

Accelerating local extinction associated with very recent climate change

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Abstract

Climate change has already caused local extinction in many plants and animals, based on surveys spanning many decades. As climate change accelerates, the pace of these extinctions may also accelerate, potentially leading to large-scale, species-level extinctions. We tested this hypothesis in a montane lizard. We resurveyed 18 mountain ranges in 2021–2022 after only ~7 years. We found rates of local extinction among the fastest ever recorded, which have tripled in the past ~7 years relative to the preceding ~42 years. Further, climate change generated local extinction in ~7 years similar to that seen in other organisms over ~70 years. Yet, contrary to expectations, populations at two of the hottest sites survived. We found that genomic data helped predict which populations survived and which went extinct. Overall, we show the increasing risk to biodiversity posed by accelerating climate change and the opportunity to study its effects over surprisingly brief timescales.

KEYWORDS

climate change, extinction, genomics, niche, range shift, reptile

INTRODUCTION

Climate change may soon be a major threat to global biodiversity. For example, some projections suggest that Earth may lose up to a third (or more) of its species to climate change in the coming decades (Bellard et al., 2012; Román-Palacios & Wiens, 2020; Thomas et al., 2004; Urban, 2015). Much of the evidence for the impacts of recent climate change has come from repeated field surveys over time (Parmesan, 2006). Numerous studies have documented that species have shifted their geographic distributions to higher elevations and higher absolute latitudes, as predicted given warming climates (Brusca et al., 2013; Chen, Hill, Ohlemüller, et al., 2011; Chen, Hill, Shiu, et al., 2011; Freeman & Class Freeman, 2014; Lenoir et al., 2020; Moritz et al., 2008; Parmesan, 2006; Rumpf et al., 2019). The loss of populations from lower elevations and latitudes suggests that climate-related local extinctions have already occurred (Sinervo et al., 2010; Wiens, 2016; Wilson et al., 2005). This process could lead to widespread, large-scale, species-level extinctions, especially if the pace of climate change increases (Román-Palacios & Wiens, 2020; Thomas et al., 2004; Urban, 2015).

The surveys and resurveys used to document these local extinctions have generally been separated by many

decades. For example, in a review of elevational range shifts (Rumpf et al., 2019), the average time between surveys was 68.5 years (range = 10–159 years, $n = 22$ studies; Table S1). Thus, a limiting factor for this research has been the need for detailed distributional data from decades ago. Yet, as climate change has accelerated (IPCC, 2021), similar effects might now be seen over much shorter timescales. An urgent question is whether local extinctions have accelerated along with the pace of climatic warming.

Here, we document dramatic and accelerating local extinctions in response to recent climate change over the past ~7 years. We focus on a montane species (Yarrow's Spiny Lizard; *Sceloporus jarrovi*) among 18 isolated mountain ranges in southeastern Arizona (Figure 1). This is an abundant, conspicuous, and approachable species that is easily found while they are basking on large rocks during daylight hours. We combine distributional, climatic, and genomic data to examine these climate-related extinctions. Specifically, we: (1) document rapid loss of many warm-edge populations between surveys in 2013–2017 and 2021–2022 (Appendix S1; Dataset S1; all datasets and Supporting Information available in Holzmann et al., 2023); (2) compare these losses to warm-edge range contractions in other studies that involved much longer timescales (Appendix S2; Dataset S2); (3)

