# The evolution of thermal performance in native and invasive populations of Mimulus guttatus — Source link ⎋

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

2 ***guttatus***

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16 **Abstract**

17 **1.** The rise of globalization has spread organisms beyond their natural range, allowing further

18 opportunity for species to adapt to novel environments and potentially become invaders. Yet, the

19 role of climatic niche evolution in promoting the success of invasive species remains poorly

20 understood. Here, we use thermal performance curves (TPCs) to test hypotheses about thermal

21 adaptation during the invasion process. First, if novel temperature regimes impose strong

22 selection in the introduced range, invasive populations may evolve distinct TPCs relative to

23 native populations. Second, invasive species may not exhibit specialist-generalist tradeoffs and

24 instead may be "masters-of-all" with high maximum performance and broad TPCs. Third, with

25 sufficient time, standing genetic variation, and temperature-mediated selection, TPCs of native

26 and invasive populations may show parallel evolution in response to thermal gradients.

27 **2.** To test these hypotheses, we built TPCs for 18 native (United States) and 13 invasive (United

28 Kingdom) populations of the yellow monkeyflower, *Mimulus guttatus*. We grew clones of

29 multiple genotypes per population across six temperature regimes in growth chambers.

30 **3.** Invasive populations have not evolved different thermal optima or performance breadths,

31 providing evidence for evolutionary stasis of thermal performance between the native and

32 invasive ranges after over 200 years post-introduction. Further, both native and invasive

33 populations experienced similar specialist-generalist tradeoffs whereby broad TPCS come at the

34 cost of lower peak performance. Inconsistent with the idea that the degree of thermal

35 specialization varies across spatial or temperature gradients, native and invasive populations did

36 not exhibit adaptive clines in thermal performance breadth with latitude or temperature

37 seasonality. However, thermal optimum increased with mean annual temperature in the native

38 range, indicating some adaptive differentiation among native populations

39    **4.** *Synthesis:* These findings suggest that thermal niches were static during the invasion process,

40    and that general-purpose genotypes, rather than rapid evolution in the introduced range, may

41    promote invasion.

42    **Key-words:** adaptive divergence, evolutionary ecology, invasion ecology, latitudinal gradient,

43    niche conservatism, phenotypic cline, specialist-generalist tradeoff, thermal performance curve,

44    thermal tolerance

45    **Introduction**

46        Invasive species are one of the greatest threats to biodiversity in the 21st century, and

47    while the importance of managing their spread is widely recognized, the factors that contribute to

48    a species becoming invasive are still debated (Sala et al., 2000; Lee, 2002; van Kleunen,

49    Dawson, et al., 2015). Baker's classic description of "ideal weeds" suggested that invasive

50    species originate from "general-purpose" genotypes with broad climatic tolerance (Baker, 1965).

51    However, it is unknown whether climatic tolerance in a species invasive range is pre-existing,

52    which predicts niche conservatism, or evolved, which predicts niche lability between the native

53    and invasive range (Petitpierre et al., 2012; Atwater et al., 2018; Liu et al., 2020). Upon

54    introduction to a new geographic region, a species may expand, contract, or maintain its climatic

55    niche space depending on how the set of environmental conditions required to support non-

56    negative population growth changes from the native to the invasive range (Broennimann et al.,

57    2012). Similarly, a species average niche conditions (often referred to as niche "centroid" or

58    "position") may or may not shift in the invasive range (Guisan et al., 2014). If climatic niches are

59    often conserved between species native and invasive ranges, then building climatic niche models

60    based on native occurrences to identify areas with high invasion risk holds great promise for

61    predicting and managing biological invasions (Thuiller et al., 2005; Chapman et al., 2017; Da Re

62    et al., 2020). Numerous studies have used correlative niche models to assess climatic niche

63    conservatism across species native and invasive ranges (Peterson et al., 2003; Kriticos et al.,

64    2013; Da Re et al., 2020), but most have neglected among-population variation in niche

65    properties and variation in physiological tolerances across climatic gradients resulting from

66    evolutionary change (some exceptions include Ebeling et al., 2008; Hill et al., 2013). We use an

67    experimental approach to evaluate the evolution of physiological tolerances within and between

68    a species native and invasive ranges.

69         One dimension of a species climatic niche that influences its ability to invade new areas

70    is temperature. Thermal performance curves (TPCs, Fig. 1A) describe the performance of a

71    genotype, individual, population, or species across a temperature gradient (Huey & Stevenson,

72    1979). Though TPCs are not strictly equivalent to thermal niches unless the performance metric

73    is total fitness, they provide a powerful means of experimentally approximating a species

74    fundamental thermal niche. Comparisons of TPCs may not explicitly test thermal niche

75    conservatism between a species native and introduced ranges, but they shed light on whether the

76    evolution of physiological tolerance plays a role in species abilities to invade new areas. Some

77    TPC parameters that have been hypothesized to influence adaptation to temperature gradients

78    include maximum performance, thermal optimum, thermal performance breadth, and area under

79    the curve (Huey & Stevenson, 1979; Angert et al., 2011; Fig. 1A). Maximum performance is the

80    highest level of performance achievable, corresponding to the peak of the TPC. Thermal

81    optimum details the temperature at which maximum performance is achieved (Huey &

82    Stevenson, 1979), analogous to thermal niche position (or centroid). Comparable to thermal

83    niche breadth, thermal performance breadth describes the span of temperatures across which a

84    specified percentage of the maximum performance is achieved (Huey & Stevenson, 1979), with

85    specialists having narrow breadth, and generalists having wide breadth. Finally, the area under

86    the curve refers to the total amount of area between a TPC and the temperature axis, analogous to

87    total thermal niche space.

88        Evolutionary divergence of TPC parameters between invasive and native populations of

89    the same species could arise through thermal niche contraction, expansion, and/or shifts in the

90    introduced range. Consistent with thermal niche shifts, changes in thermal optima may

91    accompany divergence in local thermal regimes between the native and invasive range

92    (Angiletta, 2009). Nonetheless, if populations possess broad thermal performance breadths,

93    and/or if temperature regimes are similar in both ranges, then native and invasive populations

94    may exhibit similar thermal optima (Guisan et al., 2014). Consistent with niche expansion,

95    invasive populations could evolve a broader TPC upon introduction to novel thermal regimes

96    (Zerebecki & Sorte, 2011; Bates et al., 2013). Populations can achieve broad TPCs through a

97    combination of phenotypic plasticity and standing genetic variation (Sheth & Angert, 2014),

98    particularly if there is admixture of multiple source populations introduced to the novel range

99    (Kolbe et al., 2004; Lavergne & Molofsky, 2007). Though genetic bottlenecks during founding

100    events may constrain the ability of invasive populations to adapt to novel conditions, or cause

101    reductions in breadth (consistent with thermal niche contraction) due to genetic drift (Kitayama

102    & Mueller☐Dombois, 1995; Daehler, 2003), invasive populations rarely undergo significant

103    reductions of genetic diversity relative to native populations, making this scenario unlikely

104    (Wares et al., 2005; Dlugosch & Parker, 2008). Alternatively, if source populations represent

105    general-purpose genotypes, they may be predisposed toward having a broad thermal niche which

106    may be conserved in the invasive range (Ainsworth & Drake, 2020), leading to similar thermal

107    performance breadths in native and invasive populations. To date, there are few empirical studies

108    which compare TPCs of native and invasive populations of a single species (but see Comeault et

109    al., 2020), particularly in plants.

