The evolutionary potential of an insect invader under climate change

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Although the impacts of climate change and invasive species are typically studied in isolation, they likely interact to reduce the viability of plant and animal populations. Indeed, invasive species, by definition, have succeeded in areas outside of their native range and may therefore have higher adaptive capacity relative to native species. Nevertheless, the genetic architecture of the thermal niche, which sets a limit to the potential for populations to evolve rapidly under climate change, has never been measured in an invasive species in its introduced range. Here, we estimate the genetic architecture of thermal performance in the harlequin beetle (*Harmonia axyridis*), a Central Asian species that has invaded four continents. We measured thermal performance curves in more than 400 third-generation offspring from a paternal half-sib breeding experiment and analyzed the genetic variance–covariance matrix. We show that while the critical thermal limits in this species have an additive genetic basis, most components of the thermal performance curve have low heritability. Moreover, we found evidence that genetic correlations may constrain the evolution of beetles under climate change. Our results suggest that some invasive species may have limited evolutionary capacity under climate change, despite their initial success in colonizing novel environments.

KEY WORDS: *Harmonia axyridis*, climate change, invasive species, thermal niche, thermal performance curve.

The occupation of Earth by human beings, and our ever-increasing resource use, has led to large changes in the biophysical system of the planet. For example, sustained CO_2 emissions by the fossil fuel industry have led to increases in the mean and variance of environmental temperature over large parts of the globe (IPCC 2013). Although some species (e.g., large-bodied mammals and birds) can escape warming by moving to suitable habitat, many others (e.g., small ectotherms like insects) have limited dispersal capacity or include nonmobile stages in their life cycle, necessitating *in situ* adaptation to changing conditions (Hoffmann and Sgro 2011; Kingsolver et al. 2011). Ectotherms with limited dispersal ability can compensate for rapid changes in their thermal environment through a combination of three processes: behavior, acclimation, and evolution (Angilletta 2009; Logan et al. 2015;

Cox et al. 2018; Fey et al. 2019). When organisms are unable to use behavior and acclimation to fully compensate for shifts in environmental temperatures, directional selection will begin to favor changes in the frequencies of alleles underlying thermal physiology. If individuals in a population vary in their physiological tolerances, and this variation has an additive genetic basis and is unconstrained by genetic correlations, the population will evolve (Angilletta et al. 2002; Hoffmann and Sgro 2011; van Heerwaarden and Sgro 2014). For communities of small ectotherms that interact agonistically with one another (through parasitism, predation, and competition), evolutionary potential may in large part determine the winners and losers in a warming world (Hoffmann and Sgro 2011; Urban et al. 2012; Gunderson and Stillman 2015).
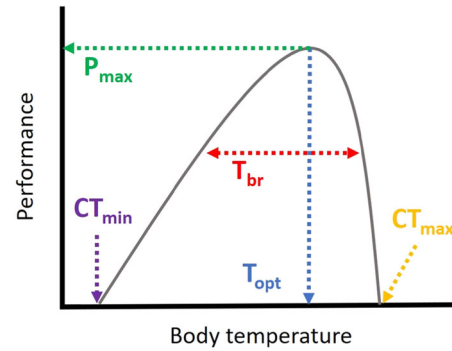
Many of the same effects of human progress that cause climate change, such as increases in global shipping, have led to a dramatic increase in the number of nonnative species established

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in different regions of the globe (Hulme 2009; Keller et al. 2011). Invasive species add an additional stressor on ecosystems as they often compete with native species for resources, or directly kill and consume them (Brown et al. 2002; Braks et al. 2004). Most studies focus on the impact of climate change or invasive species independently of one another, but these phenomena are likely to be combinatorial in their effects on native species (Stachowicz et al. 2002; Occhipinti-Ambrogi 2007; Hellmann et al. 2008; Rahel and Olden 2008).

The factors that facilitate the establishment and spread of nonnative species are varied and complex. For example, plastic responses such as acclimation or maternal effects can influence the success of invasive species (Chown et al. 2007; Davidson et al. 2011; Tepolt and Somero 2014), or their traits may be uniquely matched to the new environment (Peterson 2003; Bomford et al. 2009). Nevertheless, invasive species, by definition, have succeeded in areas outside of their native range, and the invaded environments are often climatically different from the native range (Broennimann et al. 2007; Tepolt and Somero 2014). This raises the possibility that invasive species are intrinsically capable of rapid evolutionary adaptation to novel thermal environments, and by extension, to future climate change. Additionally, prior to establishment in a new region, invasive species are often thought to undergo genetic bottlenecks that reduce genetic variance and evolutionary potential (Tsutsui et al. 2000; Dlugosch and Parker 2007; Lavergne and Molofsky 2007; Puillandre et al. 2008). Nevertheless, growing evidence suggests that rapid genetic adaptation is a key process mediating the establishment and spread of nonnative species (Lee 2002; Broennimann et al. 2007; Lavergne and Molofsky 2007; Prentis et al. 2008; Hodgins et al. 2018). If invasive species compete with natives and have greater evolutionary capacity under climate change, the competitive balance may be tipped in their favor. A key question, then, is whether the traits in invasive species that mediate fitness under climate change have a genetic architecture that is conducive to rapid evolution.
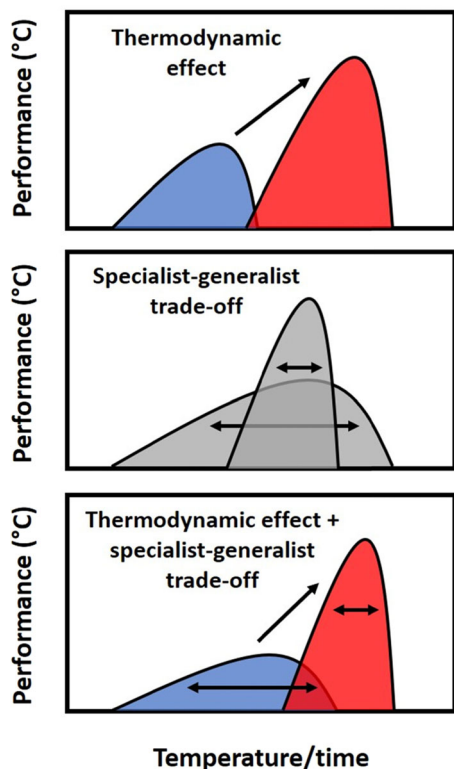
Theory suggests that some of the most important traits underlying adaptation to climate change are those that make up the "thermal performance curve" (Huey and Hertz 1984; Huey and Kingsolver 1989; Kingsolver et al. 2004; Angilletta 2009; Logan et al. 2014; Fig. 1). This curve represents the relationship between body temperature and an ecologically relevant performance (e.g., locomotor capacity, digestive efficiency) and follows a characteristically left-skewed shape that is driven by enzyme kinematics (Angilletta et al. 2002). We can break down this curve into several "thermal performance traits" that are predicted to evolve in response to different aspects of environmental variation (Huey and Kingsolver 1989; Kingsolver and Gomulkiewicz 2003; Angilletta 2009; Clusella-Trullas et al. 2011; Sunday et al. 2011; Kellermann et al. 2012; Logan et al. 2016; Logan et al. 2018; Martins et al. 2018). For example, the thermal

