the UK may have posed a selective advantage toward genotypes which exhibit greater performance under these disturbed conditions (Truscott et al. 2006). As disturbed streambanks may impose higher light availability and warmer soil temperatures, selection under these conditions may have selected for genotypes with higher T_{opt} .

Specialist-Generalist Tradeoffs

Our results provide evidence for specialist-generalist tradeoffs, independent of native or invasive status, wherein greater $T_{breadth}$ and plasticity came at the cost of reduced P_{max} (Fig. 5.1A,B). However, our finding of differing areas under the TPC among populations within each range (Appendix H) suggests that the assumption that area remains constant does not hold for *M. guttatus*. As such, there may be an additional axis of variation that explains differences in TPCs among populations (Izem & Kingsolver 2005). To explore this prediction, we performed additional linear models in which area under the curve was predicted by either P_{max} or $T_{breadth}$, range, and their interaction. Neither main nor interactive effects of range were significant, but area significantly increased with P_{max} and significantly decreased with $T_{breadth}$ (Appendix F). The increase in area with P_{max} suggests that variation in TPCs among populations is to some extent explained by vertical shifts across a fast-slow spectrum of performance, while the decrease in area with breadth indicates that high breadth comes at a cost of universally low performance. Thus, variation in TPCs in populations of both ranges of *M. guttatus* seems to be controlled by both vertical shifts where high-performing populations are ‘masters-of-all’ and the specialist-generalist tradeoff where generalist populations are ‘master-of-none’.

Evolution of Clines

We hypothesized that phenotypic clines exhibited in the native range would be repeated in the invasive range. Despite the presence of strong variation in temperature within the invasive range of *M. guttatus* (Fig. 2.1C,D), and previous documentation of high potential for rapid adaptation to facilitate invasion success (Oduor et al. 2016), our results did not support this hypothesis. Rather, we found one cline within the native range which was not mirrored in the invasive range, and several nonadaptive or maladaptive clines in the invasive range which were not present in the native range (Fig. 5.1). Phenotypic plasticity (based on SLA) increased with latitude in the native range, but latitude only explained a low proportion of variation (~10%) in plasticity. There are many possible explanations for a lack of clines in the native range. First, rather than specializing across latitudinal and thermal gradients, native populations may be composed of general-purpose genotypes which predisposed them to become invasive (van Kleunen et al. 2011). Second, since six native populations were not strictly coastal, there may also be divergent relationships between TPC parameters and environmental gradients caused by adaptation to different thermal regimes in coastal and inland environments. We tested this by conducting separate analyses of coastal populations, but results were qualitatively similar (Appendix J, K). Third, coastal *M. guttatus* populations may not display strong clines in TPCs if they occupy microhabitats containing similar pockets of temperature conditions across their range (Franco & Nobel 2003). Fourth, populations in close latitudinal proximity may experience drastically different thermal regimes due to microclimatic variation, resulting in fine-scale local adaptation that prevents us from detecting clines at broader scales. Finally, high gene flow among native populations could swamp adaptation of TPCs to local thermal regimes (Paul et al. 2011). This conclusion is consistent with genomic data which reveal high rates of gene flow

among coastal populations occupying similar latitudes in the native range relative to our study populations (Twyford & Friedman 2015). Nonetheless, our findings are particularly surprising given the numerous studies documenting local adaptation to edaphic and hydrological conditions within the *M. guttatus* species complex (Hall & Willis 2006, Wu et al. 2008, Lowry et al. 2009, Hall et al. 2010, Kooyers et al. 2015, Selby & Willis 2018, Popovic & Lowry 2020), and the evolution of parallel phenotypic clines in the introduced ranges of several species (van Boheemen et al. 2019, Hernández et al. 2019, McGoey et al. 2020). Thus, while specializing in hydrological and edaphic aspects of niche space, native *M. guttatus* populations may be generalists in thermal niche space despite spanning a broad temperature gradient in western North America.

Unexpectedly, the invasive populations of *M. guttatus* displayed what seem to be nonadaptive or maladaptive clines of TPC parameters. For example, T_{min} increased with latitude and decreased with mean annual temperature in the invasive range (Fig. 5.1E,F), suggesting that cold tolerance is lower at higher latitudes and in cooler environments. Similarly, indicative of reduced heat tolerance in warmer environments, T_{max} decreased with mean annual temperature. Although $T_{breadth}$ in the invasive range also declined with latitude (Fig. 5.1G), this relationship was weak ($R^2 = 0.062$), and $T_{breadth}$ did not vary predictably with seasonality (Fig. 5.1H) despite temperature seasonality decreasing with latitude in the invasive range (Fig. 2.1D). Genetic drift associated sequential founder events can cause a quantitative trait to rapidly increase in frequency during range expansion and result in a nonadaptive, or even maladaptive geographic cline (Colautti & Lau 2016). However, another study documented rapid evolution of parallel phenotypic clines in the invasive range, where latitudinal clines for sexual and vegetative allocation to reproduction were similar in the native and invasive ranges of *M. guttatus*, with an

increase in vegetative reproduction and a decrease in sexual reproduction at higher latitudes (van Kleunen & Fischer 2008). Future reciprocal transplant experiments are needed to assess the fitness consequences of the counterintuitive patterns documented in our study.

Caveats

There are many caveats which may have impacted the results of our study. First, given our decision to use only the cuttings for which we measured average branch length, our final dataset included only two replicates of each genotype per temperature treatment. Some replicates failed to establish roots, leading to multiple genotypes containing only one replicate for a given treatment, which could exacerbate chamber- and tray-effects on RGR of a given genotype. However, given that we used 2-4 genotypes to construct our population-level TPC curves (with the exception of one invasive population; Appendix A), these effects should be less prevalent at the population level. Second, our temperature treatments maintained constant day and night temperatures, but it is widely recognized that in natural settings plants experience daily fluctuations of temperature conditions which may influence evolutionary trends. Third, we used only one variable (RGR) in our examination of thermal performance, as well as only one variable (SLA) as a gauge of plasticity. Although we incorporated multiple growth measurements (primary stem length, branch number, and average branch length), populations may vary in their investment in stem and branch growth versus other growth parameters (such as leaf number, belowground growth, or flower number) at different temperatures. Fourth, we focused on one performance metric, RGR, but to fully understand how performance varies across temperature gradients, as well as how varying levels of tolerance may result in performance tradeoffs, multiple performance parameters (e.g., survival and fecundity) across multiple life stages should

be included in future work. Finally, we focused only on temperature, one axis of the species' climatic niche, but evolution along other niche axes such as precipitation and edaphic properties could also contribute to invasion success (Hall & Willis 2006, van Kleunen & Fischer 2008). Further, the biotic environment, including competitors, enemies, and pollinators may also differ in the introduced range (Holeski et al. 2013, Thawley et al. 2018), implying that many factors beyond abiotic conditions can play a part in adaptation to novel conditions during invasions.

Conclusions

Plant invasion is a field that has been widely studied for land management purposes, but little consensus exists on the ecological and evolutionary processes that facilitate invasion success. Our finding that native populations did not exhibit clines in TPCs indicates that general-purpose genotypes may have contributed toward successful establishment in the invasive range. Further, despite previous work showing climatic niche conservatism between the native and European invasive ranges of *M. guttatus*, novel selective forces may have caused evolutionary change of thermal optimum in the invasive range. The nonadaptive and maladaptive clines we observed in the invasive range are likely the result of unexamined factors, such as shifts in microhabitat or genetic drift, rather than temperature gradients. Additionally, we found support for similar specialist-generalist tradeoffs across both ranges, implying that the “master-of-all” scenario has not promoted the invasion of *M. guttatus* in the United Kingdom. Our results have important implications toward discovering what traits are favored for invasive organisms. For example, although having a broad thermal performance curve and general-purpose genotypes may aid in initial establishment of populations in a new environment, specialist-generalist tradeoffs may constrain the further evolution of broader TPCs. By comparing thermal niche

evolution across broad environmental gradients in a species native and invasive range, we can predict which species hold the potential to become aggressive invaders and forecast how they may fare under rapid climate change. These predictions will be invaluable in preparing for future species invasions, strengthening our efforts to manage invasive species in the face of rapid climate change and globalization.