110         Evolutionary trajectories in the introduced range may be influenced by energetic

111    tradeoffs in thermal reaction norms (Angilletta et al., 2003). Commonly referred to as "jack-of-

112    all-trades is a master of none" and specialist-generalist tradeoffs, the ability to persist over a

113    wider range of temperatures can come at the cost of lower maximum performance (Huey &

114    Hertz, 1984; Richards et al., 2006; Le Vinh Thuy et al., 2016). Such tradeoffs should result in a

115    negative relationship between maximum performance and thermal performance breadth across

116    populations, whereby populations with broader TPCs have lower peak performance due to

117    additional energetic costs (Dewitt et al., 1998; Angilletta et al., 2003; Richards et al., 2006). This

118    tradeoff operates under the assumption that the area under the TPC remains constant (Palaima &

119    Spitze, 2004), but physiological or biochemical alterations could allow higher performance

120    across a broad range of temperatures (Angilletta et al., 2003; Richards et al., 2006) and cause a

121    positive relationship between thermal performance breadth and maximum performance. This

122    phenomenon, which has been referred to as "jack-and-master", or "master of all" (Richards et al.,

123    2006; Matesanz & Sultan, 2013), may be one mechanism that advances invasion.

124         Given a temperature or latitudinal gradient, populations with sufficient time and genetic

125    variation may evolve clines in TPC parameters in response to temperature-mediated selection

126    (Endler, 1977; Diamond et al., 2017; Campbell☐Staton et al., 2018). Failure to account for the

127    presence of latitudinal or environmental clines can mask inferences of trait evolution between

128    native and invasive ranges, as divergent selection may occur among populations (Colautti et al.,

129    2009). Adaptation to local thermal regimes should result in thermal optimum increasing with

130    mean annual temperature (Angert et al., 2011), and thermal performance breadth increasing with

131    temperature seasonality (often referred to as the climate variability hypothesis, CVH;

132    Dobzhansky, 1950; Janzen, 1967; Stevens, 1989; Gutiérrez-Pesquera et al., 2016). Thus, parallel

133    phenotypic clines across latitudinal or climatic gradients in native and invasive ranges would

134    indicate that rapid evolution plays a role in the invasion process (Huey et al., 2000; Hernández et

135    al., 2019; van Boheemen et al., 2019). However, if invasive populations have not had sufficient

136    time or standing genetic variation for adaptation to novel temperature gradients, or if

137    temperature-mediated selection in the introduced range is weak, then phenotypic clines may be

138    shallower in the invasive range than in the native range, or absent altogether (Bhattarai et al.,

139    2017).

140         In this study, we compare TPCs of invasive and native perennial populations of the

141    yellow monkeyflower, *Mimulus guttatus* (Phrymaceae; Fig. 2A,B)*, also known as *Erythranthe*

142    *guttata* (Fraga, 2018; Lowry et al., 2019), to improve our understanding of species invasive

143    abilities. *Mimulus guttatus* is an herbaceous plant native to western North America, occupying

144    wet habitats across a broad latitudinal and climatic gradient from Alaska to Northern Mexico

145    (Fraga, 2018). In 1812, *M. guttatus* was brought to the United Kingdom (UK) for horticultural

146    use and has subsequently become widespread across the British Isles and to a lesser extent parts

147    of continental Europe (Preston et al., 2002; Newman, 2015). *Mimulus guttatus* is now considered

148    invasive in the UK and New Zealand (Vallejo-Marín & Lye, 2013; van Kleunen, Röckle, et al.,

149    2015; Fraga, 2018). Genomic data suggest that genotypes of *M. guttatus* in the UK originated

150    from perennial populations in Alaska (Puzey & Vallejo-Marín, 2014; Pantoja et al., 2017),

151    followed by multiple introductions of perennial populations from across the native range

152    (Vallejo-Marín et al., 2020). The invasive UK range thus consists of a highly admixed melting

153    pot of native populations and is not likely constrained by low genetic diversity. Climatic niche

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154    models indicate niche conservatism in the native and invasive European ranges of *M. guttatus*,

155    though invasive populations occur in a subset of conditions occupied in the native range (Da Re

156    et al., 2020). Because the non-native populations are locally dominant invaders in the UK

157    compared to continental Europe, and served as a bridgehead for invasions worldwide (Vallejo-

158    Marín et al., 2020), we focused exclusively on the UK portion of the invasive range.

159        Here, we assess hypotheses about whether thermal performance evolution and the ability

160    to overcome specialist-generalist tradeoffs contribute to the invasion success of *M. guttatus*.

161    First, we hypothesized that if the species has undergone changes in thermal regimes and/or

162    genetic variation in its invasive range, there would be changes in thermal optimum and

163    performance breadth between the native and invasive ranges, against the alternative hypothesis

164    that these parameters do not differ between ranges (Fig. 1B,C). Since average temperatures are

165    slightly higher in the native range (Fig. 2C), invasive populations may have evolved lower

166    thermal optima relative to native populations (Fig. 1B). Further, while admixture in the invasive

167    range could lead to broader TPCs relative to the native range, reduced temperature variation (Fig.

168    2C,D) and/or genetic bottlenecks could result in narrower TPCs in the invasive range (Fig. 1C).

169    Second, we evaluated the hypothesis that the ability to overcome specialist-generalist tradeoffs

170    has fostered the invasion of *M. guttatus* (Fig. 1D) such that native and invasive populations are

171    "masters-of-all". Alternatively, populations may exhibit specialist-generalist tradeoffs, predicting

172    that "jack-of-all-trades is a master of none". Third, given sufficient time, standing genetic

173    variation, and temperature-mediated selection, we hypothesized parallel evolution in response to

174    thermal gradients in the invasive range (Fig. 1E-H). We predicted that thermal optimum would

175    increase with mean annual temperature (Fig. 1F), which decreases with latitude in both ranges

176    (Fig. 1E; Fig. 2C), and thermal performance breadth would increase with temperature seasonality

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177 (Fig. 1H), which increases with latitude in the native range but decreases with latitude in the

178 invasive range (Fig. 1G; Fig. 2D). Alternatively, clines may be weaker or absent in the invasive

179 range (Fig. 1E-G) due to weak selection across a narrow thermal gradient or evolutionary

180 constraints imposed by bottlenecks.

181 **Materials and Methods**

182 *Plant Propagation*

183       In June 2019, we grew seeds from 18 North American perennial and 13 United Kingdom

184 populations of *Mimulus guttatus* (Fig. 2A,B) in the North Carolina State University Phytotron.

