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SYMPOSIUM

Incorporating Population-Level Variation in Thermal Performance into Predictions of Geographic Range Shifts

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Synopsis Determining how species' geographic ranges are governed by current climates and how they will respond to rapid climatic change poses a major biological challenge. Geographic ranges are often spatially fragmented and composed of genetically differentiated populations that are locally adapted to different thermal regimes. Tradeoffs between different aspects of thermal performance, such as between tolerance to high temperature and tolerance to low temperature or between maximal performance and breadth of performance, suggest that the performance of a given population will be a subset of that of the species. Therefore, species-level projections of distribution might overestimate the species' ability to persist at any given location. However, current approaches to modeling distributions often do not consider variation among populations. Here, we estimated genetically-based differences in thermal performance curves for growth among 12 populations of the scarlet monkeyflower, *Mimulus cardinalis*, a perennial herb of western North America. We inferred the maximum relative growth rate ($RGR_{\max}$), temperature optimum (T_{opt}), and temperature breadth (T_{breadth}) for each population. We used these data to test for tradeoffs in thermal performance, generate mechanistic population-level projections of distribution under current and future climates, and examine how variation in aspects of thermal performance influences forecasts of range shifts. Populations differed significantly in $RGR_{\max}$ and had variable, but overlapping, estimates of T_{opt} and T_{breadth}. T_{opt} declined with latitude and increased with temperature of origin, consistent with tradeoffs between performances at low temperatures versus those at high temperatures. Further, T_{breadth} was negatively related to $RGR_{\max}$, as expected for a specialist-generalist tradeoff. Parameters of the thermal performance curve influenced properties of projected distributions. For both current and future climates, T_{opt} was negatively related to latitudinal position, while T_{breadth} was positively related to projected range size. The magnitude and direction of range shifts also varied with T_{opt} and T_{breadth}, but sometimes in unexpected ways. For example, the fraction of habitat remaining suitable increased with T_{opt} but decreased with T_{breadth}. Northern limits of all populations were projected to shift north, but the magnitude of shift decreased with T_{opt} and increased with T_{breadth}. Median latitude was projected to shift north for populations with high T_{breadth} and low T_{opt}, but south for populations with low T_{breadth} and high T_{opt}. Distributions inferred by integrating population-level projections did not differ from a species-level projection that ignored variation among populations. However, the species-level approach masked the potential array of divergent responses by populations that might lead to genotypic sorting within the species' range. Thermal performance tradeoffs among populations within the species' range had important, but sometimes counterintuitive, effects on projected responses to climatic change.

Introduction

There is now little doubt that rapid, anthropogenically driven climatic change is having profound biological effects (Parmesan 2006; IPCC 2007). Documented biological responses to recent climatic change include plastic shifts in traits such as phenology and behavior (Nussey et al. 2005; Parmesan 2006; Durant et al. 2007), evolutionary adaptation

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to novel conditions (Visser 2008; Gardner et al. 2009), and movement to track preferred conditions (Parmesan 2006; La Sorte and Thompson 2007). Climatically-driven range shifts are well-documented in both the distant (Davis and Shaw 2001; Hadly et al. 2009; Jackson et al. 2009) and recent (La Sorte and Thompson 2007; Moritz et al. 2008) past. However, accurately forecasting the rate and extent of future range changes remains difficult due to many uncertainties, including potential for movement in fragmented landscapes and the relative importance of abiotic and biotic determinants of distribution and abundance. Refining our estimates of potential changes in range would improve assessments of the risk of extinction for individual species (Thomas et al. 2004; Loarie et al. 2008) and the composition of future communities (Gilman et al. 2010).

Species-distribution models are central to most endeavors to forecast range shifts (Elith and Leathwick 2009; Kearney and Porter 2009; Buckley et al. 2010). Approaches to modeling distribution fall into two major categories. Correlative models seek to relate presence, presence/absence, or abundance records to environmental layers such as temperature and precipitation. The statistical association between current distribution and current climate can then be used to project distributions under future scenarios (Austin 2007; Pearman et al. 2008; Thuiller et al. 2008; Austin et al. 2009). Mechanistic models, on the other hand, are built from detailed biophysical, physiological, and/or demographic data. The relationship between environmental variables and metrics such as energy gain or number of offspring can then be projected across the landscape under current or future climates (Chuine et al. 2006; Kearney and Porter 2009; Porter and Kearney 2009; Buckley et al. 2010). These modeling approaches have complementary strengths and weaknesses and differ greatly in ease and generality. Locality records, environmental data, and software that are all freely available make correlative modeling routine for many different species. However, although correlative models often do an excellent job of modeling present distributions, they have been criticized for underestimating future potential distributions in no-analog climates (Williams and Jackson 2007). On the other hand, mechanistic models might be more appropriate for isolating the effects of the abiotic environment on organismal performance and potential distribution. However, the complexity of the models and the intensive data requirements preclude mechanistic models for most species. Forecasts from both modeling approaches often cannot include important determinants of realized distributions, such as biotic interactions (Wethey 2002) and limitations to dispersal (La Sorte and Jetz 2010). Further, most applications of both modeling approaches to date have failed to consider population-level variation within the species' range, although for different reasons. Correlative models implicitly incorporate population-level variation by pooling observations from geographically differentiated populations to create a species-level inference. Attempts to create lineage-specific or population-specific models face the difficult task of accurately assigning locality records to particular subgroups (Rissler and Apodaca 2007). Mechanistic models, on the other hand, offer a framework that could be extended readily to individual populations at least in principle (Buckley 2008), yet population-specific physiological data are usually lacking.

Consideration of variation among populations is important because geographic ranges are not monolithic entities. Instead, species' ranges are often physically fragmented and composed of distinct genetic lineages (Avise 2000; Rissler and Apodaca 2007). Populations across the species' range are often phenotypically divergent and adapted to the local environment (Hereford 2009). Local adaptation is thought to incur fitness tradeoffs, whereby local genotypes have high relative fitness in their home environment but low relative fitness in more distant environments (Hereford 2009). Fitness tradeoffs impose a cost to specialization and result in either specialists that are well-adapted at home but poorly adapted to alternative environments or generalists that are broadly adapted to a range of environments but not particularly well-adapted anywhere. Such specialist-generalist tradeoffs are hypothesized to govern many aspects of the evolution of life histories and physiological traits (Futuyma and Moreno 1988; Stearns 1992; Fry 2003). Of greatest relevance to the present study, specialist–generalist tradeoffs are central to a body of theory that is particularly pertinent to understanding organismal responses to climatic change: thermal performance curve theory (Angilletta 2009).

A thermal performance curve (TPC) (Huey and Stevenson 1979) describes the relationship between temperature and an organism's ability to function (i.e., growth, survivorship, fecundity). Theory predicts constraints on area under the TPC such that the evolution of a genotype with high maximum performance across a broad range of temperatures is not possible. Such constraints would cause populations from different thermal environments to vary in TPC parameters in predictable ways. Thermal effects on important cellular functions, such as the rate of enzymatic reactions, protein conformations and membrane stability, are widespread (Berry and Bjorkman 1980; Angilletta 2009). Biochemical adaptations that improve function at low temperatures tend to incur performance costs at high temperatures, and vice versa. Therefore, during the evolution of increased performance in novel temperatures, tradeoffs between performances at low temperatures versus those at high temperatures might be manifest in the TPC shifting along the temperature axis while maintaining constant height and breadth. For example, the evolution of increased performance at low temperature would be offset by corresponding losses of performance at high temperatures (or vice versa). This pattern of shift in the position of TPC results in an expectation that thermal optima, minima and maxima increase with mean habitat temperature and decrease with latitude. However, to fully understand variation in TPC, it is important to consider temperature fluctuations and seasonality in addition to mean temperature. A population that experiences greater fluctuations in temperatures (e.g., at high latitude) is expected to have a broader TPC than would a population in a less seasonal environment (e.g., low latitude) (Janzen 1967; Ghalambor et al. 2004). However, increases in breadth of performance are expected to cause a corresponding loss of peak performance at the thermal optimum. These specialist–generalist tradeoffs underlie the expectation that "a jack of all temperatures is a master of none" (Huey and Hertz 1984). Despite the theoretical expectation of specialist–generalist tradeoffs, empirical support is mixed at best (Angilletta 2009). Instead, there is a surprising amount of evidence for master-of-all-temperatures genotypes (e.g., Mitchell and Lampert 2000; Yamahira et al. 2007). Alternative modes of population variation that encompass master-of-all-temperatures genotypes include counter-gradient and co-gradient variation, whereby master-of-all-temperatures genotypes originate from cold or warm environments, respectively. Thus, although it is clear that populations often vary in their thermal performance (e.g., Hoffmann et al. 2002), patterns of variation might be complex, and the implications of such variation for range shifts have not been explored often.