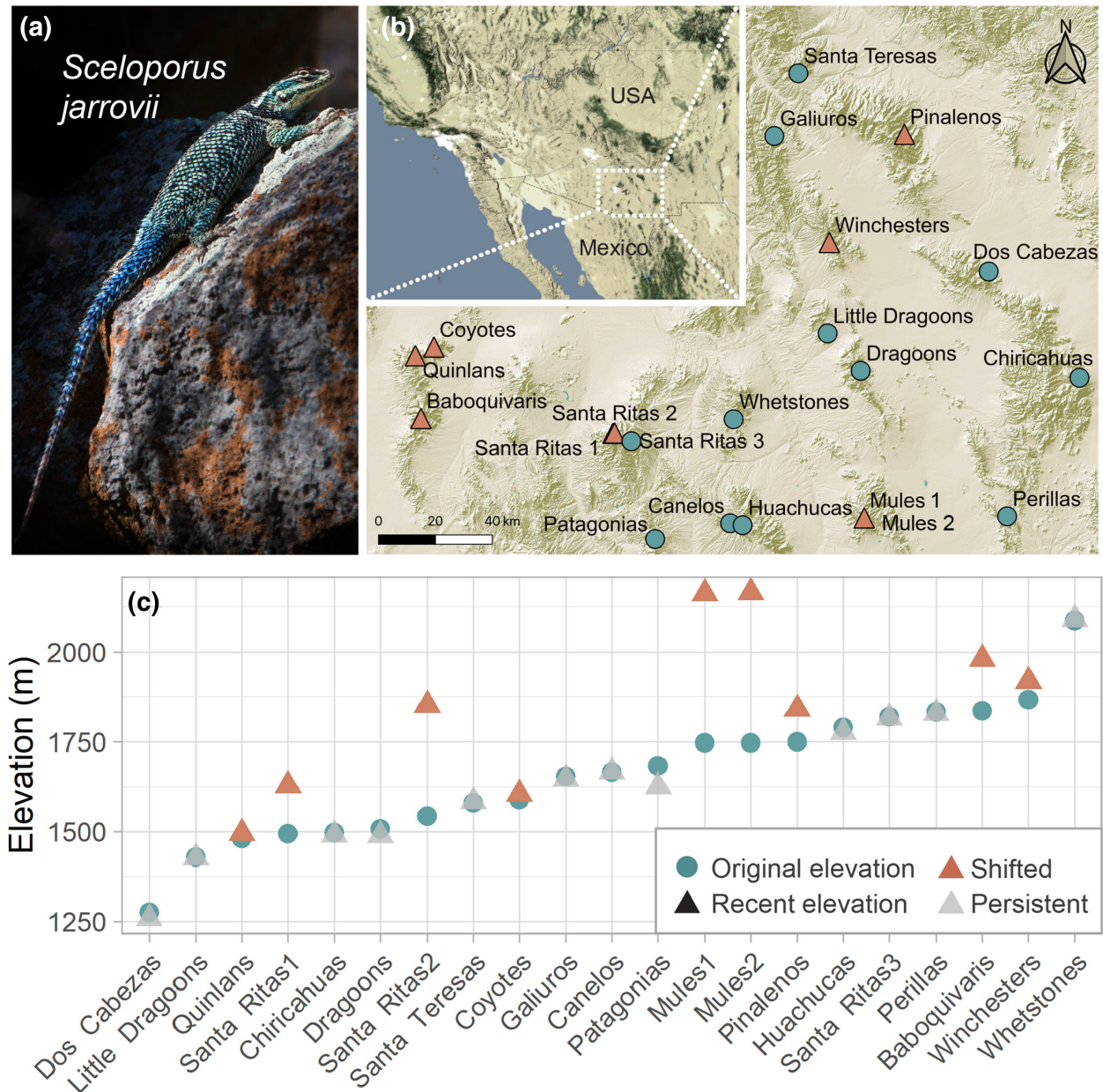


FIGURE 1 Distribution of the focal species among mountain ranges and among elevations over time. (a) An adult male Yarrow's Spiny Lizard (*Sceloporus jarrovi*). (b) Distribution of surveyed transects of *S. jarrovi* among 18 mountain ranges in southeast Arizona (see inset), showing populations that persisted at their lowest elevation between surveys (cadet blue circles) or shifted upwards due to local extinction (orange triangles). Nearby sites (Santa Ritas 1–2 and Mules 1–2) are shown together. (c) Lowest-elevation range limits for *S. jarrovi* on each transect, for the initial surveys (2013–2017; cadet blue circles) and resurveys (2021–2022; grey and orange triangles). Transects with orange triangles showed an upward shift between surveys, whereas those with grey triangles showed no shift or a small downward shift between surveys. There is one transect per mountain range, except the Santa Ritas (with 3) and the Mules (with 2).

use historical records to evaluate whether the rate of range contraction in *S. jarrovi* has accelerated recently (Appendix S3); and (4) test what factors explain the variation in climate-change responses among mountain ranges, including past climate (i.e. if populations at the lowest, hottest sites went extinct, as expected), recent climate change (i.e. if populations exposed to greater or faster warming went extinct), and levels of genetic variation (i.e. if populations with less genetic variation were more likely to go extinct).

METHODS

Field surveys

The distribution of *Sceloporus jarrovi* among 31 mountain ranges in southeast Arizona was previously documented in 2013–2017 (Wiens et al., 2019). These 2013–2017 surveys estimated its lowest elevational range limits for at least one elevational transect on each of 18 mountain ranges (Figure 1; data in Dataset S1); it is absent from the other

13 ranges. The lowest range edge is where populations are predicted to go extinct as the climate warms (e.g. Parmesan, 2006). We refer to a transect as a series of locations surveyed along an elevational gradient and a site as a specific location along the transect, defined by an elevation and a set of coordinates. A population was a site or set of nearby sites where the focal species was found.

Resurveys were conducted in 2021–2022 (Dataset S1). We resurveyed 21 transects among these 18 mountain ranges (see Appendix S1). Surveys generally started at low elevations, proceeded to higher elevations and extended below the lowest elevation previously found for *S. jarrovi* on each transect. As explained in Appendix S1, possible downward shifts were almost certainly not strongly underestimated (and downward shifts would not impact the estimates of upward shifts if they were underestimated).

The resurvey was stopped if *S. jarrovi* was found at or below its previous lower range limit on that transect (indicating no upward range contraction). If *S. jarrovi* was not found at its previous limits, the survey was repeated 1–5 additional times before inferring absence at those low-elevation sites (median = 3 total surveys/transect, $n = 9$ transects with upward shifts; Tables S2 and S3). One of the two absence sites that was visited only twice (Baboquivaris) was searched repeatedly on the second visit, so that it was searched three times in total. Details of surveys at each location are in Appendix S1. The number and duration of surveys for transects with inferred local extinction are given in Tables S2 and S3. Information for other transects is summarized in Table S4. Searches at sites with genetic samples are summarized in Table S5. Once the relevant location was arrived at, the species was generally found on the first search and in 0–27 min (if present; Tables S4 and S5). We found no changes in habitat between surveys at absence sites (e.g. deforestation).