185 We used an average of 3 seed families from populations spanning a broad latitudinal and thermal

186 gradient in the native and invasive ranges (see "Supplementary methods" for information

187 regarding population selection), totaling 95 unique genotypes (Table S1). We sowed 3-5 seeds

188 from each seed family into 72-cell plug trays filled with Fafard 4P soil (Fafard® 4P Mix, Sun

189 Gro Horticulture) and topped with germination mix (Sunshine® Redi-Earth Plug & Seedling,

190 Sun Gro Horticulture), placed them in a Percival LT-105X chamber, and subjected them to a 4°C

191 cold, dark treatment with daily misting for one week. After one week, we transferred seedlings to

192 a growth room, with a 16-hour day and 8-hour night photoperiod and a 20/15°C day/night

193 temperature regime. Cold treatments were repeated for seed families with poor initial

194 germination, which were primarily from the invasive range. After cold treatments, replanted

195 families remained in the Percival chamber with 20°C days and colder (5°C) nights for two weeks

196 before being moved to the growth room. Throughout seedling establishment and the remainder

197 of the experiment, we watered plants in the growth room with a nutrient solution (NPK +

198 micronutrients), dumped stagnant water, and randomized trays to reduce location effects twice

199 per week. Three weeks after planting, seedlings were thinned to one, central-most individual per

200    cell. Six weeks after planting, individuals were repotted into 8-inch pots with Fafard 4P. These

201    large plants served as the source of replicate cuttings for thermal performance experiments and

202    remained in the growth room for the duration of the experiment. We randomized the pots into

203    new trays, each of which held 2 plants. Eight weeks after planting, we cut the primary stem of

204    each plant to its base to encourage branching, which is ideal for taking replicate cuttings.

205    *Thermal Performance Experiment*

206         Ten weeks after planting, plants possessed sufficient vegetative growth to support many

207    cuttings. To generate thermal performance data for each genotype within each population, we

208    took cuttings of similar sizes from these plants and grew them in 2.5-inch pots within 32-pot

209    trays. As perennial *M. guttatus* often reproduces clonally in the native and invasive range

210    (Truscott et al., 2006; van Kleunen, 2007; Pantoja et al., 2018), clones permit performance

211    measurements of the same genotypes across a range of temperatures. Another advantage of using

212    cuttings rather than seedlings is that they are likely less prone to maternal effects (reviewed in

213    Roach & Wulff, 1987). Prior to temperature treatments, we allowed each set of clones 2 weeks to

214    establish roots. During this period, cuttings were kept within chambers set to 20°C day/15°C

215    night and bottom-watered daily with a nutrient solution. We randomized cuttings both within and

216    among chambers twice per week to reduce location effects. We subsequently transferred clones

217    into a growth chamber programmed to one of six temperature regimes. Over the course of the

218    experiment, we randomly assigned six temperature treatments to one of three identical Percival

219    LT-105X chambers (Percival Scientific, Inc.; Perry, Iowa, USA), resulting in two full rounds of

220    chamber use. For each temperature regime, we took two replicates (clones) of each genotype and

221    randomized them among six trays. We subjected clones to 16-hour days and 8-hour nights,

222    according to procedures previously implemented by Paul et al. (2011), Sheth & Angert (2014),

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223    and Wooliver et al. (2020), with one of the following day/night temperature regimes (°C): 10/0,

224    20/10, 25/15, 30/20, 40/30, and 45/35. Temperature regimes were replicated once, along with an

225    additional replicate of the 45°C/35°C regime. In total, we took 1,338 cuttings. However, 86

226    cuttings failed to establish, resulting in a final dataset of 1,252 individual clones from 18 native

227    and 13 invasive populations, each comprising 54 and 41 genotypes, respectively. We exposed

228    clones to a given temperature regime for one week, during which trays were sub-irrigated daily

229    with water to prevent different rates of nutrient uptake at different temperatures.

230         We measured relative change in stem length over the 7-day temperature treatment. We

231    chose this short treatment period because previous work with *M. guttatus* has documented

232    significant growth responses to temperature in one week (Sheth & Angert, 2014). We quantified

233    the length of the primary stem and the total length of branches (including stolons and side

234    branches) before and after each temperature treatment (*stem$_{in}$* and *stem$_{out}$*, respectively). Total

235    length of branches was estimated as the number of branches multiplied by the length of an

236    average branch approximately halfway down the primary stem. We then calculated relative

237    growth rate (RGR) as a proxy for fitness as the change in total stem length per initial stem length

238    per day (Eq. 1). Negative RGR values arising when clones lost stem length or branches due to

239    dieback at temperature extremes were set to zero, and we excluded negative RGR values

240    resulting from accidental damage. Although RGR is not a measure of total reproductive output,

241    we used this metric as a proxy for fitness because size has been related to reproductive output in

242    other *Mimulus* species (Sheth & Angert, 2018).

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

244    *Bayesian TPC Models*

245        We performed all analyses in R v. 3.6.2 (R Core Team, 2019). To generate TPCs for

246      native and invasive populations of *M. guttatus*, we used a hierarchical Bayesian model (R

247      package performr v0.2; Tittes et al., 2019) to simultaneously fit curves predicting RGR across

248      temperature for all populations while estimating uncertainty. As this model does not allow

249      inclusion of random effects, we first averaged total RGR across clones of each genotype at each

250      temperature. This model also required scaling RGR values by the mean RGR across all data and

251      centering daytime temperature around zero. Thus, we rescaled model outputs to reflect actual

252      RGR values and temperatures. To improve the effectiveness of posterior sampling, we altered

253      the default settings of the model to include a total of 4,000 iterations per chain and a maximum

254      tree depth of 15 (Gelman et al., 2014). This model utilizes a derivation of Kumaraswamy's

255      probability density function to fit performance curves across a continuous environmental

256      gradient. We assessed the fit of Bayesian models using a posterior predictive *P*-value, which uses

257      a test variable to give the probability that values drawn from the simulated posterior predictive

258      distribution will exceed the observed values. *P*-values closest to 0.5 indicate adequate fit

259      between the modeled and observed data (Gelman et al., 2014). The Bayesian *P*-value for the

260      overall model was 0.53, and *P*-values for each population ranged from 0.2-0.82 (Table S2).

261        From these models, we obtained estimates of thermal optimum ($T_{opt}$), thermal

262      performance breadth ($T_{breadth}$), maximum performance ($P_{max}$), and area under the curve ($AUC$)

263      for each population (Table S3). We selected critical values for $T_{breadth}$ from 100 equally spaced

264      points along the temperature axis closest to the temperatures corresponding to 50% of $P_{max}$.

265      Although these models also generated estimates of critical upper and critical lower thermal limits

266      (temperatures at which RGR decreases to zero), these estimates extended beyond our

267      temperature treatments. We thus excluded these parameters from our analyses.

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268    *Statistical Analyses for Hypothesis Testing*

269    We tested for divergence in TPC parameters between native and invasive populations of

270    *M. guttatus* independent of latitude by conducting post-hoc comparisons of TPC model

271    iterations. For all iterations, we calculated the mean and 95% credible interval of the pairwise

272    difference in each TPC parameter between the native and invasive range. We interpreted a

273    statistically significant difference if the 95% credible interval did not include zero.