Variation in thermal optima and breadth poses challenges to predicting species-level responses to climatic change. If populations are genetically differentiated and respond individualistically to changing climate, their thermal properties should strongly influence the predicted direction and magnitude of range shifts. Understanding how populations will respond requires an understanding of the structure of the variation in TPC among populations. For example, do populations exhibit specialist–generalist tradeoffs in thermal performance, and if so, are these tradeoffs associated with clear latitudinal or geographic trends, such as a low-to-high-latitude continuum from high-temperature specialist populations to low-temperature specialist populations? Evidence of specialist–generalist tradeoffs would suggest that population-level responses might vary depending on a population's TPC properties, even if all populations experience a similar magnitude of warming. For example, populations with broad TPCs may be better suited to deal with changing climate *in situ*, since they can maintain some function across a broader range of temperatures than can populations with narrow thermal breadth. Similarly, populations with higher thermal optima may be poised to take advantage of increased temperatures as currently thermally unsuitable habitat becomes available. Hence, population variation in TPCs may impact predicted range shifts, both in terms of shifts in the latitudinal position of the range (e.g., latitudinal maximum or median) and changes in range size between current and future climates. Finally, given local adaptation and specialist–generalist tradeoffs, the performance breadth of any given population will be a subset of the performance breadth of the entire species. If so, directional warming might push every population off of its local thermal optimum, and correlative models that implicitly assume species-level tolerance might yield overly optimistic projections (Harte et al. 2004). If so, a composite projection of range based on the summation of population-level forecasts might encompass a smaller suitable area than that based on a species-level TPC.

In this study, we examined TPC for vegetative growth and used TPC parameters to make mechanistic projections of potential distribution for the herbaceous perennial plant *Mimulus cardinalis* (Phrymaceae). Prior studies of *M. cardinalis* have demonstrated that photosynthetic carbon gain, vegetative growth, and reproduction are sensitive to temperature and that temperature is an important determinant of the species' upper-elevation distribution limit (Decker 1958; Hiesey et al. 1971; Angert and Schemske 2005; Angert 2006; Angert et al. 2008). We asked whether populations exhibited specialist–generalist tradeoffs for TPC parameters and how variation of TPC among populations affected projections of distributions. First, we examined the hypothesis that biochemical constraints give rise to specialist–generalist tradeoffs. We predicted that if there are tradeoffs between performances at low temperatures versus those at high temperatures, such that there is a continuum from high-temperature specialists to low-temperature specialists, then thermal optimum, minimum, and maximum should decline with latitude of origin and increase with temperature of origin. Alternatively, if there are tradeoffs between thermal breadth and maximum performance such that there is a continuum from low-latitude specialists to high-latitude generalists, then thermal breadth should increase with latitude of origin and decrease with both seasonality and maximum performance. Both types of tradeoff require that areas under the TPC are constant across populations. Second, we hypothesized that TPC parameters would affect population-level projections of distribution under both current and future climates in two main ways: (1) potential distribution position (i.e., northernmost and median latitude of all suitable habitat) would decrease with thermal optimum, and (2) potential distribution size (i.e., area and latitudinal extent of suitable habitat) would increase with thermal breadth. Third, we examined projected changes in suitable habitat from current to future climatic scenarios and hypothesized that variation in TPC parameters might affect forecasts of range shifts. We made the following predictions: (1) populations with higher thermal optima and higher thermal breadth would have a greater fraction of their current potential distributions remain suitable in the future, and (2) the magnitude of positional displacement and proportional changes in distribution size would decrease with thermal breadth and thermal optimum. Finally, we contrasted projections of distribution derived from a species-level TPC encompassing the breadth of all populations with projections of distribution derived by overlaying the projection for each individual population to test the hypothesis that ignoring population-level variation by using a species-level TPC will underestimate extinction risk due to future climatic change. We predicted that the species-level TPC would result in a larger projected suitable area and a smaller loss of future suitable area than the projection derived from the integration of population-level forecasts.

Methods

Study system

Mimulus cardinalis is a perennial herb that ranges from southern Oregon to northern Baja California and from coastal California east to the Sierra Nevada Mountains (Hiesey et al. 1971; Hickman 1993). It is also present in the southwestern United States and central Mexico, but these disjunct populations have partial crossing barriers with Californian populations and cluster into well-supported sister clades (Hiesey et al. 1971; Beardsley et al. 2003). In California, *M. cardinalis* occurs from sea level to 2400 m (Hickman 1993), although the elevational limits of the species decrease as latitude increases (Ramsey et al. 2003). The species occurs in moist habitat along seeps, creeks and rivers.

Collection of samples and propagation of plants

We collected seeds from 12 populations ranging from the southern Sierra Nevada Mountains in California to the Willamette Valley of Oregon in September 2008 (Table 1). This transect began just south of the center of the plant's range and ended near the northernmost recorded population (A. Angert and J. Paul, unpublished data). From each population, we collected fruits from 7–26 individuals. In April 2009, seeds were planted in 3″ pots containing Fafard Super-Fine Germinating Mix (Conrad Fafard, Inc., Agawam, MA, USA) in greenhouses at Colorado State University. Greenhouse temperatures averaged 24°C day/20°C night with a 16 h day/8 h night photoperiod. Trays were filled with ~2.5 cm water daily for subirrigation. Beginning six weeks after sowing, trays were subirrigated with ~2.5 cm N–P–K fertilizer solution once per week. In September 2009, plants were transferred to 3.8 l pots and apical meristems were pruned to encourage branching. In November 2009, when plants had grown sufficiently large to allow for cuttings to be taken weekly, we selected 7–10 of the largest, healthiest plants per population for assessment of responses of growth to temperature.

We estimated genotypic growth-response curves by creating vegetative clones of each genotype. We took cuttings from the base of the plant, choosing younger, newer shoots when possible. The cut was made diagonally across the stem, 2–4 nodes down from the meristem. Cuttings were then placed in 50 ml plastic tubes filled with water, ensuring that at least one node was below the water line. Cuttings were watered daily until being potted in 3″ pots filled with Fafard 4P Mix potting soil (Conrad Fafard, Inc., Agawam, MA, USA), 23–29 days after cutting. When potted, the rooting status of each cutting was recorded. Eight days after potting, clones were placed in one of two Percival LT-105 growth chambers (Percival Scientific, Inc., Perry, IA, USA) programmed for 16 h day/8 h nights and one of the following 7 day/night temperature regimes (°C): 15/0, 20/5, 25/10, 30/15, 35/20, 40/25, 45/30.

Table 1 Study population, latitude of origin, temperature of origin (July T_{ave}), maximum likelihood estimates of Gaussian thermal performance curve (TPC) parameters (RGR_{max}, T_{opt}, and $T_{breadth}$), and derived EcoCrop thresholds (T_{min}, T_{optmin}, T_{optmax}, and T_{max}; Hijmans et al. 2005)

	Site characteristics			TPC parameters			EcoCrop thresholds			
Population	Latitude (°N)	July T_{ave} (°C)	Seasonality (°C)	RGR_{max} ($g\,g^{-1}$ day^{-1})	T_{opt} (°C)	$T_{breadth}$ (°C)	T_{min} (°C)	T_{optmin} (°C)	T_{optmax} (°C)	T_{max} (°C)
American	39.12	18.4	16.0	0.32 (0.02)	25.68 (0.62)	6.71 (0.66)	5.30	17.77	33.58	46.05
Cosumnes	38.68	21.3	16.4	0.25 (0.03)	24.90 (0.90)	7.24 (0.99)	2.92	16.38	33.43	46.88
Feather	40.00	20.9	17.0	0.27 (0.03)	24.68 (0.74)	5.90 (0.78)	6.78	17.74	31.63	42.59
Kaweah	36.52	28.7	19.6	0.27 (0.03)	26.59 (1.00)	7.19 (1.12)	4.78	18.13	35.05	48.41
Klamath	41.66	20.5	16.4	0.27 (0.03)	24.01 (0.89)	6.90 (0.95)	3.07	15.89	32.14	44.96
Rogue	42.05	18.2	15.2	0.39 (0.04)	23.92 (0.92)	7.03 (0.94)	2.58	15.64	32.20	45.26
San Joaquin	37.36	23.0	17.7	0.30 (0.03)	25.75 (0.79)	6.00 (0.78)	7.52	18.68	32.82	43.97
Stanislaus	38.25	20.2	17.2	0.34 (0.03)	25.98 (0.57)	5.42 (0.60)	9.53	19.60	32.36	42.43
Tuolumne	37.82	21.6	16.9	0.41 (0.04)	25.78 (0.50)	4.86 (0.51)	11.02	20.06	31.51	40.54
Umpqua	43.37	19.6	14.0	0.32 (0.03)	24.74 (0.63)	6.38 (0.66)	5.39	17.24	32.25	44.09
Willamette	43.65	18.5	14.0	0.26 (0.02)	24.32 (0.77)	6.96 (0.84)	3.21	16.13	32.52	45.44
Yuba	39.39	23.6	16.6	0.28 (0.03)	24.76 (0.78)	6.59 (0.86)	4.77	17.01	32.52	44.75
Species average	–	–	–	0.30 (0.01)	25.10 (0.23)	6.59 (0.24)	5.09	17.34	32.87	45.12
Species envelope	–	–	–	–	–	–	2.58	15.64	35.05	48.41

Note. Standard errors of parameters of TPCs are given in parentheses beside each estimate.

