The evolution of thermal performance in native and invasive populations of *Mimulus guttatus*

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Abstract

1. The rise of globalization has spread organisms beyond their natural range, allowing further opportunity for introduced species to adapt to novel environments and potentially become aggressive invaders. Yet, the role of niche evolution in promoting the success of invasive species remains poorly understood. 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.

2. 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.

3. We found that invasive populations have not evolved different thermal optima or thermal performance breadths, and there were similar specialist-generalist tradeoffs in both native and invasive populations. Consistent with the hypothesis that they are thermal generalists, native and invasive populations did not exhibit adaptive clines in thermal performance breadth with latitude or temperature seasonality. Thermal optimum increased with mean annual temperature in the native and invasive ranges. However, this relationship was primarily driven by populations in the native range, with weak adaptive differentiation of thermal optimum across mean annual temperature in the invasive range. Because thermal breadth of native and invasive populations

did not differ and the invasive range exhibits a narrow range of thermal conditions compared to the native range, there may not have been strong selection for thermal specialization in the invasive range.

4. *Synthesis:* These findings suggest that broad thermal tolerance, rather than rapid adaptation in the novel range, may promote invasion.

Key-words: adaptive divergence, evolutionary ecology, invasion ecology, latitudinal gradient, phenotypic cline, specialist-generalist tradeoff, thermal performance curve, thermal tolerance

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, Dawson, & Maurel, 2015). Baker's classic description of "ideal weeds" suggested that invasive species originate from "general-purpose" genotypes with broad climatic tolerances and high phenotypic plasticity, allowing them to proliferate in novel environments within their introduced range (Baker, 1965). However, specialist-generalist tradeoffs suggest that broad climatic tolerance may come with energetic costs (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006; Le Vinh Thuy, VandenBrooks, & Angilletta, 2016). Invasive species may also undergo rapid climatic niche evolution in response to novel selective pressures in the introduced range, which can result in niche shifts, or even the re-establishment of latitudinal clines in phenotypic traits following environmental gradients (Harper, 1965; Lee, 2002; Davidson, Jennions, & Nicotra, 2011; Li, Du, Guan, Yu, & van Kleunen, 2016; Hernández, Poverene, Garayalde, & Presotto, 2019; van Boheemen, Atwater, & Hodgins, 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). We seek to simultaneously explore climatic niche evolution, specialist-generalist tradeoffs, and local adaptation to provide a more comprehensive view of species invasions. Examination of the ecological and evolutionary processes that 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 climatic niche that influences its ability to invade new areas is temperature. Thermal performance curves (TPCs, Fig. 1A) describe the performance of a genotype, individual, population, or species across a temperature gradient (Huey & Stevenson, 1979). Some TPC parameters that have been hypothesized to influence adaptation to temperature gradients include maximum performance, thermal optimum, thermal performance breadth, and area under the curve (Huey & Stevenson, 1979; Sheth & Angert, 2014; Wooliver, Tittes, & Sheth, 2020; Fig. 1A). 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). 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, Wilson, Dormontt, Richardson, & Lowe, 2008). Further, if invasive populations either are generalists that can tolerate a wide range of 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 (Zerebecki & Sorte, 2011; Bates et al., 2013; van Kleunen, Röckle, & Stift, 2015). Populations can achieve broad TPCs through a combination of phenotypic plasticity and standing genetic variation (Sheth & Angert, 2014). Selection for greater phenotypic plasticity, which can permit high performance across a broad range of temperatures, may occur due to rapid changes in thermal regimes upon introduction to a novel range and can promote subsequent evolutionary adaptation (Richards et al., 2006; Lande, 2009; Donohue, 2013; Valladares et al., 2014; Lande, 2015). Further, increases in thermal performance breadth are also achievable in instances of introduction from multiple differentiated source populations to the novel range, where admixture may produce invasive populations with higher genetic variation than native populations (Kolbe, Glor, Rodriguez, Ada, & Lara, 2004; Lavergne & Molofsky, 2007). However, genetic bottlenecks that occurred during founding events may constrain the ability of invasive populations 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, Diez,

Richardson, & Vila, 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. 1B). Alternatively, if source populations represent general-purpose genotypes, they may be predisposed toward having broad TPCs which can be maintained in the invasive range. 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.

The ability to persist over a wider range of temperatures can come at the cost of lower maximum performance in both native and invasive populations. 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, Sih, & Wilson, 1998; Richards et al., 2006; Fig. 1C). In contrast, populations that have a narrower TPC 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 (Palaima & Spitze, 2004; Angert, Sheth, & Paul, 2011), but some species do not meet this assumption due to physiological or biochemical alterations among genotypes or populations that allow higher performance across a broad range of temperatures (Angilletta, Wilson, Navas, & James, 2003; Richards et al., 2006). This phenomenon, which has been referred to as "jack-and-master", or "master of all" (Richards et al., 2006; Matesanz &

Sultan, 2013; Sheth & Angert, 2014), may be one mechanism that stimulates the invasive capabilities of a species.

Another TPC parameter that may track local thermal regimes is thermal optimum. Transplant experiments indicate that local adaptation is ubiquitous across many plant taxa (Savolainen, Pyhäjärvi, & Knürr, 2007; Hereford, 2009; Galliart et al., 2019). Adaptation to local climatic conditions in the introduced range may result in niche shifts in invasive populations relative to native populations (Chapman, Scalone, Štefanić, & Bullock, 2017; Konowalik & Kolanowska, 2018). Thus, shifts in thermal optima may accompany changes in local thermal regimes between the native and invasive range (Fig. 1D. Nonetheless, if invasive populations have broad TPCs, selection for other TPC parameters may be relaxed, preventing evolutionary shifts in optima 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.

Given a temperature or latitudinal gradient, populations with sufficient time and genetic variation may exhibit adaptative clines in TPC parameters in response to temperature-mediated selection, and rapid local adaptation may facilitate invasion success (Prentis et al., 2008; Oduor, Leimu, & van Kleunen, 2016). Failure to account for the presence of latitudinal or environmental clines can mask inferences of trait evolution between native and invasive ranges (Colautti, Maron, & Barrett, 2009). Adaptive phenotypic clines across geographic, latitudinal, or climatic gradients are commonly detected in both native and invasive ranges (Li et al., 2016; Thawley, Goldy-Brown, McCormick, Graham, & Langkilde, 2018; Hernández et al., 2019; van Boheemen et al., 2019; Fig. 1E-G). 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, tracking local temperatures should result in higher thermal optima at lower latitudes (Fig. 1E) and/or at higher mean annual temperatures (Angert et al., 2011; Fig. 1F). Further, as temperature seasonality typically increases with latitude, populations across a species range should show clines of increasing thermal performance breadth across both latitude and seasonality (often referred to as the climate variability hypothesis, CVH; Dobzhansky, 1950; Janzen, 1967; Stevens, 1989; Gutiérrez-Pesquera et al., 2016; Fig. 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 (Hernández et al., 2019; Fig. 1E-G). 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. 1E-G). In addition, if invasive populations have broad TPCs, selection for clines of thermal optimum 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 different thermal regimes in its invasive range, there would be shifts in TPC parameters between the native and invasive ranges (Fig. 1B,D). Second, we evaluated the hypothesis that the ability to overcome specialist-generalist tradeoffs (consistent with a "master-of-all") has fostered the invasive capabilities of *M. guttatus* (Fig. 1C). 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. 1E-G).

Materials and 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 at sea level up 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, Pearman, & Dines, 2002; Newman, 2015). In recent years, *M. guttatus* has expanded its invasive range due to climate change and altered flooding regimes (Truscott, Soulsby, Palmer, Newell, & Hulme, 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, Röckle, 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, Simón-Porcar, Puzey, & Vallejo-Marín, 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

To compare TPCs of native and invasive populations of *M. guttatus*, we propagated field-collected seeds from perennial populations of the native North American range and of the invasive United Kingdom range, totaling 346 seed families from 52 populations (see "Propagation of Mother Plants" below; Table S1). For this study, we conducted a principal component analysis of climatic variables to select focal populations that spanned the greatest amount of temperature variability within the native and invasive ranges (Supplementary Methods, Table S1, Fig. S1). From this analysis, we identified 18 populations that represented a wide breadth of temperatures within the native range (Fig. 2A). Due to lower germination

success of genotypes from the invasive range in the UK, we used all 13 available populations (Fig. 2B). Within each population, we randomly selected 1-5 seed families to represent in our experiment. On average, mean annual temperature (MAT) and temperature seasonality were higher in the native than the invasive range (Fig. 2C,D). Further, MAT increased with latitude in the native and invasive ranges (Fig. 2C), and seasonality increased with latitude in the native range but gradually decreased with latitude in the invasive range (Fig. 2D). In the native range, there was also considerably higher variation in both mean annual temperature (Fig. 2C) and temperature seasonality (Fig. 2D) relative to the invasive range.