Figure 1. The shape of a typical thermal performance curve emerges from the combined values of five "thermal performance traits," each of which are predicted to evolve in response to changes in environmental temperature in different ways (see text). Maximal performance (P_{max}) describes the height of the curve, whereas performance breadth (T_{br}) and the critical thermal limits (CT_{min} and CT_{max}, the high and low temperatures, respectively, where performance drops to zero) combine to describe its breadth. The thermal optimum (T_{opt}) describes the body temperature at which performance is maximized.

optimum (T_{opt}) is predicted to covary with mean environmental temperature, whereas the performance breadth (T_{br}) and the critical thermal limits (critical thermal minimum: CT_{min}; critical thermal maximum: CT_{max}) should covary with temperature variation (Huey and Kingsolver 1989; Angilletta et al. 2003; Angilletta 2009; Huey et al. 2009, 2012). In an idealized Darwinian world, the traits that make up the thermal performance curve could evolve independently of each other and the curve could take on a nearly infinite number of shapes. In reality, traits can be genetically correlated (through pleiotropy or linkage), and genetic correlations can produce nonintuitive evolutionary dynamics that proceed along "evolutionary lines of least resistance" (Lande and Arnold 1983; Schluter 1996). Indeed, genetic correlations between traits under selection can constrain adaptation even when heritability is high (Lande and Arnold 1983; Sadowska et al. 2007; Martins et al. 2018).

Previous studies have identified at least two important ways by which the shape of thermal performance curves may be constrained over time and space. The first is called the "thermodynamic effect" (Fig. 2, top panel), and occurs when the thermal optimum is positively correlated with maximal performance. A thermodynamic effect emerges from the fact that enzyme kinematics are more efficient at higher body temperatures (Angilletta et al. 2002; Hochachka and Somero 2002; Angilletta et al. 2003; Angilletta 2009; Knies et al. 2009; Angilletta et al. 2010). The second is called the "specialist-generalist trade-off" (Fig. 2, middle panel), and occurs when the area under the thermal performance curve remains constant over evolutionary time such that a population can either perform very well over a narrow range of

Figure 2. Correlations among parameters that describe the shape of the thermal performance curve may constrain evolutionary responses and mediate extinction risk under climate change. A "thermodynamic effect" (top panel) arises when the maximum performance capacity of a cold-adapted population (blue) increases in warm environments as an indirect effect of an evolutionary increase in the thermal optimum (red). The thermodynamic effect is also known as the "hotter is better" hypothesis because enzymatic reaction rates are typically more efficient at high temperatures. A "specialist-generalist trade-off" (middle panel) results from underlying physiological trade-offs that prevent individuals from maximizing performance across a broad range of temperatures (e.g., cell membrane fluidity can only be optimized for high or low temperatures, but not both). When both a thermodynamic effect and a specialist-generalist trade-off occur in a population experiencing climate change (bottom panel), curve shape can evolve in complex ways that leave a population better adapted to mean conditions but maladapted to variability, or vise versa. In this last scenario, evolutionary adaptation to climate change can paradoxically result in high extinction risk because the population can only adapt to high mean temperatures or extreme weather events, but not both.

temperatures or less well over a broader range of temperatures (e.g., an increase in maximal performance capacity results in a decrease in performance breadth and vice versa; Gilchrist 1996; Angilletta et al. 2002, 2003; Hochachka and Somero 2002; Izem and Kingsolver 2005; Angilletta 2009; Phillips et al. 2014). Both of these patterns have been observed at the phenotypic level when performance curves are measured across environmental gradients

(Angilletta et al. 2002, 2003, 2010; Angilletta 2009; Phillips et al. 2014), but a major outstanding question is whether phenotype-level thermodynamic effects and specialist-generalist trade-offs are driven by underlying genetic correlations. The resolution of this issue is critical because genetic correlations (unlike phenotypic correlations) represent evolutionary constraints. If both a thermodynamic effect and a specialist-generalist trade-off are driven by genetic correlations and found in the same population (Fig. 2, bottom panel), evolutionary adaptation to climate change can actually increase extinction risk over the long term by reducing the capacity of populations to deal with both high average temperatures and extreme weather events simultaneously. In general, very little is known about the genetic architecture of thermal performance curves despite the importance of these data in evaluating the adaptive capacity of species under climate change (Hoffmann and Sgro 2011; Logan et al. 2018; Martins et al. 2018).

Here, we used a South African population of the globally invasive harlequin beetle (*Harmonia axyridis*) as a model system to examine the rapid evolutionary potential of invasive species under climate change. We raised more than 400 third-generation offspring in a common-garden breeding experiment and then phenotyped these offspring for thermal tolerance limits and the thermal sensitivity of walking speed. We analyzed the genetic architecture of the thermal performance curve following both multivariate (breaking the curve down into component traits) and function-valued (treating the entire curve as a single trait) approaches. To our knowledge, our study represents the first estimates of the genetic architecture of the thermal niche in an invasive species in its invasive range.