274    We examined the potential for specialist-generalist tradeoffs within either range using a

275    general linear model with $T_{breadth}$, range (native or invasive), and their interaction as predictors

276    and $P_{max}$ as the response. We also ran a reduced linear model which removed the interaction term

277    to account for the possibility of similar tradeoffs in both ranges. We used the Akaike information

278    criterion (AIC) to assess model fit. For all linear models, we evaluated statistical significance

279    using α=0.05. A negative relationship between $T_{breadth}$ and $P_{max}$ would indicate a specialist-

280    generalist tradeoff, whereas a positive relationship would be consistent with a "master-of-all"

281    scenario. Given a final model with a significant interaction term, we ran separate models for each

282    range. To determine whether the assumption that the area under TPCs remained constant was

283    supported, we conducted pairwise comparisons of population-level mean *AUC* based on model

284    iterations. We used a 95% credible interval to assess significant differences between populations

285    within each range and between populations of different ranges.

286    To determine whether TPCs of invasive populations have rapidly adapted to temperature

287    and latitudinal gradients in the novel range, we compared latitudinal and thermal clines of TPC

288    parameters in the native and invasive range using general linear models. To test whether $T_{opt}$

289    decreased with latitude or increased with mean annual temperature, we modeled $T_{opt}$ as a

290    function of either latitude or mean annual temperature, range, and their interaction. Similarly, to

13

291    evaluate whether $T_{breadth}$ increased with latitude in the native range, decreased with latitude in the

292    invasive range, and increased with temperature seasonality in both ranges, we modeled $T_{breadth}$ as

293    a function of latitude or temperature seasonality, range, and their interaction. We used AIC to

294    compare models with and without the interaction term to account for the possibility of clines of

295    similar magnitude and direction in both ranges. If the final model for each TPC parameter

296    included a significant interaction term, we conducted range-specific models with only latitude or

297    temperature as predictors. Shallower or nonsignificant slopes within the invasive range relative

298    to the native range would suggest a lack of parallel evolution in response to thermal gradients. In

299    contrast, a significant effect of latitude or temperature, along with a nonsignificant or absent

300    interaction term would indicate parallel evolution of clines across ranges, though we note that a

301    nonsignificant interaction term could also arise due to a lack of statistical power.

302    **Results**

303    *Overall Shifts in TPC Parameters Between the Native and Invasive Ranges*

304          We found no support for the hypothesis that *M. guttatus* has evolved in response to novel

305    thermal regimes within its invasive range via TPC shifts. Pairwise comparisons revealed that $T_{opt}$

306    and $T_{breadth}$ exhibited 95% credible intervals that included zero (pairwise difference for $T_{opt}$= -

307    0.654°C, 95% CI= -1.405, 0.108; pairwise difference for $T_{breadth}$=0.018°C, 95% CI= -1.191,

308    1.239), indicating that neither differed significantly between ranges (Fig. 3, Fig. S3).

309    Additionally, pairwise comparisons showed that *AUC* and $P_{max}$ did not differ between ranges

310    (pairwise difference for *AUC*= -3.043, 95% CI= -7.485, 1.344; pairwise difference for $P_{max}$ = -

311    0.071 cm/cm/day, 95% CI= -0.194, 0.046; Fig. S3).

312    *Specialist-Generalist Tradeoffs*

313        Consistent with specialist-generalist tradeoffs, $P_{max}$ decreased with $T_{breadth}$ (Table 1, Fig.

314    4). The final model included an interaction between $T_{breadth}$ and range (Table 1). However, this

315    interaction was not statistically significant, suggesting that the direction and strength of the

316    relationship between $T_{breadth}$ and $P_{max}$ did not differ between the native and invasive ranges

317    (Table 1). The main effect of range was also non-significant (Table 1). Failing to meet the

318    assumption that area is constant when there are specialist-generalist tradeoffs, pairwise

319    comparisons indicate that $AUC$ significantly differed among populations both within and

320    between ranges (Palaima & Spitze, 2004; Fig. S2).

321    *Clines of TPC Parameters*

322        Overall, latitudinal and thermal clines varied in strength depending on the TPC parameter

323    and/or the geographic range. The final models for $T_{opt}$ as a function of latitude or mean annual

324    temperature (MAT) did not include an interaction between latitude or MAT and range (Table 1).

325    Failing to support our hypothesis, $T_{opt}$ did not decrease with latitude (Table 1, Fig. 5A). Further,

326    there was no main effect of range when assessing clines of $T_{opt}$ across latitude (Table 1). $T_{opt}$

327    increased with MAT, but there was also no main effect of range on $T_{opt}$ when assessing clines

328    across MAT (Table 1, Fig. 5B). To further dissect the relatively low variance explained by this

329    model (Adj. $R^2$=0.155), we conducted range-level models. We found that the cline of $T_{opt}$

330    increasing with MAT in our full model was primarily driven by adaptive differentiation within

331    the native range ($\beta$=0.153, $P$=0.036, Adj. $R^2$=0.199), whereas there was no relationship between

332    MAT and $T_{opt}$ in the invasive range ($\beta$=0.038, $P$=0.899, Adj. $R^2$=-0.089).

333        The final model of $T_{breadth}$ as a function of latitude included an interaction between

334    latitude and range (Table 1). Contrary to the prediction that $T_{breadth}$ would increase with latitude

335    in the native range and decrease with latitude in the invasive range, $T_{breadth}$ showed no

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336    relationship with latitude (Table 1, Fig. 5C). There was not a significant main effect of range on

337    $T_{breadth}$, and the relationship between latitude and $T_{breadth}$ did not differ between ranges (Table 1).

338    The final model of $T_{breadth}$ as a function of temperature seasonality did not include an interaction

339    term (Table 1). We found no cline of $T_{breadth}$ with temperature seasonality (Table 1; Fig. 5D),

340    failing to support the climate variability hypothesis. Further, there was no main effect of range

341    on $T_{breadth}$ when assessing clines of $T_{breadth}$ across temperature seasonality (Table 1).

**Discussion**

343        We compared thermal performance curves (TPCs) of 18 native and 13 invasive

344    populations of *Mimulus guttatus* to test key hypotheses about the role of climatic niche evolution

345    in facilitating biological invasions. First, our results provided no support for the hypothesis that

346    thermal optimum and breadth vary between the native and invasive ranges (Fig. S3). Second,

347    failing to support the hypothesis that *M. guttatus* is a "master-of-all," there were specialist-

348    generalist tradeoffs in both the native and invasive ranges (Table 1, Fig. 4). Finally, contrary to

349    the hypothesis that native and invasive ranges show parallel phenotypic clines, there was limited

350    evidence for parallel clines in TPC parameters between ranges (Table 1, Fig. 5). Rather than

351    supporting the hypothesis that TPC evolution has played a role in facilitating *M. guttatus*

352    invasion in the UK, these results provide physiological support for thermal niche conservatism in

353    the invasive range. Below, we discuss the implications of these findings in light of the

354    evolutionary processes that could contribute to biological invasion.

*Evolution of Thermal Performance Curves*

356        We found no support for the hypothesis that invasive populations have undergone

357    changes in mean TPC parameters relative to native populations (Fig. 3, Fig. S3). Instead, $T_{opt}$ and

358    $T_{breadth}$ were similar between native and invasive ranges, consistent with the finding of climatic

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359     niche conservatism between the native North American and invasive European ranges of *M.*

360     *guttatus* based on niche models (Da Re et al., 2020). However, like many other invasive species

361     (Liu et al., 2020), the invasive range of *M. guttatus* has undergone substantial niche unfilling (Da

362     Re et al., 2020), where invasive populations are found in a comparatively small subset of the

363     climatic conditions (including temperature; Fig. S1) occupied in the native range. Although the

364     range of temperatures is narrower in the introduced range (Fig. 2C), $T_{breadth}$ did not differ

365     between ranges (Fig. S3), suggesting that invasive *M. guttatus* populations are poised to occupy

366     greater climatic niche space should it become available. Maintenance of broad thermal tolerance

367     in the invasive range may allow *M. guttatus* populations to withstand rapid changes in

368     temperatures, increasing risks that invasive populations will proliferate under climate change.