Several lines of evidence suggest that the apparent absence of *S. jarrovi* at these warm-edge sites represents local extinction (and not failure to find them). These include: (1) among 29 sites where this species remained extant between surveys (Tables S4 and S5), it was found on either the first resurvey (83%) or the second (17%). (2) Conversely, there were no revisited sites where it was found only after a third (or fourth) survey. (3) When found on a given resurvey, it was found (on average) after only 8 min (29 transects; Tables S4 and S5; or 17 min including unsuccessful searches). By contrast, the total average time spent searching at locations with inferred absences was 3:44 h (range = 0:53–9:52; 10 locations; Table S3). (4) Most surveys that found *S. jarrovi* to be absent at low elevations found it present at higher elevations or at other locations that same day (65.6%; 21/32; Table S2). In the other 11 cases, it was the only transect visited that day (but related lizard species were found on the transect that day in 9/11 of these cases; Table S2). (5) Previous analyses suggest that a

low-elevation congener (Clark's Spiny Lizard; *Sceloporus clarkii*) is excluded from higher elevations by *S. jarrovi* (Wiens et al., 2019). In 8/9 transects with upward shifts for *S. jarrovi* (all but the Winchesters), we observed *S. clarkii* at specific sites where *S. jarrovi* had previously occurred, further supporting the absence of *S. jarrovi* at these sites (Appendix S1; Table S6; Dataset S1). This was the case for all transects with an upward shift in *S. jarrovi* that was >52 m elevation. We give further details about sampling and additional evidence for local extinction in Appendix S1 (including discussion of dispersal, non-climatic factors, and extinction mechanisms).

Historical records

For comparison to the recent range shifts (2013–2017 to 2021–2022), we quantified upward range shifts prior to the initial survey (2013–2017) in each mountain range (Table S7). We assembled historical records and searched for the lowest recorded site in each mountain range on or adjacent to our transects (details in Appendix S3). Absence at these sites was documented in 2013–2017 and again (for many sites) in 2021–2022.

Climate data

Climatic data were extracted from ClimateWNA (Wang et al., 2012) from 1901 to 2021. GPS coordinates (longitude, latitude and elevation) were used to determine climatic values for each site (Dataset S3). Five climatic variables were analysed: (i) mean annual temperature (MAT), (ii) mean warmest-month temperature (MWMT), (iii) mean annual precipitation (MAP), (iv) degree-days below 0°C (DD0), and (v) Hargreaves climatic-moisture deficit (CMD). MAT is a standard measure of climatic temperature and climate change. However, increases in the hottest temperatures might better predict climate-related local extinctions (Román-Palacios & Wiens, 2020). We used MWMT as the closest proxy for maximum temperature in the ClimateWNA database. Limited precipitation (MAP) might also strongly impact populations. Finally, niche-modelling analyses of *S. jarrovi* in south-east Arizona (Wiens et al., 2019) suggest that their range limits are most strongly determined by the last two variables (DD0 and CMD), which reflect cold temperatures (DD0) and climatic moisture (CMD).

Climate change between surveys was evaluated for each variable (Dataset S3). Given year-to-year variability, it may be problematic to consider only the year of each survey. Furthermore, species' responses presumably reflect temperatures from preceding years. However, the main time window here was limited (4–9 years between surveys). We therefore used mean climate data from the 2 years preceding each survey (e.g. for 2013, we

averaged 2011 and 2012 values). We estimated the rate of change in each climatic variable as the total change between surveys (using 2-year averages), divided by the time between surveys.

A few pairs of climatic variables were correlated in their distribution among low-elevation sites (Table S8), as were changes in some pairs (Table S9). However, we did not perform any single statistical analysis that included multiple climatic variables, so these correlations should not be problematic.

Population-genomic data

We used a dataset of restriction-site-associated DNA sequencing (RADseq) for *S. jarrovi* populations from a previous study (Wiens et al., 2019). The dataset included 115 individuals, 1609 loci, 3218 alleles and 428,203 aligned nucleotide sites. We also resurveyed sites where genetic samples were obtained. We give details of these data and analyses in Appendix S4.

Statistical analyses

Analyses were performed in R version 4.1.2 (R Core Team, 2019). First, we quantified upward elevational shifts in the lowest-edge range limits over time (2013–2017 vs. 2021–2022): the difference in elevation between the lowest site at which *S. jarrovi* occurred in the initial survey and the lowest site in the resurvey (Dataset S1). We also quantified the rate of elevational shift: the elevational shift divided by the years between surveys. Given that surveys and resurveys were each conducted over two or more years, we used the specific year in which we recorded the lowest-elevation individual in that survey interval (2013–2017 vs. 2021–2022). Since no *S. jarrovi* were found at all on one transect (Mules 1) in 2021–2022, we used the year of the first resurvey there (2021).

We first tested whether elevational range shifts at the lowest edge were significantly different from zero (two-sample *t*-test), given that both upward and downward shifts were possible. We next compared the rate and magnitude of the upward lowest-edge shifts here (and overall lowest-edge shifts) to those from studies of other organisms (Appendix S2; Table S1). We then compared these upward lowest-edge shifts to those inferred using historical records for *S. jarrovi* (Appendix S3; Tables S6 and S7) to see whether rates increased over time. We also compared rates of upwards lowest-edge shifts in *S. jarrovi* to upwards highest-edge shifts in *S. clarkii*. For all these analyses, we checked continuous variables for normality before applying parametric tests using the function ‘shapiro.test’ in the *stats* package in R. The one dataset that initially failed was ln-transformed, after which it passed. We treated each transect as a separate unit for analysis. Only two mountain ranges had >1 transects, and these

transects could have very different climate-change responses (compare Santa Ritas 1–3; Figure 1).