Materials and Methods
STUDY SYSTEM AND BREEDING DESIGN

The harlequin beetle is a coccinellid beetle native to Central Asia. Over the past several decades, it has been released either unintentionally or as a biocontrol agent on four continents (Europe, North America, South America, and Africa; Brown et al. 2011; Roy et al. 2016). Although there is little evidence that the harlequin beetle is an effective biocontrol agent, it likely competes with native insects (Majerus et al. 2006; Adriaens et al. 2007; Roy et al. 2016). Genetic analyses suggest that the South African population we studied originated in 2004 from an invasive North American population, likely undergoing at least two genetic bottlenecks on its roundabout way from Asia to Africa (Lombaert et al. 2010).

Over a two-week period in February 2015, we collected 300 adult (50:50 sex ratio) harlequin beetles at several adjacent sites representing one contiguous population near Stellenbosch, South Africa (33°84′76.6″S, 18°82′77.7″E). Prior to breeding, we kept between 50 and 60 adults in each of several well-ventilated 2-L plastic containers. Adults were fed frozen rose aphids

(*Macrosiphum rosae*), artificial diet (Geoghegan et al. 2000), and cotton saturated with 10% honey solution. Boxes were lined with paper towel substrate and cleaned once a week. We kept all beetles (wild-caught and lab-reared) inside incubators set to a temperature cycle of 25°C for 18 hours (diurnal) and 18°C for 6 hours (nocturnal). They were exposed to a summer photoperiod of 14L:10D for the duration of the experiment. Two weeks after field collection, we randomly selected 60 males and 60 females from our founder population and then randomly paired these individuals for mating. Each pair was kept isolated in 6-cm diameter Petri dishes and monitored daily for egg clutches. The first egg clutch from each mating pair was discarded to ensure that offspring included in the experiment were not produced from prior mating events (Nalepa et al. 1996). We isolated subsequent egg clutches from adult beetles by placing them in separate Petri dishes. When eggs hatched, 10 to 20 F_1 larvae (depending on how many larvae successfully hatched) were chosen haphazardly and split between 10 9-cm diameter Petri dishes. Each day, larvae received frozen aphids equivalent to twice their body length, two 4×4 mm blocks of artificial diet, and cotton soaked in honey solution. Once F_1 adults emerged from pupa, we placed them into separate 6-cm Petri dishes. Five days after emergence from pupae, individuals were sexed following McCornack and Ragsdale (2007). One to two weeks after emergence from pupae, when sexual maturity had been reached, F_1 beetles were divided into 55 paternal family lines. We then randomly assigned three F_1 females to mate with each F_1 male, generating both full-sib and half-sib families (only 51 of 55 full-sib families produced viable eggs). To reduce inbreeding and increase our power to detect heritability, we ensured that individuals in each F_1 pair came from different F_0 pairs (in other words, siblings did not mate). Each male was paired with one female at a time (random order) in a 6-cm Petri dish for three days to ensure successful mating. After three days, males were removed and placed with the next female. Females were kept in separate Petri dishes both before and after introduction to a male's Petri dish. Larvae hatched from the eggs of each female were divided across six 9-cm Petri dishes to reduce competition for food and the potential for cannibalism. Upon emergence from pupae, we kept F_2 individuals in separate Petri dishes for five days, sexed all individuals and ensured that elytra had hardened sufficiently before handling and experimentation. F_2 adults received the same diet as F_0 and F_1 adults (see above) except that they also received ∼20 live Russian wheat aphids (*Diuraphis noxia*) per feeding period. Not all F_2 adults survived until the experimentation period, resulting in a final sample size of 521 individuals from 51 paternal family lines (range = 5–12 offspring per family).

CRITICAL THERMAL LIMITS AND WALKING SPEED

We measured the critical thermal minimum (CT_{min}) and the critical thermal maximum (CT_{max}) on 472 and 440 F_2 adult bee-

tles, respectively. All individuals were fasted for a minimum of 14 hours before experimental trials to reduce possible effects of digestion on beetle performance. We placed individuals in a series of Perspex chambers positioned in a double-jacketed system connected to a programmable water bath (Grant, GP200, England). Each chamber was covered with a transparent lid to keep the temperature of the chamber in equilibrium with that of the water bath. A copper-constantan thermocouple connected to a datalogger (PICO Technology, TC-08 Thermocouple Datalogger, UK) was placed in the central chamber to monitor the temperature throughout the trials. After 15 minutes of acclimation to a starting temperature of 25°C, the temperature was increased (for CT_{max}) or decreased (for CT_{min}) at a rate of 0.25°C/min. We monitored individuals periodically until signs of heat or cold stress became apparent (usually after about an hour), at which time we monitored individuals continuously. We measured CT_{min} before CT_{max} for all individuals because of the greater risk of thermal stress and death associated with CT_{max}. Each individual was given a minimum of one week's rest after the walking speed trials (see below) and before CT_{min} was measured, and at least two days' rest between measurements of CT_{min} and CT_{max}. Both CT_{min} and CT_{max} were recorded as the temperature at which individuals lost muscle coordination. For these measurements, loss of muscle coordination occurred when beetles were unable to cling to a fine-tipped paintbrush, and the endpoint was reached when head, leg and antennae movement ceased despite gentle stimulation with a paintbrush (Shinner et al., manuscript in revision). Because individuals would sometimes feign death when probed with the paintbrush, we used three consecutive measurements of loss of muscle coordination to confirm that endpoints had been reached. We recorded the mass of each individual using a digital microbalance (Avery Berkel, UK; ±0.0001 g) before and after the CT_{min} trial for that individual. We used the value of mass recorded before CT_{min} in all subsequent analyses.

