



SYMPOSIUM

Thermal Performance Curves Reveal Variation in the Seasonal Niche of a Short-Lived Annual

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Synopsis An organism's environment can vary over spatial and temporal scales. Seasonal variation is an important but overlooked source of environmental variation that often shapes the ranges of organisms. The seasonal niche is a description of the spatiotemporal range of an organism resulting from spatial variation in seasonal conditions. In this study, I describe the seasonal niche of a short-lived annual plant, and variation within the species in seasonal niche breadth. I construct a seasonal species distribution model (SDM) for the species, and using thermal performance curves (TPCs), construct mechanistic SDMs (MSDMs) for individual genotypes. I quantify the correlation between the suitability scores generated in the SDM and the predicted dry weight generated by the MSDMs for each genotype, to estimate variation in seasonal niche breadth among genotypes. Thus, the parameters of TPCs reflect generalist/specialist strategies. I detected significant relationships between thermal performance breadth and maximum predicted fitness and significant correlations between optimal growth temperature and thermal performance breadth. There were large positive correlations between predictions of the SDM and MSDMs based on growth within individual genotypes. The variation in these correlations suggests variation in the degree of specialization. Genotypes with the broadest TPCs had the largest correlations between their MSDMs and the SDM, suggesting that they were generalists. The results show that correlative and MSDMs make similar predictions over the seasonal range, and that ecological specialization can vary dramatically within species.

Introduction

Environments vary over space and time. How organisms adapt to this variation depends on the scale of variation relative to the dispersal distance and generation time of the organism (Bradshaw 1965; Via and Lande 1985; Tufto 2015). Large scale spatial variation forces organisms to adapt to local ecological conditions (Hereford 2009). Small scale spatial variation occurs well within the dispersal distance of an organism, resulting in variation in performance at scales so small that selection cannot respond (e.g., Stratton 1995). Like spatial variation, temporal variation exists over large and small scales. Large scale temporal variation includes processes such as inter-annual variation and climate change. Small scale temporal variation includes diurnal variation, and seasonality. Seasonality can drive adaptation to specific seasons or select for generalist

strategies conferring adaptation to multiple seasons (Gilchrist 1995), and the seasonal niche is the realized range of spatiotemporal conditions in which a species can complete its life-cycle.

The seasonal niche includes the total spatial and temporal environment where a species is expected to grow and reproduce. For many organisms, seasonal variation determines when they reproduce as well as where they can live. If seasonal periods favorable for growth and reproduction are too short, the organism will not be able to sustain a population (Chaine 2010). In this way, the seasonal niche is a comprehensive realized niche concept, that not only describes where an organism can live, but when it is expected to express specific life stages (Hereford et al. 2017). Given the importance of seasonal variation on species distributions, it is surprising that few studies consider the role of seasonal patterns in

models of species' distribution and realized niche (but see [Nielsen et al. 2003](#); [Hereford et al. 2017](#)). An understanding of the influence of seasonal patterns can reveal not only where a species is expected to grow, but where and when alternate phenological stages are expected to occur. The influence of seasonal patterns on species distributions results because environments may vary such that growth during the wrong season can be lethal. Thus, seasonal variation exposes organisms to environmental extremes. Variation in the phenology and distribution of species reflects their physiological tolerance and performance ([Donohue et al. 2010](#)). Thus, the realized niche of the species should include not only where it is found, but when it completes its life cycle.

The seasonal niche is not only a property of the species. Variation within species in ecological specialization and physiological performance suggests variation in niche breadth within species ([Angilletta 2009](#); [Hereford 2009](#)). For example, variation within species in thermal performance ([Angert et al. 2011](#); [Latimer et al. 2011](#); [Richter-Boix et al. 2015](#)) suggests that the seasonal niche should vary within species as a result of variation in temperature. Differences among genotypes in performance suggest that the species-level niche may be an emergent property of variation in seasonal niche among genotypes. For example, the species-level niche may be large as a result of many individuals with similarly large thermal performance ranges and thus similar seasonal niches. Alternatively, the species-level niche may be large as a result of many specialist individuals with performance ranges encompassing small subsets of the total species-level range. In the former example, the individual-level seasonal niches are similar to the overall species-level niches, and in the second example, the individual niches are narrower and less similar to the species-level niche.

The degree to which an individual genotype's niche matches the species-level niche is a measure of specialization. Definitions of specialization are typically based on comparisons between groups, where specialists are able to utilize relatively fewer environments or resources than generalists ([Futuyma and Moreno 1988](#); [Forister et al. 2012](#)). The species-level realized niche can be estimated using species distribution models (SDMs). These models relate the distribution of species in space to environmental factors, to predict the distribution of the species ([Elith and Leathwick 2009](#)). Thus, the species-level realized niche is based on variation from a collection of individuals of the same species, and variation within the species is pooled to estimate a total species niche. Given the expectation that the

species-level niche is composed of the aggregate niches of genotypes that make up the species, specialist and generalist genotypes can be determined by their similarity to the species-level niche.