We acknowledge that it is unknown when exactly the range shifts occurred between surveys. Nevertheless, rates are valuable for comparing range shifts over different timescales, especially in comparisons to older records (Table S7) and other studies (Table S1).

Faster rates over shorter timescales might simply reflect the time dependence of rates (e.g. Hunt, 2012). We tested this possibility using data from the meta-analysis (with many different durations among studies; Table S1). Rates of upward range shifts were not significantly correlated with time between surveys ($r = -0.366$, $p = 0.086$, $n = 22$ studies).

We tested if the initial lowest elevation on a transect predicted if the lowest-edge populations persisted or went extinct between surveys. For each transect, we classified the lowest-elevation site as either persistent or extinct between surveys. We predicted that *S. jarrovi* would go extinct in the lowest-edge populations in mountain ranges in which the (initial) lowest-edge populations were lower than in other ranges (since these populations may be closer to the species' upper climatic temperature limits). We also tested if populations in initially hotter or drier climates (average for the 2 years preceding the first survey) were more likely to go extinct. We used logistic regression, given that we were analyzing a binary dependent variable (extinction vs. persistence) and continuous predictor variables (elevation and climate). We used the function ‘glm’ (binomial distribution) in *stats*. We estimated *p*-values with a Type-II analysis of deviance using the ‘Anova’ function of the R package *car* (Fox & Weisberg, 2018).

We also tested if those lowest-elevation populations that went extinct experienced more climate change between surveys or a faster rate of climate change. For the lowest-elevation site on each transect (in the initial survey), we quantified the difference between surveys (the average of the two preceding years) for each climatic variable as the amount of climate change. The rate of climate change was the amount of climate change divided by the years between surveys. We again divided transects into those on which *S. jarrovi* went extinct at their lowest-elevation site(s) and those on which it persisted. We used logistic regression to test if rates of change and absolute change were greater at the lowest-elevation sites at which *S. jarrovi* went locally extinct. Analyses were performed separately for each climatic variable.

We predicted that populations that went extinct would have lower genetic diversity, whereas surviving populations would have higher genetic diversity and greater potential to adapt to climate change evolutionarily (Chevin et al., 2010; Hoffmann & Sgrò, 2011; Visser, 2008). The generation time for *S. jarrovi* is ~1 year (Ballinger, 1973; Gadsden & Estrada-Rodríguez, 2008), such that there is time for genetic evolution between surveys.

For analyses of genetic diversity (unlike range shifts), individuals from nearby sites had to be grouped.

Otherwise, most sites would have only one individual, and we could not calculate population-level genetic diversity. We grouped individuals into populations ($n=25$; Table S10) based on the localities where each genetic sample was collected (detailed criteria in Appendix S4; Dataset S4). Some sites with genetic data were located at higher elevations (not the lowest site on a transect). We performed secondary analyses after excluding genetic samples that were not from the lowest-edge sites ($n=12$ populations retained; Table S10). These exclusions reduced the number of populations to one per mountain range. In another alternative analysis, we considered two populations (Santa Ritas 1 and Winchesters) as persistent that were treated as locally extinct in the main analyses (given local extinction at nearby lowest-elevation sites on these transects; see Appendix S4).

We tested if genetic variation (π) predicted which populations survived recent climate change using logistic regression (binomial distribution with two levels, extinct vs. persistent). To estimate genetic variation (details in Appendix S4), we used nucleotide diversity (π), calculated with the command-line tool *pixy* (Korunes & Samuk, 2021). Analyses were performed for the primary and reduced RADseq datasets for all populations (Datasets S5 and S6, respectively), and for only the lowest-edge populations for each mountain range ($n=12$).

We expected populations with greater genetic diversity to have greater potential for adaptive evolution and larger changes in their realized climatic niches. Therefore, we tested for a correlation between niche change (i.e. change in climatic variables between surveys; see above) in each climatic variable and nucleotide diversity (π). This was done for the lowest-edge populations (with genetic data) that persisted ($n=7$). We used Pearson's correlation with the function 'cor.test' in *stats*. Despite our prediction of a correlation between niche change and genetic diversity, changes in realized climatic niches could occur through diverse mechanisms (including genetic change, phenotypic plasticity, and changing species interactions; Hoffmann & Sgrò, 2011).

We also tested if a combination of climatic and genetic variables best predicted the survival of lowest-edge populations. We used single- and multiple-regression models with the function 'glm' (binomial distribution). We included two variables (change in MAT between surveys and π) that were significant predictors in separate analyses. We compared the fit of models based on each variable separately to one including both variables and one including both variables and an interaction term between variables. We used the Akaike (1973) information criterion (AIC) for model selection. p -values of model variables were estimated with a Type-II analysis of deviance, applying 'Anova' in *car*. Only lowest-edge populations with genetic data were included. One population (the Whetstones) had very low genetic diversity. This was identified as an outlier in the initial analyses of genetic variation and excluded ($n=11$ included), based on

Tukey's (1977) boxplot method, with π outside the interquartile range $\times 1.5$ (Figure 3b).