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 sewn 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 (NPK + micronutrients), and their location within the growth room was randomized on a bi-weekly basis. Additionally, we dumped the stagnant water from all trays on a bi-weekly basis. The cold treatment method was repeated for seed families with poor initial germination, which were primarily from the invasive range. 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 (Table S1). During this process, plants exhibiting annual characteristics (diminutive size, lack of side branches, small flowers; Hall & Willis, 2006) were excluded in favor of perennial plants. 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. 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. Prior to temperature treatments, we allowed each set of cuttings 2 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 regimes. Over the course of the experiment, we randomly assigned six temperature treatments to one of three identical Percival LT-105X chambers (Percival Scientific, Inc.; Perry, Iowa, USA), resulting in two full rounds of chamber use. For each temperature regime, we took two replicates (clones) of

each of the 95 genotypes and randomized them among six trays to reduce tray effects. We subjected replicate clones to 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), with one of the following day/night temperature regimes (°C): 10/0, 20/10, 25/15, 30/20, 40/30, and 45/35. Temperature regimes were replicated once, along with an additional replicate of the 45°C/35°C regime. In total, we took 1,338 cuttings. However, 86 of these cuttings were eliminated due to failed establishment, resulting in a final dataset of 1,252 individual clones from 18 native and 13 invasive populations, each comprising 54 and 41 genotypes, respectively. Within each chamber, we exposed these clones to a given temperature regime 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). We took measurements of the length of the primary stem and the total length of branches (including stolons and side branches) before and after each temperature treatment ($stem_{in}$ 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 dieback at temperature extremes

were set to zero, and negative RGR values in cases where clones lost stem length due to accidental damage were excluded. Although RGR is not a measure of total reproductive output, we used this metric as a proxy for fitness because size has been related to reproductive output in other *Mimulus* species (Sheth & Angert, 2018).

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

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, Walker, Torres-Martínez, & Emery, 2019) to simultaneously fit curves predicting RGR across temperature for all populations while estimating uncertainty. 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 also required that we scale values of RGR using the overall mean RGR across all data points and center daytime temperature around zero. Thus, we rescaled model 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 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 (Table S2).

From these Bayesian models, we obtained estimates of thermal optimum (T_{opt}), thermal performance breadth ($T_{breadth}$), maximum performance (P_{max}), and area under the curve (*AUC*) for each population (Table S3). We selected critical values for $T_{breadth}$ from 100 equally spaced points along the temperature axis closest to the temperature values corresponding to 50% of a TPC's P_{max}. These models also generated estimates of critical upper and critical lower thermal limits (temperatures at which RGR decreases to zero). However, these estimates extended beyond our temperature treatments. To avoid overextrapolation of temperatures which were not measured in our experiments, we excluded critical thermal limits from our analyses.

Statistical Analyses for Hypothesis Testing

We tested for divergence in TPC parameters between native and invasive populations of *M. guttatus* independent of latitude by conducting post-hoc comparisons of TPC model iterations. For all model iterations, we calculated mean TPC parameter estimates for the native and invasive ranges. 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 95% credible interval. For all pairwise differences, we interpreted a difference to be statistically significant if its 95% credible interval did not include zero. Positive mean differences would indicate higher parameter estimates within the native range, whereas negative mean differences would indicate higher parameter estimates within the invasive range.

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. We also ran a reduced linear

model which removed the interaction term to account for the possibility of tradeoffs which are similar in magnitude and direction in both ranges. We obtained the Akaike information criterion (AIC) of both models to determine which provided the better fit. For all linear models, we evaluated statistical significance using α=0.05. 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. Given a final model with 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. 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 *AUC*. Using a 95% credible interval, we determined if significant differences existed both between populations within each range and between populations of different ranges.

To determine whether invasive populations have undergone rapid adaptation 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} included predictors of either latitude or mean annual temperature, range, and their interaction. We used AIC to compare these full models to reduced models without the interaction term to account for the possibility of clines of similar magnitude and direction in both ranges. If the final model included a significant interaction term, we conducted additional range-specific models with only latitude or mean annual temperature as predictors. Shallower or nonsignificant slopes within the invasive range in comparison to the native range would suggest a 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 or absent interaction term would

indicate parallel evolution of clines across ranges. Similarly, to test whether $T_{breadth}$ increases with temperature seasonality, we modeled $T_{breadth}$ as a function of latitude or temperature seasonality, range, and their interaction, and used AIC to compare these full models to reduced models without the interaction term. Given a significant interaction term in the final model, we also conducted range-specific models with latitude or temperature seasonality as predictors.

Results

Shifts in TPC Parameters

We found no support for the hypothesis that *M. guttatus* has adapted to novel thermal regimes within its invasive range via TPC shifts. Pairwise comparisons revealed that T_{opt} and $T_{breadth}$ exhibited 95% credible intervals that included zero, indicating that neither differed significantly between ranges (Table 1, Fig. 3, Fig. S3).

Specialist-Generalist Tradeoffs

Consistent with specialist-generalist tradeoffs, P_{max} decreased with $T_{breadth}$ (Table 2, Fig. 4). The final model included an interaction between $T_{breadth}$ and range (Table 2). However, this interaction was not statistically significant, suggesting that the direction and strength of the relationship between $T_{breadth}$ and P_{max} did not differ between the native and invasive ranges (Table 2). The main effect of range was also non-significant (Table 2). Failing to meet the assumption that area is constant when there are specialist-generalist tradeoffs, pairwise comparisons indicate that *AUC* significantly differed both within and between ranges (Angert et al., 2011; Fig. S2).

Clines of TPC Parameters

Overall, latitudinal and thermal clines varied in strength depending on the TPC parameter and/or the geographic range, and there was little support for the hypothesis of adaptive clines in

either range. The final respective models for T_{opt} as a function of latitude or MAT did not include an interaction between latitude or MAT and range (Table 2). Failing to support our hypothesis, T_{opt} did not decrease with latitude (Table 2, Fig. 5A). Further, there was no main effect of range when assessing clines of T_{opt} across latitude (Table 2). T_{opt} increased with MAT, but there was also no main effect of range on T_{opt} when assessing clines across MAT (Table 2, Fig. 5B). To further dissect the relatively low variance explained by this model (Adj. R^2=0.155), we conducted range-level models. We found that the cline of T_{opt} across MAT in our full model was primarily driven by adaptive differentiation within the native range (β=0.153, P=0.036, Adj. R^2=0.199), whereas there was no relationship between MAT and T_{opt} in the invasive range (β=0.038, P=0.899, Adj. R^2=-0.089).

A model with an interaction between latitude and range best explained the relationship between $T_{breadth}$ and latitude (Table 2). Contrary to the prediction that $T_{breadth}$ would increase with latitude, $T_{breadth}$ showed no relationship with latitude (Table 2, Fig. 5C). There was not a significant main effect of range on $T_{breadth}$, and the relationship between latitude and $T_{breadth}$ did not differ between ranges (Table 2). The model that best explained the relationship between $T_{breadth}$ and temperature seasonality did not include an interaction term (Table 2). We found no cline of $T_{breadth}$ with temperature seasonality (Table 2; Fig. 5D), failing to support the climate variability hypothesis. Further, there was no main effect of range on $T_{breadth}$ when assessing clines of $T_{breadth}$ across temperature seasonality (Table 2).

