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Limited potential for adaptation to climate change in a broadly distributed marine crustacean

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The extent to which acclimation and genetic adaptation might buffer natural populations against climate change is largely unknown. Most models predicting biological responses to environmental change assume that species' climatic envelopes are homogeneous both in space and time. Although recent discussions have questioned this assumption, few empirical studies have characterized intraspecific patterns of genetic variation in traits directly related to environmental tolerance limits. We test the extent of such variation in the broadly distributed tidepool copepod *Tigriopus californicus* using laboratory rearing and selection experiments to quantify thermal tolerance and scope for adaptation in eight populations spanning more than 17° of latitude. *Tigriopus californicus* exhibit striking local adaptation to temperature, with less than 1 per cent of the total quantitative variance for thermal tolerance partitioned within populations. Moreover, heat-tolerant phenotypes observed in low-latitude populations cannot be achieved in high-latitude populations, either through acclimation or 10 generations of strong selection. Finally, in four populations there was no increase in thermal tolerance between generations 5 and 10 of selection, suggesting that standing variation had already been depleted. Thus, plasticity and adaptation appear to have limited capacity to buffer these isolated populations against further increases in temperature. Our results suggest that models assuming a uniform climatic envelope may greatly underestimate extinction risk in species with strong local adaptation.

Keywords: climate envelope model; local adaptation; thermal tolerance; experimental evolution

1. INTRODUCTION

The rapid pace of anthropogenic climate change poses an unprecedented threat to the planet's biological diversity [1]. The extent to which plastic physiological responses and evolutionary change might rescue natural populations threatened by climate change is largely unknown [2–9]. Until recently, most models predicting biological responses to climate change have assumed that species' environmental tolerances are static both in space and time. Predictions of geographical range shifts and extinction risk are most commonly generated by correlative models that use a species' occurrence data to describe its environmental niche, and then map that niche onto space under changing environmental conditions [10]. The merits of correlative models have been debated extensively in the literature [11–17]. In particular, theory predicts that adaptation or differences in environmental tolerance among populations might modify predicted outcomes [18–20], and there is a growing interest in accounting for these factors in trait-based mechanistic models [21]. However, few empirical studies have examined the effects of trait variation in space and time on predictions of extinction risk [22–24]. These are important considerations: models that assume a constant climatic envelope for a species will underestimate extinction risk when local adaptation creates individual populations that contain a subset of the tolerance phenotypes found in the species as a whole, and they will overestimate extinction risk when populations can evolve greater tolerance (figure 1) [26,27]. The ability to estimate extinction risks reliably therefore depends critically on evaluating (i) the range of plastic physiological responses possible, (ii) the magnitude of genetic variation for traits that govern environmental tolerance, and (iii) how this variation is distributed among populations. Although some of these data exist for a handful of species [28–30], our study is the first to describe each of these components in a single species over most of its geographical range.

Several recent studies suggest that species with narrow geographical distributions may have lower genetic variation for traits related to environmental tolerance, and hence diminished capacity to evolve in response to climate change [31]. This pattern is consistent with a larger body of work predicting that species with large geographical ranges will be less vulnerable to climate change [1,14]. However, a critical assumption underlying these predictions is that the broad tolerance present at the species level reflects the variation contained within individual populations. The possibility remains that even in wide-ranging species, strong local adaptation may create populations that contain only a subset of the tolerances found in the species as a whole.

Here, we test the hypothesis that populations of a broadly distributed species vary in their ability to respond to climate change, either through adaptation or physiological acclimation. We measured plasticity of thermal tolerance and the scope for adaptation to increased

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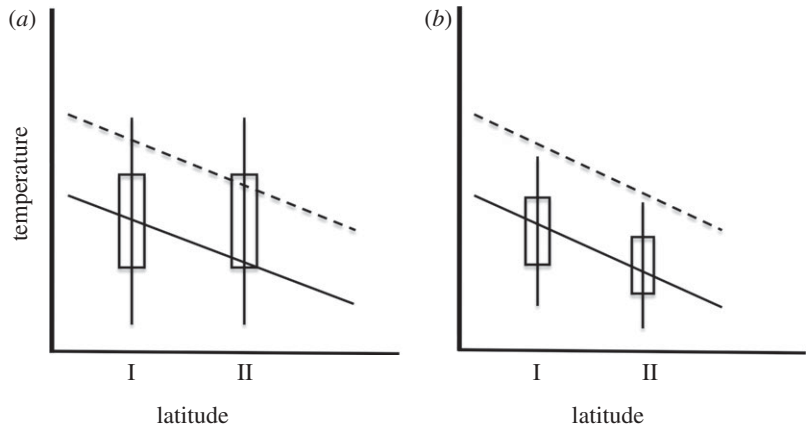