The methods employed in SDMs to estimate the distribution of species cannot be used to estimate the realized niche of an individual because the individual is located in a single population. Mechanistic species distribution modeling (MSDM) can be used to estimate the realized niche of an individual. In an MSDM, the distribution of the species is predicted by estimating the relationship between performance and environmental factors ([Kearney and Porter 2009](#)). Both SDMs and MSDMs predict the distribution of species, and both methods can predict the seasonal niche. The predictions from SDMs and MSDM should be correlated ([Rougier et al. 2015](#); [Shabani et al. 2016](#)). The suitability of the environment is predicted in an SDM and a measure of performance or fitness is predicted in an MSDM. Points in space and time that are more suitable should be those that lead to higher fitness. Thus, there is an expected correlation between suitability and fitness. The MSDM of an individual with a seasonal niche that mirrors the species-level niche should make similar predictions as the SDM of the species as a whole. The MSDM of an individual with an extreme phenotype or that has a very limited physiological performance range should be dissimilar to the species-level SDM.

Here I estimate the correlations between the results of a seasonal SDM and seasonal MSDMs of individuals of a short-lived annual plant species. The goals of this study are first to test the hypothesis that genotypes that make up the species are thermal specialists on specific conditions or generalists that largely mirror the species-level niche. Quantifying these relationships will shed light on whether the species is made up of a collection of specialists adapted to different conditions or generalists that mirror the species niche. I estimate the correlation between the predictions of the species-level SDM and the predictions of the genotype's MSDMs. The second goal is to determine the aspects of thermal performance that are correlated with a specialist or generalist genotype. Here I quantify genetic correlations between parameters of thermal performance curves (TPCs), and I estimate relationships between TPC parameters and the degree of specialization. Quantifying the actual realized niche is difficult and requires multivariate methods to disentangle the influence of correlated variables. In this study, I use seasonal range as a proxy for the realized niche (e.g. [Lee-Yaw et al. 2016](#)), where range is the

distribution in space and time of suitability and fitness. This approach is general not only to short-lived organisms. Specific life-stages of long-lived organisms, such as migrations of birds or diapause in insects can be modeled with these methods as well.

Materials and methods

Mollugo verticillata is a short-lived annual, native to South and Central America (Kearney and Peebles 1964). It is considered naturalized to California (Baldwin et al. 2012). There is strong evidence that the species is highly selfing given the small flower size (1.5–2.5 mm diameter) and lack of pollination in the field (J. Hereford, personal observation). In California, *M. verticillata* is found in moist soil along the shores of lakes and reservoirs. Germination in these environments does not occur in response to rainfall, but in response to warm temperatures and soil desiccation along the shores. In other parts of its range, germination appears to coincide with warm weather rains (J. Hereford, personal observation). In this experiment, I sampled genotypes from six source populations, spanning the range of climate and seasonality within California.

The species level seasonal niche within California can be estimated by understanding where and when *M. verticillata* is likely to be growing and reproducing. I used an SDM to predict the species level niche and determine the factors that limit the distribution of *M. verticillata*. The construction of the seasonal SDM has been previously published (Hereford et al. 2017). Briefly, an SDM was constructed for *M. verticillata* that incorporated variation in seasonal patterns at the locations that specimens were collected. While conventional SDMs focus on how variation in average conditions predicts the distribution of a species, the seasonal SDM utilizes climate data from the time and place that each observed collection was made to predict not only where a species is likely to be found, but also when the species is predicted to be growing and reproducing at that location. The climate data in the seasonal SDM were collected from the Basin Characterization Model (BCM) described in Flint et al. (2013). This model produces 270 m gridded maps of California and surrounding watersheds for each month and year from 1896 to the present. The seasonal SDM for *M. verticillata* showed that mean monthly temperature was responsible for 78.8% of the variance in suitability of habitat and season (Hereford et al. 2017). Thus, temperature is the major determinant of the presence of *M. verticillata* across the landscape and seasons.