TABLES

Table 1.1: Pairwise comparisons of thermal performance parameters between ranges. For each Bayesian model iteration, we calculated range-level mean thermal parameter estimates and found their pairwise differences by subtracting the parameter estimate of the native range from the invasive range. We used these comparisons to generate a mean pairwise difference, as well as a 90% credible interval for this difference.

| Parameter | Pairwise Difference | 90% CI |
|-----------------------|---------------------|-------------------|
| T_{min} (°C) | 0.034 | [-0.525, 0.607] |
| T_{max} (°C) | -0.04 | [-0.532, 0.459] |
| T_{opt} (°C) | -0.654 | [-1.296, -0.014]* |
| P_{max} (cm/cm/day) | -0.071 | [-0.175, 0.028] |
| $T_{breadth}$ (°C) | 0.018 | [-0.993, 1.041] |
| Area | -3.043 | [-6.758, 0.617] |

*=credible interval does not include zero

Table 2.1: Regression coefficients and adjusted R^2 of general linear models relating response variables to latitude, range, and latitude*range.

| Response | Latitude | Range | Latitude x Range | Adj. R^2 |
|---------------|-----------|----------|------------------|------------|
| T_{opt} | 0.0453 | 3.812 | -0.0870 | -0.00182 |
| $T_{breadth}$ | -0.201* | -11.209* | 0.204* | 0.0197 |
| Plasticity | -0.00192* | -0.150** | 0.00296** | 0.0716 |
| T_{max} | 0.0596 | 3.256 | -0.0599 | -0.0206 |
| T_{min} | 0.0642*** | 3.865*** | -0.0704*** | 0.356 |

*= $p < 0.1$, **= $p < 0.05$, ***= $p < 0.01$

Table 3.1: Regression coefficients and adjusted R^2 of general linear models relating response variables to mean annual temperature (MAT), range, and MAT*range.

| <i>Response</i> | <i>MAT</i> | <i>Range</i> | <i>MAT x Range</i> | <i>Adj. R²</i> |
|-----------------|------------|--------------|--------------------|---------------------------|
| T_{opt} | 0.0383 | -1.738 | 0.115 | 0.104 |
| T_{max} | -0.168 | -1.620* | 0.183* | 0.00941 |
| T_{min} | -0.112** | -1.0409** | 0.125** | 0.130 |

*= $p < 0.1$, **= $p < 0.05$, ***= $p < 0.01$

FIGURES

Figure 1.1: Hypotheses describing the evolution of thermal performance curves (TPCs) and clines in the native vs. invasive ranges of *Mimulus guttatus*, where grey, orange, and purple may describe the TPC of a native or invasive population in panels B-D, and red corresponds to invasive populations and blue corresponds to native populations in panels E-G. (A) TPC parameters of interest include P_{max} , T_{opt} , $T_{breadth}$, T_{max} , and T_{min} . (B) Invasive populations may have wider (grey) or narrower (orange) $T_{breadth}$ relative to native populations. Alternatively, if general-purpose genotypes from native source populations facilitate invasion, $T_{breadth}$ may be equally wide in both ranges. (C) Invasive populations exhibit different T_{opt} , T_{max} , and T_{min} relative to native populations. (D) Within native and invasive populations, there may be specialist-generalist tradeoffs such that populations with greater $T_{breadth}$ have a lower P_{max} (grey) and populations with narrower $T_{breadth}$ have a higher P_{max} (orange). However, some invasive species may be able to overcome these tradeoffs and achieve a wide $T_{breadth}$ accompanied by a high P_{max} (purple). (E-G) Solid lines indicate steep clines, indicating sufficient time, genetic variation, and selective pressure for local adaptation in TPC parameters across latitudinal and temperature gradients, whereas dashed lines indicate weaker/no clines. (E) The native range (solid blue line) exhibits clines such that T_{opt} , T_{max} , and T_{min} decrease with latitude, whereas the invasive range (solid red line) exhibits repeated/parallel clines (solid red line), or weaker/no clines (dashed red line), or repeated/parallel clines. (F) The native range (solid blue line) exhibits clines such that T_{opt} , T_{max} , and T_{min} increase with mean annual temperature, whereas the invasive range exhibits repeated/parallel clines (solid red line), or weaker/no clines (dashed red line). (G) The native range (solid blue line) exhibits clines such that $T_{breadth}$ and/or phenotypic plasticity increases with both latitude and temperature, whereas the invasive range exhibits repeated/parallel clines (solid red line), or weaker/no clines (dashed red line).