The order of the temperature regimes was determined randomly. We replicated each temperature regime twice, once in each of two identical growth chambers, with the exception of the 40/25 regime, which was conducted twice in the same growth chamber. Up to two cuttings per plant were made each week beginning in November, resulting in a series of sequential trials that ended in April 2010. In total, up to four clones per genotype were placed in each temperature regime, resulting in 2432 clones.

Thermal performance curves

The following measurements of size were taken on each clone immediately prior to, and seven days after, being placed in the growth chamber: length of primary stem, number of secondary stems, length of an average secondary stem, number of rhizome sprouts, and length of an average rhizome sprout. From these measurements we estimated total stem length at each time of measurement as the sum of primary, secondary, and rhizome lengths. We then calculated relative growth rate (RGR) as the change in total stem length per initial total stem length per day. Prior to conducting statistical analyses, we examined the effect of rooting status on RGR. Because RGR was often negative for unrooted cuttings, we excluded these individuals from analysis ($N = 426$).

We compared the fit of several functions that could describe RGR as a function of temperature using the Akaike Information Criterion (Angilletta et al. 2006). Except for the integrations described below, we used genotypic means (mean RGR across clones of each genotype at each temperature) rather than individual clones as data lines to avoid pseudoreplication. We fit the following functions using the ‘nls’ function in R: a symmetrical Gaussian, a second-order polynomial, a higher-order polynomial that would permit asymmetry, and a generalized additive model with two degrees of freedom (Supplementary Table 1). Asymmetrical curves requiring four or more parameters were not estimable from our data. For all populations, AIC values were lowest for the symmetrical Gaussian function (Supplementary Table 1), which is the basis of all subsequent analyses reported here. The equation for the Gaussian curve is

$$RGR = ae^{-0.5(\frac{T-b}{c})^2},$$

where a is maximum RGR (RGR_{max}), b is the temperature optimum for RGR (T_{opt}), and c is one half of the breadth of the curve, from T_{opt} to the inflection point ($T_{breadth}$). We calculated the temperature minimum (T_{min}) and maximum (T_{max}) for growth as the temperatures at which RGR was 1% of RGR_{max}.

Tests for generalist-specialist tradeoffs

To test for population shifts in TPC position (high-temperature versus low-temperature specialists), we regressed T_{opt}, T_{min} and T_{max} on latitude and on average temperature for July. We use latitude in addition to a temperature metric because latitude might serve as a synthetic proxy for additional aspects of variation in temperature across our sampling gradient. To test for population shifts in TPC breadth (low-latitude specialists versus high-latitude generalists), we regressed $T_{breadth}$ on latitude and on seasonality of temperature (i.e., maximum temperature of the warmest month minus minimum temperature of the coolest month) and we also tested for a negative correlation between $T_{breadth}$ and RGR_{max}. We obtained climatic variables for each population from the ClimateWNA database, which uses digital elevation models to continuously downscale climatic variables and has been shown to perform well in topographically complex landscapes (Wang et al. 2006). We chose the month of July to represent the peak of the growing season, matching the growth phase we simulated in growth chambers. However, climatic variables were highly correlated and different months yielded qualitatively similar results. To test for counter-gradient and co-gradient variation, we regressed RGR_{max} and area under the TPC on latitude and on average temperature for July.

Specialist–generalist tradeoffs assume fixed areas under TPCs. We tested for differences in area under the curve among populations in two ways. First, we bootstrapped genotypic mean data lines with replacement to generate 95% confidence intervals around each estimate of population area (Supplementary Fig. 1). Second, we fit TPCs to clone data to calculate the area under the curve for each genotype. We then tested for differences among populations using analysis of variance where data lines were estimates of genotypic area.

Locality records

We used known occurrences of *M. cardinalis* along with randomly generated absences (“pseudoabsences”) to aid in selection of parameters and in comparisons of the models, described in detail below. In 2005, we compiled locality records for *M. cardinalis* from the following online databases: Jepson Interchange, Southwest Environmental Information Network (SEINet), Oregon Flora, Burke Museum, Intermountain Herbarium, Missouri Botanical Garden, and Conabio. In 2009, we obtained records from the San Diego Natural History Museum and re-compiled locality records from SEInet, and in 2010 we re-compiled locality records from Jepson Interchange. We supplemented these records with our own field observations from 1998–2010 from central Oregon through southern California, yielding a total of ~600 non-duplicated records (Fig. 1). In Diva-GIS, version 5.2 (Hijmans et al. 2005) we created an equal number of pseudoabsences randomly occupying the minimum convex-range polygon of *M. cardinalis* buffered by ~100 km. We then used these presences and pseudoabsences to compute the area under the receiver operating characteristic curve (AUC) to evaluate performance of the models (Fielding and Bell 1997).

Mechanistic distribution models

We used the EcoCrop module in Diva-GIS, version 5.2 (Hijmans et al. 2005) to generate mechanistic distribution projections. The following EcoCrop parameters were derived from TPC estimates: minimum temperature for growth (T_{min}), maximum temperature for growth (T_{max}), minimum temperature for optimal growth (T_{optmin}), and maximum temperature for optimal growth (T_{optmax}) (Table 1). We defined possible T_{min} and T_{max} as average monthly temperatures where predicted RGR was either 1 or 5% of RGR_{max}. We chose 1% based on higher AUC values (Supplementary Table 2). We defined possible T_{optmin} and T_{optmax} as average monthly temperatures where predicted RGR was either 50 or 80% of RGR_{max}. We chose 50% based on higher AUC values (Supplementary Table 2). We calculated T_{min}, T_{max}, T_{optmin}, and T_{optmax} separately for each population. We also created two different species-level models. The first, which we refer to as the species-average model, was based on parameters from a Gaussian curve fit to RGR data pooled across populations. The second, which we refer to as the species-envelope model, was created by combining the lowest T_{min} and T_{optmin} (from the Rogue population) and the highest T_{max} and T_{optmax} (from the Kaweah population; Table 1), creating a species-level model that encompassed the extremes of population-level variation. The following additional EcoCrop parameters were invariant in our models: killing temperature (KT), minimum rainfall for growth (R_{min}), maximum rainfall for growth (R_{max}), minimum rainfall for optimum growth (R_{optmin}), maximum rainfall for optimal growth (R_{optmax}), minimum growing period (G_{min}), and maximum growing period in days (G_{max}). In initial trials we varied KT from 0 to −8°C and chose −4°C, the value with the greatest AUC (Supplementary Table 2). To select values of rainfall parameters,