We also examined the RADseq data for specific, climatic-related SNPs (single-nucleotide polymorphisms) that were absent in extinct *S. jarrovi* populations but present in persistent populations. We then examined these candidate SNPs for their correspondence to proteins with known functions. Details are in Appendix S4. Note that RADseq data sample the genome only sparsely, so many other relevant variants may also exist. Along these lines, we only examined SNPs that were strongly related to climatic variables, to be conservative. Overall, this analysis of SNPs should be considered preliminary.

For all statistical analyses, we used standard methods rather than phylogenetic methods. Populations on most mountain ranges were separated for ~ 1 million years or more (Wiens et al., 2019), but our analyses pertain to very recent changes in distribution and climate.

RESULTS

Survey results

We conducted resurveys in 2021–2022 of populations initially surveyed in 2013–2017 (Dataset S1). We resurveyed 18 mountain ranges (Figure 1) along 21 transects. We found dramatic but highly heterogeneous responses to climatic change in the last 4–9 years (median = 7 years, $n=21$ transects; 85.7% from 6 to 8 years; Table S6). Twelve transects showed either no range contractions or small downward shifts at the lower range edge (Figure 1; Table S6). Nine others showed upward shifts, indicating local extinction of the lowest-elevation

TABLE 1 Upward elevational range shifts in two lizard species among mountain ranges.

Mountain range	<i>Sceloporus jarrovi</i>		<i>Sceloporus clarkii</i>	
	Shift (m)	Rate (m/year)	Shift (m)	Rate (m/year)
Mules 1	414.83	59.26	249.02	35.57
Mules 2	417.58	52.20	141.12	17.64
Santa Ritas 2	309.98	34.44	275.54	45.92
Santa Ritas 1	133.81	33.45	76.81	8.53
Baboquivaris	144.78	20.68	171.30	24.47
Pinalenos	91.44	15.24	170.69	28.45
Winchesters	51.82	7.40	—	—
Coyotes	16.46	2.35	10.67	1.52
Quinlans	14.63	1.63	60.96	6.77

Note: Shifts are between the initial survey (2013–2017) and resurvey (2021–2022), for the lower range edge (*S. jarrovi*) or upper range edge (*S. clarkii*) for each species. Only mountain ranges with upward shifts in *S. jarrovi* are shown. Ranges are listed in order of descending rates for *S. jarrovi*. The presence of *S. clarkii* was not conclusively documented in the resurveys of the transect in the Winchesters. Full data for both species are in Table S6.

populations (Figure 1; Table 1; Table S6). The overall pattern across all 21 transects was a mean net upward shift of 70.66 ± 140.04 meters in elevation at the lowest range edges (significantly different from zero; $p=0.032$, $n=21$ transects, two-tailed, one-sample t -test).

In some mountain ranges, rates of population loss were among the highest ever recorded. We compared our results to a meta-analysis (Rumpf et al., 2019) of upward elevational shifts at the lowest (warm) edge of species' elevational ranges (Appendix S2; Table S1; Dataset S2). The mean rate of upward lower-edge range shifts found here (25.18 ± 21.09 m/year, $n=9$ transects) was ~5 times higher than the mean rate from the meta-analysis (5.39 ± 7.49 m/year, $n=648$ species with upward shifts) and significantly different ($p=0.005$, one-tailed, two-sample t -test; data ln-transformed for normality). Across all our transects, the overall rate was a mean upward shift of 10.08 ± 18.98 m/year ($n=21$ transects, including transects with no or downward shifts; Table S6), and in the meta-analysis it was 2.08 ± 7.28 m/year ($n=1026$ species, including those with no or downward shifts; $p=0.036$, one-tailed, two-sample t -test). The most rapid shift observed here (59.26 m/year: Mules 1; Table 1) was in the upper 99.5th percentile among upward warm-edge range shifts for the 648 species in the meta-analysis (Dataset S2).

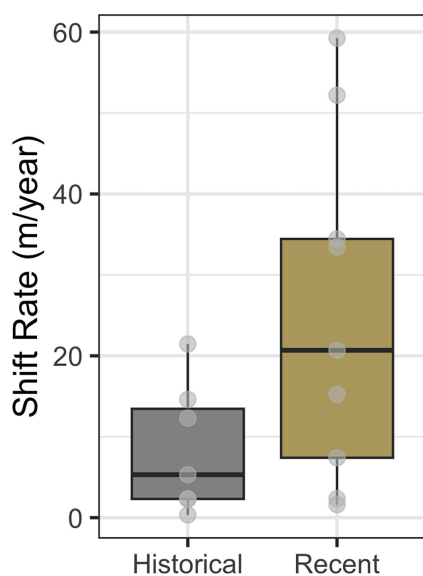


FIGURE 2 Rates of upward elevational shifts in the lowest-edge range limits of *Sceloporus jarrovi* populations, comparing historical and recent shifts. Each grey dot is a shift on one transect. Historical shifts (left, grey; $n=7$ transects with upward shifts) are between 1956–2005 and 2013–2017 (median=42 years between surveys). Recent shifts (right, gold; $n=9$ transects with upward shifts) are between 2013–2017 and 2021–2022 (median=7 years between surveys). The recent mean rate (25.18 m/year) is significantly higher than the historical mean rate (8.38 m/year; $p=0.025$, one-tailed, two-sample t -test). Boxplots show the median shift rate (black line) with first (lower hinge) and third (upper hinge) quartiles. Whiskers represent minimum and maximum values. Data are in Table 1 (recent shifts) and Table S7 (historic shifts).