369     Future TPC comparisons that include introduced populations from additional regions would

370     further contribute to our understanding of the role of thermal niche evolution in the global range

371     expansion of *M. guttatus*.

372        One factor that could contribute to the evolutionary stasis of TPC parameters in the

373     invasive range is insufficient standing genetic variation (Prentis et al., 2008; Dlugosch et al.,

374     2015; Colautti et al., 2017). Although lower neutral genetic variation in the introduced range

375     (Puzey & Vallejo-Marín, 2014; Pantoja et al., 2017) could have constrained the rapid evolution

376     of $T_{opt}$ and $T_{breadth}$ in *M. guttatus*, the highly admixed nature of invasive populations (Vallejo-

377     Marín et al., 2020) make this possibility unlikely. Instead, genetic variation resulting from

378     admixed invasive populations likely contributed to the maintenance of broad TPCs and allowed

379     these populations to easily tolerate the narrower range of temperatures in the UK. In sum, the

380     invasive populations have yet to undergo significant divergence in TPCs from native populations

381     due to overlap in thermal niche space, rather than lacking the genetic variation necessary for

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382    evolution to occur. If invasive populations exhibit high admixture, they may spread further via

383    thermal niche evolution in the face of climate change.

384    *Specialist-Generalist Tradeoffs*

385          We found that TPCs in both ranges were constrained by specialist-generalist tradeoffs,

386    such that broad TPCs came at the cost of lower maximum performance (Table 1, Fig. 4).

387    Considering the similar $T_{breadth}$ across ranges, maintenance of broad thermal tolerance in the

388    narrow thermal conditions of the invasive range may incur significant performance costs via

389    specialist-generalist tradeoffs. However, variation in $AUC$ among populations within each range

390    (Fig. S2) suggests that the assumption that area remains constant does not hold for *M. guttatus*

391    (Palaima & Spitze, 2004). As such, the tradeoff between $T_{breadth}$ and $P_{max}$ is only partial.

392    Although $AUC$ and $T_{breadth}$ were not correlated ($\rho$=-0.2692, *P*= 0.1431), suggesting that thermal

393    niche space is not affected by variance in $T_{breadth}$, $AUC$ was positively correlated with $P_{max}$,

394    ($\rho$=0.9767, *P*<0.001). These results imply that variation in TPCs among populations is partly

395    explained by vertical shifts across a fast-slow spectrum of performance (Izem & Kingsolver,

396    2005), where some populations achieve a greater $AUC$ by having both a high maximum

397    performance and a broad TPC (Palaima & Spitze, 2004). Thus, variation in TPCs in native and

398    invasive populations of *M. guttatus* seems to be controlled by both vertical shifts where high-

399    performing populations are 'masters-of-all' and specialist-generalist tradeoffs where generalist

400    populations are 'masters-of-none'.

401    *Evolution of Clines*

402          We hypothesized that phenotypic clines exhibited in the native range would be repeated

403    in the invasive range. Although temperature varies predictably with latitude in the invasive range

404    (Fig. 2C,D), and there is ample evidence that rapid adaptation can facilitate invasion success

405    (Oduor et al., 2016), our results did not support the hypothesis of parallel clines. Rather, $T_{opt}$

406    increased with mean annual temperature across both ranges, though the amount of variance

407    explained was modest (*Adj. $R^2$*=0.155). As native populations were the primary driver of the

408    cline detected in the full model (Fig. 5B), adaptive differentiation of $T_{opt}$ to mean annual

409    temperature may contribute to the success of this species in its native range. The absence of this

410    cline in the invasive range implies weaker selection on $T_{opt}$ or insufficient time for adaptation in

411    the invasive range. Given that invasive populations of *M. guttatus* have maintained similar

412    $T_{breadth}$ as native populations, selection in the invasive range with a relatively narrow range of

413    mean annual temperatures would not likely favor adaptive differentiation in $T_{opt}$ (Fig. 2C).

414         Failing to support the climate variability hypothesis (Dobzhansky, 1950; Janzen, 1967;

415    Stevens, 1989; Gutiérrez-Pesquera et al., 2016), $T_{breadth}$ was not related to latitude or temperature

416    seasonality in either range. There are many possible explanations for a lack of clines in $T_{breadth}$ in

417    native populations. First, since six native populations were inland perennials, differing regimes

418    of temperature seasonality in coastal and inland environments of perennial *M. guttatus* could

419    mask latitudinal and macroclimatic trends in  $T_{breadth}$ (Hall & Willis, 2006; Lowry et al., 2009).

420    Second, microclimatic variation could cause populations of *M. guttatus* to occupy areas with

421    either highly similar or drastically different regimes of temperature seasonality, which could

422    hinder the detection of clines at broader macroclimatic scales (Franco & Nobel, 2003;

423    Rashkovetsky et al., 2006; De Frenne et al., 2013). While additional analyses of variation in TPC

424    parameters within populations would be helpful for dissecting this hypothesis, our model was

425    unable to fit genotype-level curves due to insufficient replication. Finally, high gene flow among

426    native populations could swamp adaptation of TPCs to local thermal regimes (Paul et al., 2011).

427    Rather than evolving TPCs in response to thermal variation, native populations may consist of

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428   general-purpose genotypes with wide TPCs which contributed to their successful establishment

429   as an invasive species (van Kleunen et al., 2011). This conclusion is consistent with the finding

430   of high rates of gene flow among coastal populations occupying similar latitudes in the native

431   range relative to our study populations (Twyford & Friedman, 2015). Nonetheless, our findings

432   are particularly surprising given the evolution of parallel phenotypic clines in the introduced

433   ranges of several species (van Boheemen et al., 2019; Hernández et al., 2019; McGoey et al.,

434   2020). Overall, our results suggest that though native *M. guttatus* populations are adaptively

435   differentiated by thermal optima, populations are equally tolerant across a broad temperature

436   gradient in western North America. Such homogenization of $T_{breadth}$ among native populations

437   may have allowed *M. guttatus* to maintain a broad thermal niche space upon introduction.

438   *Caveats*

439   There are many caveats which may have impacted the results of our study. First, our

440   temperature regimes maintained constant respective day and night temperatures, but in nature

441   plants experience temperature fluctuations. Second, although we incorporated multiple

442   measurements of stem and branch growth, populations may vary in their investment in stem and

443   branch growth versus other growth parameters (such as leaf number or belowground growth) at

444   different temperatures. Third, we focused on one performance metric, RGR over a week-long

445   period, but to fully understand performance tradeoffs and variation in performance across

446   temperatures, multiple performance metrics (e.g., survival and fecundity) should be measured

447   over longer experimental periods and across multiple life stages. Ultimately, performance

448   metrics that better approximate lifetime fitness could yield stronger phenotypic clines.