To quantify the relationship between performance and body temperature, we measured the walking speeds of beetles at each of six temperatures in the following random order: 24°C, 18°C, 30°C, 36°C, 12°C, and 43°C. We determined suitable high and low temperatures by assessing changes in performance across a broad range of temperatures during pilot trials. Intermediate temperatures were chosen to be roughly equidistant from one another (6–7°C intervals) between the high and low temperatures. Walking speed is commonly used as an estimate of performance in harlequin beetles because they regularly engage in this behavior in nature to access food resources and avoid predators, and are rather awkward fliers (Noriyuki et al. 2011; Verheggen et al. 2017; Xiao et al. 2017). As with the experiment to determine the critical thermal limits, beetles were fasted for a minimum of 14 hours prior to walking speed trials to reduce possible effects of digestion on performance. One individual at a time was placed inside

an enclosed runway (1 cm × 1 cm × 22 cm) that was embedded in a custom-made Perspex unit. The track was marked at 1 cm intervals to evaluate distance traveled. The Perspex unit was placed within a walk-in climate chamber set to the target temperature. Individuals were allowed to come to thermal equilibrium with the target temperature for 10–15 minutes before trials were conducted. We verified that the air inside the runway had equilibrated to the target temperature using a thermocouple probe inserted into the center of the runway just prior to the start of each trial. Individuals were encouraged to walk by releasing them into one side of the track and then gently poking them with a fine-tipped paintbrush. For each individual at each temperature, we recorded three separate trials that were done in quick succession. At the intermediate temperatures, we considered a trial viable if the individual walked for at least 5 cm continuously. At the highest and lowest temperature, if the individual could not walk for at least 5 cm, its performance was recorded as zero. Trials were filmed with fast-framed digital video (60 frames per second) using a Kodak Zi8 camera placed directly above the Perspex runway. We used the frame rate of these videos to calculate the fastest speed (in cm/s) an individual walked over any 1 cm segment of the track. All individuals rested for a minimum of two days between trials at different temperatures. We only included individuals in final analyses if we were able to get at least two viable walking speed estimates at each experimental temperature. We did not consider a trial viable if individuals walked on the upper surface or sides of the track.

We fitted thermal performance curves to the raw walking speed data for each individual following Angilletta (2003) and Logan et al. (2014, 2018). We removed aberrant performance curves from final analyses when they clearly resulted from experimental error or injuries to beetles (~17% of the curves were removed from final analyses). We fitted the full set of asymmetrical, parabolic functions built into the curve-fitting program TableCurve 2D to the raw data for all individuals ($N = 432$). Additionally, following Battles and Kolbe (2019), we used CT_{min} and CT_{max} values to anchor thermal performance curves (we forced the curve for an individual to go through the x-axis at the critical thermal limits for that individual). We chose the best-fit equation for each individual using AIC criteria and then extracted the thermal performance traits (T_{opt}, T_{br}, and P_{max}) as well as the area under the curve (AUC) by solving the equation for every 0.1°C between CT_{min} and CT_{max}. Our estimate for T_{br} was the range of body temperatures over which the individual achieved at least 80% of P_{max} (a standard estimate of performance breadth in thermophysiological studies; Angilletta 2009; Logan et al. 2013, 2014, 2016, 2018; Martins et al. 2018).

QUANTITATIVE GENETIC ANALYSES

To estimate additive genetic variances and covariances underlying the thermal performance curve, we implemented a restricted maximum-likelihood based "animal model" in R (ASReml-R package; Butler et al. 2017) using our full population pedigree (Wilson et al. 2010). The animal model is a type of mixed effects model where the additive genetic variance of each individual is included as a random effect (Kruuk 2004). We ran analyses on two separate sets of data: one including the traits that compose the thermal performance curve (CT_{min}, CT_{max}, T_{opt}, T_{br}, and P_{max}; hereafter referred to as "thermal performance traits"), and another that included walking speed at each experimental temperature, CT_{min}, and CT_{max} (hereafter referred to as "walking speed traits"). We included the critical thermal limits in the latter model to test for trade-offs between performance at intermediate and extreme temperatures. All values were log-transformed to conform to the assumption of normality, and standardized to a mean of zero and unit variance to improve model convergence. Additionally, we added one to all CT_{min} values to allow for log transformation. We analyzed thermal performance and walking speed traits following Wilson et al. (2010). We obtained estimates for additive genetic (V_A) and maternal (V_M) effects by including "individual" and "dam" as random effects, respectively. We also included mass and sex as fixed effects. For each trait, we calculated the narrow-sense heritability by dividing V_A by the total phenotypic variance (which included V_A, V_M and residual variance, or V_R). Standard error of heritability was estimated using the "pin" function in the *nadiv* R package (Wolak 2012). To test for the significance of additive genetic and maternal effects, we compared the log-likelihood of models with different random structures using likelihood ratio tests (Wilson et al. 2010; Houslay and Wilson 2017). To determine the significance of mass and sex, we compared the log-likelihood of models that included both V_A and V_M effects to models with and without the fixed effect of mass or sex. To estimate genetic covariances (and correlations), separate bivariate models were run for each pairwise trait combination (for the thermal performance and walking speed traits, separately). We did not include terms for maternal or sex effects in models for genetic covariances because these did not emerge as significant in our univariate analyses. Additive genetic effects, maternal effects, and residual variances and covariances were specified as unstructured matrices. We determined the significance of genetic covariances between traits by comparing the log-likelihood of models with and without a covariance term specified. Genetic correlations [CORR(G)] were calculated using the following formula (Wilson et al. 2010):

$$\text{CORR}(G) = \text{COVA}_{12}/\sqrt{VA_1 * VA_2},$$

Table 1. Additive genetic ($V_A \pm$ SE), maternal ($V_M \pm$ SE), and residual variances ($V_R \pm$ SE), as well as narrow-sense heritabilities ($h^2 \pm$ SE) for thermal performance traits in the harlequin beetle.