To estimate TPCs, I grew six successive cohorts of the same maternal families (genotypes) throughout the spring, summer, and fall. Individuals of these genotypes were repeatedly planted approximately every 6 weeks from May to November of 2014. I grew plants from 20 genotypes of each of the six populations in a screen house. The screen house is a controlled growth facility that allows ambient temperature and nearly ambient sunlight. I planted two seeds per pot, and planted three such pots in each of three randomized blocks for each maternal family (genotype). The first seed to germinate in a pot was allowed to grow, and the second seed to germinate was removed. If both seeds germinated on the same day the smallest was removed. Plantings where no seeds germinated were not included in any analyses, and differences in sample size among genotypes result from variation in germination. Plants were watered daily such that soil never completely dried out, to simulate the conditions of the lakeshore habitat. The temperature from the time of germination to senescence was recorded at 5 min intervals for all seeds that germinated. The final dry weight at senescence was used as the measure of fitness, as the correlation between flower number and final dry weight is 0.95 (J. Hereford, unpublished data). Plants begin flowering within 10 days of germination, and no plant was ever weighed without flower buds present. Therefore, all plants were reproductive. The TPC for each genotype was estimated by the non-linear regression of growth temperature on final dry-weight (Huey and Stevenson 1979). Members of each genotype could have germinated during warm or cool periods, therefore each genotype experienced a wide range of growth temperatures. This range allowed individuals of each genotype to be grown in cool or warm times of the growing season.

I followed the methods in Angilletta (2006) to construct TPCs for each genotype. The maximum number of seedlings that could germinate from each genotype across the entire experiment was 18 (3 in each of 6 experiments). This limited the forms of TPCs that could be fit to the data. I used two formulas to estimate four parameters to characterize the relationship between growth temperature and dry weight, the Quadratic and the Gaussian. Following Angilletta (2006), I fit Quadratic and Gaussian models to the relationship between dry weight and mean growth temperature for each genotype. I chose the model with the lower AIC score to estimate the TPC. The relationships between dry weight and mean growth temperature can be used to predict the fitness of a plant growing at any temperature. In 41 out of 120 genotypes, no non-linear regression

would converge on estimates of curve parameters as a result of small sample sizes within those genotypes. These genotypes were not included in any analyses.

The MSDMs were generated using temperature maps and the TPCs to predict fitness across the seasons. I used the relationships between dry weight and average growth temperature from the TPCs, to predict what the dry weight of an individual plant would be at any location during any month. Mean monthly temperature maps were generated from the BCM maps. I obtained 12 maps of average temperature, one for each month. Mean monthly temperature was calculated as the mean of the minimum and maximum temperature of each month. This calculation of the average was used because only minimum and maximum temperature monthly rasters are available. These means were calculated for each month in the period from 1981 to 2010. Therefore, the maps present average conditions during each month in the period from 1981 to 2010. The predicted fitness of each genotype at each point in the 270 m grid during each month can be estimated from the TPC and the temperature values from the monthly temperature maps. This procedure generates an MSDM for each genotype.

The SDM and the MSDMs are independent estimates of the realized niche. The species-level SDM is constructed from species collection records using several climatic variables to predict the suitability of the environment for *M. verticillata* (Hereford et al. 2017). The MSDMs are based on TPCs where fitness of a genotype is predicted exclusively by variation in temperature. The SDM is taken from a large collection of multiple individuals throughout California. Temperature explains the majority of the variation in the SDM, and with the exception of soil depth, the remainder of the variation is explained by factors that have a functional relationship with temperature. The SDM characterizes the species-level realized niche in California (Elith and Leathwick 2009). The MSDMs show the predicted fitness of individual genotypes, and thus represent the realized niche of genotypes within the species. Genotypes with wider niches will encompass more of the species-level niche than genotypes with narrower niches. One measure of the size of a genotype's niche is the correlation between its predicted performance and the species-level suitability at that same time and place. Genotypes with niches that more closely match the species-level niche will have greater correlations between species-level suitability and predicted dry weight. It is possible for genotypes to have large niches that do not overlap with the species-level niche, resulting in

small or negative correlations between suitability and predicted dry weight. The major assumption of this analysis is that genotype-level niches are not larger than the species-level niche. This assumption is reasonable because it is improbable that genotypes would have realized niches larger than the species-level niche. To quantify how well a genotype's niche breadth matched the species-level niche, I calculated the correlation between the predicted dry-weight (from TPCs) of an individual of that genotype at a site and the predicted suitability of the site for the species, this correlation was calculated for all 12 months. To calculate the correlation between suitability and predicted dry weight I first chose 1050 random locations from the 270 m grid of California and surrounding watersheds. I then quantified the correlation between predicted suitability of the locations and the predicted dry weight of plants at those locations and months. Large positive correlations indicate more overlap between the species-level and genotype-level niches.