Figure 1. Correlative models of species' distributions may underestimate extinction risk if individual populations contain a narrower range of tolerance phenotypes than the species as a whole. In this simplified scenario, box plots show the hypothetical distribution of temperature-tolerance phenotypes in two populations lying along a latitudinal temperature gradient. Solid line shows current gradient; dashed line shows the future gradient. Populations can persist if they have some tolerance values lying above the new threshold. (*a*) With a broad range of phenotypes within populations and no local adaptation, both populations persist. (*b*) With a narrower range of phenotypes within populations and local adaptation, neither population persists, although population II could persist with gene flow from population I. The persistence of each population depends not just on the range of tolerance phenotypes in the species as a whole, but on the distribution of those phenotypes among and within populations (Redrawn from [25]).

temperatures in populations of *Tigriopus californicus*, a harpacticoid copepod that ranges over 3000 km of latitude from Baja California, Mexico (27°N), to southeast Alaska, USA (57°N). This species is an ideal system for examining the impacts of climate change on populations that occur in fragmented landscapes, because it is restricted to high intertidal and supralittoral rocky pools with low connectivity among populations [32,33]. High intertidal pools are subject to long periods of tidal emersion; thus, this copepod must tolerate a broad range of diurnal and seasonal variation in temperature. Prior work suggests that eurythermal species characteristic of such environments are often less sensitive to climatic variation than species that inhabit more stable environments [29,30]. On the other hand, many warm-adapted intertidal species and corals presently live close to the edge of their upper thermal limits, and thus *T. californicus* could be unexpectedly vulnerable to increased temperatures [34,35].

2. MATERIAL AND METHODS

(a) *Field collection*

We established 30 laboratory cultures of *T. californicus* from eight sites spanning more than 17° of the species range (figure 2, inset). For each site, we collected individuals from three to four pools encompassing as wide as possible a spectrum of potential thermal conditions (exposed and shallow versus shaded and deep). We initiated one laboratory culture (line) from each pool with 50 gravid females each, allowing us to sample the majority of the standing variation occurring within that pool [36]. We also installed a temperature datalogger (Thermochron ibuttons, no. DS1921G, Dallas Semiconductor) in each pool to collect hourly temperatures over the course of the following year. Dataloggers were attached to the rock surface at the bottom of the pool and thus likely recorded the coolest temperatures available to copepods in stratified pools. Cultures were each maintained in 250 ml of filtered sea water (32–34 ppt salinity) at 19°C under 12 L : 12 D conditions. Copepods were fed ad libitum (approx. 50 mg Aquadine ground spirulina fish food per culture per week), and 50–75% of the water in each culture was changed weekly. Cultures were maintained in the laboratory for two generations (four to six weeks per generation at this temperature) before measuring thermal tolerance.

(b) *Thermal tolerance measurements*

We measured thermal tolerance in the second laboratory reared generation for each of the 30 copepod lines as follows. We exposed copepods to a range of temperatures from the temperature that maintained 100 per cent survival to the temperature that produced 100 per cent mortality. Set temperatures ($n = 5–7$) were spaced at 0.2°C intervals and each line was tested with four to six replicate tubes per temperature, each holding five to six adult males. To control temperature as precisely as possible, trials were conducted in an ABI 2720 thermocycler with the copepods placed in 120 µl fresh sea water in a 400 µl thin-walled polymerase chain reaction (PCR) tube. We used a 2 h ramp up from 20°C followed by 1 h of exposure at the target temperature. Records from field dataloggers show that this is a realistic rate of change: temperatures in shallow pools may increase by 20°C over the course of 3 h on warm days (see the electronic supplementary material, figure S1*b*). Although tubes remained closed during thermal trials to prevent water loss, anecdotal evidence suggests that our thermal tolerance assays were not influenced by oxygen depletion: there was substantial head space in each tube, and decreasing the number of animals per tube and/or increasing the surface area exposed to air by performing assays in shallow containers did not change mortality rates. Mortality was assessed under a dissecting microscope at least 40 h after the temperature exposure ended. We then estimated the LT_{50} for each copepod line by plotting the proportion of surviving individuals versus temperature ($n = 4–6$ tubes per temperature per line) and fitting a logistic regression to obtain a point estimate for 50 per cent mortality.