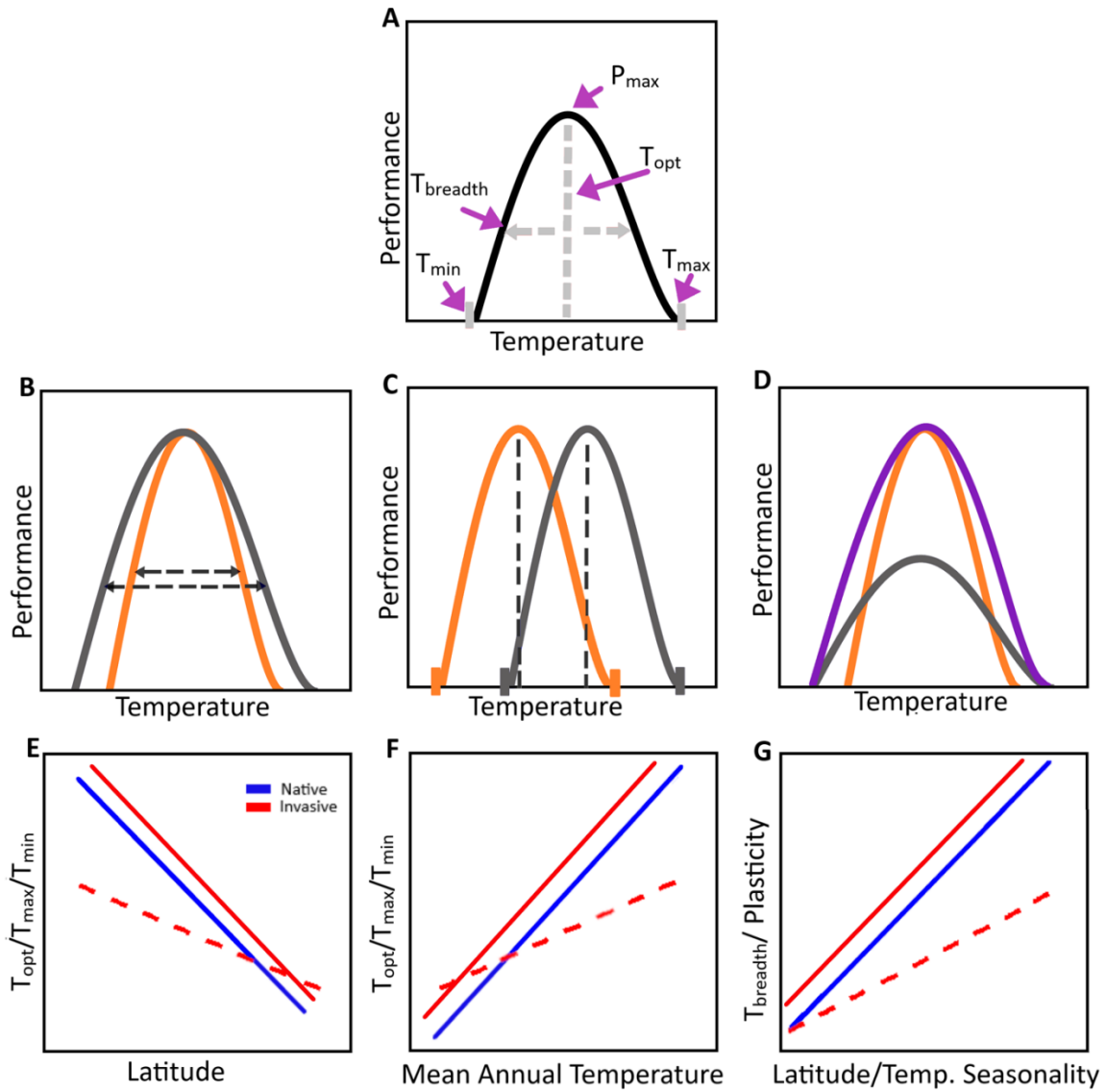
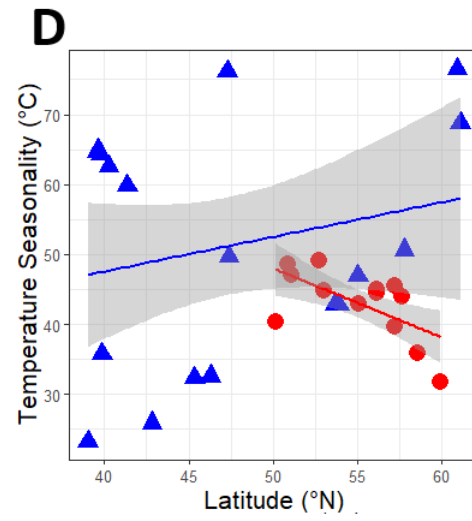
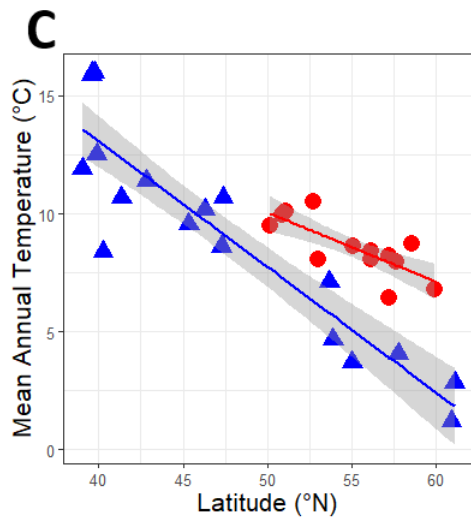
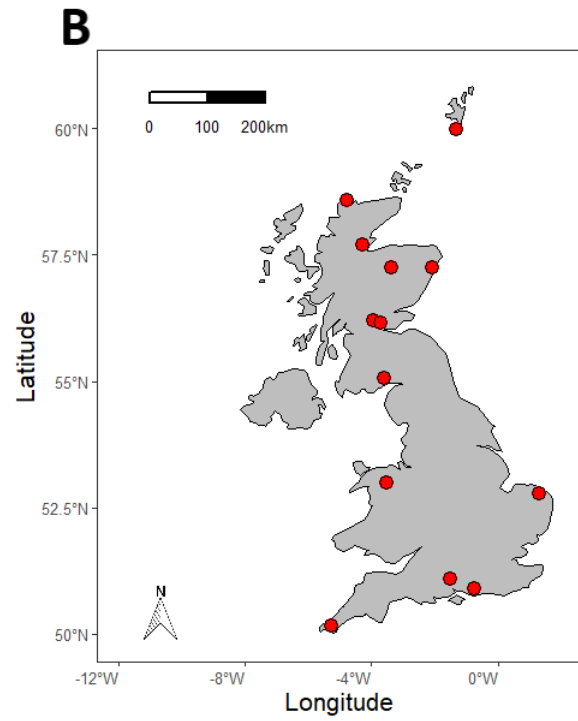
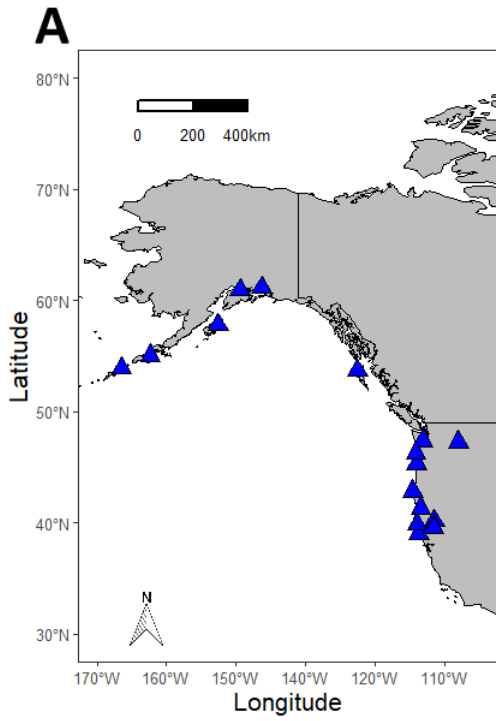


Figure 2.1: Map of focal populations of *M. guttatus* in (A) native range in North America and (B) invasive range in the United Kingdom. (C-D) Observed values of (C) mean annual temperature (°C) and (D) temperature seasonality (°C) across latitude (°N) for native (blue triangles) and invasive (red circles) populations. Fitted lines indicate predicted mean annual temperature or seasonality based on observed values across latitudes. The gray shaded area indicates a 90% confidence interval for these predictions. Climate data were obtained from WorldClim v.2 (~1-km resolution, 1970-2000, Fick & Hijmans 2017).



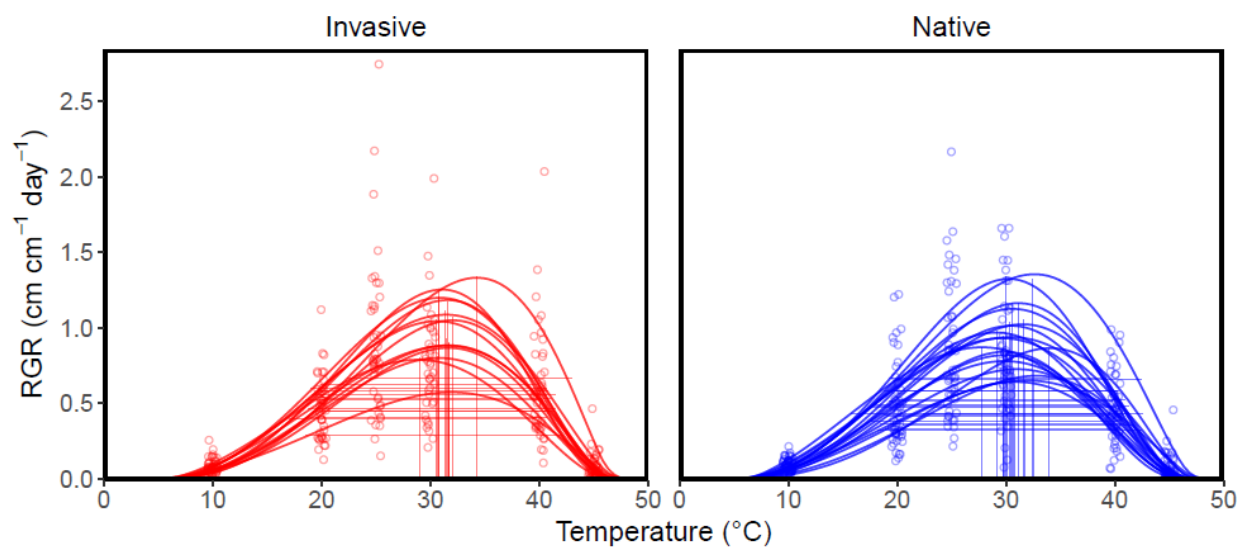


Figure 3.1: TPCs of 18 native (blue) and 13 invasive (red) populations of *Mimulus guttatus*. T_{opt} is represented by vertical lines, and $T_{breadth}$ is represented by horizontal lines. Points represent genotype-level mean RGR at a given daytime temperature.