Discussion

In this study, we compared thermal performance curves (TPCs) 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 no support for the hypothesis that thermal optimum and breadth vary between the native and invasive ranges (Table 1, Fig. S3). Second, our findings did not support the hypothesis that *M. guttatus* has overcome specialist-generalist tradeoffs. Instead, TPCs in both ranges were constrained by specialist-generalist tradeoffs, such that broad TPCs came at the cost of lower maximum performance (Table 2, Fig. 4). Finally, contrary to the hypothesis that native and invasive ranges show parallel phenotypic clines, there was limited evidence for parallel clines in TPC parameters between ranges (Table 2, Fig. 5). Although the cline of thermal optimum across mean annual temperature was similar in both ranges, which could suggest repeated evolution of thermal optimum in the invasive range, the effect was driven primarily by native populations. Together, these results suggest that the invasive capabilities of *M. guttatus* are an outcome of general-purpose genotypes (as evidenced by a lack of clines in thermal breadth across latitude). Yet, specialist-generalist tradeoffs still constrained the evolution of thermal performance in both ranges of *M. guttatus*. Further, despite a lower range of temperatures in the introduced range, TPCs of invasive populations were just as broad as those of native populations spanning a greater range of temperatures (Fig. 2B). As a result, it is unlikely that invasive populations experienced strong temperature-mediated selection on thermal optimum across latitudinal and temperature gradients in the UK. Below, we discuss the implications of these findings in light of the evolutionary processes that could contribute to biological invasion.

Evolution of Thermal Performance Curves

We found no support for the hypothesis that invasive populations have undergone changes in mean TPC parameters relative to native populations (Table 1, Fig. 3, Fig. S3). Instead, T_{opt} and $T_{breadth}$ were similar between native and invasive ranges. 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, Olivares, Smith, & Vallejo-Marín, 2020). However, while a portion of the climatic niche was conserved, the invasive range of *M. guttatus* 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 (Fig. S1), and that T_{opt} and $T_{breadth}$ did not differ between ranges (Table 1, Fig. S3), are consistent with the study modeling climatic niches. These results are consistent with a recent meta-analysis showing niche conservatism between the native and introduced ranges of many invasive species (Liu, Wolter, Xian, & Jeschke, 2020). Although the climatic niche in the introduced range is not currently as wide as that of the native range, invasive *M. guttatus* populations seem poised to occupy a greater climatic niche space should it become available. As a result, maintenance of a broad thermal tolerance in the invasive range may allow *M. guttatus* populations to withstand rapid changes in temperatures, posing greater risk that invasive populations may prosper under climate change. Collectively, a lack of divergence in thermal niches 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 contribute to the evolutionary stasis of TPC parameters in the invasive range is insufficient standing genetic variation (Prentis et al., 2008; Dlugosch, Anderson, Braasch, Cang, & Gillette, 2015; Colautti, Alexander, Dlugosch, Keller, & Sultan, 2017). On one hand, invasive populations experiencing the introduction and recombination of

multiple genotypes are more likely to adapt to novel temperature regimes (Colautti et al., 2017). On the other hand, genetic bottlenecks that occurred during founding events may 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 and are closely related to northern native populations (Puzey & Vallejo-Marín, 2014; Pantoja et al., 2017). Low genetic variation in the introduced range could have constrained the rapid evolution of T_{opt} and $T_{breadth}$ in this species. However, the initial invasion of *M. guttatus* in the UK originating from Alaskan native populations was followed by multiple introductions from across the native range (Vallejo-Marín et al., 2020). As a result, the invasive range consists of a highly admixed melting pot of native populations and is unlikely to be constrained by low genetic diversity. Thus, invasive populations may arise from admixed thermal genotypes that contributed toward population-level TPCs remaining as wide as those in the native range, allowing invasive *M. guttatus* to tolerate the narrower breadth of thermal conditions in the UK. Collectively, these results suggest that the invasive populations have yet to undergo significant divergence in TPCs from native populations due to overlap in thermal niche space, rather than lacking the fodder which evolution may act upon. Invasive populations may present a high risk for thermal niche expansion and evolution in the face of climate change.

Specialist-Generalist Tradeoffs

Our results provide evidence for specialist-generalist tradeoffs, independent of native or invasive status, wherein greater $T_{breadth}$ came at the cost of reduced P_{max} (Fig. 5A). However, our finding of differing *AUC* among populations within each range (Fig. S2) suggests that the assumption that area remains constant does not hold for *M. guttatus* (Palaima & Spitze, 2004;

Angert et al., 2011). As such, there may be an additional axis of variation that explains differences in TPCs among populations. We found a strong positive correlation between *AUC* and P_{max}, (ρ=0.9767, P<0.001), which suggests that variation in TPCs among populations is partly explained by vertical shifts across a fast-slow spectrum of performance (Izem & Kingsolver, 2005). As a result, higher performing populations achieve a larger thermal niche than populations with lower peak performance. These results are consistent with the idea of "winner" genotypes and populations, which may achieve a greater AUC by having both a high maximum performance and broad thermal breadth (Palaima & Spitze, 2004). However, *AUC* and $T_{breadth}$ were not correlated (ρ=-0.2692, P= 0.1431), meaning that although having a broad TPC may constrain maximum performance, thermal breadth is not a key predictor of thermal niche space as approximated by *AUC*. In other words, thermal generalist qualities may reduce performance, but do not always result in functionally inferior individuals. Rather, higher performers are more likely to have larger niche spaces. Thus, variation in TPCs in native and invasive populations of *M. guttatus* seems to be controlled by both vertical shifts where high-performing populations are 'masters-of-all' and specialist-generalist tradeoffs where generalist populations are 'masters-of-none'.

Evolution of Clines

We hypothesized that phenotypic clines exhibited in the native range would be repeated in the invasive range. Although temperature varies predictably with latitude in the invasive range (Fig. 2C,D), and there is ample evidence that rapid adaptation can facilitate invasion success (Oduor et al., 2016), our results did not support the hypothesis of parallel clines. Rather, T_{opt} increased with MAT across both ranges, though the amount of variance explained was relatively modest (*Adj*. R^2=0.155). To further understand this pattern, we conducted separate range-level

models of T_{opt} as a function of MAT. There was a weak cline in the native range, although the amount of variation explained was modest. However, there was no effect of MAT on T_{opt} in the invasive range. Thus, native populations were the primary driver of the weak cline detected in the full model (Table 2). Albeit weak, adaptive differentiation of T_{opt} to mean annual temperature may contribute toward the success of this species in its native range. The absence of this cline in the invasive range implies weaker selection on T_{opt} or insufficient time for adaptation in the invasive range. Given that invasive populations of *M. guttatus* have maintained similar $T_{breadth}$ as native populations, it is unlikely that selection in the invasive range with a relatively narrow range of mean annual temperatures would favor specialization in T_{opt} (Fig. 2C).

Although T_{opt} increased with mean annual temperature in the native range, $T_{breadth}$ was not related to latitude or temperature seasonality in either range. These results do not support the climate variability hypothesis (Dobzhansky, 1950; Janzen, 1967; Stevens, 1989; Gutiérrez-Pesquera et al., 2016), which predicts a positive relationship between $T_{breadth}$ and temperature seasonality and latitude. There are many possible explanations for a lack of clines in $T_{breadth}$ in native populations. First, since six native populations were not coastal, there may also be divergent relationships between TPC parameters and environmental gradients caused by adaptation to differing regimes of temperature seasonality in coastal and inland environments. Multiple studies have documented instances of adaptive differentiation between *M. guttatus* in coastal and inland habitats (Hall & Willis, 2006; Lowry, Hall, Salt, & Willis, 2009) resulting from contrasting environmental conditions. Second, *M. guttatus* populations may not display strong clines in $T_{breadth}$ if they occupy microhabitats with similar temperature seasonality across their range (Franco & Nobel, 2003). Third, populations in close latitudinal proximity may experience drastically different regimes of temperature seasonality due to microclimatic

variation, resulting in fine-scale local adaptation that prevented us from detecting clines at broader macroclimatic scales (Rashkovetsky et al., 2006; De Frenne et al., 2013). Finally, high gene flow among native populations could swamp adaptation of TPCs to local thermal regimes (Paul et al., 2011). Rather than evolving TPCs in response to latitudinal and thermal gradients, native populations may be generalists with wide TPCs which predisposed them to become invasive (van Kleunen, Schlaepfer, Glaettli, & Fischer, 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, Lowry, & Willis, 2010; Kooyers, Greenlee, Colicchio, Oh, & Blackman, 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, Hodgins, & Stinchcombe, 2020). Overall, our results suggest that while specializing in hydrological and edaphic aspects of niche space, native *M. guttatus* populations may be thermal generalists despite spanning a broad temperature gradient in western North America.