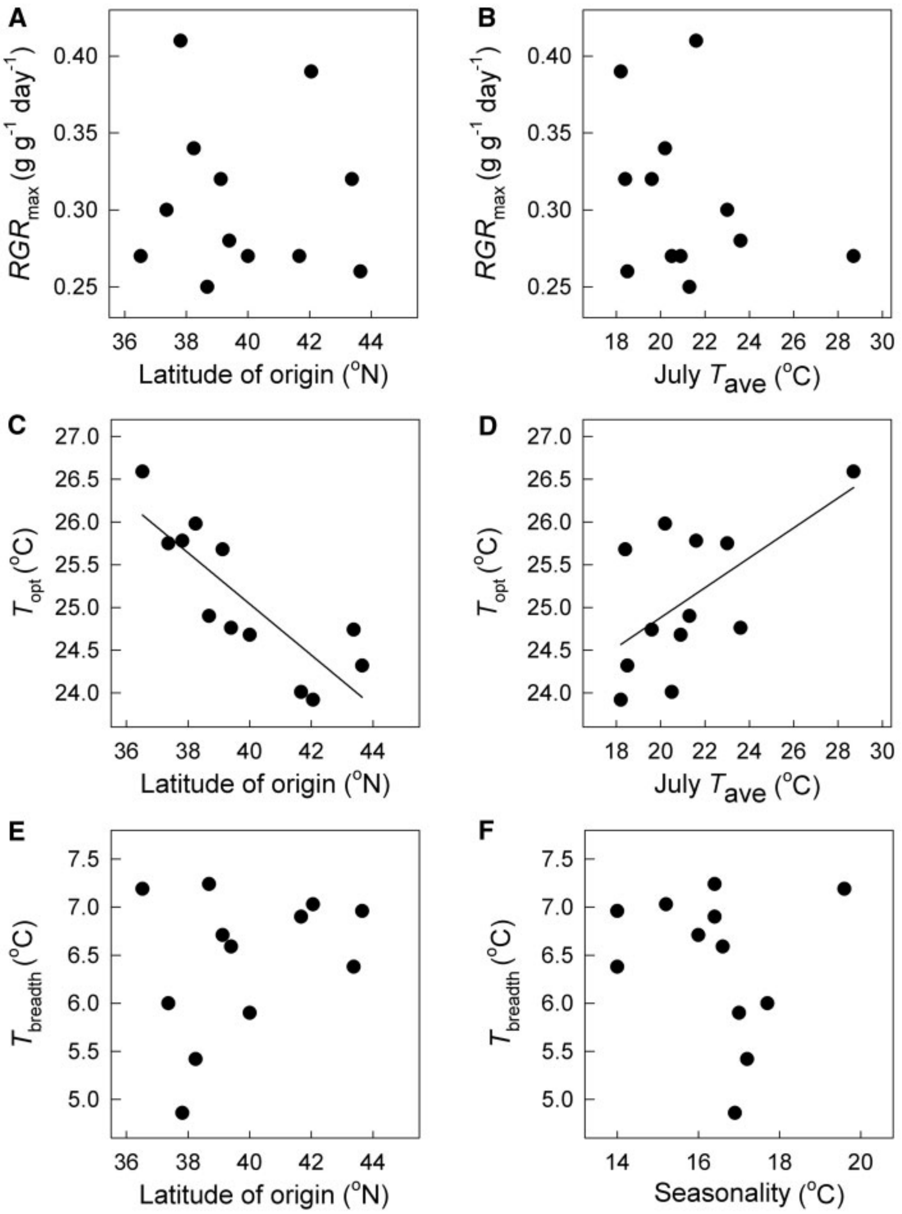

Fig. 1 Maximum likelihood estimates of parameters of thermal performance curves versus latitude of origin and temperature at site of origin. (**A**) Performance maximum (RGR_{max}; g g^{-1} day^{-1}) versus latitude (°N). (**B**) RGR_{max} versus July mean temperature (T_{ave}; °C). (**C**) Temperature optimum (T_{opt}; °C) versus latitude. (**D**) T_{opt} versus July T_{ave}. (**E**) Temperature breadth ($T_{breadth}$; °C) versus latitude. (**F**). $T_{breadth}$ versus temperature seasonality (°C).

we extracted data on annual rainfall from locality records using the ClimateWNA database (Wang et al. 2006). We defined R_{min} and R_{max} as the minimum and maximum observed annual rainfall: 105 and 2276 mm/year, respectively. We defined possible R_{optmin} and R_{optmax} as values where annual rainfall is 50, 80 or 90% of the maximum observed total and chose 90% based on higher AUC values, resulting in $R_{optmin} = 526$ and $R_{optmax} = 911$ mm/year (Supplementary Table 2). We estimated G_{min} to be 65 days based on census dates (A. Angert, unpublished data) at a montane reciprocal transplant garden where *M. cardinalis* was unable to complete its life cycle before killing frosts (Angert and Schemske 2005; Angert et al. 2008). We estimated G_{max} to be 300 days because the species is reported to be occasionally winter-active in coastal habitats (Hiesey et al. 1971).

We ran EcoCrop under both current and future climates. Spatial layers for current and future average minimum and maximum monthly temperatures and total monthly precipitation were obtained at a 30 s resolution from the Worldclim database (version 1.4, release 3; www.worldclim.org; Hijmans et al. 2005). Future climate-layers are available for any combination of three climate models (CCCMA, HADCM3, and CSIRO), two emissions scenarios (a2a and b2a), and three future years (2020, 2050, and 2080). For simplicity, we present results using the CCCMA model and a2a scenario projected to 2080. Projections using alternative models, scenarios, and dates yielded qualitatively similar patterns of variation among populations. We clipped all climate-layers to encompass British Columbia (Canada); Washington, Oregon, and California (United States); and Baja California and Baja California Sur (Mexico) to prevent models from predicting occurrence across major biogeographic barriers such as the Great Basin. We converted EcoCrop outputs ranging from 0 (lowest suitability) to 100 (highest suitability) into binary presence/absence maps based on a threshold of 60, such that grid cells with suitability less than 60 were excluded from projections. For each re-classified EcoCrop output, we extracted the minimum, maximum, median and midpoint latitude (L_{min}, L_{max}, L_{med}, and L_{mid}, respectively) and elevation of all grid cells predicted to be suitable, the area (A) predicted to be suitable, and the latitudinal extent (E) of suitable habitat (maximum–minimum latitude) using the package "raster" (Hijmans and van Etten 2011) in R, version 10.1 (R Core Development Team 2009). Analyses using different thresholds yielded qualitatively similar patterns. Because all populations had projected suitable habitat at the southern tip of the Baja Peninsula, L_{min} was invariant and we focused our subsequent analyses on L_{max} and L_{med}. We calculated several metrics to compare current and future projections for each population: the fraction of currently suitable grid cells that was projected to remain suitable under future climates (A_{rem}), change in range position ($\Delta L_{max} = L_{max,\ future} - L_{max,\ current}$ and $\Delta L_{med} = L_{med,\ future} - L_{med,\ current}$), and proportional change in range size [$\Delta A = (A_{future} - A_{current})/A_{current}$ and $\Delta E = (E_{future} - E_{current})/E_{current}$]. To examine the effect of variation in thermal optimum on projections of range, we regressed L_{max}, L_{med}, ΔL_{max}, $\Delta L_{med,}$ and A_{rem} on T_{opt}. To examine the effect of variation in thermal breadth on projections of range, we regressed A, E, ΔA, ΔE, and A_{rem} on $T_{breadth}$. We also created a concatenated species-level projection by overlaying each population's projection and comparing this projection to that generated by the species-average and species-envelope models.

Results

Population variation in TPCs

Populations differed in estimated RGR_{max} (range 0.25–0.41 g g^{-1} day^{-1}; Table 1, Supplementary Fig. 2). Maximum likelihood estimates of T_{opt} ranged from 23.92°C to 26.59°C, while estimates of $T_{breadth}$ ranged from 4.86°C to 7.24°C (Table 1; Supplementary Fig. 2). While differences in RGR_{max} among populations are statistically significant, the standard errors of T_{opt} and $T_{breadth}$ overlap among populations (Table 1). As expected, the average TPC had intermediate parameter estimates, resulting in EcoCrop thresholds that did not encompass population extremes of thermal tolerance (Table 1). T_{opt} and $T_{breadth}$ varied independently across populations ($r = -0.37$, $P = 0.24$), hence we use them as independent measures of variation in TPC in the analyses that follow.

Tests for specialist–generalist tradeoffs

RGR_{max} and area under the curve were unrelated to latitude or temperature of origin (Table 2; Fig. 1A, B). T_{opt} declined with latitude (Fig. 1C) and increased with temperature (Fig. 1D; Table 2). T_{min} also declined with latitude, albeit weakly, while T_{max} was unrelated to latitude (Table 2). Neither T_{min} nor T_{max} were related to habitat temperature (Table 2). $T_{breadth}$ was unrelated to latitude or temperature seasonality (Table 2; Fig. 1E, F). However, $T_{breadth}$ was negatively correlated with RGR_{max} ($r = -0.57$, $P = 0.055$ with all populations;

Table 2 Summary of linear regression analyses of parameters from thermal performance curves versus latitude and temperature of origin

Response	Predictor	B	R^2	P
RGR_{max}	Latitude	−0.00	0.00	0.86
RGR_{max}	July T_{ave}	−0.01	0.09	0.35
AUC	Latitude	0.06	0.05	0.50
AUC	July T_{ave}	−0.07	0.09	0.35
T_{opt}	Latitude	**−0.30**	**0.70**	**0.0007**
T_{opt}	July T_{ave}	**−0.17**	**0.36**	**0.038**
T_{min}	Latitude	−0.59	0.27	0.081
T_{min}	July T_{ave}	0.12	0.02	0.68
T_{max}	Latitude	0.00	0.00	0.99
T_{max}	July T_{ave}	0.23	0.10	0.32
$T_{breadth}$	Latitude	0.10	0.10	0.32
$T_{breadth}$	Seasonality	−0.08	0.02	0.63

Note. Values given in bold are significant at $P < 0.05$.