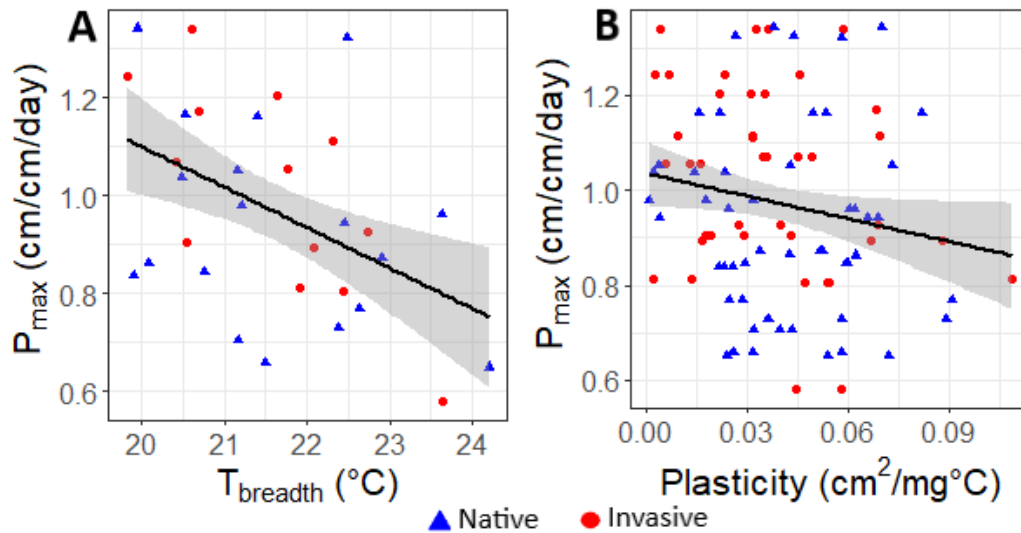
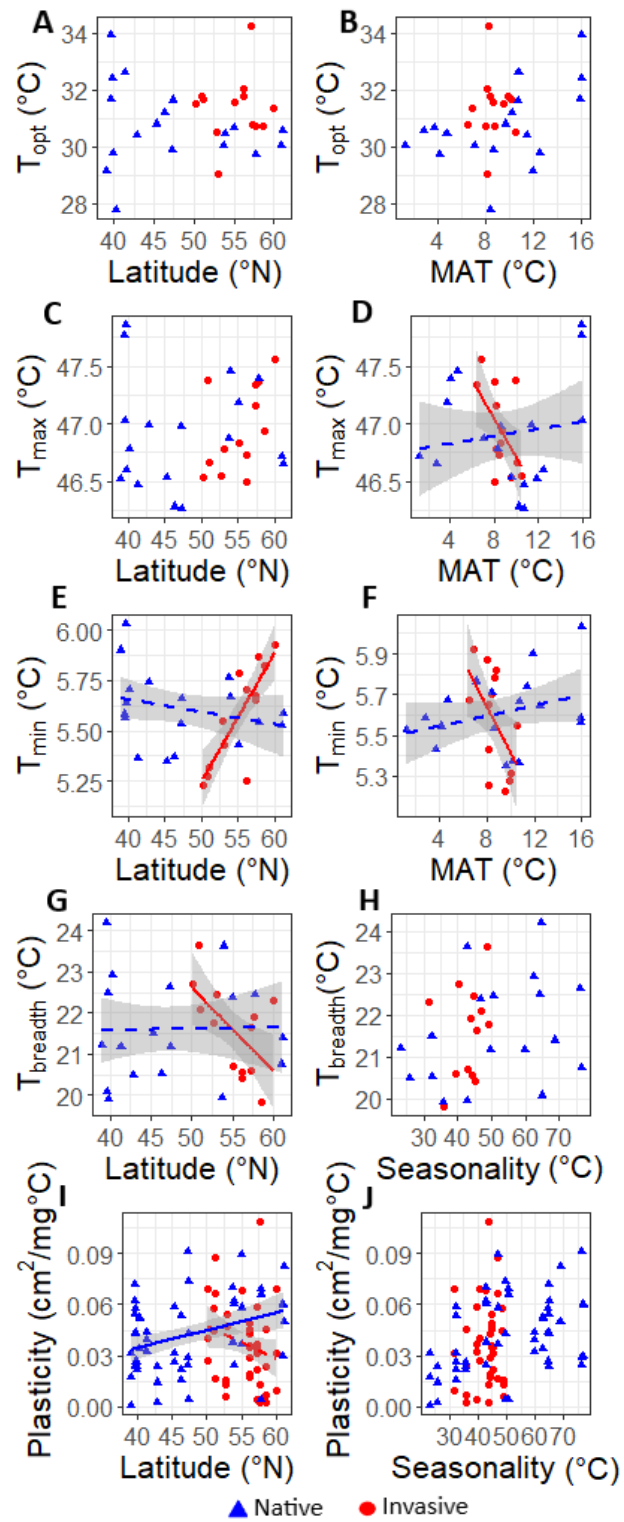


Figure 4.1: Specialist-generalist tradeoffs as shown by general linear models relating population-level P_{max} to either (A) population-level $T_{breadth}$ or (B) genotype-level SLA plasticity. Grey shading indicates a 90% confidence interval. Both figures show the slope from the full model with a black line, as the main effects of (A) $T_{breadth}$ and (B) plasticity were significant in the full model ($p < 0.1$ for both effects), but there was not a statistically significant interaction between either predictor variable and range, indicating that the direction and magnitude of these relationships did not differ between the ranges.

Figure 5.1: Latitudinal and thermal clines of (A-H) population-level TPC parameters and (I-J) genotype-level SLA plasticity across predictors of either latitude, mean annual temperature (MAT), or temperature seasonality. Range-level regression lines are shown if there was a significant interaction with range in full general linear models. Solid lines indicate a range-level model where the p-value for a given predictor is <0.1 . Dashed lines indicate a range-level model where the p-value for a given predictor is >0.1 .



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APPENDICES

Appendix A

Seed collection sites for potential *Mimulus guttatus* populations to be included in thermal performance experiments. “Donor” describes the labs or individual collectors who donated seeds from each population. Population codes have been assigned to each geographical occurrence. “Number of Genotypes” describes the total number of seed families within each population which were donated for our experiment. “Genotypes Selected” describes the number of seed families within each population used in thermal performance experiments, given germination success and population selection criteria. “Range” describes whether the population exists within the North American/native range or United Kingdom/invasive range of *M. guttatus*.

| <i>Donor</i> | <i>Population Code</i> | <i>Latitude</i> | <i>Longitude</i> | <i>Number of Genotypes</i> | <i>Genotypes Selected</i> | <i>Range</i> |
|--------------|------------------------|-----------------|------------------|----------------------------|---------------------------|---------------|
| Lowry | N1 | 39.0083 | -123.69395 | 7 | 3 | North America |
| Coughlan | N2 | 39.53903 | -121.58286 | 15 | 0 | North America |
| Coughlan | N3 | 39.55229 | -121.567 | 15 | 3 | North America |
| Coughlan | N4 | 39.60485 | -121.598 | 15 | 3 | North America |
| Coughlan | N5 | 39.6153 | -121.6 | 15 | 0 | North America |
| Lowry | N6 | 39.73687 | -123.631 | 11 | 0 | North America |
| Coughlan | N7 | 39.7462 | -121.6728833 | 14 | 3 | North America |
| Coughlan | N8 | 39.813717 | -121.57175 | 2 | 0 | North America |
| Lowry | N9 | 39.860529 | -123.902367 | 11 | 3 | North America |
| Coughlan | N10 | 40.1028 | -121.4993 | 15 | 0 | North America |
| Coughlan | N11 | 40.2476 | -121.447433 | 12 | 3 | North America |
| Lowry | N12 | 41.339663 | -123.388162 | 11 | 3 | North America |
| Blackman | N13 | 42.690011 | -124.447772 | 5 | 0 | North America |
| Lowry | N14 | 42.83772 | -124.56 | 7 | 3 | North America |
| Colicchio | N15 | 43.235261 | -124.392128 | 7 | 0 | North America |
| Lowry | N16 | 43.989674 | -123.177453 | 11 | 0 | North America |
| Coliccho | N17 | 44.143124 | -124.122314 | 2 | 0 | North America |
| Coliccho | N18 | 44.26739 | -124.108563 | 2 | 0 | North America |