449   Nevertheless, short-term RGR of cuttings captures performance of clonally reproducing plants

450   characteristic of perennial *M. guttatus*. Finally, we focused on temperature, one axis of the

451    climatic niche, but evolution along other niche axes such as precipitation and edaphic properties

452    could also contribute to invasion success (Hall & Willis, 2006; van Kleunen & Fischer, 2008).

453    Further, the biotic environment may also differ in the introduced range (Holeski et al., 2013;

454    Thawley et al., 2018), implying that many factors beyond abiotic conditions can play a part in

455    adaptation to novel conditions during invasions.

456    **Conclusions**

457          Plant invasions have been widely studied for land management purposes, but little

458    consensus exists on the ecological and evolutionary processes that facilitate invasion success.

459    Our findings that thermal optima and breadth are similar in the invasive and native ranges, and

460    that populations did not exhibit clines in thermal breadth even in the native range, suggest that

461    general-purpose genotypes, rather than rapid TPC evolution, may have contributed toward

462    successful establishment in the invasive range. Our results have important implications toward

463    discovering what traits are favored for invasive organisms. For example, although having a broad

464    thermal performance curve may aid in initial establishment of populations in a new environment,

465    specialist-generalist tradeoffs may constrain the further evolution of broader TPCs. By

466    comparing the evolution of thermal performance across broad environmental gradients in a

467    species native and invasive range, we can predict which species hold the potential to become

468    aggressive invaders and forecast how they may fare under rapid climate change. Species that are

469    genetically predisposed towards a broad thermal tolerance may rapidly expand in their invasive

470    range as climatic conditions shift. These predictions will be invaluable in preparing for future

471    species invasions, strengthening our efforts to manage invasive species in the face of rapid

472    climate change and globalization.

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482    **Author Contributions**

483    A.Q. and S.N.S. conceived of and designed the study with feedback from M.V.M. A.Q.

484    collected the data. A.Q. and R.W. analyzed the data. A.Q. and S.N.S. led the writing, with

485    substantial contributions from R.W. and M.V.M. All authors contributed critically to the drafts

486    and gave final approval for publication.

487    **Data Availability**

488    All data and scripts associated with this study are available at

489    https://github.com/akquerns/Guttatus_EvolTPCClines.

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756

**Tables**

**Table 1.** 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), thermal performance breadth ($T_{breadth}$), temperature seasonality (TS), or performance maximum ($P_{max}$). 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.

| Response | Predictor (β1, β2, β3) | β1, *P* | β2, *P* | β3, *P* | AIC | *Adj. R²* |
|---|---|---|---|---|---|---|
| | | | Full Model | | | |
| $P_{max}$ | **$T_{breadth}$, 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** |