$r = -0.83$, $P = 0.0014$ with one outlier removed; Fig. 2). Area under the curve did not differ significantly among populations ($F_{11,78} = 0.76$, $P = 0.67$).

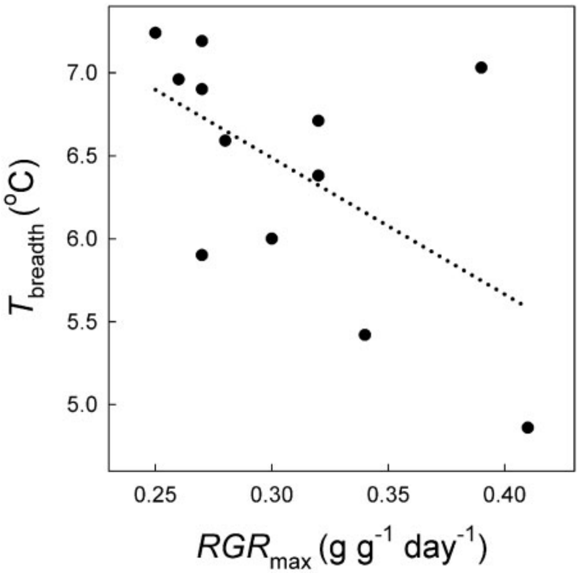

Fig. 2 Specialist-generalist tradeoff between thermal breadth ($T_{breadth}$; °C) and maximum performance (RGR_{max}; g g^{-1} day^{-1}). Dotted line depicts marginally significant tradeoff between $T_{breadth}$ and RGR_{max} ($P < 0.10$); when the outlier is removed, relationship becomes statistically significant ($P < 0.01$).

Effects of TPC parameters on projections of range

Variation in T_{opt} and $T_{breadth}$ among populations influenced current and future population-level projections of potential distribution (Table 3; Fig. 3; Supplementary Fig. 3). The latitudinal position of projected distributions was negatively related to population T_{opt} using either current or future climate-layers (Table 4; Fig. 4A, B). The amount of projected suitable area was positively related to population $T_{breadth}$ using either current or future climate-layers (Table 4; Fig. 4C and D).

Effects of TPC parameters on forecasts of range shifts

Projected changes from current to future climates were related to T_{opt} and $T_{breadth}$. The fraction of currently suitable habitat projected to remain suitable, A_{rem}, was positively related to T_{opt} (Table 4; Fig. 5A) and negatively related to $T_{breadth}$ (Table 4; Fig. 6A). Although northern limits were projected to shift northward for all populations (all $\Delta L_{max} > 0$; Table 3), the magnitude of northward shift declined with T_{opt} (Table 4; Fig. 5B) and increased with $T_{breadth}$ (Table 4; Fig. 6B). Shifts in L_{med} were also negatively related to T_{opt} and positively related to $T_{breadth}$ (Table 4), but ΔL_{med} varied in both magnitude and direction (Table 3). Median latitudes for populations with the lowest T_{opt} and highest

Table 3 Summary metrics from EcoCrop mechanistic distribution projections (Hijmans et al. 2005) for population-level and species-level models under current and future climatic regimes: northernmost suitable grid cell (L_{max}), median latitude of all suitable grid cells (L_{med}), number of suitable grid cells (A), and latitudinal extent of suitable grid cells (E)

	Current				Future				Change				
Population	L_{max}	L_{med}	A	E	L_{max}	L_{med}	A	E	ΔL_{max}	ΔL_{med}	A_{rem}	$\Delta A/A$	$\Delta E/E$
American	43.30	37.58	150,893	20.43	51.26	36.35	277,825	28.38	7.96	−1.23	0.76	0.84	0.39
Cosumnes	48.00	37.68	194,275	25.12	57.78	37.75	400,674	34.90	9.79	0.07	0.73	1.06	0.39
Feather	40.82	37.67	140,574	17.94	51.00	36.15	252,500	28.12	10.18	−1.53	0.77	0.80	0.57
Kaweah	43.30	37.60	148,018	20.43	51.26	36.33	276,185	28.38	7.96	−1.27	0.75	0.87	0.39
Klamath	48.23	37.79	205,445	25.35	57.79	38.15	424,172	34.91	9.56	0.36	0.73	1.06	0.38
Rogue	48.82	37.95	218,202	25.94	57.82	38.67	451,443	34.94	9.00	0.73	0.72	1.07	0.35
San Joaquin	40.75	37.99	115,276	17.87	46.24	35.99	236,587	23.36	5.49	−2.00	0.77	1.05	0.31
Stanislaus	40.68	38.49	70,945	17.80	44.25	35.97	215,258	21.37	3.57	−2.52	0.79	2.03	0.20
Tuolumne	40.66	38.65	48,727	17.78	43.72	36.09	199,332	20.84	3.06	−2.57	0.84	3.09	0.17
Umpqua	43.33	37.53	159,157	20.45	51.32	36.53	293,770	28.44	7.99	−1.00	0.75	0.85	0.39
Willamette	43.40	37.52	166,926	20.53	51.45	36.77	319,011	28.58	8.05	−0.75	0.75	0.91	0.39
Yuba	48.05	37.69	197,067	25.17	57.78	37.85	406,253	34.90	9.73	0.17	0.74	1.06	0.39
Population overlay	43.25	37.94	115,000	20.37	51.14	36.28	207,001	28.26	7.89	−1.66	0.72	0.80	0.39
Species envelope	43.25	37.94	115,000	20.37	51.14	36.28	207,001	28.26	7.89	−1.66	0.72	0.80	0.39
Species average	40.66	38.48	75,352	17.78	45.72	35.92	175,308	22.84	5.06	−2.56	0.40	1.33	0.28

Note. Changes in projected distribution from current to future time periods are given as the change in L_{max}, the change in L_{med}, the fraction of currently suitable habitat projected to remain suitable (A_{rem}), the proportional change in A ($\Delta A/A$), and the proportional change in E ($\Delta E/E$).

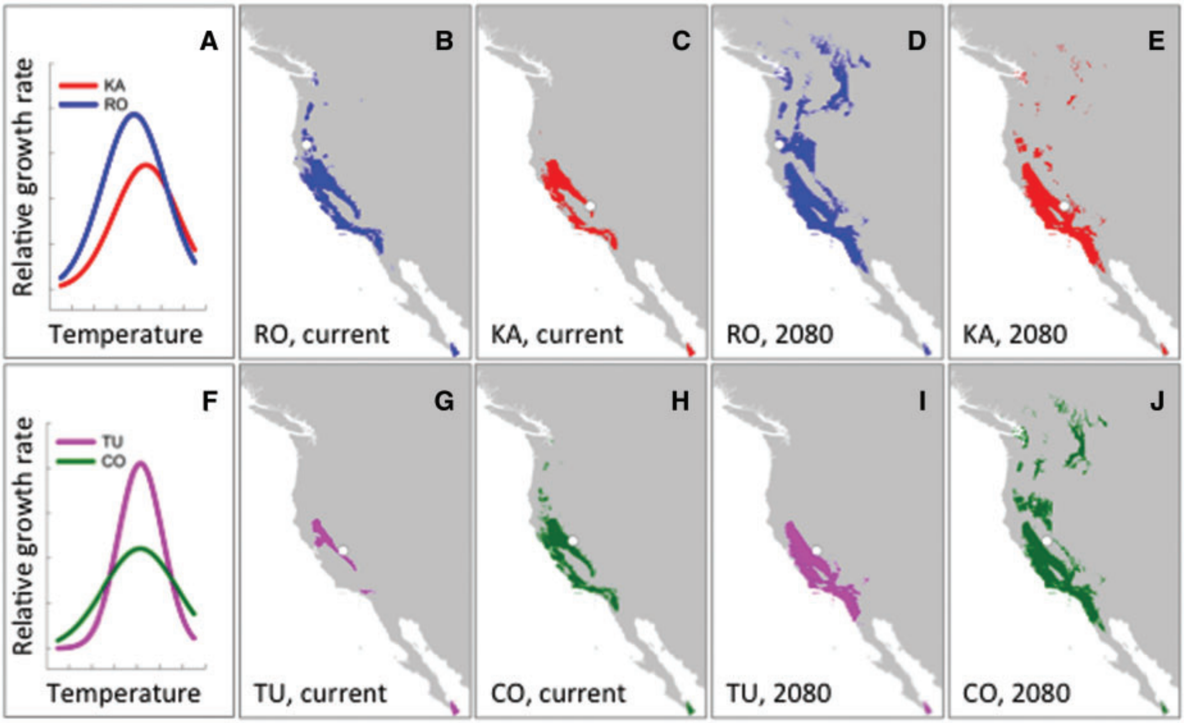

Fig. 3 Projections of potential distribution for representative populations. (**A**) Projections for populations with low (blue) versus high (red) T_{opt} under current (**B** and **C**) and future (**D** and **E**) climates. (**F**) For populations with low (pink) versus high (green) T_{breadth}, projections under current (**G** and **H**) and future (**I** and **J**) climates. White dot indicates location of each population.

