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Climate change, extinction, and Sky Island biogeography in a montane lizard

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Abstract

Around the world, many species are confined to "Sky Islands," with different populations in isolated patches of montane habitat. How does this pattern arise? One scenario is that montane species were widespread in lowlands when climates were cooler, and were isolated by local extinction caused by warming conditions. This scenario implies that many montane species may be highly susceptible to anthropogenic warming. Here, we test this scenario in a montane lizard (*Sceloporus jarrovii*) from the Madrean Sky Islands of southeastern Arizona. We combined data from field surveys, climate, population genomics, and physiology. Overall, our results support the hypothesis that this species' current distribution is explained by local extinction caused by past climate change. However, our results for this species differ from simple expectations in several ways: (a) their absence at lower elevations is related to warm winter temperatures, not hot summer temperatures; (b) they appear to exclude a low-elevation congener from higher elevations, not the converse; (c) they are apparently absent from many climatically suitable but low mountain ranges, seemingly "pushed off the top" by climates even warmer than those today; (d) despite the potential for dispersal among ranges during recent glacial periods (~18,000 years ago), populations in different ranges diverged ~4.5–0.5 million years ago and remained largely distinct; and (e) body temperatures are inversely related to climatic temperatures among sites. These results may have implications for many other Sky Island systems. More broadly, we suggest that Sky Island species may be relevant for predicting responses to future warming.

KEYWORDS
biogeography, climate change, extinction, phylogeography, physiology, Sky Island

1 | INTRODUCTION

One of the most urgent questions in biology today is: how will species and populations respond to anthropogenic climate change? For example, will species be able to adjust to the changing conditions, or will they go extinct (Holt, 1990; Moritz & Agudo, 2013; Wiens, 2016; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008)? This topic is particularly important for two reasons. First, there may be extensive loss of biodiversity caused by global warming (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Thomas et al., 2004; Urban, 2015). Second, impacts of climate change on some species may have negative consequences for

human populations (e.g., losses of crops in the developing world; Challinor et al., 2014).

Predicting the future impacts of climate change on species may be challenging, and diverse approaches have been used (e.g., Williams et al., 2008; Moritz & Agudo, 2013). These range from theoretical (Chevin, Lande, & Mace, 2010) to experimental (Etterson & Shaw, 2001) to macroevolutionary (Quintero & Wiens, 2013). Perhaps the most widespread approach is to use niche models to project future species distributions and persistence under different climate change scenarios (Thomas et al., 2004; Urban, 2015). This approach assumes that climatic niches will remain similar over time, and distributions will change instead (through local extinction and/or dispersal).

Here, we analyze distribution patterns in a montane "Sky Island" species, test the causes of these patterns, and address the potential relevance of these results to climate change and extinction. Around the world, many species are confined to "islands" of montane habitat, often with different populations (or closely related endemic species) isolated on different nearby mountain ranges or peaks (review in McCormack, Huang, & Knowles, 2009). How do such distributions arise? One hypothesis is that these species were widespread in the lowlands when climates were cooler, and were forced into high-elevation refuges as climates warmed (McCormack et al., 2009), long before anthropogenic climate change. Thus, this hypothesis implies that the pace of climate change exceeded that of local adaptation for the lowland populations, and that these populations went extinct rather than shifting their niches to accommodate warmer conditions. This hypothesis has been explored to some extent in the literature relating speciation and climatic-niche conservatism (e.g., Kozak & Wiens, 2006; Hoskin et al., 2011; Hua & Wiens, 2013). However, the "Sky Island" pattern might be more widespread among populations of montane species than speciation, and more straightforward to study (e.g., intrinsic reproductive isolation of populations is not necessary). Of course, climate-driven local extinction is only one hypothesis to explain the geographic distribution of Sky Island species. Another possibility is that species dispersed among mountain ranges without occurring in the intervening lowlands. A third possibility is that lowlands are climatically suitable, but species are prevented from occurring there by nonclimatic factors (e.g., competition, microhabitat). Here, we develop a series of analyses to test whether Sky Island distributions are caused by climate-related local extinctions, integrating data from distributional surveys, climate, population genomics, and thermal physiology.