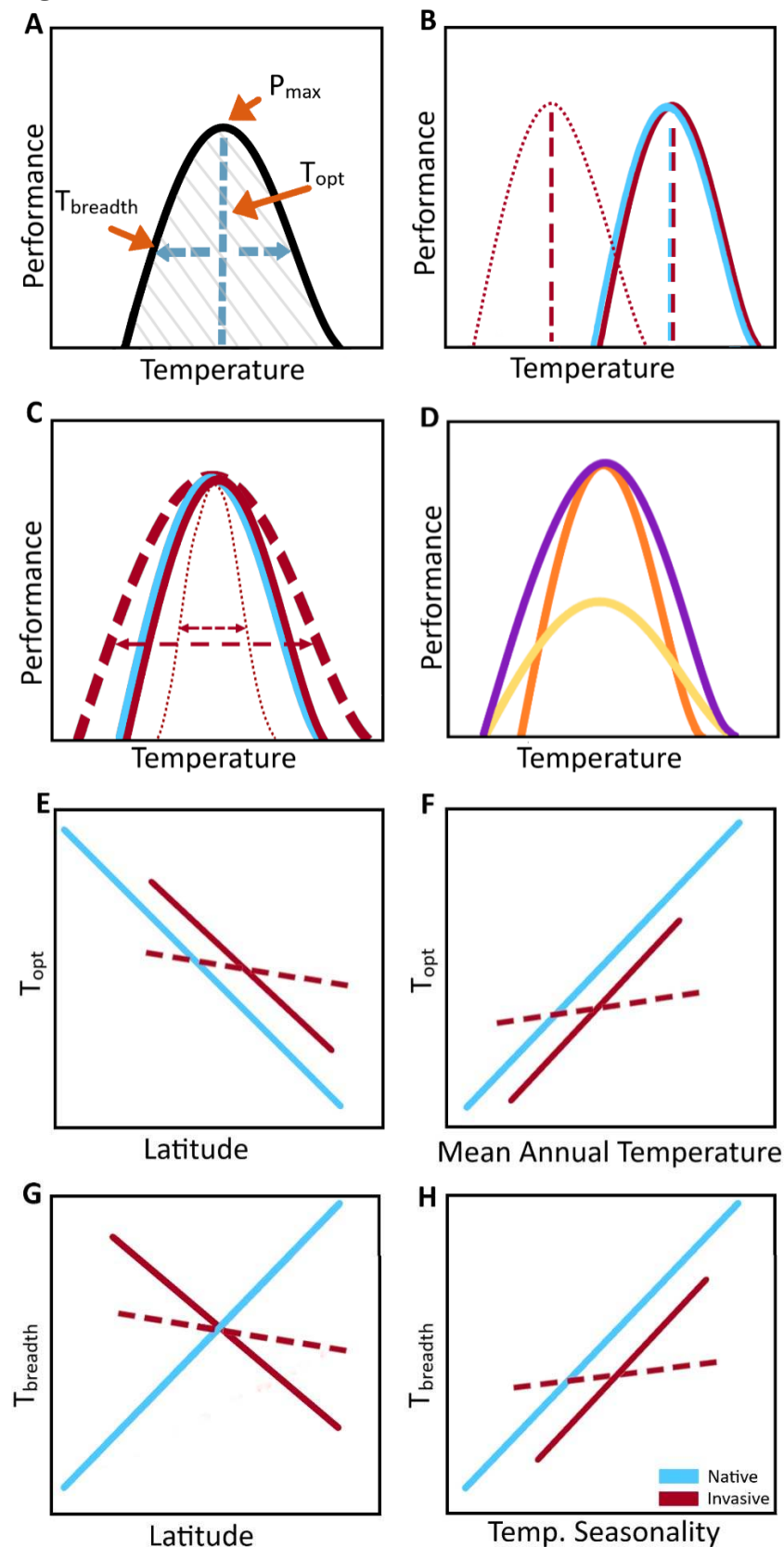*\*=P<0.05, \*\*=P<0.01, \*\*\*=P<0.001*

763 **Figures**



764

**Figure 1.** Hypotheses describing the evolution of thermal performance curves (TPCs) and clines in native and invasive populations of *M. guttatus*. (A) TPC parameters of interest include maximum performance ($P_{max}$), thermal optimum ($T_{opt}$), thermal performance breadth ($T_{breadth}$), and area under the curve (shaded region) (B) Invasive populations may exhibit a lower $T_{opt}$ relative to native populations (dotted line) due to lower average mean annual temperatures (MAT; Fig. 2C; native average MAT= 9.2°C, invasive average MAT=8.6°C). Alternatively, native and invasive populations may exhibit similar $T_{opt}$ if populations occupy similar thermal regimes or if $T_{breadth}$ is maintained (solid lines) in the invasive range. (C) Invasive populations may evolve wider (dashed line) or narrower (dotted line) $T_{breadth}$ relative to native populations due to admixture or bottlenecks/reduced temperature variation, respectively. Alternatively, if general-purpose genotypes from native populations facilitate invasion, $T_{breadth}$ may be maintained (solid line). (D) Within native and invasive populations, there may be specialist-generalist tradeoffs such that populations with greater $T_{breadth}$ have a lower $P_{max}$ (yellow) and populations with narrower $T_{breadth}$ have a higher $P_{max}$ (orange). However, some invasive species may not exhibit these tradeoffs and instead achieve a wide $T_{breadth}$ and a high $P_{max}$ (purple). (E-F) The native range (solid blue line) may exhibit clines such that $T_{opt}$ decreases with latitude (E) and increases with MAT (F), and these clines may be parallel (solid red) or weaker/nonexistent (dashed red) in the invasive range. (G-H) The native range may exhibit clines such that $T_{breadth}$ increases with latitude (G) and temperature seasonality (H). The invasive range, where temperature seasonality increases with latitude (Fig. 2D), may evolve parallel clines (solid line) such that $T_{breadth}$ decreases with latitude (G) and increases with temperature seasonality (H), or may exhibit weaker/no clines (dashed line).
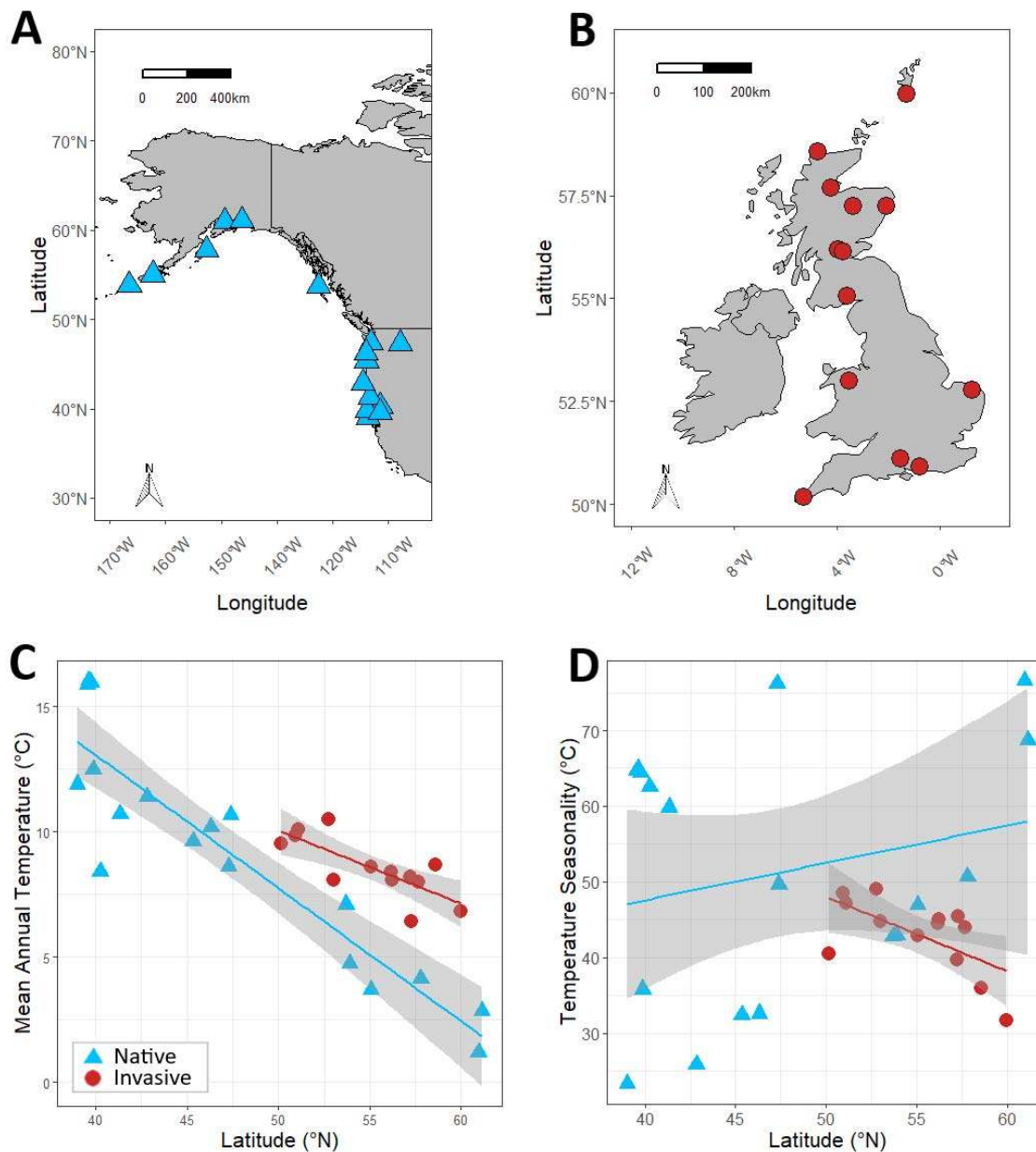
**Figure 2.** Map of focal populations of *M. guttatus* in (A) native range in North America and (B)

invasive range in the United Kingdom. Relationships between (C) mean annual temperature and

(D) temperature seasonality with latitude for native and invasive 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.

793    Climate data were obtained from WorldClim v.2 (~1-km resolution, 1970-2000, Fick & Hijmans,
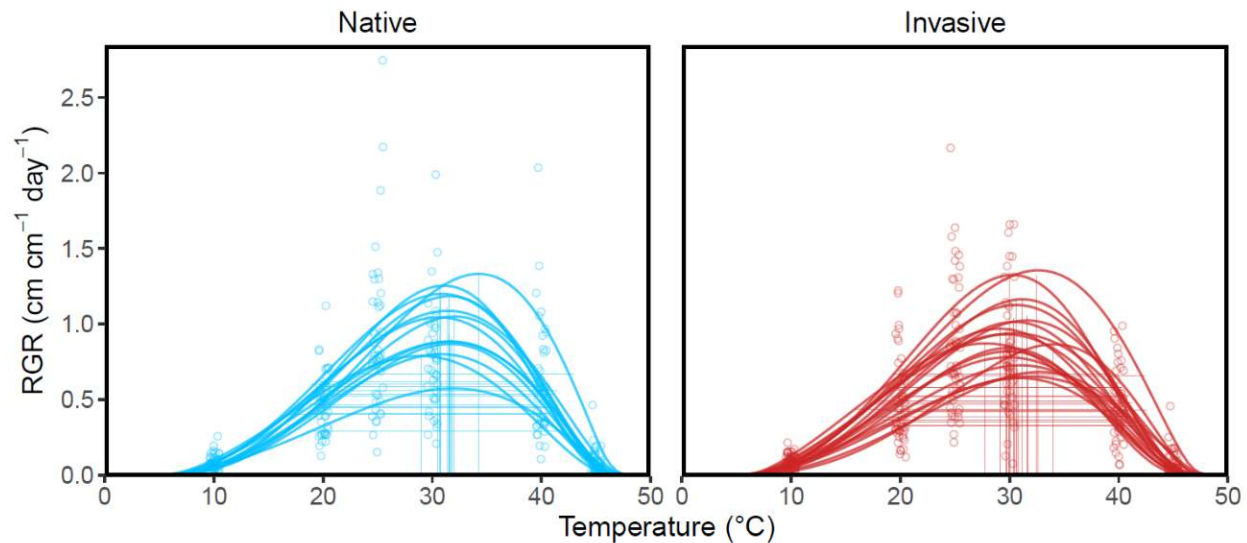
794    2017).