Furthermore, the magnitude of these shifts was similar between our study and the meta-analysis (mean upward shift here= 177.26 ± 162.08 m vs. 205.57 ± 118.49 m for 648 species, $p=0.678$, one-tailed, two-sample t -test; mean change for all 21 transects= 70.66 ± 140.04 m vs. 81.97 ± 113.81 m for all 1026 species, $p=0.613$). Yet, the mean time between surveys for those studies was almost 10 times longer (mean= 7.0 ± 1.16 years here vs. mean= 68.5 ± 37.65 years among the 22 studies, $p<0.001$, one-tailed, two-sample t -test). Importantly, the resurveys included in the meta-analysis generally ended well before our initial surveys (resurveys in the 22 studies were from 2003 to 2015, median=2008; Table S1), with most completed decades before our recent resurveys.

We found that rates of local extinction have accelerated among these *S. jarrovi* populations over time (Figure 2). We estimated lower elevational range limits from museum and literature records (spanning 1956–2005) and compared them to lower-edge elevational limits from our surveys in 2013–2017 (Dataset S1). We found relevant historical data for 10 mountain ranges (12 transects), with upward shifts on seven transects (Appendix S3; Figure S1; Table S7). The average rate of upward change from 2013–2017 to 2021–2022 tripled relative to that from 1956–2005 to 2013–2017. The historical mean rate of upward change was 8.38 ± 7.88 m/year ($n=7$ transects; median=42 years between surveys; Table S7), whereas the recent mean rate was significantly higher with 25.18 ± 21.09 m/year ($n=9$ transects; $p=0.025$, one-tailed, two-sample t -test; Table S6; median=7 years between surveys). We analysed only upward shifts for this comparison since historical records were not based on systematic elevational transects (see Appendix S3).

We also found striking upward shifts in a lower-elevation congener (*Sceloporus clarkii*; Figure S2). Previous analyses suggested that this distantly related congener is kept at lower elevations by *S. jarrovi* at higher elevations, and they rarely occur in local-scale sympatry (Wiens et al., 2019). Between 2013–2017 and 2021–2022, *S. clarkii* shifted upslope at their upper-range edge on 10 transects (Figure S2; Table S6). Further, *S. clarkii* was found in one mountain range (Perillas), where it was not observed in previous surveys. The upward shifts in *S. clarkii* included those transects where *S. jarrovi* had the largest upward shifts (Table 1; Figure S2). Upward elevational shifts in the two species were correlated ($r=0.717$, $p=0.045$, $n=8$ transects where both species shifted upwards; Figure S3; Table S6).

Patterns of extinction

Patterns of extinction within mountain ranges followed predictions from climate change, but patterns among mountain ranges did not. Within mountain ranges, the lowest-elevation populations (i.e. warmest) were those that went extinct, as predicted given climatic warming.

Conversely, populations surveyed at higher elevations on these transects remained extant (Table S6), except for one (Mules 1, see Discussion).

The prediction of extinction at the warmest sites was not supported among mountain ranges, however. In the initial surveys (2013–2017), *S. jarrovi* had very different lower-elevation range limits among mountain ranges, from 1275 to 2087 meters above sea level (Figure 1; Table S6). Surprisingly, the populations where the species occurred at the lowest elevations remained extant in 2021–2022 (Dos Cabezas, Little Dragons; Figure 1; Table S6). Thus, this species survived at two of the two hottest sites, whereas many populations in cooler and wetter climates apparently succumbed to rising temperatures (Dataset S3). Neither lower elevations, higher temperatures, nor lower precipitation predicted local extinctions, but local extinctions were associated with sites that were initially wetter (higher MAP, lower CMD; Table S11). Results were similar using the 2021–2022 climate at each site (Table S12).

This surprising variation in local extinctions among mountain ranges was related to both climate change and genetic variation (Figure 3). Lowest-elevation sites where populations went extinct between surveys showed larger total increases in MAT (logistic regression: $p=0.029$; $n=20$ lowest-elevation populations; the two transects in the Mules were combined here given their shared lowest site; Figure 3). These sites also showed a higher rate of change in MAT ($^{\circ}\text{C}/\text{year}$, $p=0.045$) than sites where they persisted (other variables were not significant, including annual precipitation; Table S13). These results reflect variation in climate change among sites.

Levels of genetic variation also differed between persistent and extinct populations. We analysed RAD-seq data for 25 populations, largely from 2014 to 2015 (Table S10; Datasets S4–S7). Populations that remained extant in 2021–2022 had significantly higher nucleotide diversity (π) than those that went extinct (Figure 3; logistic regression: $p=0.004$, $n=25$ populations; Table S14; Dataset S7). These results were generally robust across alternative analyses (Tables S14 and S15). A model-fitting analysis of lowest-edge populations ($n=11$) showed that models including both climatic and genetic data had the best fit (Table S16). Thus, the lowest-edge populations that went extinct had less genetic variation and/or experienced greater climate change. These results may help explain why populations at the two lowest sites persisted and why climate change alone did not strongly predict which populations went extinct.