We focus on a broadly distributed species (Mountain Spiny Lizard; *Sceloporus jarrovii*) in the Madrean Sky Islands of southeastern Arizona. The Madrean Sky Islands consist of ~30–40 mountain ranges separated by arid lowlands (desert and semi-desert grassland), situated south of the Rocky Mountains and north of the Sierra Madre Occidental (McCormack et al., 2009). They most likely formed ~30 Myr ago (Coblentz & Ritter, 2004), although other estimates imply some uplift ~15–7 Myr ago (Wilson & Pitts, 2010). The Madrean Sky Islands range from relatively low mountains (~1,700 m above sea level, "m" hereafter) with only a few scattered oaks, to larger ranges with extensive forest and one or more peaks >3,000 m (Figure 1; Table S1). *Sceloporus jarrovii* occurs from this region southwards into the Sierra Madre Occidental (Schwalbe, 2009). In southeastern Arizona, this species has been reported in at least 12 mountain ranges, in habitats ranging from oak woodlands to alpine spruce-fir forests (Schwalbe, 2009). *Sceloporus jarrovii* is easy to find and observe (i.e., they bask on exposed rocks on sunny days throughout the year; Schwalbe, 2009), making it relatively straightforward to distinguish between localities where they are present versus absent, and locations with suitable microhabitat where this species is absent are typically occupied by a congener instead (see below). Based on data from fossil pack-rat middens (Betancourt, Van Devender, & Martin, 1990), the pine-oak woodlands where this species occurs today were widespread in the lowlands between mountains during the Last Glacial Maximum (LGM; ~18,000 years ago). Thus, this species could have been broadly distributed in the lowlands during these cooler periods, and their current distribution might be explained by widespread extinction of these lowland populations caused by their inability to adapt to climate change.

The distribution of *S. jarrovii* is representative of many other species that are also confined to two or more Madrean Sky Island ranges (within the region), including other lizards (*Elgaria kingii*, *Sceloporus slevini*, *Sceloporus virgatus*, and *Plestiodon callicephalus*) and snakes (*Crotalus pricei*, *Crotalus lepidus*, *Crotalus willardi*, *Lampropeltis pyromelana*, *Senticolis triaspis*, *Tantilla yaquia*; Brennan & Holycross, 2006). Similar distribution patterns are known in many other taxa, including birds (e.g., McCormack, Bowen, & Smith, 2008; Manthey & Moyle, 2015), amphibians (Barber, 1999; Streicher et al., 2014), snails (Weaver, Weaver, & Guralnick, 2010), insects (Downie, 2004; Dyer & Jaenicke, 2005; Smith & Farrell, 2005; Ober, Matthews, Ferrieri, & Kuhn, 2011), spiders (Masta, 2000), and plants (e.g., Moreno-Letelier & Pinero, 2009; Perez-Alquicira et al., 2010).

Several studies have addressed the genetic divergence of Madrean Sky Island populations in different taxonomic groups (see citations in the preceding sentence). However, these studies have generally not focused on explaining species distributions within and between mountain ranges, and especially not on how climate change, niche change, and extinction may be related to these patterns. Moreover, previous genetic studies have not focused on comprehensive sampling of mountain ranges in the region, instead sampling only a fraction of the >30 ranges present (map in Figure 1). For example, Masta and Maddison (2002) included spiders from 13 ranges, whereas other studies (cited above) sampled <10. Previous studies may have sampled relatively few mountain ranges simply because their focal taxa occurred in few mountain ranges. However, it is unclear if the distribution of taxa among mountain ranges was well known in these cases (i.e., from systematic surveys of all ranges in the region).