Appendix A (continued)

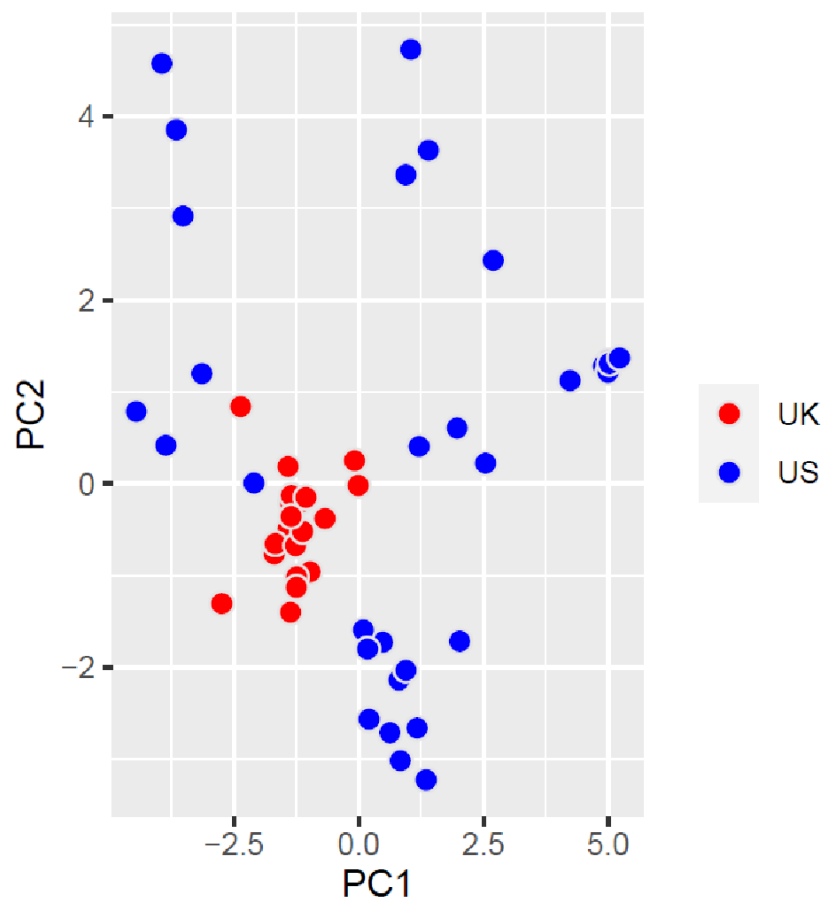
| | | | | | | |
|----------------|-----|------------|--------------|----|---|----------------|
| Colicchio | N19 | 44.309916 | -124.101597 | 3 | 0 | North America |
| Coliccho | N20 | 44.623434 | -124.067267 | 10 | 0 | North America |
| Coliccho | N21 | 44.677008 | -124.07399 | 4 | 0 | North America |
| Lowry | N22 | 45.3382533 | -123.9771333 | 12 | 4 | North America |
| Lowry | N23 | 46.3053 | -124.072 | 10 | 3 | North America |
| Holeski | N24 | 47.287683 | -117.962933 | 5 | 3 | North America |
| Lowry | N25 | 47.3854 | -123.147 | 11 | 3 | North America |
| Holeski/Rotter | N26 | 53.698133 | -132.526217 | 3 | 3 | North America |
| Friedman | N27 | 53.90448 | -166.51068 | 5 | 3 | North America |
| Friedman | N28 | 55.05603 | -162.32816 | 5 | 3 | North America |
| Friedman | N29 | 57.79456 | -152.59483 | 5 | 3 | North America |
| Holeski/Rotter | N30 | 59.741133 | -151.7475 | 5 | 0 | North America |
| Holeski/Rotter | N31 | 60.95245 | -149.4112167 | 5 | 3 | North America |
| Holeski/Rotter | N32 | 61.13825 | -146.32465 | 5 | 2 | North America |
| Vallejo-Marín | I1 | 50.162 | -5.293 | 5 | 3 | United Kingdom |
| Vallejo-Marín | I2 | 50.904513 | -0.77971674 | 3 | 2 | United Kingdom |
| Vallejo-Marín | I3 | 51.09699 | -1.5084 | 5 | 3 | United Kingdom |
| Holeski/Rotter | I4 | 51.133 | -3.64177 | 3 | 0 | United Kingdom |
| Vallejo-Marín | I5 | 52.768 | 1.297 | 5 | 3 | United Kingdom |
| Holeski/Rotter | I6 | 52.98935 | -3.466 | 3 | 0 | United Kingdom |
| Vallejo-Marín | I7 | 53.00598 | -3.54927 | 4 | 3 | United Kingdom |
| Holeski/Rotter | I8 | 55.0635 | -3.60888 | 3 | 1 | United Kingdom |
| Holeski/Rotter | I9 | 55.4615 | -4.6257 | 3 | 0 | United Kingdom |
| Holeski/Rotter | I10 | 55.6548 | -2.23938 | 3 | 0 | United Kingdom |
| Holeski/Rotter | I11 | 55.99497 | -2.55667 | 3 | 0 | United Kingdom |
| Holeski/Rotter | I12 | 56.0653 | -4.39088 | 3 | 0 | United Kingdom |
| Vallejo-Marín | I13 | 56.1473 | -3.74477 | 5 | 4 | United Kingdom |
| Vallejo-Marín | I14 | 56.19654 | -3.96856 | 5 | 4 | United Kingdom |

Appendix A (continued)

| | | | | | | |
|----------------|-----|-----------|------------|---|---|----------------|
| Vallejo-Marín | I15 | 57.23748 | -2.06385 | 5 | 4 | United Kingdom |
| Vallejo-Marín | I16 | 57.25499 | -3.36777 | 5 | 3 | United Kingdom |
| Vallejo-Marín | I17 | 57.682614 | -4.2652576 | 5 | 3 | United Kingdom |
| Holeski/Rotter | I18 | 57.82897 | -5.06625 | 3 | 0 | United Kingdom |
| Vallejo-Marín | I19 | 58.575 | -4.767 | 5 | 4 | United Kingdom |
| Vallejo-Marín | I20 | 59.97777 | -1.30036 | 5 | 4 | United Kingdom |

Appendix B

Results of PCA exploring variation in 11 temperature variables taken from WorldClim v. 2.0 across all populations considered for use in our study (Appendix A; 1970-2000, Fick & Hijmans 2017). These variables include mean annual temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, and mean temperature of the coldest quarter.



Appendix C

About Decision to Use Subsetted Dataset

Given that we only measured the length of an average branch on plants from one chamber run of each temperature, we explored the potential of using the genotype-level and population-level mean for average branch length. This method would involve taking the mean of the average branch length for each genotype and population at the beginning of the chamber run, as well as the mean of average branch length for each genotype*temperature and population*temperature combination at the end of each chamber run. Then, we would use genotype-level and population-level means of average branch length to calculate total relative growth rates for each cutting replicate.

We tested the plausibility of using either genotype- or population-level means using a cross validation method. The 1,252 cuttings which possessed measurements of average branch length were split into a training and validation set. We used the training set to calculate genotype- and population-level mean values of average branch length. Then, we used genotype- and population-level mean values of average branch length taken from the training set to calculate total relative growth within the validation set. Using the validation set, we plotted a linear regression model of the proxy relative growth rates (using the mean values) versus actual relative growth rate (using the actual measurement of average branch length taken from each individual cutting). We found that calculations using genotype-level average showed a low correlation with actual relative growth rate which explained only 35% of the variation in our data ($\beta=0.57$, Adj. $R^2= 0.3509$). Population-level average showed only a slightly higher correlation with actual relative growth rate which explained 40% of the variation in our data ($\beta=0.60784$, Adj. $R^2= 0.4024$).