Trait	V_A	V_M	V_R	Effect of mass	Effect of sex	h^2
CT_{min}	**0.26 ± 0.15**	0.09 ± 0.07	0.63 ± 0.10	No	No	**0.27 ± 0.15**
CT_{max}	**0.36 ± 0.12**	0	0.65 ± 0.10	No	No	**0.35 ± 0.11**
T_{opt}	0	0.05 ± 0.05	0.95 ± 0.08	No	No	0
P_{max}	**0.18 ± 0.16**	0	0.84 ± 0.09	No	No	**0.16 ± 0.08**
T_{br}	0.07 ± 0.07	0	0.93 ± 0.09	Yes	No	0.07 ± 0.07
AUC	0.08 ± 0.10	0.01 ± 0.06	0.86 ± 0.09	Yes	No	0.08 ± 0.10
v12	0	0.02 ± 0.05	0.96 ± 0.08	No	No	0
v18	0	0	0.98 ± 0.07	Yes	No	0
v24	**0.06 ± 0.11**	0.09 ± 0.07	0.81 ± 0.09	Yes	No	**0.06 ± 0.11**
v30	0	0.08 ± 0.06	0.90 ± 0.08	Yes	No	0
v36	0.03 ± 0.10	0.07 ± 0.07	0.89 ± 0.09	Yes	No	0.03 ± 0.10
v43	0.10 ± 0.08	0	0.88 ± 0.09	No	Yes	0.10 ± 0.08

These include the traits that define the shape of thermal performance curve: the critical thermal minimum and maximum (CT_{min} and CT_{max}, respectively), thermal optimum (T_{opt}), maximal performance (P_{max}), and performance breadth (T_{br}). Additional traits include the area under the thermal performance curve (AUC) and walking speed at each experimental temperature (v12, v18, etc.), as well as whether sex or mass effects were significant for each trait in the model. All estimates are from univariate models. Statistically significant values are in bold.

Table 2. Genetic correlations (below diagonal) and corresponding genetic covariances (above diagonal) for the traits that compose the shape of the thermal performance curve, as well as the area under the curve.

	CT_{min}	CT_{max}	T_{opt}	P_{max}	T_{br}	AUC
CT_{min}	–	0.11	**0.16**	0.12	−0.11	0.05
CT_{max}	0.28	–	−0.01	0.02	−0.01	−0.01
T_{opt}	**0.98**	−0.13	–	0.08	−0.03	0.07
P_{max}	0.50	0.08	0.93	–	−0.01	0.11
T_{br}	−0.68	−0.09	−0.43	−0.99	–	−0.07
AUC	0.26	−0.04	1.00	0.91	−0.94	–

Thermal performance traits include the critical thermal minimum and maximum (CT_{min} and CT_{max}, respectively), thermal optimum (T_{opt}), maximal performance (P_{max}), and performance breadth (T_{br}). All values are taken from bivariate models. Significant values are in bold.

where $COVA_{12}$ is the additive covariance between traits 1 and 2, and VA_1 and VA_2 are the additive genetic variances of traits 1 and 2, respectively.

Lastly, we constructed two G-matrices using multivariate models that included all thermal performance and walking speed traits, respectively. To be able to compare results from these G-matrices to previous univariate and bivariate analyses, we ran two models for each set of traits: one with V_A, V_M, sex and mass, and the other with only V_A and mass. This was done to match the predictors included in univariate and bivariate models. The results of these different approaches were very similar, so we only

present the G-matrices generated from univariate and bivariate models in the main text. We include the results of the multivariate models in the Supporting Information (Tables S1–S3).

In addition to breaking down the thermal performance curve into component traits and analyzing genetic architecture using multivariate methods, we can also treat the curve as a single "function-valued" trait (Gomulkiewicz and Kirkpatrick 1992; Kingsolver et al. 2001; Stinchcombe and Kirkpatrick 2012; Gomulkiewicz et al. 2018). In other words, the trait under selection can be thought of as the entire curve relating performance to body temperature. We therefore analyzed the genetic architecture of the thermal performance curve of the harlequin beetle using the template mode of variation (TMV) method developed by Izem and Kingsolver (2005). TMV capitalizes on the fact that thermal performance curves follow an archetypical shape with a clear maximum (Huey and Kingsolver 1989; Angilletta 2009). The method constructs a template curve from the raw data for each family that is then used to compare axes of genetic variation. Variation in thermal performance curves is broken down into the portion of variance that follows each of three biologically relevant axes: vertical shift (genetic variation in maximal performance), horizontal shift (genetic variation in the thermal optimum), and a specialist-generalist trade-off (better performance over some temperatures leads to worse performance over other temperatures). The higher the genetic variance associated with a given axis, the more likely it is that evolution will proceed along that axis. TMV has several advantages over alternative function-valued methods. First, unlike other approaches (e.g., principle components

Table 3. Genetic correlations (below diagonal) and corresponding genetic covariances (above diagonal) between walking speed at each experimental temperature (v12, v18, etc.), as well as between walking speeds and the critical thermal limits (CT_{min} and CT_{max}, respectively).

	v12	v18	v24	v30	v36	v43	CT_{min}	CT_{max}
v12	–	−0.03	−0.02	0	0.05	0.02	−0.02	**−0.13**
v18	−0.47	–	−0.03	−0.02	0.04	0.01	−0.04	**−0.03**
v24	−0.73	−0.81	–	0	−0.03	−0.07	**−0.21**	−0.06
v30	−0.03	−0.79	−0.05	–	0.04	0.05	0.03	−0.01
v36	0.64	0.73	−0.22	0.50	–	0.08	0.13	0.03
v43	0.75	0.39	−0.57	0.70	0.97	–	**0.18**	0
CT_{min}	−0.61	−0.43	**−0.77**	0.23	0.70	**0.82**	–	–
CT_{max}	**−0.83**	**−0.61**	−0.22	−0.10	0.17	0.03	–	–

We included the critical thermal limits to test for constraints between performance at intermediate and extreme temperatures. All values are taken from bivariate models. Significant values are in bold.

analysis), the output of TMV is easy to interpret in terms of real-world biology (Izem and Kingsolver 2005; the axes of variation apply to *a priori* theories of thermal adaptation; Angilletta 2009; Stinchcombe and Kirkpatrick 2012), and second, one can use TMV to estimate the amount of genetic variation in the thermal optimum (Izem and Kingsolver 2005; Stinchcombe and Kirkpatrick 2012), an important consideration under climate change scenarios. We implemented the MatLab code for TMV provided by Izem and Kingsolver (2005) using our full data set of half-sib families (51 families, median number of individuals per family = 10). We did not include the critical thermal limits in this analysis to ensure that the template for each family was calculated for an identical range of temperatures. We also conducted a sensitivity analysis using smaller subsets of our data based on different selection criteria (e.g., removing individuals of whom we were unable to obtain optimal curve fits during multivariate analyses), but this did not appreciably change the results. Following recommendations in Izem and Kingsolver (2005), we used a fourth-order polynomial as our template model and verified that this model fit the raw data for each family to a high degree of accuracy (Fig. S1).