Some previous studies (mostly in other regions) have also combined phylogeography with niche modelling to address the impacts of past climate change (e.g., Carstens & Richards, 2007; Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009), including some that focused on montane species (Bryson, Murphy, Graham, Lathrop, & Lazcano, 2011; Gutierrez-Tapia & Palma, 2016; Mastretta-Yanes et al., 2018) and some that discussed implications for future climate

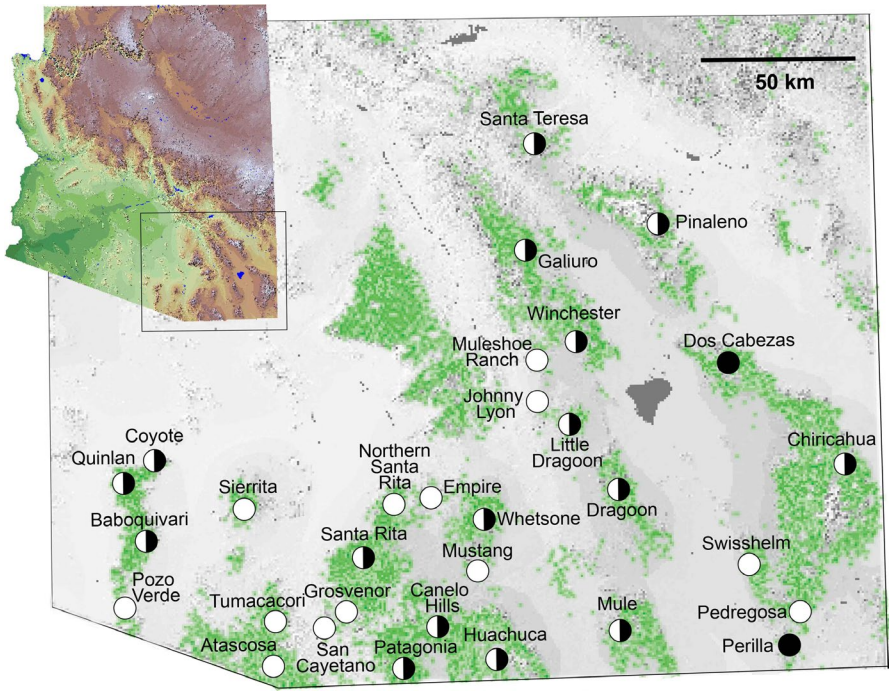

FIGURE 1 Distribution of the 31 Madrean Sky Island mountain ranges in southeastern Arizona included in this study. Circles indicate the location of transects. White circles indicate mountain ranges where only *Sceloporus clarkii* was found on our transects. Black circles indicate mountain ranges where only *Sceloporus jarrovii* was found. Half-black and half-white circles indicate mountain ranges where both species occur. Green indicates distribution of Madrean oak woodlands. We did not include the two mountain ranges west of the Johnny Lyon Hills and Galiuros (Rincon, Santa Catalinas) because they lack native *S. jarrovii*, and other taxa typical of Madrean Sky Islands (Appendix S1). However, there is an introduced population of *S. jarrovii* at one site in the Santa Catalinas (Schwalbe, 2009)

change (Cordellier & Pfenninger, 2009). Here, we integrate these two approaches (niche modelling, phylogeography) with analyses of distributional, climatic, and physiological data to address the causes of Sky Island distributions and their implications for future climate change. We also focus specifically on climatic warming, and not simply past climatic fluctuations in general.

In this study, we address the following questions. (a) What is the current distribution of *S. jarrovii* among Madrean Sky Islands in southeast Arizona, and what explains its current absence at lower elevations? Specifically, is its distribution explained by unsuitable climatic conditions and/or by competition with a congeneric species (*S. clarkii*) at lower elevations? This potential competitor (*S. clarkii*) has similar body size and diet and occurs in the same saxicolous microhabitats near the lower-elevation range limits of *S. jarrovii* (see Section 4; Schwalbe, 2009; Schwalbe & Rosen, 2009). (b) Is the phylogeny among populations of *S. jarrovii* in the region consistent with that of a formerly widespread species that went extinct in the lowlands as climates warmed? For example, are there clades of populations from different mountain ranges that correspond to higher elevation ridges, separated by lower elevation valleys? Do sampled individuals from each mountain range form a monophyletic group, or do they show a pattern more consistent with recent dispersal among ranges? (c) Is there evidence for conservatism or local adaptation in relevant physiological traits among populations? Specifically, are temperature-related physiological variables similar across populations in different mountain ranges with different lower-elevational range limits (as expected if these variables failed to adapt to warming conditions over time)? Or do they show evidence of local adaptation, with physiological variables covarying with climatic variables among populations? We also address how quickly climatic and physiological variables change among populations over time, and (possibly for the first time) whether these two types of variables change at similar rates. We present our methods and results in the approximate order listed above, given that each set of analyses depends largely on the preceding ones.