Next, we attempted to implement general linear models and linear mixed effect models (using the lmer function of the lme4 package; Bates et al. 2014) to predict average branch length using the same cross-validation method. Our general linear models included stem length, population, and the total number of branches as possible predictors. For our mixed effect models, potential fixed effects were stem length and total number of branches. Potential random effects were population and genotype nested within population. Multiple models were generated for each possible combination of variables. The models which provided the lowest AIC values were used to predict proxy total relative growth rate, and that proxy was plotted using a linear regression versus actual growth rate. This model produced a slightly better fit than mean-values alone ($\beta=0.77$, Adj. $R^2= 0.5958$). Given the low correlation between both proxies and actual relative growth rate values, we decided to use only the subset of cuttings which contained actual measurements of average branch length in our final dataset.

Appendix D

Posterior predictive p-values generated for each *Mimulus guttatus* population's TPC curve. P-values close to 0.5 indicate adequate fit between the modeled and observed data (Gelman et al. 2014). Invasive populations are indicated by I1-13, and native populations are indicated by N1-N18 (Appendix A).

| Population | Bayesian p-value |
|-------------------|-------------------------|
| I1 | 0.30525 |
| I2 | 0.56975 |
| I3 | 0.198375 |
| I4 | 0.482125 |
| I5 | 0.565375 |
| I6 | 0.54275 |
| I7 | 0.638 |
| I8 | 0.5215 |
| I9 | 0.532125 |
| I10 | 0.711625 |
| I11 | 0.698 |
| I12 | 0.821375 |
| I13 | 0.457125 |
| N1 | 0.542375 |
| N2 | 0.426 |
| N3 | 0.671375 |
| N4 | 0.33275 |
| N5 | 0.694625 |
| N6 | 0.64025 |
| N7 | 0.2865 |
| N8 | 0.668625 |
| N9 | 0.3945 |
| N10 | 0.3935 |
| N11 | 0.644875 |
| N12 | 0.473875 |
| N13 | 0.565625 |
| N14 | 0.741375 |
| N15 | 0.493375 |
| N16 | 0.6755 |
| N17 | 0.50725 |
| N18 | 0.401875 |

Appendix E

Genotype-level plasticity (in units of $\text{cm}^2/\text{mg}^\circ\text{C}$) calculated as the absolute value of the slope of the reaction norm which displays change in specific leaf area between 10°C and 40°C for native (N1-N18) and invasive (I1-I13) populations of *Mimulus guttatus*. Three genotypes were excluded due to insufficient data.

| Genotype | Population | Plasticity |
|----------|------------|------------|
| 1 | N1 | 0.018 |
| 2 | N1 | 0.001 |
| 3 | N1 | 0.032 |
| 4 | N2 | 0.024 |
| 5 | N2 | 0.072 |
| 6 | N2 | 0.054 |
| 7 | N3 | 0.043 |
| 8 | N3 | 0.062 |
| 9 | N4 | 0.027 |
| 10 | N4 | 0.044 |
| 11 | N4 | 0.058 |
| 12 | N5 | 0.023 |
| 13 | N5 | 0.022 |
| 14 | N5 | 0.026 |
| 15 | N6 | 0.034 |
| 16 | N6 | 0.052 |
| 17 | N6 | 0.053 |
| 18 | N7 | 0.032 |
| 19 | N7 | 0.040 |
| 20 | N7 | 0.043 |
| 21 | N8 | 0.014 |
| 22 | N8 | 0.002 |
| 23 | N8 | 0.024 |
| 24 | N9 | 0.026 |
| 25 | N9 | 0.032 |
| 26 | N9 | 0.058 |
| 27 | N10 | 0.053 |
| 28 | N10 | 0.022 |
| 29 | N10 | 0.016 |
| 30 | N11 | 0.029 |
| 31 | N11 | 0.091 |
| 32 | N11 | 0.025 |

Appendix E (continued)

| | | |
|----|-----|-------|
| 33 | N12 | 0.073 |
| 34 | N12 | 0.004 |
| 35 | N12 | 0.043 |
| 36 | N13 | 0.038 |
| 37 | N13 | 0.070 |
| 38 | N14 | 0.024 |
| 39 | N14 | 0.060 |
| 40 | N14 | 0.062 |
| 41 | N15 | 0.089 |
| 42 | N15 | 0.036 |
| 43 | N15 | 0.058 |
| 44 | N16 | 0.004 |
| 45 | N16 | 0.069 |
| 46 | N16 | 0.066 |
| 47 | N17 | 0.060 |
| 48 | N17 | 0.060 |
| 49 | N17 | 0.030 |
| 50 | N18 | 0.050 |
| 51 | N18 | 0.082 |
| 52 | I1 | 0.069 |
| 53 | I1 | 0.040 |
| 54 | I1 | 0.027 |
| 55 | I2 | 0.058 |
| 56 | I2 | 0.044 |
| 57 | I3 | 0.067 |
| 58 | I3 | 0.088 |
| 59 | I3 | 0.017 |
| 60 | I4 | 0.013 |
| 61 | I4 | 0.016 |
| 62 | I4 | 0.006 |
| 63 | I5 | 0.054 |
| 64 | I5 | 0.054 |
| 65 | I5 | 0.047 |
| 66 | I6 | 0.068 |
| 67 | I7 | 0.029 |
| 68 | I7 | 0.018 |
| 69 | I7 | 0.043 |
| 70 | I7 | 0.019 |

Appendix E (continued)

| | | |
|----|-----|-------|
| 71 | I8 | 0.045 |
| 72 | I8 | 0.035 |
| 73 | I8 | 0.049 |
| 74 | I8 | 0.036 |
| 75 | I9 | 0.033 |
| 76 | I9 | 0.004 |
| 77 | I9 | 0.036 |
| 78 | I9 | 0.059 |
| 79 | I10 | 0.035 |
| 80 | I10 | 0.022 |
| 81 | I10 | 0.031 |
| 82 | I11 | 0.013 |
| 83 | I11 | 0.109 |
| 84 | I11 | 0.002 |
| 85 | I12 | 0.007 |
| 86 | I12 | 0.046 |
| 87 | I12 | 0.002 |
| 88 | I12 | 0.023 |
| 89 | I13 | 0.069 |
| 90 | I13 | 0.032 |
| 91 | I13 | 0.032 |
| 92 | I13 | 0.010 |

Appendix F

Regression coefficients and p-values from full general linear models relating response variables to predictors. β_1 indicates the main effect of either latitude, mean annual temperature (MAT), $T_{breadth}$, plasticity, temperature seasonality (TS), or P_{max} . β_2 indicates the main effect of range. β_3 indicates the interaction between range and the predictor corresponding to β_1 .