Lastly, we determined phenotypic covariances and correlations between traits that correspond to the thermodynamic effect and specialist-generalist trade-off, respectively. Specifically, we used bivariate models to estimate the phenotypic covariances and correlations between CT_{min} and CT_{max}, T_{opt} and P_{max}, and AUC and P_{max}. As in previous bivariate models, only mass was included as a fixed effect, although "dam" was not specified as a random effect. To determine the significance of phenotypic covariances and correlations, we compared the log-likelihood of models with and without among-individual covariance between traits (Houslay and Wilson 2017). Phenotypic covariance was estimated by summing the V_A and V_R estimates in models that included the covariance of traits among individuals. Phenotypic correlations [CORR(P)] were estimated using the formula given in Butler et al. (2017) (with standard error estimated using the

"pin" function in the *nadiv* R package):

$$CORR\,(P) = \;COVA_{12} + \;COVR_{12}/$$
$$\sqrt{(VA_1 + VA_2)} * \sqrt{(VR_1 + VR_2)},$$

where $COVR_{12}$ is the residual covariance between trait 1 and 2, and VR_1 and VR_2 are the residual variances of traits 1 and 2, respectively.
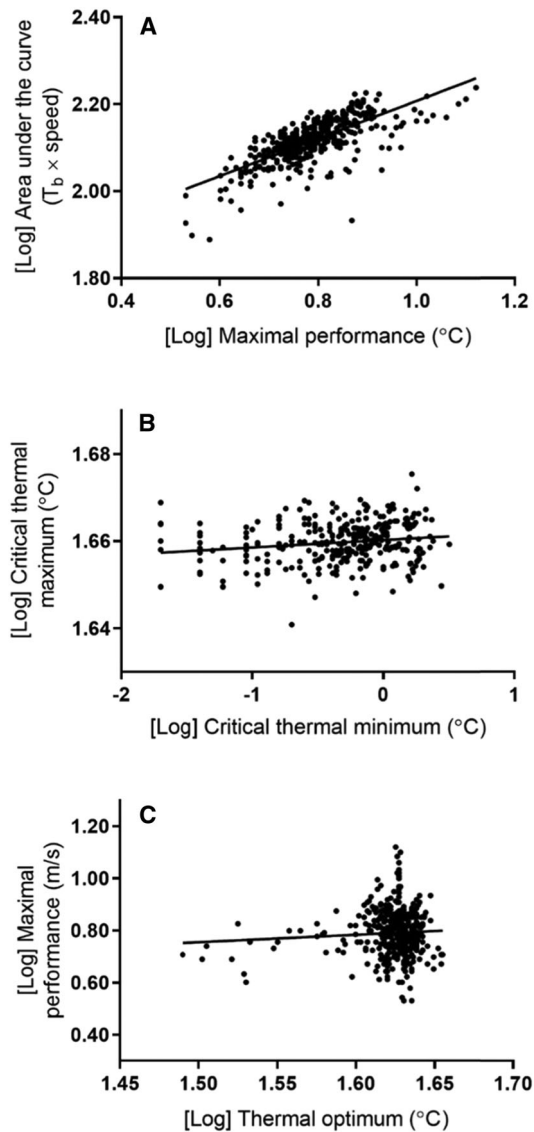
Results
MULTIVARIATE ANALYSES

The distributions of walking speeds at each trial temperature are displayed in Figure S2. The mean values for CT_{min}, CT_{max}, T_{opt}, P_{max}, T_{br}, and AUC (± SEM) for our focal population of harlequin beetles were 0.42 ± 0.03°C, 45.65 ± 0.02°C, 42.07 ± 0.09°C, 6.30 ± 0.06 cm/s, 11.86 ± 0.19°C, and 131.81 ± 0.70 (T_b × walking speed), respectively. The critical thermal limits (CT_{min} and CT_{max}), P_{max}, and walking speed at 24°C were the only traits that were heritable (Table 1). There were no significant maternal effects on any trait, whereas mass and sex affected some traits but not others (Table 1). CT_{min} was strongly positively genetically correlated with T_{opt} (Table 2) and walking speed at 43°C (Table 3), whereas CT_{min} was strongly negatively genetically correlated with walking speed at 24°C (Table 3). CT_{max} was strongly negatively genetically correlated with walking speed at both 12°C and 18°C (Table 3).

At the phenotypic level, AUC was positively correlated with P_{max} (0.72 ± 0.03, $P < 0.001$; Fig. 3A), whereas CT_{min} was positively correlated with CT_{max} (0.16 ± 0.05, $P = 0.02$; Fig. 3B). P_{max} and T_{opt} were not significantly correlated (0.07 ± 0.05, $P = 0.09$; Fig. 3C).

FUNCTION-VALUED ANALYSES

The TMV model explained a total of 45.2% of the genetic variation in the thermal performance curves (the rest was error

Figure 3. Phenotypic correlations between thermal performance traits. Area under the curve was positively correlated with maximal performance (A), whereas the critical thermal limits were positively correlated with one another (B), providing mixed evidence for a specialist-generalist trade-off at the phenotypic level. The correlation between the thermal optimum and maximal performance (C) suggests that harlequin beetle phenotypes are only weakly constrained by a thermodynamic effect.

variation). Of the explained variation, 9% could be attributed to a horizontal shift in the curve (genetic variation in T_{opt}), 11% to a vertical shift in the curve (genetic variation in P_{max}), and 26% to a specialist-generalist trade-off (Fig. 4).