(c) *Selection experiments*

We tested the ability of each population to respond to selection for increased thermal tolerance by exposing each of

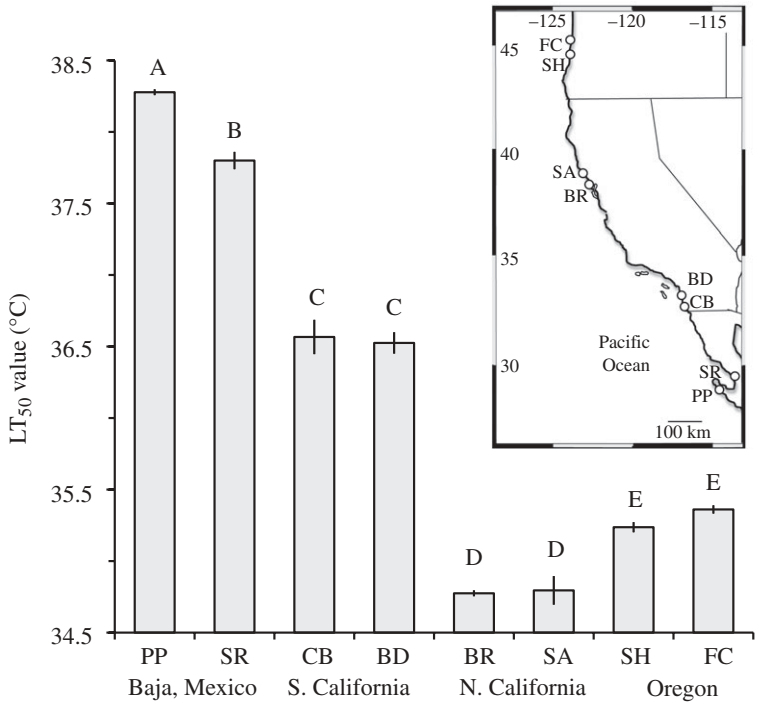

Figure 2. Mean thermal tolerance (LT_{50}) ± s.e. of adult male *T. californicus* from eight North American populations ($n = 3–4$ lines per population) ranging from Baja California, Mexico to OR, USA. Values shown are for the second laboratory reared generation, raised under a constant 19°C environment. Thermal tolerance varied among populations (ANOVA: $F_{7,22} = 608.0$, $p < 0.0001$). Shared letters above bars indicate populations whose means do not differ (Tukey–Kramer, $p > 0.05$). Inset: Sampling locations: Punta Prieta, MX (PP) 27°00′ N, 114°03′ W; Santa Rosalia, MX (SR) 28°39′ N, 114°15′ W; Cabrillo Point, CA (CB) 32°04′ N, 117°15′ W; Bird Rock, CA (BD) 32°49′ N, 117°16′ W; Bodega Marine Reserve, CA (BR) 38°04′ N, 123°19′ W; Salt Point, CA (SA) 38° 20′ N, 123° 33′ W; Strawberry Hill, OR (SH), 44°15′ N, 124°06′ W; Fogarty Creek, OR (FC) 44° 50′ N, 124°03′ W.

the 30 lines to nine to 10 generations of mass selection for the six northern populations, and four to five generations of mass selection for the two populations from Baja California, Mexico, where cultures were initiated later than for California and Oregon. For each laboratory reared culture, we exposed all available mate-guarding pairs (100–400 pairs of males + virgin females) to the temperature that produced 40–90% mortality in adult males (2 h ramp up, 1 h at target temperature). These same temperatures typically produce about 20 per cent lower mortality in females, which have higher thermal tolerance than males. To accommodate the larger numbers of copepods, we performed these experiments in 50 ml containers of filtered sea water, floated in temperature-controlled water baths. We founded the next generation in each culture using exactly 40 mate-guarding pairs, selected randomly from the surviving individuals in each line. For each culture, we also maintained an unselected line, established each generation using 40 randomly selected mate-guarding pairs. Maintaining large effective population sizes in each generation minimized the loss of variation to drift [36]. We estimated the LT_{50} values in all selected and unselected lines after 5 and 10 generations following the procedure described above. We then calculated realized heritability of thermal tolerance in each line as the total response to selection divided by the cumulative selection differential (see additional description in the electronic supplementary material).