We then tested whether populations with greater genetic variation had larger changes in their realized climatic niches, allowing them to survive recent climate change. Persistent populations with genetic data showed a significant positive correlation between nucleotide diversity and niche change in MWMTs ($r=0.795$, $p=0.033$, $n=6$, Figure 3c; other variables in Figure S4; MAT showed a similar trend). Overall, populations with more genetic variation shifted their climatic niches and survived hotter temperatures (Figure 3c), whereas populations with less genetic variation tended to go extinct (Figure 3b).

Finally, we identified specific nucleotide variants (SNPs) that may be associated with surviving recent climate change. Based on latent-factor mixed models (LFMMs; Fricot et al., 2013), we identified eight SNPs

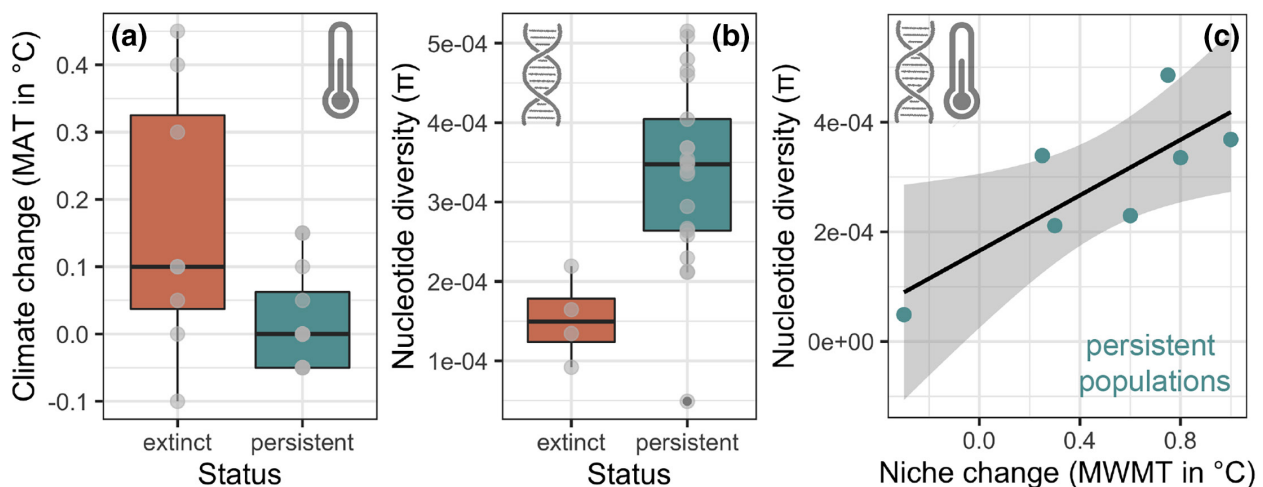


FIGURE 3 Climate change, genetic diversity, and niche change in populations of *Sceloporus jarrovi*. (a) Change in mean annual temperature between surveys at the lowest-elevation sites on each transect, contrasting populations that went locally extinct with those that persisted (logistic regression: $p=0.029$, $n=20$ populations, with the two transects in the Mules combined). Some grey circles overlap fully. (b) Nucleotide diversity (π) within extinct and persistent populations (logistic regression: $p=0.004$, $n=25$ populations; Table S14). Boxplots show median values (black line) with first (lower hinge) and third (upper hinge) quartiles. Whiskers represent minimum and maximum values, excluding one outlier (Whetstones). (c) Correlation between nucleotide diversity and niche change in the mean warmest month temperature among persisting populations ($r=0.795$, $p=0.033$, $n=6$).

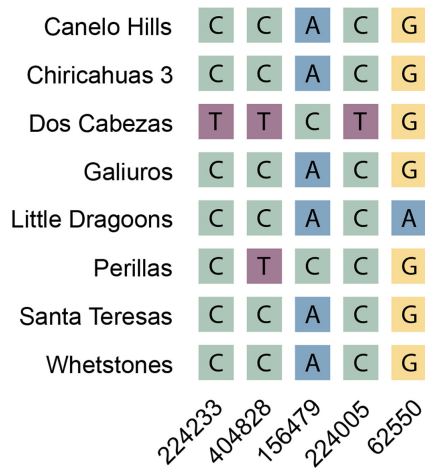


FIGURE 4 Climate-associated nucleotide variants in surviving low-elevation populations. These five single-nucleotide polymorphisms were strongly related to climatic variables (Table S17) and varied among the eight lowest-edge populations (with genetic data) that survived recent climate change (Table S20). The most common base (A=adenine, T=thymine, G=guanine and C=cytosine) in each population is shown (all frequencies in Table S20). These five variants were absent in all extinct populations, but present in the three hottest sites with surviving populations (Dos Cabezas, Little Dragons, and Perillas).

that were most strongly correlated with these five climatic variables, and seven of these SNPs were within described genes (Appendix S4; Figure S5; Tables S17–S19; functions in Table S18; Dataset S8). For all three annotated genes, the SNPs were associated with non-synonymous changes (i.e. changes in amino acids).