Discussion

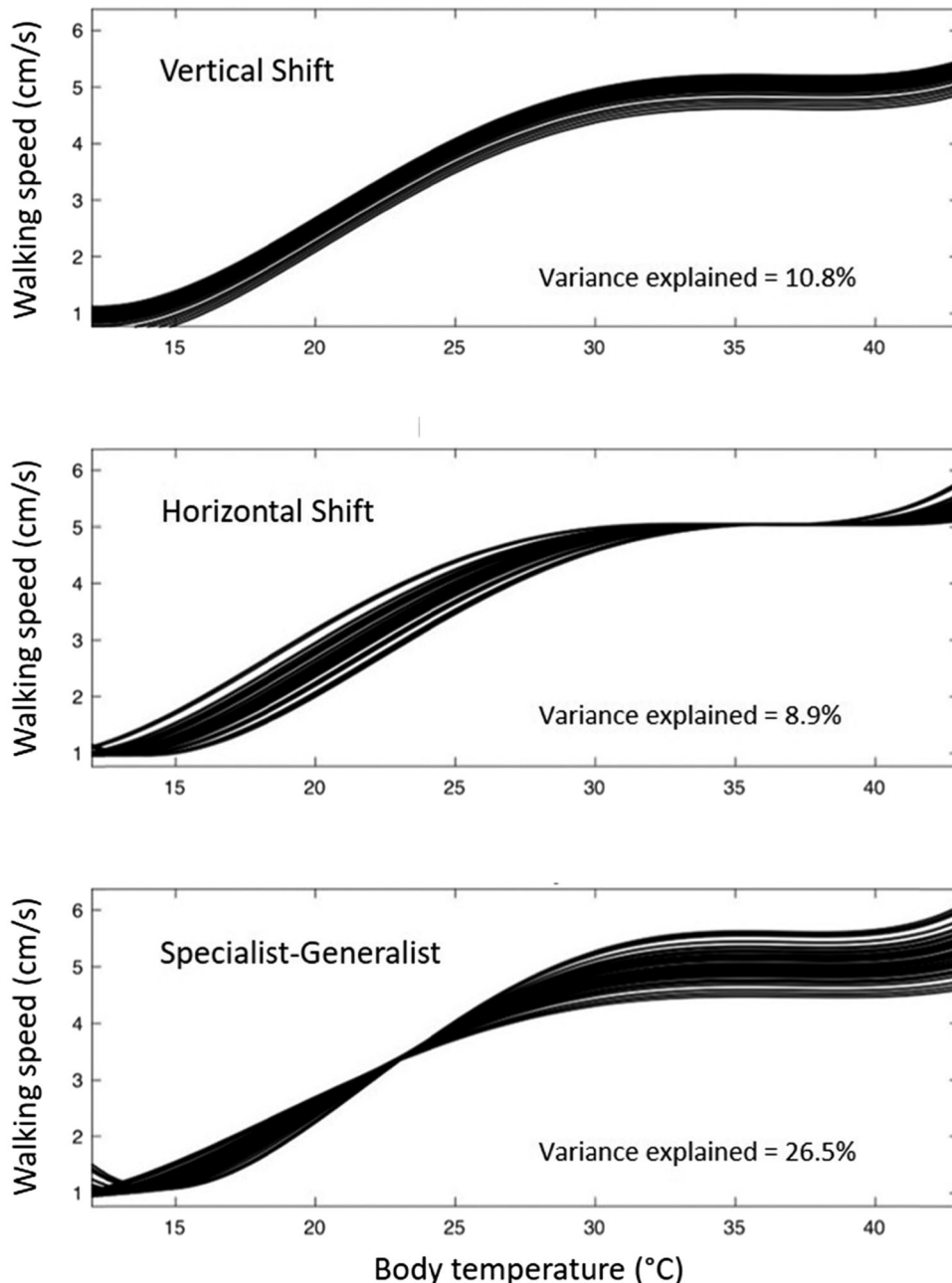We did not detect significant additive genetic variance underlying most components of the thermal performance curve in the invasive harlequin beetle in South Africa. For example, the thermal optimum and performance breadth, two traits thought to be critical in the response of ectotherms to increases in the mean and variance of environmental temperature, respectively, lacked heritability. Moreover, walking speeds at most of our experimental temperatures were not heritable (with the sole exception of walking speed at 24°C, which had low but significant heritability). By contrast, the critical thermal limits (CT_{min} and CT_{max}) were both moderately heritable and genetically correlated with performance at various temperatures in ways that suggest their evolution may be constrained. Taken together, our results indicate that the harlequin beetle has relatively low evolutionary capacity in the face of rapid climate change.

Two recent experiments on lizards (Logan et al. 2018; Martins et al. 2018) were the first to measure additive genetic variances of full thermal performance curves. These studies reported low or nonexistent heritability underlying most components of the thermal performance curve (estimated as the thermal sensitivity of sprint speed). Nevertheless, because of the difficulty of raising large numbers of lizards in a captive setting, these studies used comparably low sample sizes and may not have had the power to detect low but significant heritability if it was present. Here, although we used much larger sample sizes, we nevertheless found similarly low levels of heritability underlying important traits like the thermal optimum and performance breadth. By contrast, in congruence with Martins et al. (2018) and several studies on insects (Blackburn et al. 2014; van Heerwaarden et al. 2016), we detected significant heritability for the critical thermal limits.

It was perhaps not surprising to find relatively low heritability in most traits given the likelihood that the ancestors of our study population had passed through at least two genetic bottlenecks in the recent past (Lombaert et al. 2010; Bock et al. 2015). A previous meta-analysis (Dlugosch and Parker 2007) showed that genetic bottlenecks do not result in the loss of broad-sense heritability in many invasive species but noted that few estimates of narrow-sense heritability exist for invasive species in their invasive range (but see Nespolo et al. 2014 for a rare exception). It is important to understand the extent to which invasive populations maintain additive genetic variance in fitness-related traits as this is a critical determinant of their capacity to evolve rapidly under novel environmental conditions.