A second goal of this study is to determine the aspects of thermal performance that are most associated with variation in the realized niche. Here I compare the parameters generated from TPCs with the correlations between the SDM and MSDMs. To perform this analysis, the TPCs must be of the same general shape. I chose the Gaussian as the template shape, as 55 out of the 79 TPCs that could be estimated had lower AIC scores under a Gaussian model. In addition, the quadratic results in biologically impossible values of dry weight at low and high temperatures. Therefore, all comparisons of TPC parameters are based on the following Gaussian function from Angilletta (2006).

$$W = z_{\max} e^{[-0.5((T - T_o)/T_b)^2]},$$

where T is the growth temperature, T_o is the optimum growth temperature, $z_{\max}$ is the maximum dry weight, and T_b is the thermal performance breadth. These parameters are the same as T , b , k , and c , in Angilletta (2006), respectively.

To demonstrate the methods, Fig. 1 illustrates how the MSDMs and individual correlations between genotype-level MSDM and the overall SDM are calculated. The three genotypes with the smallest correlations between their MSDM and the SDM in July and the three genotypes with the largest correlations are presented. The nonlinear regressions in the first column show the TPCs for each of the six genotypes. The maps show the predicted biomass resulting from the TPC and the raster of mean temperature. The third column shows the correlations

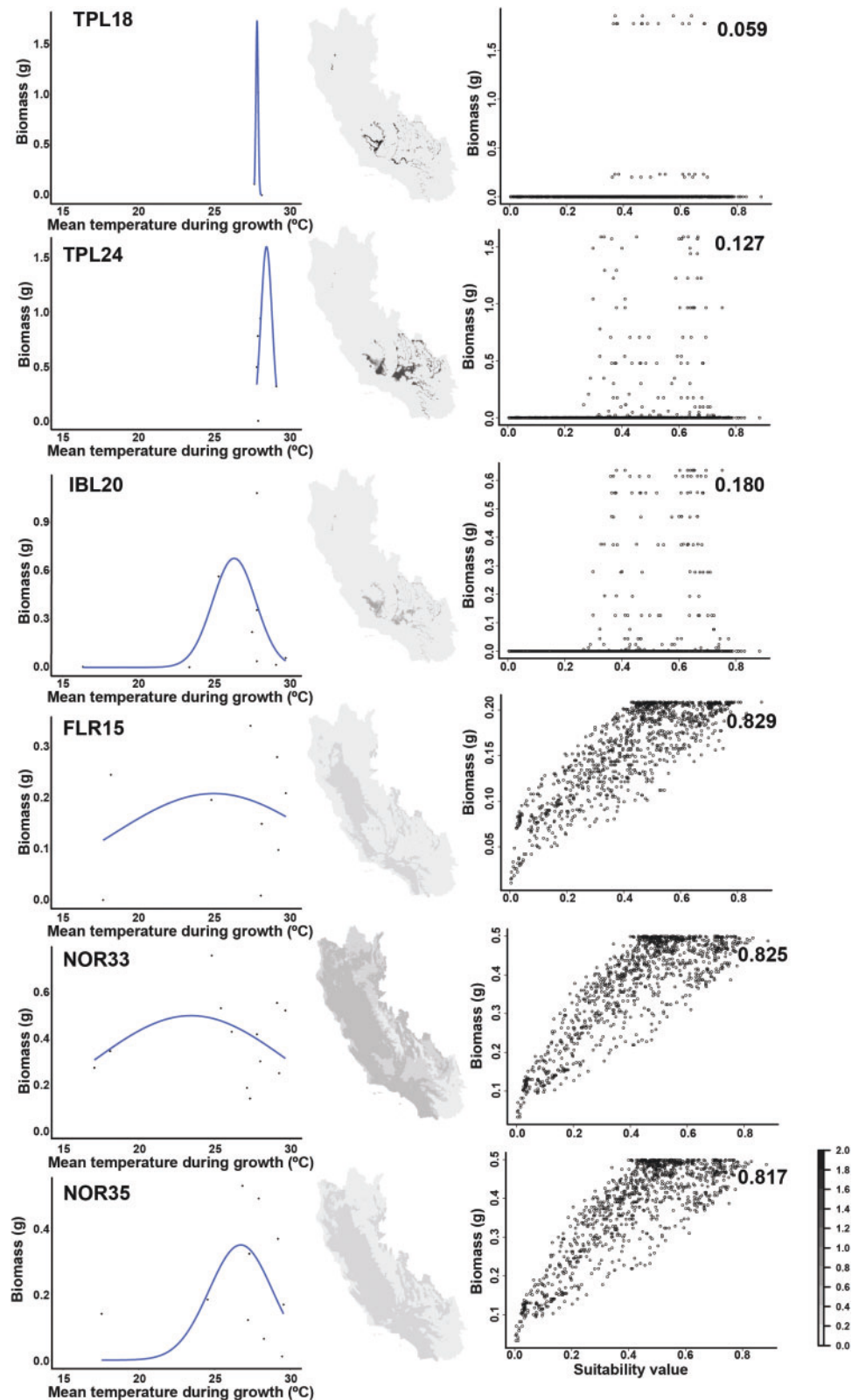


Fig. 1 Six examples showing calculation of the mechanistic species distribution models (MSDMs) for the three genotypes with the smallest and greatest correlations between the SDM and MSDMs. The first column shows the thermal performance curves with each point showing the biomass (final dry weight) and average growth temperature of each plant (replicate of a genotype). The second column shows maps of predicted dry weight across the study area in July. The third column shows the relationship between the overall SDM and the genotype's MSDM for July. The correlation coefficient is shown on the upper right of each plot.