(d) *Plasticity experiments*

To test the ability of copepods to respond to increased thermal stress through acclimation, we compared the thermal tolerance of six of the eight populations reared under warm and cool temperature regimes. To minimize effects of laboratory adaptation, plasticity experiments were conducted on the first laboratory reared generation for lines collected separately from the lines used for the selection experiment. For this experiment, we established four cultures for each population × temperature treatment. To avoid confounding the effects of selection and plasticity, each culture was initially established with six newly gravid females, and each female was maintained separately at first to ensure that she survived to produce her first brood, after which all females and offspring for one treatment were combined into a single culture. Experiments were conducted on the offspring once they had been reared to adulthood under their respective temperature treatments. The cool treatment consisted of a constant 19°C, while the warm treatment consisted of a 19°C for 18 h/28°C for 6 h cycle, which was the warmest treatment we were able to use without producing mortality in some populations. Temperatures were maintained at ±1°C using Percival incubators (Iowa 50036). We used diurnal cycling rather than constant temperatures for the warm treatment because constant 28°C temperatures produced some mortality, and because cycling warm and cool temperatures approximates conditions observed in pools during spring and summer months (electronic supplementary material, figure S1*b*). We measured LT_{50} in all warm- and cool-raised lines as described above.

(e) *Molecular methods*

We estimated neutral molecular diversity in all eight populations by genotyping 30 copepods from each population at

four microsatellite markers (TC1202, TC1203, TC56J2, and TCS030) originally described by Harrison *et al.* [37]. We chose these four loci because they reliably amplified in all eight populations. DNA extraction followed Lee & Frost [38]. Three markers (TC1202, TC56J2 and TCS030) were amplified in a multiplex PCR reaction, while one marker (TC1203) was amplified singly. Both multiplex and single-marker reactions were carried out in 10 µl final volume, with 1X PCR buffer, 200 µM each dNTP, 1.5 mM $MgCl_2$, 0.75 pmol each forward and reverse primer (forward primers were fluorescently labelled with FAM, VIC or NED), 0.125 U Qiagen HotStar Taq DNA polymerase and 5–10 ng genomic DNA. PCR conditions consisted of 95°C for 15 min, followed by 32 cycles of 94°C for 30 s, 55°C or 53°C (depending on the locus and population) for 90 s, 72°C for 1 min and concluded with a 30 min extension at 72°C. For genotyping, 0.5 µl of product from each PCR reaction was added to 9 µl formamide containing GeneScan-500 (LIZ) size standard (Applied Biosystems, Foster City, CA, USA) and run on an ABI Prism 3100 Genetic Analyzer in the UC Davis DNA sequencing facility. F_{ST} and expected heterozygosity were estimated in GENEPOP v. 1.2 [35].

We compared F_{ST} with the Q_{ST} for thermal tolerance. Q_{ST} was estimated from phenotypic variance among populations and mean realized heritability of thermal tolerance × phenotypic variance within populations as an estimate of additive variance (see additional description in electronic supplementary material).

(f) *Statistical methods*

For both the plasticity and selection experiments, we estimated LT_{50} values via logistic regression and analysed variation in LT_{50} among populations using a one-way ANOVA, with lines as replicates. A *post hoc* Tukey–Kramer analysis was used to test for significant differences between pairs of populations. All analyses were performed in R v. 2.8.1 [39].

3. RESULTS

We sampled eight populations of *T. californicus* from the centre of the species' distribution to near the southern range edge and spanning 17° of latitude (figure 2, inset). Our laboratory assays of heat tolerance show that *T. californicus* populations are locally adapted to temperature, with the highest thermal tolerance found in populations at warm, low-latitude sites (figure 2 and electronic supplementary material, figure S1). Moreover, the distribution of thermal tolerance phenotypes within populations is extremely narrow compared with the range of thermal tolerances found in the species as a whole: 3.5°C separate the mean tolerances of the most and least tolerant populations, whereas the standard deviation in lethal temperatures within populations is 0.29 (±0.03)°C. Less than 1 per cent of the additive variance for thermal tolerance was partitioned within populations, with a Q_{ST} for lethal temperature greater than 0.99.