Caveats

There are many caveats which may have impacted the results of our study. First, 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; Table S1), these effects should be less prevalent at the population level. Second, our temperature regimes maintained constant respective 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, although we incorporated multiple measurements of stem and branch growth (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 or belowground growth) at different temperatures. Thus, some populations in this study may allocate more resources toward unmeasured parameters, providing an inadequate measure of total performance. Fourth, we focused on one performance metric, RGR, but to fully understand how performance varies across temperature gradients, as well as how varying thermal 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, Keefover-Ring, Deane Bowers, Harnenz, & Lindroth, 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 populations did not exhibit clines in thermal breadth across the native

range, and that invasive populations have not undergone changes in thermal breadth relative to native populations, indicates that general-purpose genotypes may have contributed toward successful establishment in the invasive range. Because of these thermal generalist qualities combined with a comparatively small thermal niche space in the invasive range, invasive populations likely exhibit weaker selection on thermal optimum across latitudinal and temperature gradients. Additionally, there were 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.

Acknowledgements

We thank B. Caldwell, E. Coughlin, N. Gold, M. Kidd, D. Ryan, J. Torres, E. Vtipil, and M. Wiegmann for assistance with data collection and plant care. We also thank NCSU Phytotron staff members for assistance with plant care and chamber maintenance. We are grateful to B. Blackman, J. Colicchio, J. Coughlan, J. Friedman, L. Holeski, D. Lowry, and M. Rotter for generously providing seeds for this work. W. Hoffmann and M. Burford-Reiskind provided valuable feedback on an earlier version of this work, and M. Flores-Vergara provided guidance

about plant propagation. This project was funded by USDA National Institute of Food and Agriculture Hatch 1016272.

Author Contributions

A.Q. and S.S. conceived of and designed the study. A.Q. collected the data. A.Q. and R.W. analyzed the data. A.Q. led the writing of this manuscript. R.W., M.V.M., and S.S. provided feedback on this manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability

All data and scripts associated with this study are available at https://github.com/akquerns/Guttatus_EvolTPCClines.

References

Angert, A. L., Sheth, S. N., & Paul, J. R. (2011). Incorporating Population-Level Variation in Thermal Performance into Predictions of Geographic Range Shifts. *Integrative and Comparative Biology*, *51*(5), 733–750. doi: 10.1093/icb/icr048

Angilletta, M. J., Wilson, R. S., Navas, C. A., & James, R. S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution*, *18*(5), 234–240. doi: 10.1016/S0169-5347(03)00087-9

Baker, H. G. (1965). Characteristics and modes of origin of weeds. In H. G. Baker & G. L. Stebbins (Eds.), *The genetics of colonizing species* (pp. 147–172). New York, New York: Academic Press.

Bates, A. E., McKelvie, C. M., Sorte, C. J. B., Morley, S. A., Jones, N. A. R., Mondon, J. A., … Quinn, G. (2013). Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1772). doi: 10.1098/rspb.2013.1958

Bhattarai, G. P., Meyerson, L. A., Anderson, J., Cummings, D., Allen, W. J., & Cronin, J. T. (2017). Biogeography of a plant invasion: Genetic variation and plasticity in latitudinal clines for traits related to herbivory. *Ecological Monographs*, *87*(1), 57–75. doi: 10.1002/ecm.1233

Chapman, D. S., Scalone, R., Štefanić, E., & Bullock, J. M. (2017). Mechanistic species distribution modeling reveals a niche shift during invasion. *Ecology*, *98*(6), 1671–1680. doi: 10.1002/ecy.1835

Colautti, R. I., Alexander, J. M., Dlugosch, K. M., Keller, S. R., & Sultan, S. E. (2017). Invasions and extinctions through the looking glass of evolutionary ecology.

Philosophical Transactions of the Royal Society B: Biological Sciences, *372*. doi: 10.1098/rstb.2016.0031

Colautti, R. I., Maron, J. L., & Barrett, S. C. H. (2009). Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evolutionary Applications*, *2*(2), 187–199. doi: 10.1111/j.1752-4571.2008.00053.x

Comeault, A. A., Wang, J., Tittes, S., Isbell, K., Ingley, S., Hurlbert, A. H., & Matute, D. R. (2020). Genetic diversity and thermal performance in invasive and native populations of African fig flies. *Molecular Biology and Evolution*, *37*(7), 1893–1906. doi: 10.1093/molbev/msaa050

Da Re, D., Olivares, A. P., Smith, W., & Vallejo-Marín, M. (2020). Global analysis of ecological niche conservation and niche shift in exotic populations of monkeyflowers (*Mimulus guttatus, M. luteus*) and their hybrid (*M.* × *robertsii*). *Plant Ecology & Diversity*, *13*(2), 133–146. doi: 10.1080/17550874.2020.1750721

Daehler, C. C. (2003). Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 183–211. doi: 10.1146/annurev.ecolsys.34.011802.132403

Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, *14*(4), 419–431. doi: 10.1111/j.1461-0248.2011.01596.x

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate

warming. *Proceedings of the National Academy of Sciences*, *110*(46), 18561–18565. doi: 10.1073/pnas.1311190110

Dewitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution*, *13*(2), 77–81. doi: 10.1016/s0169-5347(97)01274-3

Dlugosch, K. M., Anderson, S. R., Braasch, J., Cang, F. A., & Gillette, H. D. (2015). The devil is in the details: Genetic variation in introduced populations and its contributions to invasion. *Molecular Ecology*, *24*(9), 2095–2111. doi: 10.1111/mec.13183

Dobzhansky, T. (1950). Evolution in the Tropics. *American Scientist*, *38*, 209–221.

Donohue, K. (2013). Development in the Wild: Phenotypic Plasticity. *Annual Plant Reviews*, *45*, 321–355. doi: 10.1002/9781118305881.ch10

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. doi: 10.1002/joc.5086

Fraga, N. S. (2018). *Erythranthe guttata*, in Jepson Flora Project. Retrieved March 20, 2020, from Jepson eFlora website: https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=99131

Franco, A. C., & Nobel, P. S. (2003). Effect of Nurse Plants on the Microhabitat and Growth of Cacti. *Journal of Ecology*, *77*(3), 870–886. doi: 10.2307/2260991

Galliart, M., Bello, N., Knapp, M., Poland, J., St Amand, P., Baer, S., … Johnson, L. (2019). Local adaptation, genetic divergence, and experimental selection in a foundation grass across the US Great Plains' climate gradient. *Global Change Biology*, *25*(3), 850–868. doi: 10.1111/gcb.14534

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2014). *Bayesian data analysis* (3rd ed.). London, UK: Chapman and Hall.

González-Moreno, P., Diez, J. M., Richardson, D. M., & Vila, M. (2015). Beyond climate: Disturbance niche shifts in invasive species. *Global Ecology and Biogeography*, *24*, 360–370. doi: 10.1111/geb.12271

Gutiérrez-Pesquera, L. M., Tejedo, M., Olalla-Tárraga, M. A., Duarte, H., Nicieza, A., & Solé, M. (2016). Testing the climate variability hypothesis in thermal tolerance limits of tropical and temperate tadpoles. *Journal of Biogeography*, *43*(6), 1166–1178. doi: 10.1111/jbi.12700

Hall, M. C., Lowry, D. B., & Willis, J. H. (2010). Is local adaptation in *Mimulus guttatus* caused by trade-offs at individual loci? *Molecular Ecology*, *19*(13), 2739–2753. doi: 10.1111/j.1365-294X.2010.04680.x

Hall, M. C., & Willis, J. H. (2006). Divergent Selection on Flowering Time Contributes to Local Adaptation in *Mimulus guttatus* Populations. *Evolution*, *60*(12), 2466–2477. doi: 10.1111/j.0014-3820.2006.tb01882.x

Harper, J. L. (1965). Establishment, Aggression, and Cohabitation in Weedy Species. In H. G. Baker & G. L. Stebbins (Eds.), *The genetics of colonizing species* (pp. 243–268). New York, New York: Academic Press. CABDirect. Retrieved from https://www.cabdirect.org/cabdirect/abstract/19682301817

Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist*, *173*(5), 579–588. doi: 10.1086/597611