| Full Model | | | | | |
|---------------|---|-------------------------------|------------------------------|--------------------------------|------------|
| Response | Predictor ($\beta_1, \beta_2, \beta_3$) | β_1, p | β_2, p | β_3, p | Adj. R^2 |
| T_{opt} | Lat, R, Lat*R | -0.002, $p=0.712$ | 3.812, $p=0.590$ | -0.087, $p=0.504$ | -0.002 |
| | MAT,R, MAT*R | 0.038, $p=0.899$ | -1.738, $p=0.521$ | 0.115, $p=0.710$ | 0.128 |
| P_{max} | $T_{breadth}$, R, $T_{breadth}$ *Range | -0.140, $p=0.00817^{***}$ | -1.963, $p=0.146$ | 0.0877, $p=0.159$ | 0.219 |
| | Plasticity, R, Plasticity*Range | -2.278, $p=0.0848^*$ | -0.160, $p=0.0548^*$ | 1.716, $p=0.345$ | 0.0615 |
| $T_{breadth}$ | Lat, R, Lat*R | -0.201, $p=0.0689^*$ | -11.207, $p=0.0769^*$ | 0.204, $p=0.0790^*$ | 0.0197 |
| | TS, R, TS*R | 0.0581, $p=0.407$ | 1.265, $p=0.689$ | -0.0336, $p=0.640$ | -0.00760 |
| Plasticity | Lat, R, Lat*R | -0.00192, $p=0.0960^*$ | -0.150, $p=0.0263^{**}$ | 0.00296, $p=0.0171^{**}$ | 0.0716 |
| | TS, R, TS*R | 4.713e-04, $p=0.499$ | -3.818e-03, $p=0.903$ | 9.641e-05, $p=0.894$ | 0.0772 |
| T_{max} | Lat, R, Lat*R | 0.0596, $p=0.139$ | 3.256, $p=0.159$ | -0.0599, $p=0.158$ | -0.0206 |
| | MAT, R, MAT*R | -0.168, $p=0.111$ | -1.620, $p=0.0853^*$ | 0.183, $p=0.0891^*$ | 0.00941 |
| T_{min} | Lat, R, Lat*R | 0.0642, $p=0.000243^{***}$ | 3.865, $p=0.000145^{***}$ | -0.0704, $p=0.000159^{***}$ | 0.356 |
| | MAT, R, MAT*R | -0.112, $p=0.0233^{**}$ | -1.0409, $p=0.0189^{**}$ | 0.125, $p=0.0146^{**}$ | 0.130 |

Appendix F (continued)

| | | | | | |
|-------------------------|--|-------------------------------|--------------------------|------------------------|--------|
| <i>Area Under Curve</i> | <i>T</i> _{breadth} , Range, <i>T</i> - <i>breadth</i> *Range | -4.497, <i>p</i> =0.0521* | -86.081, <i>p</i> =0.157 | 3.847, <i>p</i> =0.171 | 0.0705 |
| | <i>P</i> _{max} , Range, <i>P</i> _{max} *Range | 38.594, <i>p</i> =2.49e-14*** | -3.217, <i>p</i> =0.363 | 3.107, <i>p</i> =0.378 | 0.9504 |

*=*p*<0.1, **=*p*<0.05, ***=*p*<0.01

Appendix G

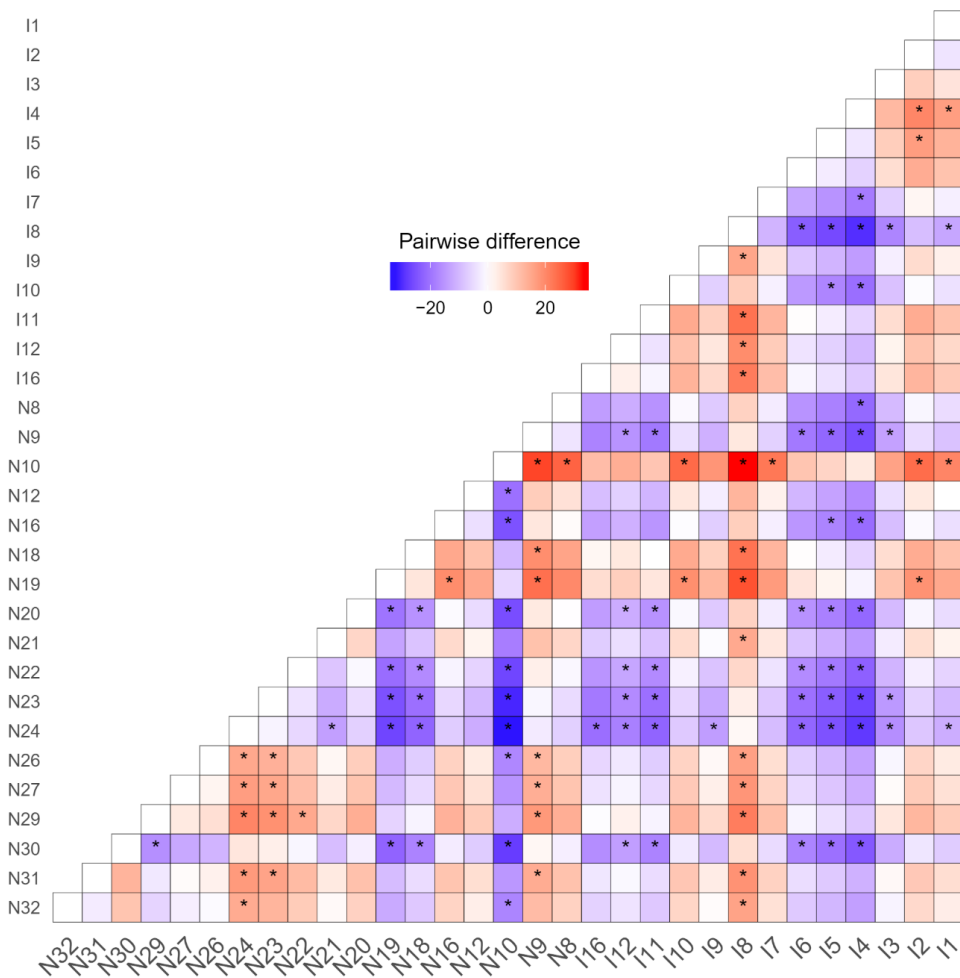
Regression coefficients and p-values from individual range models which were conducted if interaction term from full model (Appendix F) was significant. These models removed the range-level effect and range-level interaction included in full linear models. Instead, we ran individual models for the populations of the native (North American) and invasive (United Kingdom) ranges respectively. β_1 indicates the main effect of either latitude or mean annual temperature.

| Response | Predictor (β_1) | Native | | Invasive | |
|-----------------------------|-------------------------|-------------------------------|----------------------------|----------------------------------|----------------------------|
| | | β_1, p | <i>Adj. R</i> ² | β_1, p | <i>Adj. R</i> ² |
| <i>P</i> _{max} | Lat | 0.00482, <i>p</i> =0.476 | -0.0283 | 0.0401, <i>p</i> =0.0299** | 0.303 |
| <i>T</i> _{breadth} | Lat | 0.00364, <i>p</i> = 0.929 | -0.0620 | -0.201, <i>p</i> =0.0369** | 0.279 |
| Plasticity | Lat | 0.00104, <i>p</i> =0.013** | 0.102 | -0.00192, <i>p</i> =0.118 | 0.0373 |
| <i>T</i> _{max} | MAT | 0.0159, <i>p</i> =0.544 | -0.0375 | -0.168, <i>p</i> =0.0529* | 0.236 |
| <i>T</i> _{min} | Lat | -0.00620, <i>p</i> =0.282 | 0.0139 | 0.0642, <i>p</i> =0.000574*** | 0.645 |
| | MAT | 0.0125, <i>p</i> =0.204 | 0.0424 | -0.112, <i>p</i> =0.0549* | 0.231 |