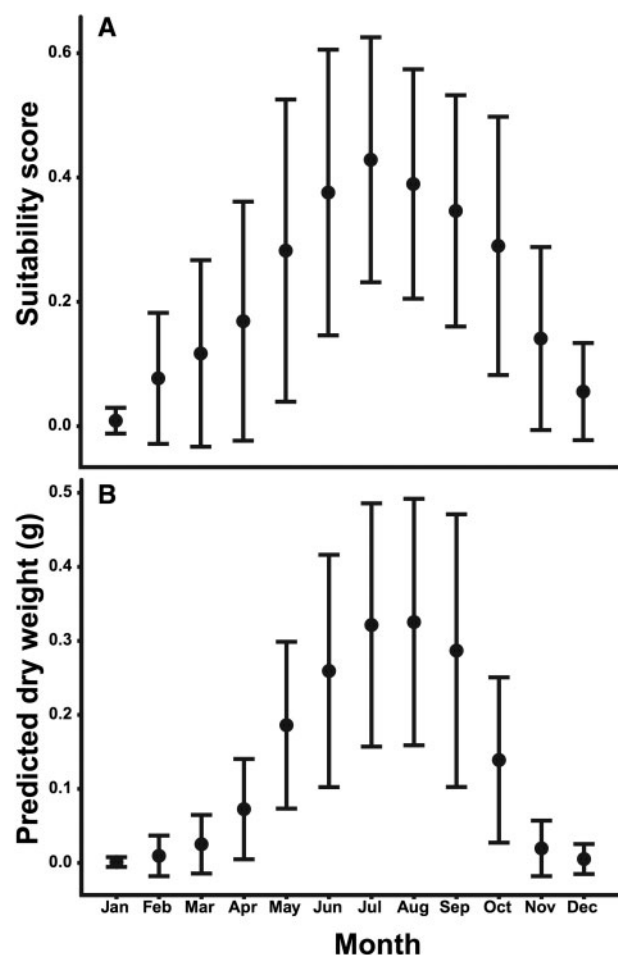


Fig. 2 Plots of mean monthly suitability of the 1050 points generated from the SDM (A), and mean predicted dry weight for the same points across the 79 genotypes (B). Points indicate means and bars are standard deviations. The standard deviations for plot A are based on variation among the 1050 points for each month ($n = 1050$ points). The standard deviations for plot B are calculated from the average predicted dry weight of each genotype at the 1050 points ($n = 79$ genotypes).

between the genotype's MSDM and the SDM for July. All analyses were performed in R version 3.3.

Results

Predicted suitability and predicted dry weight changed monthly, with both measures predicting peak growth in summer months. For the 1050 randomly chosen points, the seasonal SDM predicted monthly changes in median suitability, with highest suitability from April to October. Predicted dry weight among the 79 genotypes followed the same pattern (Fig. 2). June was the month with peak predicted dry weight and suitability. Variation in suitability and predicted dry weight also followed a seasonal pattern. There was little variation in both measures from January to March, and variation

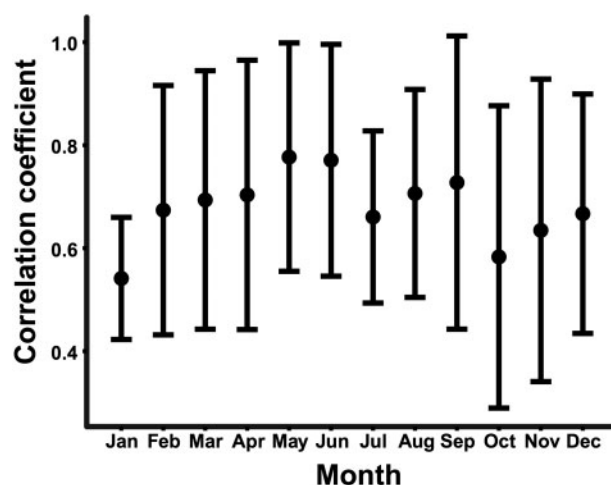


Fig. 3 Median correlation coefficients for each month between the predictions of the SDM and the MSDMs of all genotypes. Bars represent one standard deviation of 79 genotype-level correlations.

increased from April to October. A nonlinear regression of suitability on temperature for the 1050 points was performed for July. This regression estimated an optimum temperature value of 24.26, similar to the value for the data pooled across all genotypes (24.21). The estimated variance from that regression was 5.74, larger than the value of 3.63 for all genotypes. The plot of the relationship between suitability and temperature for July is shown in Supplementary Fig. S1.