Hernández, F., Poverene, M., Garayalde, A., & Presotto, A. (2019). Re-establishment of latitudinal clines and local adaptation within the invaded area suggest rapid evolution of

seed traits in Argentinean sunflower (*Helianthus annuus* L.). *Biological Invasions*, *21*(8), 2599–2612. doi: 10.1007/s10530-019-01998-8

Holeski, L. M., Keefover-Ring, K., Deane Bowers, M., Harnenz, Z. T., & Lindroth, R. L. (2013). Patterns of Phytochemical Variation in *Mimulus guttatus* (Yellow Monkeyflower). *Journal of Chemical Ecology*, *39*, 525–536. doi: 10.1007/s10886-013-0270-7

Huey, R. B., & Hertz, P. E. (1984). Is a Jack-of-All-Temperatures a Master of None? *Evolution*, *38*(2), 441–444. JSTOR. doi: 10.2307/2408502

Huey, R. B., & Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Integrative and Comparative Biology*, *19*(1), 357–366. doi: 10.1093/icb/19.1.357

Izem, R., & Kingsolver, J. G. (2005). Variation in continuous reaction norms: Quantifying directions of biological interest. *American Naturalist*, *166*(2), 277–289. doi: 10.1086/431314

Janzen, D. H. (1967). Why Mountain Passes are Higher in the Tropics. *The American Naturalist*, *101*(919), 233–249. doi: 10.1086/282487

Kitayama, K., & Mueller□Dombois, D. (1995). Biological invasion on an oceanic island mountain: Do alien plant species have wider ecological ranges than native species? *Journal of Vegetation Science*, *6*(5), 667–674. doi: 10.2307/3236436

Kolbe, J. J., Glor, R. E., Rodriguez, L., Ada, S., & Lara, C. (2004). Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, *431*, 177–181.

Konowalik, K., & Kolanowska, M. (2018). Climatic niche shift and possible future spread of the invasive South African Orchid *Disa bracteata* in Australia and adjacent areas. *PeerJ*, *6*. doi: 10.7717/peerj.6107

Kooyers, N. J., Greenlee, A. B., Colicchio, J. M., Oh, M., & Blackman, B. K. (2015). Replicate altitudinal clines reveal that evolutionary flexibility underlies adaptation to drought stress in annual *Mimulus guttatus*. *New Phytologist*, *206*(1), 152–165. doi: 10.1111/nph.13153

Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, *22*(7), 1435–1446. doi: 10.1111/j.1420-9101.2009.01754.x

Lande, R. (2015). Evolution of phenotypic plasticity in colonizing species. *Molecular Ecology*, *24*(9), 2038–2045. doi: 10.1111/mec.13037

Lavergne, S., & Molofsky, J. (2007). Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proceedings of the National Academy of Sciences*, *104*(10), 3883–3888. doi: 10.1073/pnas.0607324104

Le Vinh Thuy, J., VandenBrooks, J. M., & Angilletta, M. J. (2016). Developmental plasticity evolved according to specialist-generalist trade-offs in experimental populations of *Drosophila melanogaster*. *Biology Letters*, *12*(7). doi: 10.1098/rsbl.2016.0379

Lee, C. E. (2002). Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, *17*(8), 386–391. doi: 10.1016/S0169-5347(02)02554-5

Li, J., Du, L., Guan, W., Yu, F. H., & van Kleunen, M. (2016). Latitudinal and longitudinal clines of phenotypic plasticity in the invasive herb *Solidago canadensis* in China. *Oecologia*, *182*(3), 755–764. doi: 10.1007/s00442-016-3699-x

Liu, C., Wolter, C., Xian, W., & Jeschke, J. M. (2020). Most invasive species largely conserve their climatic niche. *Proceedings of the National Academy of Sciences*. doi: 10.1073/pnas.2004289117

Lowry, D. B., Hall, M. C., Salt, D. E., & Willis, J. H. (2009). Genetic and physiological basis of adaptive salt tolerance divergence between coastal and inland *Mimulus guttatus*. *New Phytologist*, *183*(3), 776–788. doi: 10.1111/j.1469-8137.2009.02901.x

Lowry, D. B., Sobel, J. M., Angert, A. L., Ashman, T. L., Baker, R. L., Blackman, B. K., … Yuan, Y. W. (2019). The case for the continued use of the genus name *Mimulus* for all monkeyflowers. *Taxon*, *68*(4), 617–623. doi: 10.1002/tax.12122

Matesanz, S., & Sultan, S. E. (2013). High-performance genotypes in an introduced plant: insights to future invasiveness. *Ecology*, *94*(11), 2464–2474. doi: 10.1890/12-1359.1

McGoey, B. V., Hodgins, K. A., & Stinchcombe, J. R. (2020). Parallel clines in native and introduced ragweed populations are likely due to adaptation. *Ecology and Evolution*, 4594–4608. doi: 10.1002/ece3.6163

Murren, C. J., Auld, J. R., Callahan, H., Ghalambor, C. K., Handelsman, C. A., Heskel, M. A., … Steiner, U. K. (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity*, *115*(4), 293–301. doi: 10.1038/hdy.2015.8

Newman, J. (2015). Rapid Risk Assessment Summary Sheet: Monkey flower (*Mimulus guttatus*). *GB Non-Native Species Secretariat*.

Oduor, A. M. O., Leimu, R., & van Kleunen, M. (2016). Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *Journal of Ecology*, *104*(4), 957–968. doi: 10.1111/1365-2745.12578

Palaima, A., & Spitze, K. (2004). Is a jack-of-all-temperatures a master of none? An experimental test with *Daphnia pulicaria* (Crustacea: Cladocera). *Evolutionary Ecology Research*, *6*, 215–225.

Pantoja, P. O., Simón-Porcar, V. I., Puzey, J. R., & Vallejo-Marín, M. (2017). Genetic variation and clonal diversity in introduced populations of *Mimulus guttatus* assessed by genotyping at 62 single nucleotide polymorphism loci. *Plant Ecology and Diversity*, *10*(1), 5–15. doi: 10.1080/17550874.2017.1287785

Paul, J. R., Sheth, S. N., & Angert, A. L. (2011). Quantifying the impact of gene flow on phenotype- environment mismatch: A demonstration with the scarlet monkeyflower *Mimulus cardinalis*. *American Naturalist*, *178*(S1), S62–S79. doi: 10.1086/661781

Popovic, D., & Lowry, D. B. (2020). Contrasting environmental factors drive local adaptation at opposite ends of an environmental gradient in the yellow monkeyflower (*Mimulus guttatus*). *American Journal of Botany*, *107*(2), 298–307. doi: 10.1002/ajb2.1419

Prentis, P. J., Wilson, J. R. U., Dormontt, E. E., Richardson, D. M., & Lowe, A. J. (2008). Adaptive evolution in invasive species. *Trends in Plant Science*, *13*(6), 288–294. doi: 10.1016/j.tplants.2008.03.004

Preston, C. D., Pearman, D. A., & Dines, T. D. (Eds.). (2002). *New Atlas of the British and Irish Flora* (Vol. 1). Oxford University Press.

Puzey, J., & Vallejo-Marín, M. (2014). Genomics of invasion: diversity and selection in introduced populations of monkeyflowers (*Mimulus guttatus*). *Molecular Ecology*, *23*(18), 4472–4485. doi: 10.1111/mec.12875

R Core Team. (2019). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rashkovetsky, E., Iliadi, K., Michalak, P., Lupu, A., Nevo, E., Feder, M. E., & Korol, A. (2006). Adaptive differentiation of thermotolerance in *Drosophila* along a microclimatic gradient. *Heredity*, *96*(5), 353–359. doi: 10.1038/sj.hdy.6800784

Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J., & Pigliucci, M. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, *9*, 981–993. doi: 10.1111/j.1461-0248.2006.00950.x

Sala, O. E., Chapin, F. S., Armesto, J. J., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., … Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, *287*(5459), 1770–1774. doi: 10.1126/science.287.5459.1770

Savolainen, O., Pyhäjärvi, T., & Knürr, T. (2007). Gene Flow and Local Adaptation in Trees. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 595–619. doi: 10.1146/annurev.ecolsys.38.091206.095646

Selby, J. P., & Willis, J. H. (2018). Major QTL controls adaptation to serpentine soils in *Mimulus guttatus*. *Molecular Ecology*, *27*(24), 5073–5087. doi: 10.1111/mec.14922

Sheth, S. N., & Angert, A. L. (2014). The evolution of environmental tolerance and range size: a comparison of geographically restricted and widespread *Mimulus*. *Evolution*, *68*(10), 2917–2931. doi: 10.1111/evo.12494

Sheth, S. N., & Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, *115*(10), 2413–2418. doi: 10.1073/pnas.1715899115

Stevens, G. C. (1989). The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in the Tropics. *The American Naturalist*, *133*(2), 240–256.