Our data suggest that changes in the thermal optimum (T_{opt}) and performance breadth (T_{br}), which are predicted to occur as a result of shifts in the mean and variance of environmental temperature, respectively, are likely to occur much slower than changes in the critical thermal limits in the harlequin beetle. A critical question moving forward is whether climate change acts as an agent of selection primarily on performance at extreme temperatures (more relevant to CT_{min} and CT_{max}) or on performance at

Figure 4. Genetic variation in thermal performance curves (each line represents a family) associated with a vertical shift (potential change in maximal performance; top panel), horizontal shift (potential change in the thermal optimum; middle panel), and a specialist-generalist trade-off (a change in performance at high temperatures necessitates a decrease in performance at low temperatures, and vice versa; bottom panel). Most of the variation follows a specialist-generalist trade-off that suggests that it may represent an important evolutionary constraint in harlequin beetles. This figure was produced using MatLab code provided by Izem and Kingsolver (2005).

intermediate temperatures (more relevant to T_{opt} and T_{br}). Recent studies have emphasized the importance of extreme weather events as agents of selection (Campbell-Staton et al. 2017; Grant et al. 2017), suggesting that the evolvability of the critical thermal limits may be particularly important. On the other hand, if selection on performance at intermediate temperatures is stronger, then climate change may reduce the population mean fitness of the harlequin beetle because the thermal optimum and performance breadth are only weakly heritable.

Although several of the traits we examined were heritable, we also found evidence of genetic correlations that may constrain the evolution of thermal performance curves. We found weak evidence for a thermodynamic effect at both the phenotypic (correlation between T_{opt} and P_{max}; $P = 0.09$) and genetic (genetic

correlation between T_{opt} and $P_{max} = 0.93$, although this estimate was also statistically insignificant) levels. We also found evidence for a specialist-generalist trade-off. At the phenotypic level, CT_{min} and CT_{max} were positively correlated, demonstrating that individuals which performed best at the warmest temperatures were also likely to perform poorly at the coolest temperatures. At the genetic level, CT_{min} and T_{opt} were positively correlated, indicating that an evolutionary increase in the thermal optimum would reduce the capacity of the population to withstand extremely cold conditions. Finally, CT_{max} was strongly negatively correlated at the genetic level with performance at the two lowest temperatures, suggesting than an evolutionary increase in performance during heat waves would decrease the capacity for the population to withstand cold snaps. Similarly, when we analyzed thermal performance curves as a single function-valued trait, the majority of explained variation in thermal performance curves (26%) was described by a specialist-generalist trade-off. By contrast, P_{max} and AUC were positively correlated at the genetic level (although this correlation was not statistically significant), suggesting that an increase in maximal performance may lead to an increase in total performance capacity. On balance, our data suggest that thermal adaptation in the harlequin beetle will be constrained by a specialist-generalist trade-off, a pattern also observed in other insects (Gilchrist 1996; Latimer et al. 2011; Condon et al. 2015).

Our results should be interpreted with caution for several reasons. First, although our sample sizes were two- to fourfold larger than related studies, they may still have been insufficient to detect low to moderate heritability in thermal traits that are based on locomotor performance given the intrinsically high error associated with measuring such traits (Logan et al. 2018). Indeed, quantitative genetics studies often use sample sizes of many hundreds to thousands of individuals (Klein et al. 1973; Lynch and Walsh 1998). Nevertheless, logistical constraints limit the sample sizes of such studies, and the heritability of many traits have been successfully estimated with far smaller sample sizes than the ones we used here (e.g., Cox et al. 2017a,b). Moreover, locomotor performance and some physiological traits have been shown to be highly repeatable in a number species (e.g., Huey and Dunham 1987; Van Berkel and Clusella-Trullas 2018; K. Alujević, unpubl. PhD thesis), suggesting that, in the absence of overwhelming measurement error, single estimates of locomotor performance are likely to capture the "real" value. Additionally, we urge caution in interpreting our results in terms of extinction probabilities because other processes (e.g., behavior and acclimation) may also mediate the response of the harlequin beetle to climate change. Finally, our analyses are based on a single, invasive population. It is possible that other populations of the harlequin beetle have greater evolutionary potential, especially if those populations have gone through fewer genetic bottlenecks (as is likely the case with native populations in Central Asia).

In summary, the biological impacts of invasive species and climate change are often studied in isolation from one another, despite the fact that these phenomena will interact. For example, climate change may tip the competitive balance in favor of native or invasive species based on their adaptive potential relative to one another. We hypothesized that invasive species may be intrinsically more capable of adaptation to environmental change, given that many of them have already overcome rapid environmental change to become invasive in the first place (Dlugosch and Parker 2007; Lavergne and Molofsky 2007; Bock et al. 2015; Hodgins et al. 2018). Moreover, previous work has suggested that genetic bottlenecks may not appreciably reduce the evolutionary capacity of invasive species (Dlugosch and Parker 2007; Lavergne and Molofsky 2007). Instead, we found that a South African population of the harlequin beetle has relatively low evolutionary potential in the face of climate change, especially if selection gradients are strongest or selection events are most common at intermediate temperatures. The unique colonization history of this population (likely at least two recent bottlenecks) or strong selection in the first few generations after colonization may have contributed to this low genetic variation, but better historical information is needed to evaluate these possibilities. Whether invasive species elsewhere typically have lower evolutionary potential than their native counterparts is an outstanding question that requires the estimation of genetic architecture in native and invasive competitors from diverse taxa and from around the globe.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Additive genetic ($V_A \pm SE$), maternal ($V_M \pm SE$), and residual variances ($V_R \pm SE$), as well as narrow-sense heritabilities ($h^2 \pm SE$) for thermal performance traits in the harlequin beetle.

Table S2. Genetic correlations (below diagonal) and corresponding genetic covariances (above diagonal) for the traits that compose the shape of the thermal performance curve, as well as the area under the curve.

Table S3. Genetic correlations (below diagonal) and corresponding genetic covariances (above diagonal) between walking speed at each experimental temperature (v12, v18, etc.), as well as between walking speeds and the critical thermal limits (CT_{min} and CT_{max}, respectively).

Figure S1. Mean thermal performance curves (green lines) and associated model fits (fourth-order polynomial; black dashed lines) for 16 representative families in our study (ss = sample size for each family).

Figure S2. Variation in walking speed among harlequin beetles at each experimental temperature.