The suitabilities generated by the SDM and the predicted dry weight generated by the MSDM were correlated, and the magnitude of the correlations changed with season. The distribution of correlations was not normal for any month and the distributions tended to be left skewed. Therefore, median values of the correlations are presented. Correlations between SDM and MSDM were greatest in May and June (Fig. 3). The median correlations in all months were greater than 0.54, and the first quartile was greater than 0.23 in all months. Each correlation was based on the same 1050 spatial points. Thus, any correlations larger than 0.07 are significant. There was ample variation among correlations across genotypes for most months. January was the exception, where there was little variation among genotypes in SDM/MSDM correlation (Fig. 3).

The TPCs for each genotype revealed relationships between thermal performance breadth and maximum performance. There was a significant negative correlation ($r = -0.51$, $P < 0.0001$) between the thermal performance breadth and maximum performance, where greater thermal performance breadth was significantly correlated with decreased

maximum performance (Fig. 4A). There was a significant correlation ($r = -0.27$, $P = 0.015$) between optimum growth temperature and thermal performance breadth (Fig. 4B), but no significant correlation ($r = 0.18$, $P = 0.11$) between optimum growth temperature and maximum performance (Fig. 4C).

The relationship between parameters of the TPCs and the SDM/MSDM correlation was significant in all months for all parameters. The correlations between thermal performance breadth and SDM/MSDM relationship were positive and significant in all months (Table 1). The correlation between maximum performance and SDM/MSDM relationship was negative in all months, as was the correlation between optimum growth temperature and SDM/MSDM relationship (Table 1).

Discussion

Genotypes with larger SDM/MSDM correlations were those with larger thermal performance breadth, lower optimum temperature, and lower predicted maximum performance. Taken together the relationships between TPC parameters and the relationship between the TPC parameters and the SDM/MSDM correlations suggest that generalist genotypes reflect the overall species realized niche, and that being a generalist comes at a cost to performance at high temperatures. These patterns did not differ among months (Table 1). The correlations among parameters of the TPCs suggest that greater niche breadth comes at a fitness cost, as there was a negative correlation between thermal performance breadth and maximum performance (Fig. 4A). The correlation between optimum growth temperature and performance breadth suggests that increasing optimum growth temperature results in lower thermal performance breadth (Fig. 4B). Predicted suitabilities and predicted dry weight showed similar seasonal patterns, where they were projected to be greatest in summer and near zero in winter (Fig. 2). This pattern suggests a mechanism for the observation that fewer collections of *M. verticillata* are made in winter and late fall (Hereford et al. 2017). The correlations between SDM and MSDM were generally positive and significant (Fig. 3), suggesting that most genotypes should have high fitness in areas and times predicted to be suitable for *M. verticillata*, and that most genotypes are more generalized. MSDMs with only temperature as the explanatory variable were highly correlated in their predictions to an SDM based on the five most important variables. This is not surprising, given that mean monthly temperature