Thawley, C. J., Goldy-Brown, M., McCormick, G. L., Graham, S. P., & Langkilde, T. (2018). Presence of an invasive species reverses latitudinal clines of multiple traits in a native species. *Global Change Biology*, *25*(2), 620–628. doi: 10.1111/gcb.14510

Tittes, S. B., Walker, J. F., Torres-Martínez, L., & Emery, N. C. (2019). Grow Where You Thrive, or Where Only You Can Survive? An Analysis of Performance Curve Evolution in a Clade with Diverse Habitat Affinities. *The American Naturalist*, *193*(4), 530–544. doi: 10.1086/701827

Truscott, A. M., Soulsby, C., Palmer, S. C. F., Newell, L., & Hulme, P. E. (2006). The dispersal characteristics of the invasive plant *Mimulus guttatus* and the ecological significance of increased occurrence of high-flow events. *Journal of Ecology*, *94*(6), 1080–1091. doi: 10.1111/j.1365-2745.2006.01171.x

Twyford, A. D., & Friedman, J. (2015). Adaptive divergence in the monkey flower *Mimulus guttatus* is maintained by a chromosomal inversion. *Evolution*, *69*(6), 1476–1486. doi: 10.1111/evo.12663

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., … Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, *17*(11), 1351–1364. doi: 10.1111/ele.12348

Vallejo-Marín, M., Friedman, J., Twyford, A. D., Lepais, O., Ickert-Bond, S. M., Streisfeld, M. A., … Puzey, J. R. (2020). Population genomic and historical analysis reveals a global invasion by bridgehead processes in *Mimulus guttatus*. *BioRxiv*. doi: 10.1101/2020.06.26.173286

Vallejo-Marín, M., & Lye, G. C. (2013). Hybridisation and genetic diversity in introduced *Mimulus* (Phrymaceae). *Heredity*, *110*, 111–122. doi: 10.1038/hdy.2012.91

van Boheemen, L. A., Atwater, D. Z., & Hodgins, K. A. (2019). Rapid and repeated local adaptation to climate in an invasive plant. *New Phytologist*, *222*(1), 614–627. doi: 10.1111/nph.15564

van Kleunen, M., Dawson, W., & Maurel, N. (2015). Characteristics of successful alien plants. *Molecular Ecology*, *24*(9), 1954–1968. doi: 10.1111/mec.13013

van Kleunen, M., & Fischer, M. (2008). Adaptive rather than non-adaptive evolution of *Mimulus guttatus* in its invasive range. *Basic and Applied Ecology*, *9*(3), 213–223. doi: 10.1016/j.baae.2007.03.006

van Kleunen, M., Röckle, M., & Stift, M. (2015). Admixture between native and invasive populations may increase invasiveness of *Mimulus guttatus*. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1815). doi: 10.1098/rspb.2015.1487

van Kleunen, M., Schlaepfer, D. R., Glaettli, M., & Fischer, M. (2011). Preadapted for invasiveness: do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? *Journal of Biogeography*, *38*(7), 1294–1304. doi: 10.1111/j.1365-2699.2011.02495.x

Whitney, K. D., & Gabler, C. A. (2008). Rapid evolution in introduced species, "invasive traits" and recipient communities: Challenges for predicting invasive potential. *Diversity and Distributions*, *14*(4), 569–580. doi: 10.1111/j.1472-4642.2008.00473.x

Wooliver, R., Tittes, S. B., & Sheth, S. N. (2020). A resurrection study reveals limited evolution of thermal performance in response to recent climate change across the geographic range of the scarlet monkeyflower. *Evolution*, *74*(8), 1699–1710. doi: 10.1111/evo.14041

Wu, C. A., Lowry, D. B., Cooley, A. M., Wright, K. M., Lee, Y. W., & Willis, J. H. (2008). *Mimulus* is an emerging model system for the integration of ecological and genomic studies. *Heredity*, *100*, 220–230. doi: 10.1038/sj.hdy.6801018

Zerebecki, R. A., & Sorte, C. J. B. (2011). Temperature tolerance and stress proteins as mechanisms of invasive species success. *PLoS ONE*, *6*(4). doi: 10.1371/journal.pone.0014806

Tables

Table 1. Pairwise comparisons of TPC parameters between ranges. For each Bayesian model iteration, we calculated range-level mean parameter estimates and found their pairwise differences by subtracting the parameter estimate of the invasive range from the native range, such that a positive difference indicates that the mean parameter estimate was greater in the native range. We used these comparisons to generate mean pairwise differences and 95% credible intervals.

Parameter	Pairwise Difference	95% CI
T_{opt} (°C)	-0.654	[-1.405, 0.108]
$T_{breadth}$ (°C)	0.018	[-1.191, 1.239]
AUC	-3.043	[-7.485, 1.344]

Table 2. Regression coefficients and *P*-values from full general linear models relating response variables to predictors. β1 indicates the main effect of either latitude, mean annual temperature (MAT), $T_{breadth}$, temperature seasonality (TS), or P_{max}. β2 indicates the main effect of range (invasive vs. native). β3 indicates the interaction between range and the predictor corresponding to β1. Based on AIC, we chose bolded models as the final model for each respective cline.

		Full Model				
Response	**Predictor (β1, β2, β3)**	**β1, *P***	**β2, *P***	**β3, *P***	**AIC**	***Adj. R²***
P_{max}	**$T_{breadth}$, R, $T_{breadth}$*Range**	**-0.140, *P*=0.008****	**-1.963, *P*=0.146**	**0.088, *P*=0.159**	**-10.448**	**0.219**
	$T_{breadth}$, R	-0.083, *P*=0.009**	-0.070, *P*=0.323	---	-10.131	0.188
T_{opt}	Lat, R, Lat*R	0.045, *P*=0.712	3.812, *P*=0.590	-0.087, *P*=0.504	111.848	-0.002
	Lat, R	**-0.033, *P*=0.409**	**-0.908, *P*= 0.123**	**---**	**110.372**	**0.018**
	MAT, R, MAT*R	0.038, *P*=0.899	-1.738, *P*=0.521	0.115, *P*=0.710	107.545	0.128
	MAT, R	**0.148, *P*=0.028***	**-0.748, *P*=0.108**	**---**	**105.708**	**0.155**
$T_{breadth}$	**Lat, R, Lat*R**	**-0.201, *P*=0.069**	**-11.209, *P*=0.077**	**0.204, *P*=0.079**	**103.385**	**0.020**
	Lat, R	-0.018, *P*=0.623	-0.120, *P*=0.820	---	104.993	-0.062
	TS, R, TS*R	0.058, *P*=0.407	1.265, *P*=0.689	-0.034, *P*=0.640	104.236	-0.008
	TS, R	**0.026, *P*=0.117**	**-0.197, *P*=0.662**	**---**	**102.492**	**0.020**