2 | MATERIALS AND METHODS

2.1 | Sampling of mountain ranges

We first documented the distribution of *Sceloporus jarrovii* among mountain ranges in southeastern Arizona. We initially compiled distributional data from museum records (Dataset S1). However, georeferenced localities were lacking for some ranges, and it was unclear whether some were surveyed at all. Therefore, we systematically sampled almost all mountain ranges in the region (details in Appendix S1). These surveys provided information on the presence (and potential absence) of *S. jarrovii* in 31 ranges. They also generated estimates of the lower elevational limit of *S. jarrovii* and upper limit of *Sceloporus clarkii* along an elevational transect in most ranges (Dataset S2). Most ranges had both *S. jarrovii* and *S. clarkii*, or only *S. clarkii* (Figure 1). In Appendix S1, we also discuss the precise geographic scope of our study, the possible impacts of recent climate change on our results, and other potential methodological concerns. These datasets and other supplementary material are available on Dryad (https://doi.org/10.5061/dryad.dp13668).

2.2 | Testing the factors driving species distributions

We tested several hypotheses to explain the distribution of *S. jarrovii* among mountain ranges and adjacent lowlands. We first used niche

modelling with Maxent (Phillips, Anderson, & Schapire, 2006) to test if mountains and lowlands where *S. jarrovii* is currently absent are climatically suitable or unsuitable for this species (details in Appendix S2). To do this, we combined georeferenced museum records with localities from our field surveys (Dataset S3) and then systematically thinned them to a final set of localities (Dataset S4). We used climatic data from the standard WorldClim dataset (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and the ClimateWNA dataset (Wang, Hamann, Spittlehouse, & Murdock, 2012). However, we focused primarily on the latter dataset, given their finer geographic scale. Results of Maxent model selection are provided in Dataset S5. Maxent models for both datasets had very good fit (AUC > 0.90), and results were insensitive to removing correlated climatic variables (Appendix S2).

We also assessed the distribution of suitable climatic conditions for *S. jarrovii* during the LGM to test the hypothesis that the lowlands between Sky Islands were suitable during colder periods. We used two models of LGM climate: the community-climate-system-model (CCSM version 3; Otto-Bliesner et al., 2006) and the model-for-interdisciplinary-research-on-climate (MIROC version 3.2; Sugiyama, Shiogama, & Emori, 2010).

We also used more fine-scale analyses of distributional and climatic data to test whether *S. jarrovii* was absent from lowlands and from mountain ranges presently containing only *S. clarkii* because of (a) unsuitable climatic conditions, and/or (b) competition. Using the georeferenced localities (sites) from our transects, we first tested whether climatic conditions in the highest-elevation *clarkii* site in each of the *clarkii*-only ranges (n = 13) were significantly hotter or drier than the lowest-elevation site for *S. jarrovii* in ranges where it occurs (n = 17, excluding the Whetstones, see Appendix S1 for justification). We used a single site from each range, and tested for a significant difference in mean values of variables between the two categories of sites (*jarrovii*, *clarkii* only) among ranges, using an unpaired *t*-test (for all variables, Shapiro-Wilk tests failed to reject normality). A significant difference would suggest that absence of *S. jarrovii* in *clarkii*-only ranges is explained by their climatic tolerances. We obtained high-resolution climatic data (for 1981–2010) for each locality from the Climate WNA database (Wang et al., 2012), which includes fine-scale climatic data informed by elevations. We focused on four variables that describe overall temperature and precipitation: mean-annual temperature (MAT), mean warmest-month temperature (MWMT), mean-annual precipitation (MAP), and mean-annual summer precipitation (MSP). We also included two variables identified as the most important in determining the distribution of *S. jarrovii* from niche-modelling analyses with the ClimateWNA data (Appendix S2): number-of-days-below 0°C (DD_0) and Hargreave's climatic-moisture deficit index (CMD). Climatic data for each site are provided in Dataset S2.