Table 4 Summary of linear regression analyses of distribution projection metrics versus parameters of thermal performance curves

Response	Predictor	*B*	R^2	*P*
Current L_{max}	T_{opt}	**−2.70**	**0.49**	**0.011**
Future L_{max}	T_{opt}	**−4.54**	**0.54**	**0.0062**
Current L_{med}	T_{opt}	0.14	0.10	0.32
Future L_{med}	T_{opt}	**−0.89**	**0.62**	**0.0023**
ΔL_{max}	T_{opt}	**−1.85**	**0.42**	**0.022**
ΔL_{med}	T_{opt}	**−1.03**	**0.61**	**0.0026**
A_{rem}	T_{opt}	**0.02**	**0.41**	**0.025**
ΔA / A	T_{opt}	0.26	0.11	0.30
ΔE / E	T_{opt}	−0.04	0.16	0.19
Current A	T_{breadth}	**62,984**	**0.81**	**<0.0001**
Future A	T_{breadth}	**91,334**	**0.62**	**0.0024**
Current E	T_{breadth}	**3.44**	**0.62**	**0.0025**
Future E	T_{breadth}	**6.01**	**0.74**	**0.0003**
ΔL_{max}	T_{breadth}	**2.57**	**0.64**	**0.0018**
ΔL_{med}	T_{breadth}	**1.24**	**0.70**	**0.0007**
A_{rem}	T_{breadth}	**−0.04**	**0.86**	**<0.0001**
ΔA / A	T_{breadth}	**−0.69**	**0.59**	**0.0036**
ΔE / E	T_{breadth}	0.07	0.28	0.075

Note. Values given in boldface are significant at $P < 0.05$.

T_{breadth} were projected to shift northward, whereas median latitudes for populations with the highest T_{opt} and lowest T_{breadth} were projected to shift southward (Figs. 5C and 6C). For all populations, projected distributions under future climates were larger than projected distributions under current climates (Fig. 4C, D). Proportional changes in range size were unrelated to variation in T_{opt} (Table 4; Fig. 5D, E) and weakly related to variation in T_{breadth} (Table 4). Proportional change in number of suitable grid cells declined with T_{breadth}, although this relationship was driven entirely by two populations with low T_{breadth} (Fig. 6D). Proportional change in extent was not significantly related to T_{breadth} (Fig. 6E).

Effects of species-level versus population-level TPCs on range projections and on forecasts of range shifts

Contrary to our prediction, the projection for the species-envelope model was identical to that obtained by overlaying population projections under either current or future climates (Table 3). The projection for the species-average model was similar to projections for populations of intermediate T_{opt} and T_{breadth} under both current and future climatic regimes, but it resulted in a substantially lower

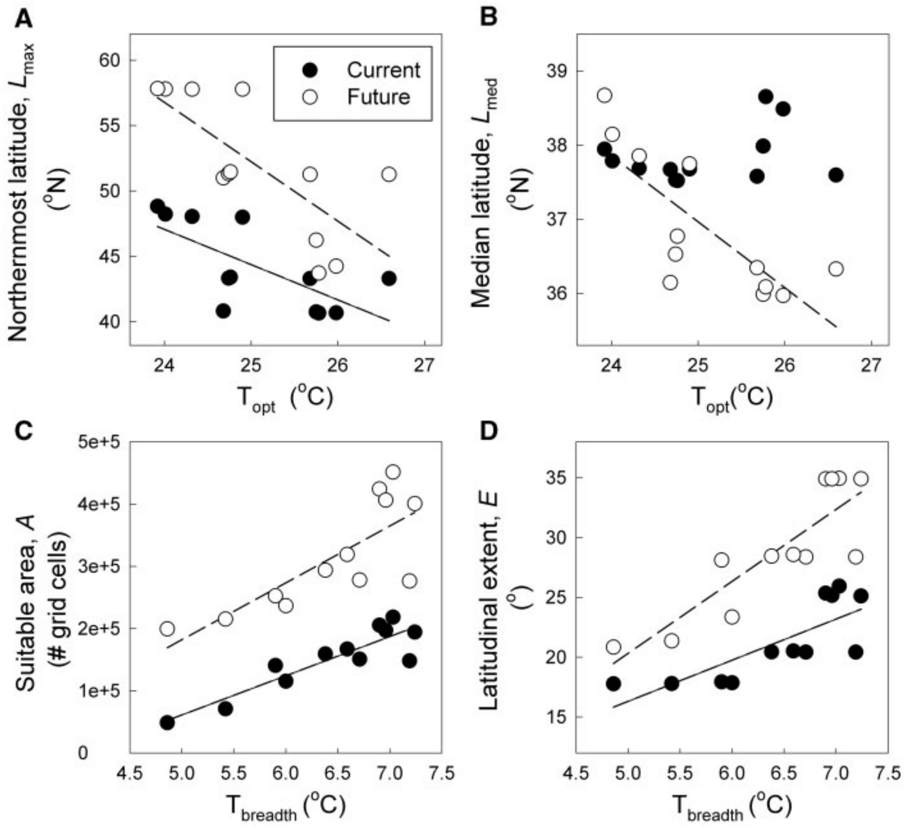

Fig. 4 The effect of variation in the parameters of thermal performance curves on population-level projected distributions under current (filled symbols) and future (open symbols) climates. (**A**) Northernmost suitable latitude (L_{max}; °N) versus temperature optimum (T_{opt}; °C). (**B**) Median suitable latitude (L_{med}; °N) versus T_{opt}. (**C**) Suitable area (*A*; hash grid cells) versus thermal breadth ($T_{breadth}$; °C). (**D**) Latitudinal extent (*E*; °N) versus $T_{breadth}$. Statistically significant regressions ($P < 0.05$) are shown as solid (current climate) or dashed (future climate) lines.

fraction of suitable habitat remaining (Table 3). Both species-level models predicted a net northward shift of L_{max} and a southward shift of L_{med} (Table 3). The species-average model predicted a relatively small change in L_{max} but a relatively large change in L_{med}. The species-envelope model predicted intermediate changes in L_{max} and L_{med}.

Discussion

In this study, we evaluated whether populations exhibit specialist–generalist tradeoffs for TPC parameters and then determined how variation in TPC among populations affected projections of current and future distributions. To do so, we estimated genetically based differences in growth rate as a function of temperature among 12 populations of *M. cardinalis* and then used these growth curves to generate mechanistic projections of potential distribution for each population. Many additional factors are likely to influence species' realized distributions, including limitations to dispersal, abiotic variables other than temperature, and various sorts of biotic interactions. The projections presented in this article are not intended to fully represent the determinants of the species' present distribution, nor are they likely to be accurate forecasts of the species' future distribution. The projections are valuable for illustrating how genetic differentiation among populations influences estimates of potential geographic ranges and the effect that variation might have on species' responses to climatic change. First, our results partially supported the hypothesis that there are thermal tradeoffs between performances at low temperatures versus those at high temperatures and between breadth of performance and maximal performance. Second, our results supported the hypothesis that T_{opt} and $T_{breadth}$ influence the position and size of current and future potential distributions. Third, our results demonstrated that $T_{breadth}$ and T_{opt} affect the magnitude of projected future range shifts, but not always in the expected manner.