795

**Figure 3.** Thermal performance curves of 18 native and 13 invasive populations of *M. guttatus*.

Vertical lines represent thermal optima ($T_{opt}$) and horizontal lines denote thermal performance

breadth ($T_{breadth}$). Points represent genotype-level mean relative growth rate (RGR) at a given
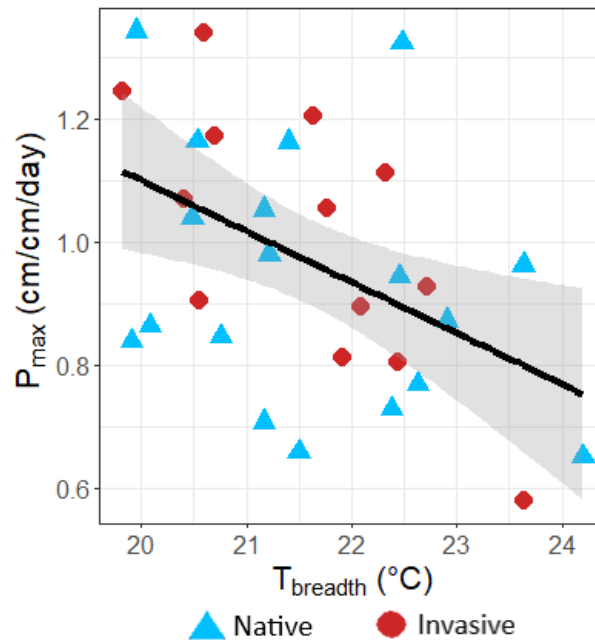
daytime temperature.

800

**Figure 4.** Specialist-generalist tradeoffs as shown by a relationship between maximum

performance ($P_{max}$) and thermal performance breadth ($T_{breadth}$) across populations of *M. guttatus*.

Black line indicates the main effect of $T_{breadth}$ ($\alpha$=0.05; Table 1) from the full model with the

interaction term removed, and grey shading shows 95% confidence interval.
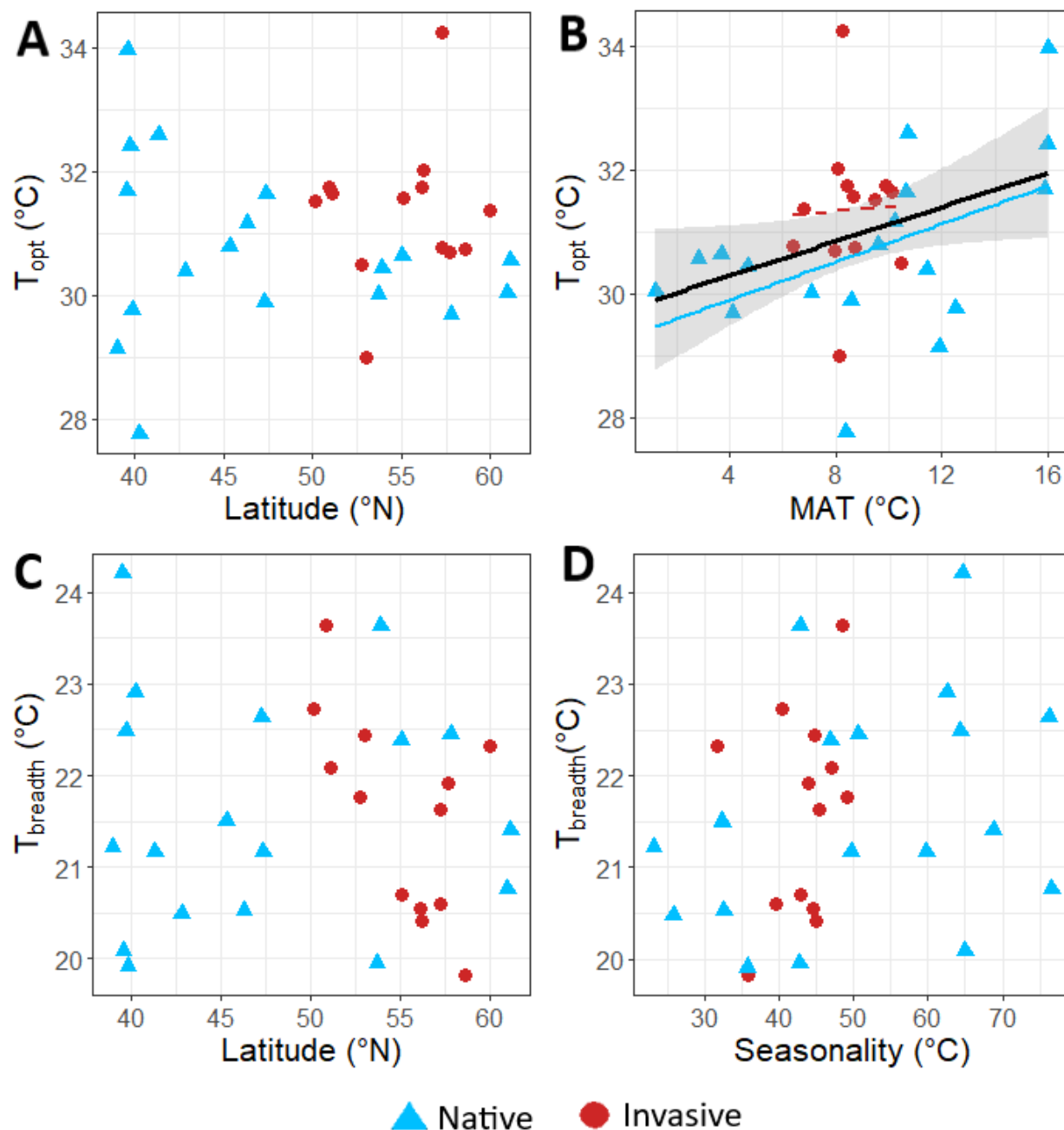
**Figure 5.** Relationships between population-level thermal optimum ($T_{opt}$) or thermal

performance breadth ($T_{breadth}$) and latitude, mean annual temperature (MAT), or temperature

seasonality. A main effect regression line (black) is shown to indicate an overall cline of MAT

($\alpha = 0.05$; Table 1) with $T_{opt}$. However, this cline was driven by significant adaptive differentiation

810    within the native range (solid blue line; $P<0.05$), rather than the invasive range (dashed red line;

811    $P>0.05$).