We measured the plasticity of thermal tolerance by rearing *T. californicus* from six of the eight sampled populations under chronic heat stress. Warm-reared lines expressed an additional 0.5–1.0°C of thermal tolerance in each population (figure 3). There was a negative relationship between latitude and plasticity, with low-latitude populations showing greater plasticity (figure 3). Although all populations expressed plasticity for thermal tolerance, the magnitude of plasticity was still small in comparison with the range of variation found across the species as a whole: none of the northern populations exhibited a capacity for acclimation that reached the tolerances found in southern populations (figures 2 and 3).

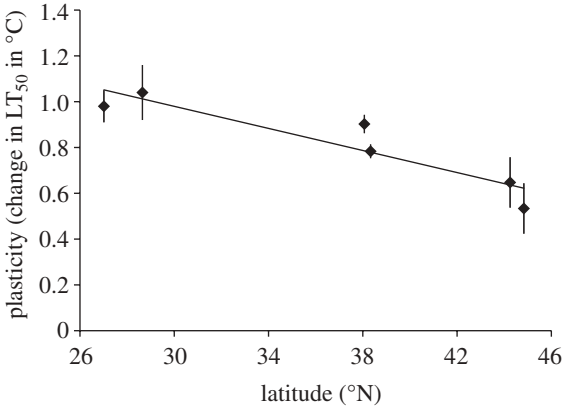

Figure 3. Plasticity of thermal tolerance versus latitude for six populations of *T. californicus*. Plasticity was measured in the second laboratory reared generation as the difference in LT_{50} values ± s.e. between lines raised under cool (constant 19°C) and warm (daily cycles of 19°C for 18 h, 28°C for 6 h) conditions ($n = 4$ lines per population × treatment combination). A linear regression reveals a negative relationship between latitude and plasticity ($R^2 = 0.82$, $p = 0.01$).

To test the ability of populations to adapt to increasing temperatures, we measured the realized heritability of thermal tolerance by exposing three to four lines from each of the eight sites to four to 10 generations of mass selection on thermal tolerance, maintaining population sizes of 40 pairs per line in each generation. Six of eight populations responded to selection; however the maximum response was 0.53°C (in population BR; figure 4). Ten generations of strong selection did not bring the tolerances of northern populations to the levels found in southern populations. Furthermore, only two populations (BD and SH) exhibited a significant increase in the cumulative response to selection between generations five and 10.

Analysis of the distribution of genetic variation at four presumably neutral microsatellite loci [37] in all eight populations revealed a high level of subdivision at the microsatellite loci, mirroring quantitative subdivision ($F_{ST} = 0.72$, $Q_{ST} = 0.995$). Microsatellite variation within populations was low, with an average of 1.6 loci per population that were fixed for one allele and a mean heterozygosity of 0.22 (figure 5). To test for an effect of drift on quantitative variation, we compared the heritability of thermal tolerance to neutral heterozygosity; however, regression of heritability on heterozygosity reveals a non-significant relationship ($R^2 = 0.18$, $p = 0.30$). To test for the reduction of variance by selection, we compared heritability of thermal tolerance to the initial thermal tolerance for each line, and this regression reveals a negative relationship between the two variables ($R^2 = 0.14$, $p = 0.049$).

4. DISCUSSION

Recent models of extinction risk imposed by climate change highlight the theoretical influence of temporal and spatial