If these eight SNPs were beneficial for survival under climate change, we would expect some of these variants to be present in surviving populations at the lowest and hottest sites (Figure 4). Conversely, these same variants should be absent in extinct populations. Among these lowest-edge populations with genetic data ($n=13$), we found five climate-associated variants present at the three hottest sites (highest MAT) where *S. jarrovi* remained extant (Figure S6; Table S20). Four of these variants (Figure 4) were present at high frequencies at the hottest of these persistent sites (Dos Cabezas). Two of these four were shared with the third hottest extant site (Perillas), including a non-synonymous change in fibrillin 2 (which regulates body-fluid levels, among other functions; Table S18). Populations from the Perillas and Chiricahuas appear to be sister taxa (Wiens et al., 2019), suggesting that these two variants (absent in the Chiricahuas) might have evolved independently in the Dos Cabezas and Perillas. At the second hottest of these persistent sites (Little Dragons), only one variant was present, which was apparently fixed at this site but absent at the first and third hottest of these sites (Figure 4; Table S20). None of these variants were present in the extinct populations. In summary, these climate-associated variants may help explain the surprising persistence of *S. jarrovi* at three of the hottest sites among these transects

(although further work will be needed to confirm this and address potential mechanisms). Intriguingly, our results hint that different variants might have been important for survival at different sites.

DISCUSSION

We show here that there has been an accelerating local extinction associated with very recent climate change in the past ~ 7 years in a montane lizard species. Although there is an extensive literature that predicts that climate-related extinction will accelerate with increasing temperatures (e.g. Román-Palacios & Wiens, 2020; Thomas et al., 2004; Urban, 2015), the results here support these predictions based on local extinctions that have already occurred. Furthermore, there is a large literature that has documented local extinctions in other organisms, but generally by comparing surveys separated by many decades (reviews in Rumpf et al., 2019; Wiens, 2016). Our results show that similar levels of local extinction are now occurring over dramatically shorter timescales.

We also document extensive heterogeneity in these local extinctions among mountain ranges, and we show that genomic data can help explain this otherwise puzzling variability. There has been burgeoning interest in using genomic data to predict species' future responses to climate change (e.g. Bay et al., 2018; Exposito-Alonso et al., 2019; Razgour et al., 2019). However, few studies (if any) have addressed whether specific genetic variants or overall genome-wide variation have allowed certain natural populations to survive recent warming when others have gone extinct. We show here that levels of genome-wide variation can help predict patterns of population persistence and extinction based on extinctions that have already occurred, strongly supporting the emphasis on this variable (Kardos et al., 2021). We also identify specific climate-associated nucleotide variants that are present in surviving populations at the hottest sites but lacking in extinct populations (although further research is needed on their function). Our results suggest that such genomic analyses may now become increasingly feasible as rapid climate change reduces the time between genetic sampling and local extinction.

The local extinctions documented here were primarily in low-elevation populations, which implies that none of these 18 montane lineages are in imminent danger of extinction. Yet, one of the most genetically distinct populations (Mule Mountains) is now almost entirely extinct. This lineage has been separated from all others for ~ 3 million years (Wiens et al., 2019), similar in age to many described lizard species (Jezkova & Wiens, 2018). We found this population absent at high elevations on one transect (Mules 1; up to 2163 m), and on the other transect (Mules 2), we found it persisting only within 83 meters elevation of the highest peak in

this mountain range (lowest *S. jarrovii*=2165 m; Fisure Peak=2248 m). Their rapid disappearance from both low- and high-elevation sites suggests that this lineage might soon be extinct. Specifically, extrapolating from the estimated rate of upward shifts (52.2 m/year, Mules 2; Table 1), they will likely be extinct by 2025. Few such lineage-level extinctions related primarily to climate change have been recorded so far (Cahill et al., 2013; Parmesan, 2006; Waller et al., 2017), but they are expected to become increasingly common (Thomas et al., 2004; Urban, 2015).

Understanding how climate change impacts biodiversity is one of the most pressing challenges for biologists. We show that the pace of local extinction from climate change has accelerated over time in this lizard species, and the changes seen over the past ~7 years are similar to those seen over ~70 years in earlier studies. These results also demonstrate the potential to study climate-related extinctions in wild populations over surprisingly brief timescales rather than relying on historical records or projections of future changes. They also show that some populations have rapidly disappeared from both low and high elevations. Similar surveys are urgently needed for other species and regions. Overall, these results imply that we may soon have an unparalleled (and horrific) view of biodiversity loss in our lifetimes.

AUTHOR CONTRIBUTIONS

Kim L. Holzmann and John J. Wiens designed the study and wrote the paper. Kim L. Holzmann, Ramona L. Walls, and John J. Wiens collected data. Kim L. Holzmann performed analyses. All authors contributed to revisions.

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DATA AVAILABILITY STATEMENT

All data and code are available as Datasets S1–S9. Scripts for all statistical analyses are provided in Dataset S9. Datasets S1–S9 and Supporting Information (Appendices S1–S4; Figures S1–S7; Tables S1–S20) are publicly available on Dryad (<https://doi.org/10.5061/dryad.dz08kps3k>).

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SUPPORTING INFORMATION

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

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