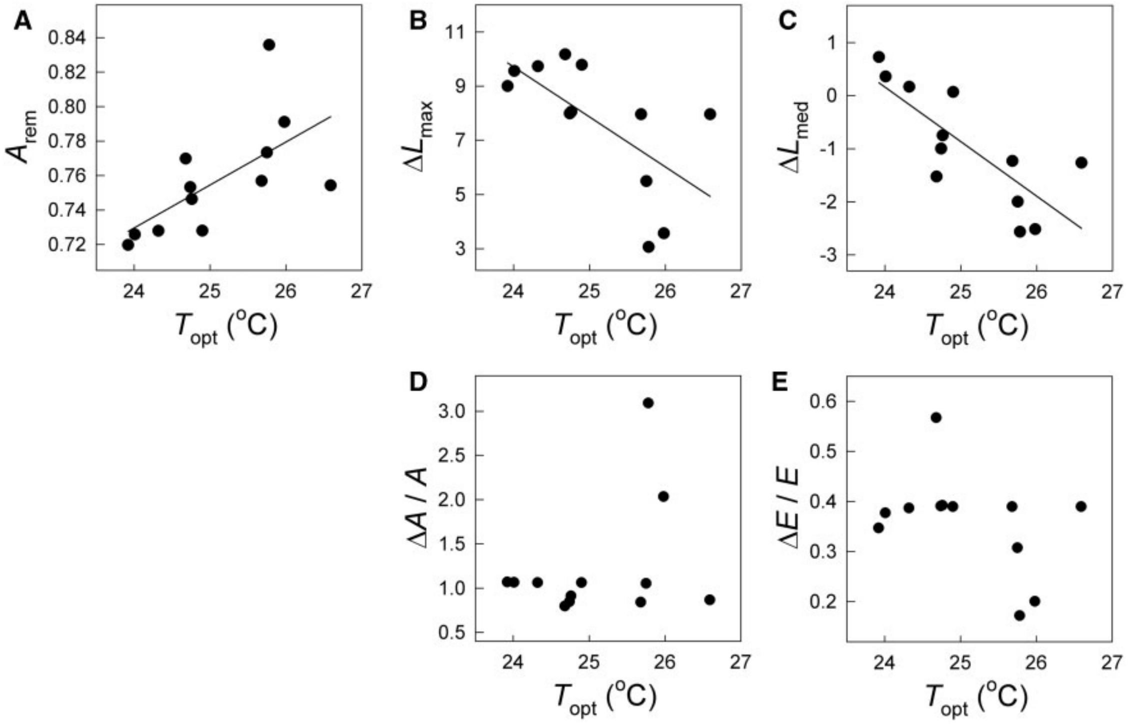

Fig. 5 The effect of thermal optimum (T_{opt}; °C) on range shift calculations: (**A**) the fraction of currently suitable habitat projected to remain suitable in future climates (A_{rem}); (**B**) the change in the latitude of the northernmost suitable grid cell (ΔL_{max}); (**C**) the change in latitude of the median suitable grid cell (ΔL_{med}); (**D**) the proportional change in the number of suitable grid cells ($\Delta A/A$); and (**E**) the proportional change in the latitudinal extent of suitable habitat ($\Delta E/E$). Statistically significant regressions ($P < 0.05$) are shown as solid lines.

Finally, we found no evidence for the hypothesis that ignoring population-level variation by using a species-level TPC will result in an underestimate of risk of extinction due to future climatic change. Below we discuss each of these results in turn, along with their implications for understanding organismal responses to climatic change.

Our study provides partial evidence for specialist-generalist tradeoffs for thermal performance curves. As predicted, T_{opt} and T_{min} declined with latitude and T_{opt} increased with temperature of origin, supporting the idea that there is a continuum from high-temperature specialists to low-temperature specialists. However, T_{min} and T_{max} were not related to temperature of origin and T_{max} did not decline with latitude, suggesting additional important variation among populations in breadth of performance. We did detect a tradeoff between performance breadth and peak performance, and areas under the TPC did not vary among populations, consistent with a tradeoff between generalization and specialization. We did not, however, detect a positive relationship between $T_{breadth}$ and latitude or a negative relationship between $T_{breadth}$ and seasonality of temperature, thus providing no support for the idea that specialist populations originate from less variable environments at lower latitudes than do generalist populations. In general, the relationship between population-specific TPC parameters and local environmental temperatures was either nonexistent (T_{min}, T_{max}, $T_{breadth}$) or surprisingly weak (T_{opt}). It is possible that our climatic data do not accurately reflect microclimates experienced in the riparian habitat occupied by the study species, where factors like drainage of cold air can cause substantial temperature inversions over small spatial scales. However, the ClimateWNA database where we obtained site-specific climatic data has been shown to perform well in topographically complex landscapes (Wang et al. 2006). It is also possible that observed phenotypes are maladapted to local conditions. For example, while we detected a significant trend of T_{opt} declining with latitude, the gradient was much shallower than the concordant change in local environmental temperature ($b = -0.31$ versus -0.90). In a companion study to the present one, Paul et al. (2011) estimated gene flow among 11 of the populations represented here. They found that the magnitude of gene flow into a given population (weighted by environmental temperature, such that gene flow from donor populations that are more

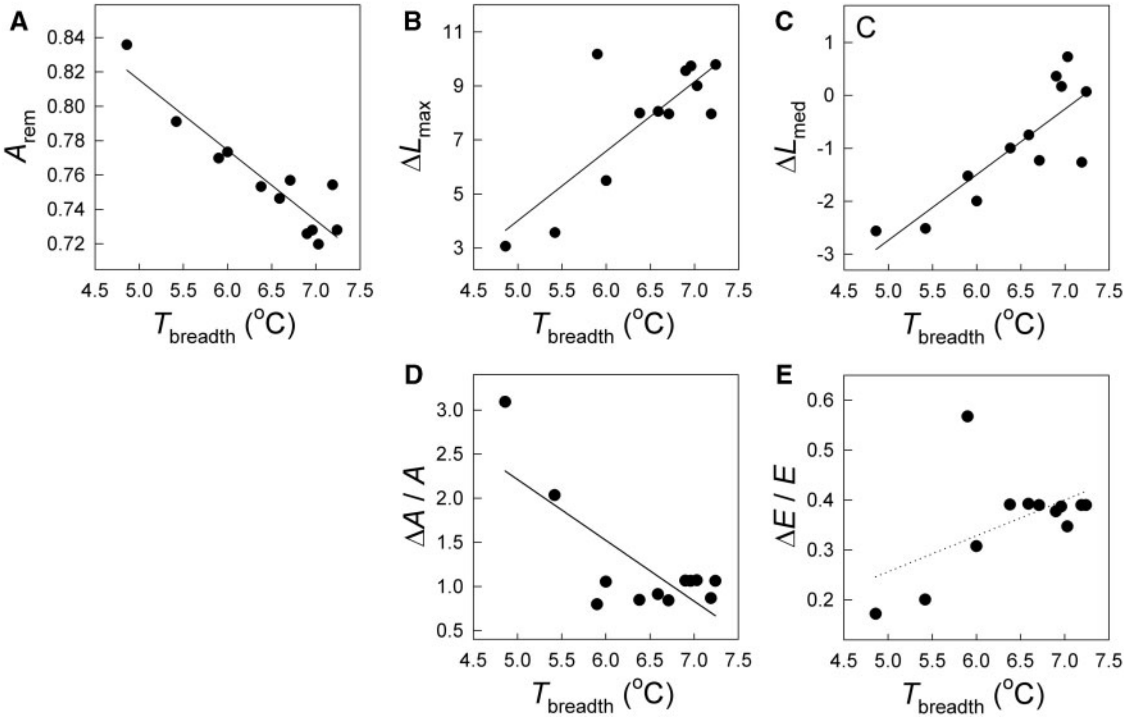

Fig. 6 The effect of thermal breadth ($T_{breadth}$; °C) on calculations of shifts in range: (**A**) the fraction of currently suitable habitat projected to remain suitable under future climates (A_{rem}); (**B**) the change in the latitude of the northernmost suitable grid cell (ΔL_{max}); (**C**) the change in latitude of the median suitable grid cell (ΔL_{med}); (**D**) the proportional change in the number of suitable grid cells ($\Delta A/A$); and (**E**) the proportional change in the latitudinal extent of suitable habitat ($\Delta E/E$). Statistically significant regressions ($P < 0.05$) are shown as solid lines, and marginally significant regressions ($P < 0.10$) are shown as dashed lines.

climatically different from the recipient population are given greater weight) significantly explained the mismatch between temperature optima for growth and local environmental temperature. These results suggest that gene flow may be pushing some populations off of their local phenotypic optima, resulting in varying degrees of maladaptation to local conditions. Under such a scenario, expected specialist–generalist tradeoffs between populations may not be fully realized, as population-level growth curves include some genotypes that are not adapted to local temperature. Although gene flow may push populations off of current local optima, it might also aid future persistence by increasing genetic variation within populations and providing alleles that are pre-adapted to future climates.