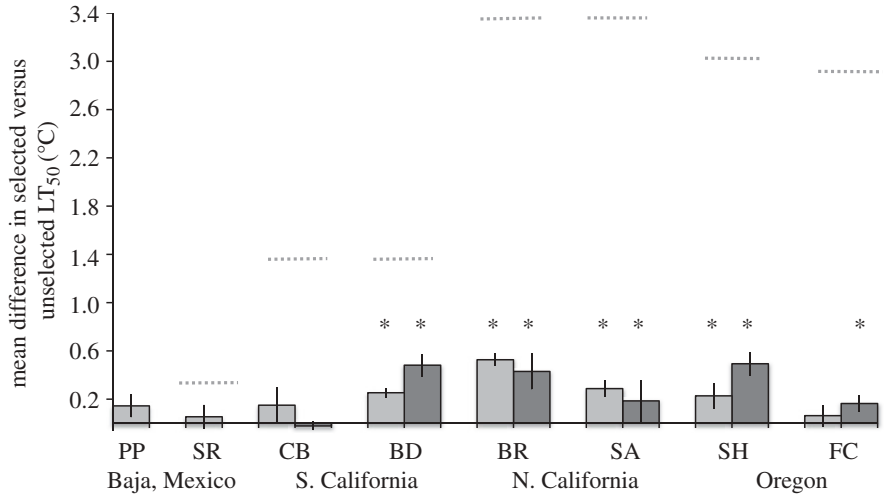

Figure 4. Response to selection on thermal tolerance in *T. californicus* measured as mean difference ± s.e. between the thermal tolerance (LT_{50} value) of selected versus unselected lines within a site ($n = 3–4$ selected and unselected lines per site). Asterisks denote means which were significantly different from 0 at $p = 0.05$. Dashed lines show the difference between unselected lines in a site and the most tolerant population found for the species as a whole (PP). Response to selection was measured in generations 5 and 10 in all populations but PP and SR, where each was exposed to only five generations of selection. In only two populations (BD and SH) was the cumulative response significantly different between generations 5 and 10 (Student's *t*-test, $p < 0.05$). Light grey bars, generations 4–5; dark grey bars, generations 9–10.

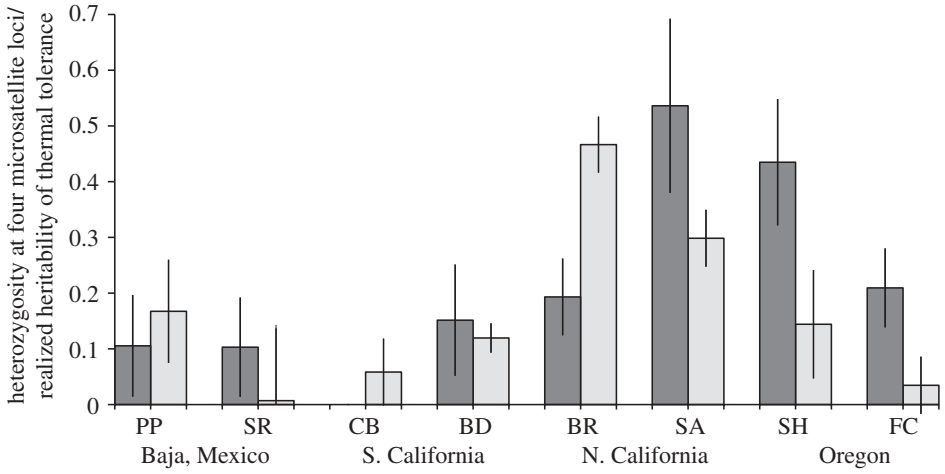

Figure 5. Mean quantitative diversity in thermal tolerance (±s.e.) as measured by realized heritability ($n = 3–4$ lines per population; light grey bars), measured after five generations of selection, and mean neutral diversity as measured by expected heterozygosity (dark grey bars) (±s.e.) across four microsatellite loci [37] for eight populations of *T. californicus*.

variation in tolerance on the reliability of predicted responses [18–20]. The present study demonstrates empirically that these are important considerations. The distribution of thermal tolerance phenotypes within populations of the copepod *T. californicus* is extremely narrow when compared with the range of thermal tolerances found in the species as a whole, with a Q_{ST} for thermal tolerance >0.99. Consequently, models based on the climate envelope for the species as a whole would fail to predict extinctions in locally adapted populations with a narrower range of tolerances. Nevertheless, the possibility remains that the tolerances of individual populations could change through genetic adaptation or phenotypic plasticity.

All of the populations exhibited some phenotypic plasticity for thermal tolerance. However, all of the northern populations lacked the capacity for acclimation that would allow them to reach the tolerances found in southern populations (figures 2 and 3). In our selection experiments, six populations evolved increased tolerance; however, even 10 generations of strong selection could not bring the tolerances of northern populations to the levels found in southern populations (figure 4). Furthermore, only two populations (BD and SH) exhibited a significant increase in the cumulative response to selection between generations five and 10. This suggests that the maximum response to selection may already have been achieved in four populations, including the two with the lowest initial tolerance.