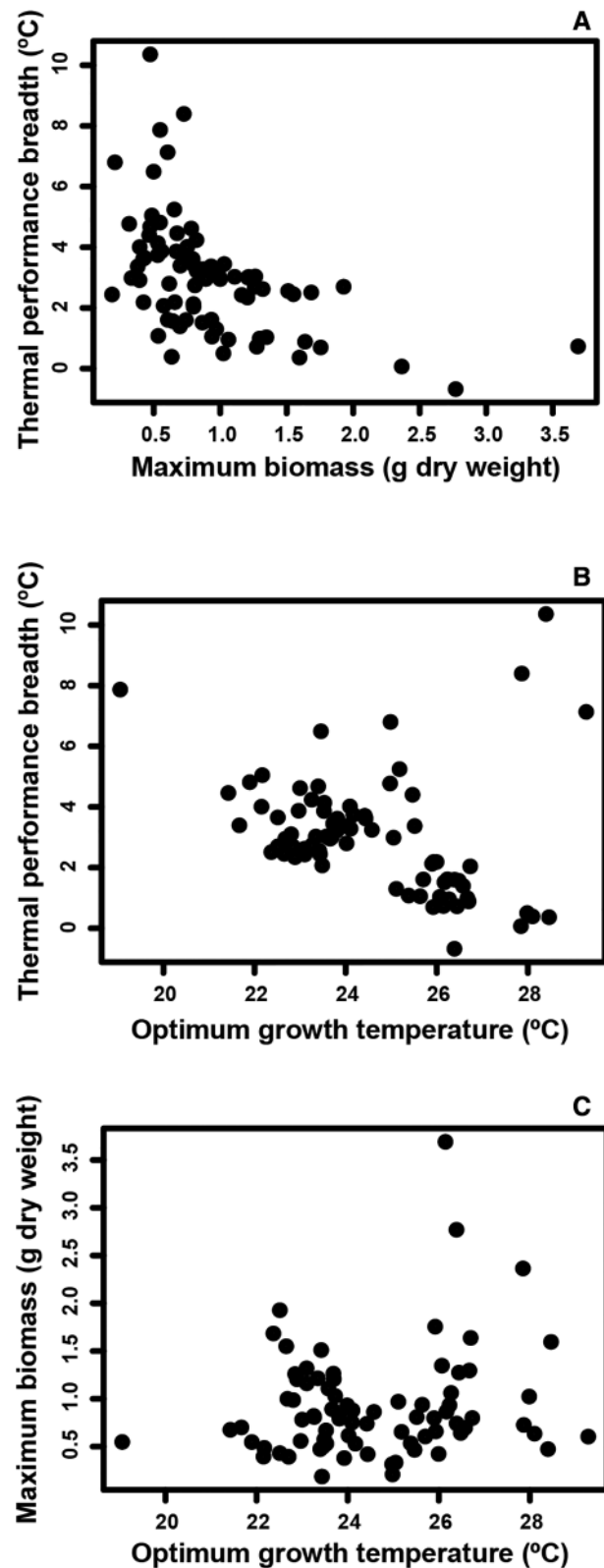


Fig. 4 Scatter plots between thermal performance breadth and maximum dry weight (A), thermal performance breadth and optimum growth temperature (B), and maximum dry weight and optimum growth temperature (C). Individual points show the parameter estimates of a single genotype.

Table 1 The correlation coefficients between broadness of the realized niche and the three parameters of the thermal performance curves

	January	February	March	April	May	June	July	August	September	October	November	December
T_o	−0.34	−0.59	−0.60	−0.62	−0.68	−0.56	−0.57	−0.75	−0.79	−0.64	−0.58	−0.53
T_b	0.88	0.82	0.82	0.81	0.74	0.60	0.44	0.44	0.60	0.85	0.86	0.85
Z_{max}	−0.49	−0.51	−0.45	−0.46	−0.42	−0.48	−0.47	−0.42	−0.41	−0.44	−0.46	−0.43

Notes: All correlations are significant. T_o indicates the optimum growth temperature, Z_{max} is the maximum dry weight, and T_b is the thermal performance breadth.

is by far the most important variable in seasonal suitability for *M. verticillata* (Importance = 78.8; Hereford et al. 2017). The TPCs were based on mean temperature during growth, which ignores variation in temperature during the life cycle (Kingsolver and Woods 2016), yet the models make similar predictions. The variation among genotypes in SDM/MSDM correlations and the relationship between TPC parameters and monthly SDM/MSDM correlations suggest variation among genotypes in niche breadth.

The relationship between the results of the models in this study suggests that the seasonal SDM accurately predicts the realized niche of genotypes with broad niches, but does not predict the niche of more specialized genotypes. The correlations between the SDM and the MSDMs largely agree in their predictions of when and where the environment is most suitable for *M. verticillata*. The large positive correlations between the SDM and MSDMs of most genotypes show that areas that are most suitable are predicted to lead to greatest fitness. The magnitude of the correlations show that there is strong agreement between the models for all months (Fig. 3). Few studies have compared the predictions of SDMs and MSDMs. Two studies found agreement between the predictions of correlative and mechanistic models in terrestrial and aquatic species (Rougier et al. 2015; Shabani et al. 2016). The mechanistic models in those studies were based on more than a single variable. In this study, temperature has such a large influence on the seasonal SDM that the mechanistic model based only on thermal performance is likely to capture a large portion of the variation in fitness. Including the influence of other variables such as soil moisture/evapotranspiration should improve the accuracy of the predictions of the mechanistic models and increase the correlations between SDM and MSDMs for some genotypes. However, many genotypes showed correlations between the SDM and MSDM that were greater than 0.80, suggesting that temperature is the major niche axis in this species (Hereford et al. 2017).