**=P<0.05, **=P<0.01, ***=P<0.001*

Figures

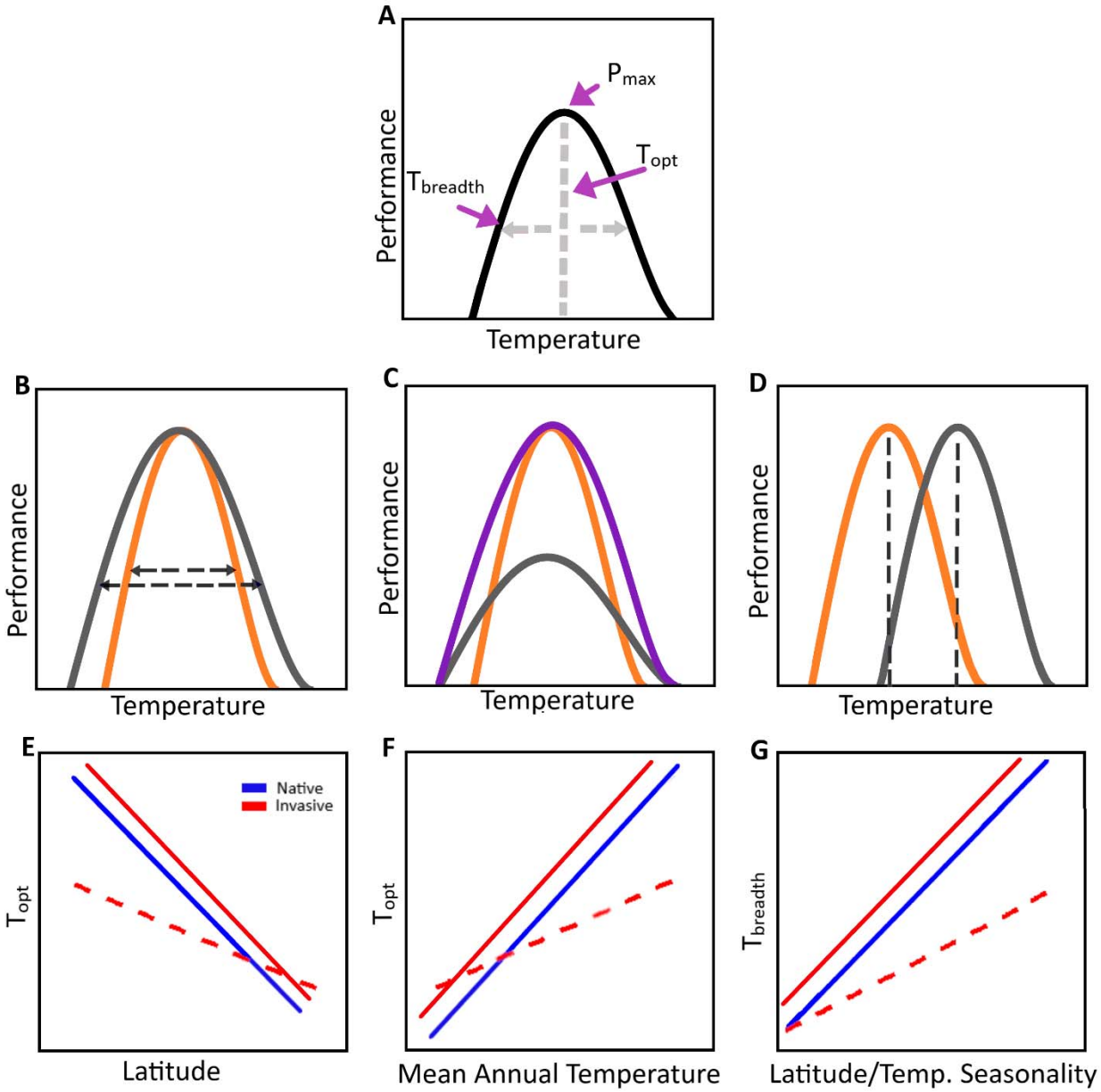

Figure 1. Hypotheses describing the evolution of thermal performance curves (TPCs) and clines in a species' native and invasive range, where grey, orange, and purple describe the TPC of a native or invasive population in panels B-D, and red corresponds to invasive populations and blue corresponds to native populations in panels E-G. (A) TPC parameters of interest include maximum performance (P_{max}), thermal optimum (T_{opt}), and thermal performance breadth

($T_{breadth}$). (B) Invasive populations may have wider (grey) or narrower (orange) $T_{breadth}$ relative to native populations. Alternatively, if general-purpose genotypes from native populations facilitate invasion, $T_{breadth}$ may be equally wide in both ranges. (C) 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 $T_{breadth}$ and a high P_{max} (purple). (D) Invasive populations exhibit a different T_{opt} relative to native populations. (E-G) Solid lines represent 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-G) The native range (solid blue line) exhibits clines such that T_{opt} decreases with latitude (E) and increases with mean annual temperature (F), and $T_{breadth}$ increases with latitude and temperature seasonality (G). In these panels, the invasive range (red lines) may exhibit repeated/parallel clines (solid lines), or weaker/no clines (dashed lines).

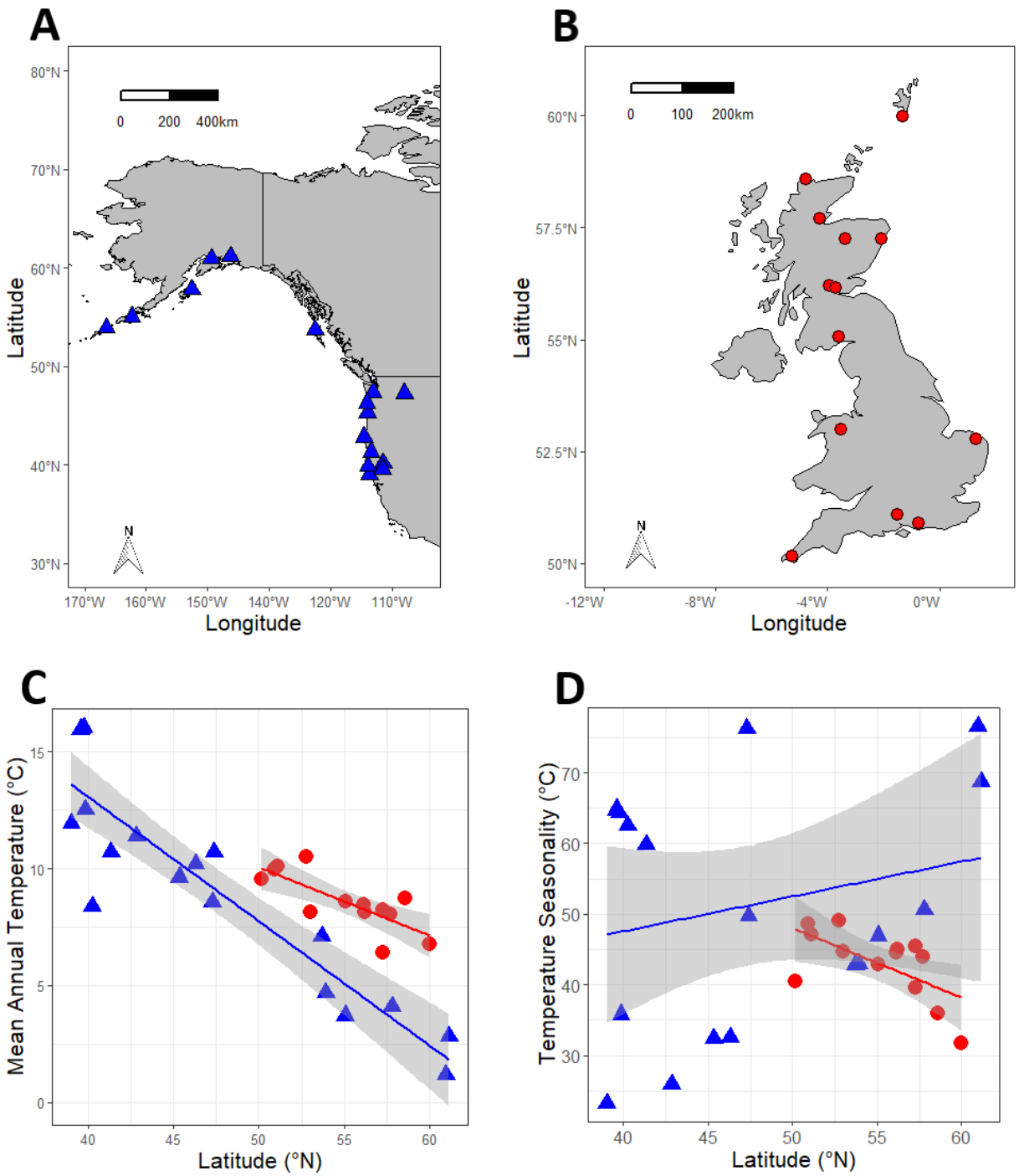

Figure 2. Map of focal populations of *M. guttatus* in (A) native range in North America and (B) invasive range in the United Kingdom. Relationships between (C) mean annual temperature and (D) temperature seasonality with latitude for native (blue triangles) and invasive (red circles) populations. Fitted lines indicate predicted mean annual temperature or seasonality as a function

of latitude based on linear models. The gray shaded area represents a 95% confidence interval for these predictions. Climate data were obtained from WorldClim v.2 (~1-km resolution, 1970-2000, Fick & Hijmans, 2017).