Lack of genetic variation is not generally thought to limit evolutionary response, given the evidence for variation in most traits in most taxa [40]. The paucity of additive genetic variation for increased thermal tolerance within populations of *T. californicus* (and hence diminished capacity to respond to selection) is striking given evidence for abundant variance in this trait in other taxa [41], and substantial variation among populations in *T. californicus*

(figure 2). Low potential for adaptation within populations may be caused by genetic drift owing to small effective population sizes, the removal of variation by selection or strong correlations with other traits [8,42]. In the first case, there should be a correlation between neutral and quantitative diversity, whereas in the second case variation should be reduced only in the trait(s) under selection, and across populations the amount of variation should be correlated with the mean value of the trait. Drift is especially plausible for *T. californicus* because of bottlenecks during extinction–recolonization events [43]. The lack of a significant relationship between neutral heterozygosity and heritability of thermal tolerance suggests that variation in the capacity to respond to selection is not driven solely by drift. However, the low observed levels of microsatellite diversity reduced the power to detect a relationship between neutral and quantitative variation. There was a negative relationship between thermal tolerance and realized heritability of thermal tolerance, suggesting that variation is being removed by selection. Nevertheless, low levels of microsatellite variation and high F_{ST} values imply that genetic drift also plays a role in reducing levels of variation within populations.

The distribution of variation for environmental tolerance among populations also clarifies mechanisms setting this species' southern geographical range limit. A geographical range limit is an evolutionary limit in the sense that it represents a failure to adapt to the conditions beyond the range boundary. Hypotheses for why a species should fail to adapt to conditions beyond its range boundary fall into two classes: (i) antagonistic gene flow from more central populations [44] and (ii) limited variation at the edge, either owing to genetic drift or fundamental limits in the traits themselves [31,45,46]. If adaptation in edge populations is limited by antagonistic gene flow, then populations at the edge of a species range should contain variation for environmental tolerance (and hence the capacity to evolve increased tolerance during periods of environmental change). On the other hand, if edge populations have no additional variation in the range-limit setting trait(s) [28,29], then populations at the equatorward edge may have no capacity to evolve increased tolerance in the face of increasing temperatures. The pattern of subdivision for neutral markers and quantitative variation in thermal tolerance in *T. californicus* does not fit our expectations for either of these processes. Heritable variation in thermal tolerance is low in southern range edge populations of *T. californicus*, but it is also low in some populations throughout the species' range (figure 5).

The fact that variation among populations so greatly exceeds variation within populations in *T. californicus* highlights a fundamental limitation of present attempts to model biological responses to climate change. Although local adaptation to temperature is common [25,47,48], most correlative approaches to species distribution modelling assume that every population of a species has the same environmental tolerance. As such, these models do not predict extinction for a given population until conditions reach the most extreme found within the species' range. In *T. californicus*, however, 3.5°C (more than 10 phenotypic standard deviations) separate the lethal temperatures of the least and most thermally tolerant populations. Notably, in northern populations neither phenotypic plasticity nor selection on standing genetic variation can achieve the tolerances observed in southern populations. Moreover, temperature dataloggers from the six northern sites show that pools at each site currently heat to within 1.0°C of lethal temperatures in spring and summer months, suggesting that *T. californicus* already exists close to its upper thermal limit within the interior of its range (see the electronic supplementary material, figure S1). This raises the possibility of a patchwork of population-level extirpations with warming temperatures, rather than a simple poleward range shift, a scenario that has also been suggested for other locally adapted taxa [49,50]. Interestingly, short-term selection on standing variation does not lead to the evolution of greater tolerance in northern populations, even though southern populations have evolved greater tolerance over millions of years of evolutionary time. This is an important distinction, as contemporary climate change is likely to act on much shorter timescales than those that separate divergent populations in this species.

Tigriopus californicus are restricted to high intertidal and supralittoral pools. Behaviour and strong predation pressure appear to constrain dispersal and gene flow between rocky outcrops; however, pools within an outcrop appear to be relatively homogeneous at neutral loci [32,43]. Although *T. californicus* may be extreme in its level of genetic divergence among populations, a growing body of evidence suggests that many other terrestrial and marine organisms also live in fragmented landscapes, with weak demographic and genetic connections among populations, and strong local adaptation to prevailing abiotic conditions [25,33,47,48,51]. Our results suggest that many local populations of *T. californicus* are at or near their capacity to respond physiologically or adaptively to further warming, at least at the rate that temperature is presently increasing. Most attempts to model species' responses to climate change neglect these potentially widespread biological features, and are likely to underestimate extinction threats posed by ongoing anthropogenically driven increases in both sea water and atmospheric temperatures. Before these climate envelope models can be reliably used to predict extinction risk, they may therefore need to be modified to include critical factors such as population structure, genetic connectivity and the capacity for local populations to respond to changing environments.

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