*=*p*<0.1, **=*p*<0.05, ***=*p*<0.01

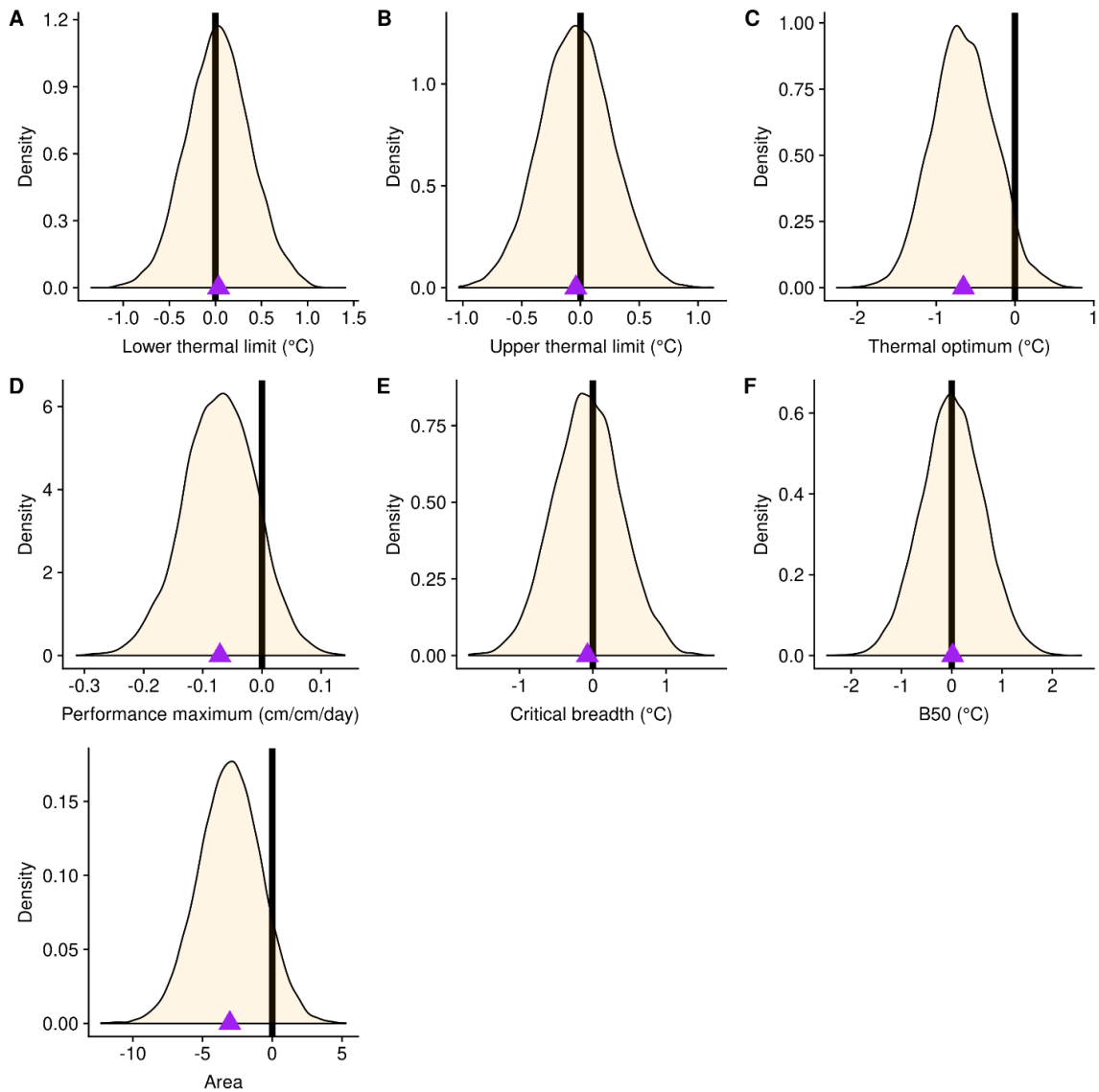
Appendix H

Pairwise comparisons of area under the thermal performance curve across 31 invasive and native populations of *Mimulus guttatus*. Population codes are in Appendix A. The color of each box represents the mean pairwise difference between the x group (columns) and the y group (rows) for 8,000 iterations of a Bayesian model. Red indicates cases where the y group has a parameter value that is greater than the x group, and blue indicates cases where the y group has a parameter value that is less than the x group. Asterisks represent pairwise comparisons where the 90% credible interval for differences across all iterations of the model does not overlap zero.



Appendix I

Pairwise comparisons of range-level mean TPC parameters. Pairwise differences are calculated by subtracting native range parameter estimates from invasive range parameter estimates. Each bell curve shows a probability density curve for pairwise differences based on 90% credibility. The mean pairwise difference is indicated by a purple triangle, and a vertical black line is shown to indicate a lack of difference in parameter estimates between the native and invasive range.



Appendix J

Additional analyses excluding inland populations from native range

Mimulus guttatus includes inland annuals and coastal perennials, both of which exhibit life history strategies specific to their environment, coupled with genomic distinctions (Hall & Willis 2006, Wu et al. 2008, Lowry et al. 2009, Hall & Willis 2010). Although we excluded annuals due to their absence within the invasive range, perennials located close to the coastline may also exhibit different adaptations of TPCs to environmental gradients relative to perennials found more inland. To test whether inland populations of *M. guttatus* pose different adaptive phenotypic clines in comparison to coastal populations, we generated the same linear models after excluding the six inland perennial populations. We chose to exclude inland populations (rather than excluding coastal populations or adding an additional factor to our model which explained coastal vs. inland status) due to the low number of inland populations included in our experiment. These models resulted in no compelling differences in clines (Appendix J). One exception was that T_{max} decreased with MAT, but this relationship explained a low amount of variation in the full model (Appendix J).

Appendix K

Regression coefficients and p-values from full general linear models relating response variables to predictors with inland native populations removed. β_1 indicates the main effect of either latitude, mean annual temperature (MAT), $T_{breadth}$, plasticity, temperature seasonality (TS), or P_{max} . β_2 indicates the main effect of range. β_3 indicates the interaction between range and the predictor corresponding to β_1 .

| Full Model | | | | | |
|----------------------------|---|------------------------------------|------------------------------------|-----------------------------------|------------------------------|
| Response | Predictor ($\beta_1, \beta_2, \beta_3$) | β_1, p | β_2, p | β_3, p | Adj. R^2 |
| <i>T_{opt}</i> | Lat, R, Lat*R | 0.04527, <i>p</i> =0.627 | 1.12814, <i>p</i> =0.838 | -0.03792, <i>p</i> =0.707 | 0.1213 |
| | MAT,R, MAT*R | 0.03832, <i>p</i> =0.877 | -0.71475, <i>p</i> =0.749 | -0.03207, <i>p</i> =0.901 | 0.1109 |
| <i>P_{max}</i> | <i>T_{breadth}</i> , R, <i>T_{breadth}</i> *Range | -0.13981, <i>p</i> =0.005490*** | -1.73893, <i>p</i> =0.228070 | 0.07813, <i>p</i> =0.244695 | 0.2622 |
| | Plasticity, R, Plasticity*Range | -2.27832, <i>p</i> =0.0694* | -0.14454, <i>p</i> =0.0836* | 2.10106, <i>p</i> =0.2526 | 0.03682 |
| <i>T_{breadth}</i> | Lat, R, Lat*R | -0.20069, <i>p</i> =0.0374** | -14.10804, <i>p</i> =0.0154** | 0.25540, <i>p</i> =0.0166** | 0.1592 |
| | TS, R, TS*R | 0.05808, <i>p</i> =0.385 | 1.75626, <i>p</i> =0.564 | -0.04813, <i>p</i> =0.491 | - 0.06829 |
| Plasticity | Lat, R, Lat*R | -0.001922, <i>p</i> =0.09322* | -0.197050, <i>p</i> =0.00489*** | 0.003792, <i>p</i> =0.00312*** | 0.1561 |
| | TS, R, TS*R | 0.0004713, <i>p</i> =0.513 | -0.0106867, <i>p</i> =0.746 | 0.0003029, <i>p</i> =0.693 | 0.08225 |
| <i>T_{max}</i> | Lat, R, Lat*R | 0.05957, <i>p</i> =0.0764* | 1.98416, <i>p</i> =0.3065 | -0.03695, <i>p</i> =0.2993 | 0.1588 |
| | MAT, R, MAT*R | -0.16746, <i>p</i> =0.0512* | -1.19872, <i>p</i> =0.1163 | 0.11476, <i>p</i> =0.1908 | 0.2248 |

Appendix K (continued)

| | | | | | |
|-----------|---------------|--------------------------------|--------------------------------|---------------------------------|--------|
| T_{min} | Lat, R, Lat*R | 0.06421, $p=0.000186^{***}$ | 3.87723, $p=0.000151^{***}$ | -0.07051, $p=0.000166^{***}$ | 0.4378 |
| | MAT, R, MAT*R | -0.11216, $p=0.0253^{**}$ | -1.03067, $p=0.0232^{**}$ | 0.12474, $p=0.0185^{**}$ | 0.1313 |

= $p < 0.1$, **= $p < 0.05$, *= $p < 0.01$*