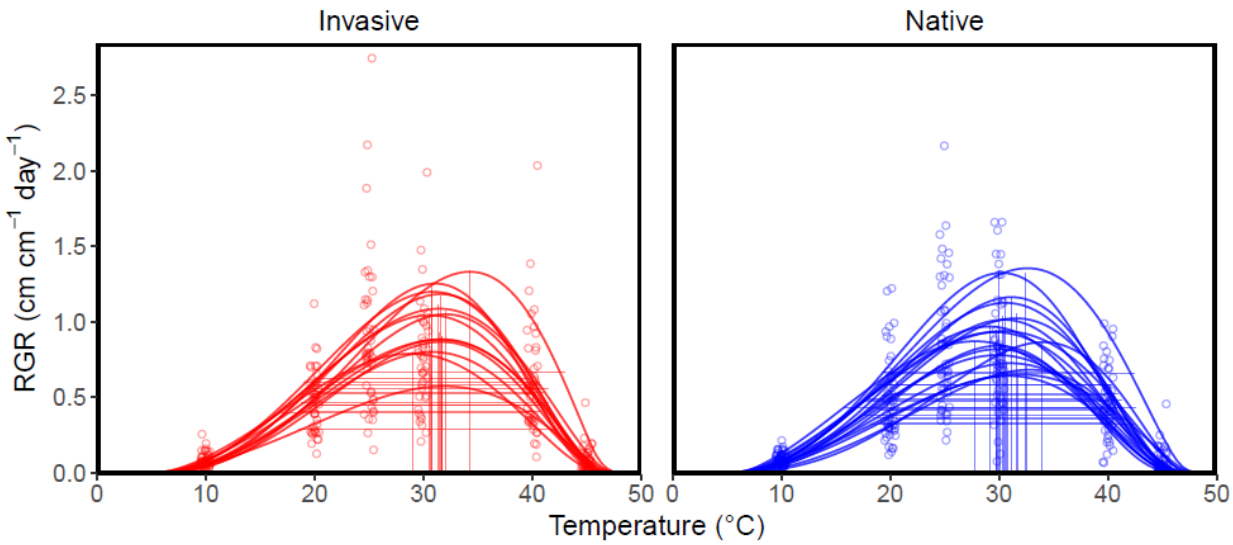

Figure 3. TPCs of 18 native (blue) and 13 invasive (red) populations of *M. guttatus*. Vertical lines represent T_{opt}, and horizontal lines denote $T_{breadth}$. Points represent genotype-level mean RGR at a given daytime temperature.

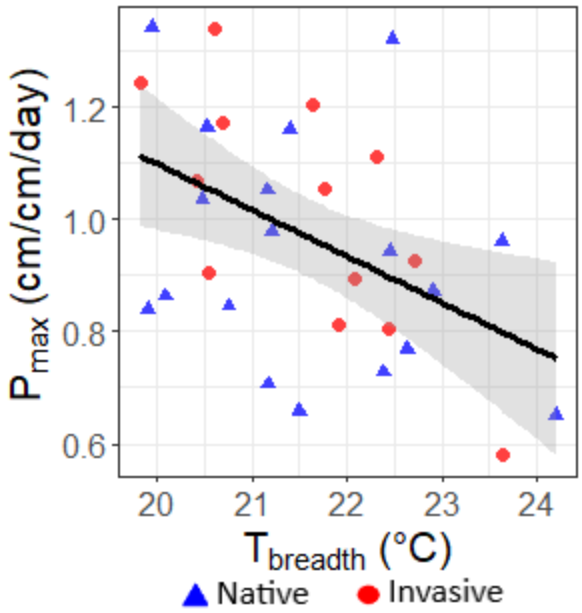

Figure 4. Specialist-generalist tradeoffs as shown by a relationship between P_{max} and $T_{breadth}$ across populations of *M. guttatus*. Black line indicates the main effect of $T_{breadth}$ (α=0.05; Table 2) from the full model with the interaction term removed, and grey shading shows 95% confidence interval.

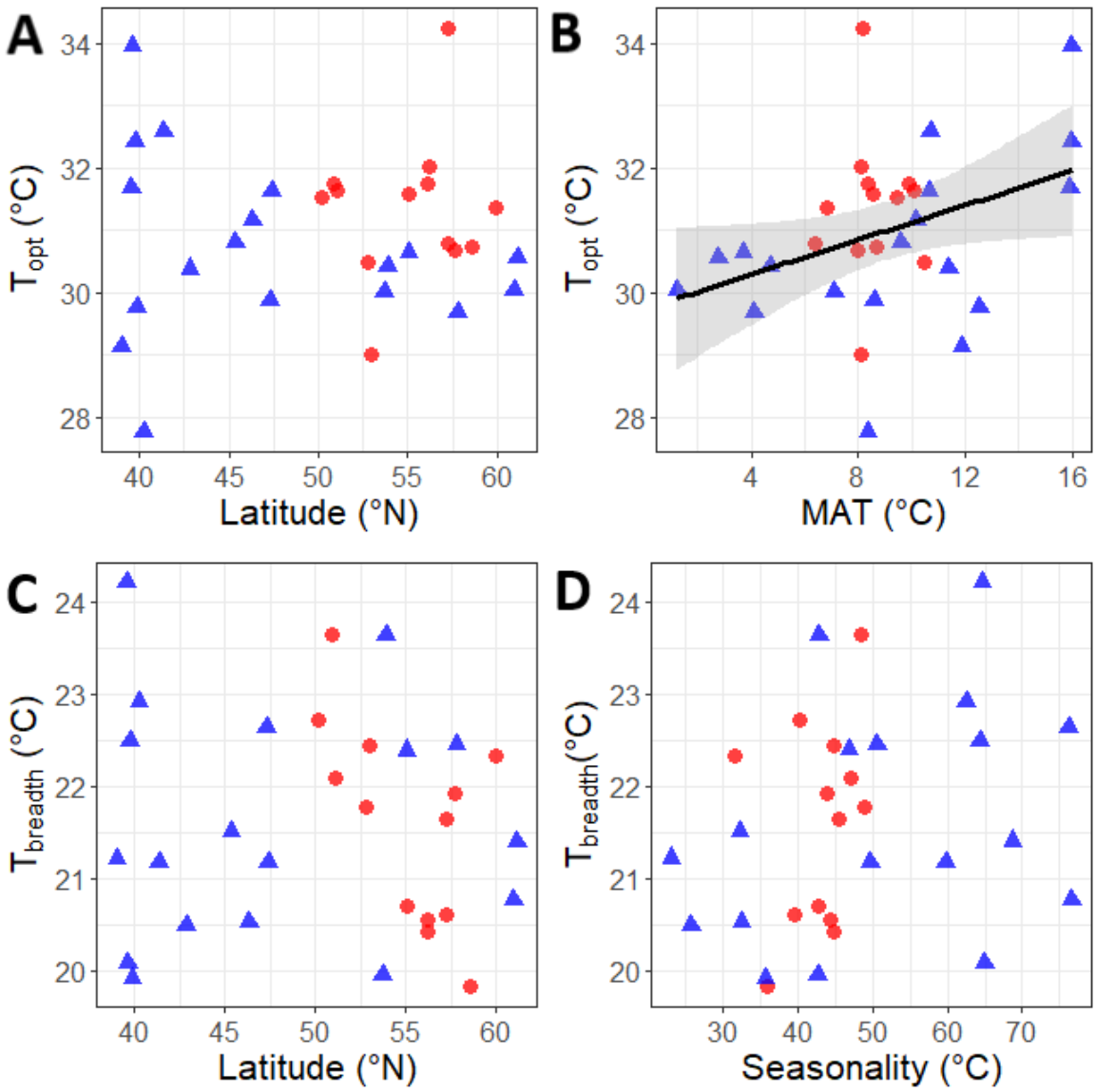

Figure 5. Relationships between population-level TPC parameters and latitude, mean annual temperature (MAT), and temperature seasonality. A main effect regression line (black) is shown if there was a significant effect of latitude, MAT, or temperature seasonality (α=0.05; Table 2).