These analyses estimate the spatiotemporal ranges of genotypes within a species, quantify variation in specialization within the species, and reveal constraints on the evolution of thermal performance. Formal tests of genetic variation in niche breadth within and among populations are the focus of a different study (J. Hereford, manuscript in preparation), yet the range of variation in the correlations between SDMs and MSDMs and the correlations between parameters of the TPCs suggest that there is genetic variation among genotypes in the degree of specialization. The relationships between parameters of TPCs reveal possible constraints on the evolution of thermal performance. Two processes may constrain evolution of thermal performance to warmer temperatures. First there is a negative correlation between temperature optimum and performance breadth, suggesting that warm temperature performance comes at a cost to performance breadth. Adaptation to warmer temperatures may result in limited growth across a wide range of temperatures. This within species pattern is in agreement with a species-level pattern, where thermal performance at high temperatures is associated with a more narrow range of thermal performance (Dillon et al. 2010; Dell et al. 2011). An implication of this result is that increased performance in July will come at a cost to April performance. The results are not in agreement with the 'hotter is better and broader' conclusion of Kneis et al. (2012). Higher optimum growth temperature was associated with lower thermal performance breadth (Fig. 4B), and there was no association with maximum performance (Fig. 4C). Warmer optimum growth temperatures were associated with smaller correlations between SDM and MSDMs, suggesting genotypes with higher optimum growth temperatures were more specialized.

Related to the pattern of lower thermal performance range associated with increased optimum growth temperature is the pattern of lower thermal performance range associated with increased maximum fitness (Fig. 4A). This result suggests that genotypes that have high maximum fitness at a given

temperature have a lower range of high thermal performance. The result also suggests that niche space is limited, such that it is not possible to maintain high fitness across a wide range of temperatures. The correlation between maximum dry weight and thermal performance breadth indicates the specialist–generalist dimension of TPCs (Huey and Kingsolver 1989; Gilchrist 1995; Izem and Kingsolver 2005). This relationship illustrates the limits to thermal evolution in this species. Genotypes that adapt to high seasonal temperatures to expand the seasonal niche will be limited to a smaller range of temperatures over which they could maintain high fitness. Specialist–generalist constraints have been detected in other species (Angert et al. 2011; Latimer et al. 2011, 2015), suggesting that increasing fitness in a specific season generally comes at a cost to fitness across seasons.

It is not clear that the variation among genotypes in the degree of specialization is adaptive. Thermal performance can respond to selection (Logan et al. 2014), but parameters of TPCs may respond to selection at different rates (Latimer et al. 2014). Optimum growth temperature does not appear to evolve in response to overall climate or warmest seasonal temperatures. Thermal performance breadth, optimal growth temperatures, and maximum performance are not related to seasonality of the genotype's native site or overall summer temperatures (J. Hereford, unpublished data; Supplementary Table S1). The parameters that determine thermal performance may evolve in response to genetic drift and evolutionary history similar to other traits (Travisano et al. 1995). The genotypes in this study were collected from populations that occur in man-made reservoirs that are between 95 and 57 years old. It is possible that not enough time has occurred to allow adaptation to those conditions (Phillips 1996). Alternatively, genotypes with high thermal optima may be maintained within all populations as a result of rare extreme thermal events. A period of extreme temperatures during a growing season can be a highly effective agent of selection that may override the effects of selection for optimum growth under more moderate temperatures (Buckley and Huey 2016). These events may maintain variation within populations depending on the frequency of extreme temperatures during the growing season. It is possible that seasonal patterns of selection may drive the evolution of thermal performance in ways that are not clear from simply quantifying the length of the growing season. Seasonal variation in selection may result in unpredictable patterns of thermal adaptation in this species given the genetic relationships

between parameters of TPCs and seasonal variation (Table 1). Despite variation in overall climate, genotypes may vary in their degree of thermal specialization as a result of environmental variation within and between generations (Gilchrist 1995). Future studies in this system should determine the patterns of seasonally varying selection, to quantify the role of seasonal adaptation in the evolution of thermal performance (e.g., Kingsolver et al. 2001; Chevin et al. 2015).

The seasonal context of the organism should be considered in studies of adaptation. This study reveals variation within a species in niche breadth by quantifying variation in across seasons. The seasonal niche of *M. verticillata* is not a static feature of the species, but may evolve. This study demonstrates the robustness of correlative estimates of the seasonal niche by comparing the correlations between the SDM and the MSDMs for each genotype in the study. Considering the seasonal aspects of an organism's environment provides a more complete characterization of the environment. Seasonal patterns can shape responses to selection in ways that are not obvious when considering only overall differences between environments. For example, many reciprocal transplant studies find evidence of generalists despite strong environmental differences between native sites (Hereford 2009). If seasonal variation within the sites results in greater overlap in conditions, or if there are genetic constraints among the factors that make up the niche as seen in this study, the classic pattern of local adaptation where both populations are specialists on their native sites will not be detected.

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Supplementary data

Supplementary data are available at *ICB* online.

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