The evidence we find for specialist–generalist tradeoffs is at odds with many other empirical tests for such tradeoffs. Previous studies focusing on growth as a measure of performance have often documented patterns of counter-gradient (e.g., Yamahira et al. 2007) or cogradient (e.g., Mitchell and Lampert 2000) variation by which "master-of-all-temperatures" genotypes are possible (reviewed by Angilletta 2009). Other studies testing for specialist-generalist tradeoffs have found no support for a tradeoff between performance breadth and maximal performance (e.g., Huey and Hertz 1984; Palaima and Spitze 2004), although a few studies have provided evidence for such tradeoffs (Bennett et al. 1992; Gilchrist 1996; Cooper et al. 2001; Izem and Kingsolver 2005; Latimer et al. 2011). A recent study of latitudinal variation in thermal performance among populations of the intertidal copepod *Tigriopus californicus* in western North America also revealed partial support for both types of specialist–generalist tradeoffs by including measures of fitness when different population-pairs were allowed to compete (Willett 2010). In that study, low-latitude populations with highest survival under high temperature stress had lower competitive fitness than did high-latitude populations at moderate temperatures, but they had higher competitive fitness than did high-latitude populations at high temperatures (Willett 2010). The inclusion of a more realistic competitive environment highlights the importance of environmental context when detecting tradeoffs. It might be particularly difficult to detect tradeoffs under permissive laboratory conditions. Also, a focus on only certain dimensions of an organisms' life history may obscure tradeoffs that arise with other, unexamined components of fitness, such as tradeoffs among growth, survival and fecundity.

We found strong support for the hypothesis that TPC parameters influence the position and size of current and future potential distributions. As predicted, the latitudinal position of current and future projections decreased with T_{opt}. Also consistent with our predictions, distribution size in current and future climates increased with T_{breadth}. Together, these results demonstrate biological realism in our models of current and future potential distributions for each population. Nevertheless, projections of current and future suitable habitat could be refined in several ways. First, incorporating population-specific killing temperatures into our distribution models could reveal further variation among population-level projections. Second, more detailed parameters for rainfall and snowpack for riparian zones could improve performance of the model. Third, incorporating variation in phenology among populations into our models could also reveal differences among population projections and improve performance of the model. Finally, we lack information about thermal acclimation, which might expand the temperature range over which optimal growth occurs (Atkin and Tjoelker 2003) and is likely to be important for organismal responses to climatic change (Chown et al. 2010).

Our results supported some of the predictions stemming from the hypothesis that TPC parameters influence range-shift forecasts. Populations with a higher T_{opt} had a greater fraction of their current potential distributions predicted to remain suitable in the future, consistent with our predictions. Furthermore, the northward displacement of the northern margin decreased with T_{opt}. Together, these results suggest that populations with lower thermal optima may be at a higher risk of extinction due to climatic change than are populations with higher thermal optima. Inconsistent with the above conclusion, populations with higher thermal optima were projected to have the greatest southward displacement of the latitudinal median. The results for T_{breadth} were also somewhat mixed. Proportional changes in the number of suitable grid cells decreased weakly with T_{breadth}, consistent with our prediction that populations with greater breadth of performance would exhibit smaller changes in distribution. However, the fraction of current potential distributions remaining suitable in the future decreased strongly with T_{breadth}, and the magnitude of latitudinal displacement increased with T_{breadth}. These results suggest that populations with higher T_{breadth} may undergo greater distributional changes due to climatic change, which is the opposite of what we predicted. This counter-intuitive result may be because populations with greater breadth were projected to expand in multiple directions; projected distributions of these populations expanded northward and eastward at the northern periphery of the range as well as southward and westward from the center of the range. Populations with lower breadth were mainly projected to expand southward and westward from the center of the range while showing very little northward expansion. Implications of variation in TPC for range shifts can be framed in terms of the magnitude of warming relative to the thermal optimum and thermal breadth of the organism. This framework has been applied to assess the risk of extinction for temperate versus tropical species, yielding the counterintuitive result that tropical organisms with narrow TPC may be relatively more vulnerable than temperate organisms, despite a greater magnitude of projected warming at high latitudes (Deutsch et al. 2008). In contrast, our results suggest that wider thermal breadth does not necessarily buffer populations from risk of extinction associated with climatic change.

The amount of suitable habitat was projected to increase in future climates for all populations, though by different amounts. Some projections also showed somewhat unexpected shifts southward. At least some of the projected shifts to the south might be explained by the physical geography of the study region, which includes the high-elevation areas of the southern Sierra Nevada Mountains and the Transverse Ranges. Consistent with this idea, the mean and maximum elevation of suitable habitat shifted to higher elevations in the future climatic scenario. However, populations with the greatest projected southward shifts did not also exhibit the greatest projected upward shifts, suggesting that additional factors are involved in these counterintuitive southward shifts. Recent studies have shown that species may track their climatic niches in different directions depending on the relative changes in different limiting factors (Tingley et al. 2009; Crimmins et al. 2010). Our results suggest that the growth physiology of *M. cardinalis* may be well suited to warmer climates of the future, but we caution that many factors (e.g., fragmentation and destruction of habitat, alteration of stream flow, limitations to dispersal, and biotic interactions) are likely to prevent these populations from expanding into all projected suitable habitat. It is unclear whether these projected range expansions are due to an increase in the spatial extent of currently suitable habitat, or whether future climates might foster a niche shift into warmer, wetter areas that are physiologically suitable but not presently available on the landscape (Williams and Jackson 2007). Projected expansions of range are interesting in light of the biogeography of *M. cardinalis* and other closely related *Mimulus* species in the Erythranthe clade, many of which presently occur in the deserts of Mexico and southwestern United States. Beardsley et al. (2003) hypothesized that the clade originated in the Sierra Nevada Mountains and that a common ancestor migrated out of the Sierras before diversifying into distinct endemic desert species. A migration across what is presently vastly unsuitable habitat may have been facilitated by historically warmer and wetter climates that permitted broader distributions.

Our results do not support the predictions arising from the hypothesis that ignoring population-level variation in TPCs will result in an underestimate of the risk of extinction due to future climatic change. The species-envelope model did not result in a larger projected suitable area or a smaller loss of future suitable area than did the projection of range derived from the integration of population-level forecasts. The lack of difference in future area between the species-envelope model and integrated population projections likely is due to high overlap among population-level TPCs. However, the species-average model, which did not reflect population extremes of thermal tolerance, resulted in a substantially smaller future suitable area and a smaller fraction of current habitat remaining suitable compared to the integrated population projections. This finding suggests that averaging data from multiple distinct populations into a single mechanistic model can yield misleading projections. Despite lack of support for our initial predictions, having only one estimate of net direction of change from a single species-level curve obscured the array of potential responses by different populations. Populations were projected to undergo net displacement in different directions, which could cause substantial reassortment of genotypes within the confines of the species' range. Such heterogeneity is not revealed by species-level models, even though the net result, in terms of area occupied by the species' range, is the same. In the present study, we did not build the species-level TPCs from all of the populations across the range of *M. cardinalis*, and it is possible that the subset of populations we used does not encompass the extremes of $T_{\max}$ and $T_{\min}$ of the species. Thus, there is potentially even more variation among population-level TPCs than we have documented in the present study, and perhaps capturing this variation would reveal differences in projections of range and in forecasts of shifts in range between species-level and population-level TPCs.

In summary, we show that specialist–generalist tradeoffs in TPC parameters among populations leads to variation in current and future projections of suitable habitat, and to differences in forecasts of range shifts, revealing limitations of most species-distribution models that do not account for genetic variation across the species' range (Yates et al. 2010). We are aware of only a few previous studies that have incorporated genetic and/or phenotypic variation among populations into projections of species' ranges. In a study that incorporated geographic variation among populations of a North American lizard species to assess current and future range projections, Buckley (2008) found that variation in morphology and life history among populations resulted in differences in projections of distribution. Kolbe et al. (2010) documented latitudinal variation in thermal sensitivity of hopping speed and lower thermal tolerance (estimated as critical thermal minimum) among populations of invasive cane toad in Australia. Consistent with our results, they also showed that variation in TPCs among populations resulted in differences in population-level projections of distribution. Apart from phenotypic differences in TPCs among populations as documented by Kolbe et al. (2010), we also detected genotypic variation in TPCs among populations. In the present study, this genetic variation is the result of historical evolutionary processes that resulted in current genetic differentiation among populations. However, additive genetic variation within populations also should influence future evolutionary potential to respond to novel selection pressures. We are now examining the evolutionary potential for future adaptation in populations of *M. cardinalis* to improve our understanding of variation among populations in their abilities to persist in the face of rapid climatic change.

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Supplementary Data

Supplementary Data are available at *ICB* online.

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