We tested whether variation in lower-elevational range limits of *S. jarrovii* were related to climatic variables at a fine scale. Across 17 mountain ranges where *S. jarrovii* occurs (all but the Whetstones), we conducted a regression between the elevation of the lowest site with *S. jarrovii* and the corresponding values of each of the six variables. We would expect that if a climatic variable sets the lower elevational limits of *S. jarrovii*, it should have similar values at the lowest sites for *S. jarrovii* across different ranges, rather than simply covarying with elevation across ranges. We applied a sequential Bonferroni correction to these and similar analyses (Rice, 1989), in sets of six (asterisks indicate results considered nonsignificant after this correction). Applying this correction across all tests in the study would be inappropriate (Rice, 1989), and applying such a correction at all is controversial (Nakagawa, 2004).

We also tested whether sites for *S. clarkii* and sites for *S. jarrovii* were climatically distinct along our elevational transect for each mountain range (using unpaired *t*-tests). We did this for those mountain ranges for which the transect included at least two sites for each species and six or more sites overall.

We then performed analyses to evaluate if *S. jarrovii* and *S. clarkii* may have influenced each other's elevational distributions. Elevational distributions of species on mountain ranges with one versus two species have been considered natural experiments that can provide evidence of competitive exclusion (Brown & Lomolino, 1998). Most ranges with only one species were *clarkii*-only ranges (see Section 3, Figure 1). We tested if *S. jarrovii* occurred at lower elevations in ranges where *S. clarkii* is absent (suggesting that *S. clarkii* prevents *S. jarrovii* from invading lowlands). Conversely, we tested if *S. clarkii* occurred at higher elevations in the absence of *S. jarrovii* (suggesting that *S. jarrovii* excludes *S. clarkii* from higher elevations where they occur together). A complicating factor here is that some *clarkii*-only ranges were very low, such that species interactions could not explain their maximum elevation. Therefore, we repeated this latter analysis after removing the six sites with the lowest elevations (<1,750 m), just above the mean lower-elevational range limit for *S. jarrovii*. We also performed similar analyses focusing on climatic variables, instead of elevation. However, our main emphasis was on elevational ranges, given our goal of explaining the current elevational distribution of *S. jarrovii*.

Finally, we tested if the current distribution of *S. jarrovii* among mountains might simply be related to higher maximum elevations. We determined the maximum elevation present in each range (Table S1), using Peakbagger.com. We used logistic regression ("glm" function in R) to test if the maximum elevation of a range predicted whether *S. jarrovii* occurred there.

2.3 | Population genomic data

We obtained population genomic data from *S. jarrovii* populations from all 18 mountain ranges in our study area where it occurs and estimated a phylogeny among individuals and populations on these ranges. Given the hypothesis that the current distribution of this species among Sky Islands reflects climate-driven local extinction of lowland populations in the past, we made two main predictions. First, given a widespread ancestor and a warming climate, populations in deeper valleys should go extinct first, generating monophyletic groups of populations associated with elevated groups of mountain ranges. Second, individuals sampled from each range

should form monophyletic groups in our tree, assuming that each range has Madrean woodland habitat that has been disjunct for long time periods. A pattern of nonmonophyly of elevated ridges and ranges could be consistent with more recent dispersal among ranges (but also incomplete lineage sorting; e.g., Masta & Maddison, 2002).

We obtained DNA from tail tips or blood samples from lizards that were noosed in the field and then immediately released. A listing of individuals sampled and their localities is given in Table S2. Many ranges were represented by a single locality, given that road access was limited. However, the larger and more accessible ranges were represented by two or more distinct localities (Chiricahuas, Dragoons, Huachucas, Pinalenos, Santa Ritas).

We included other populations and species to root the tree. In recent phylogenetic studies, *S. jarrovii* is sister to a clade containing *S. bulleri*, *S. insignis*, and *S. torquatus* (Wiens, Kozak, & Silva, 2013; Leaché, Banbury, Linkem, & Nieto Montes de Oca, 2016). We included *S. insignis* and *S. torquatus* as outgroups, and *S. megalepidurus* as a more distant outgroup. We also included two *S. jarrovii* from the southern Sierra Madre Occidental. The latter should provide a better root for the phylogeny of populations in Arizona than individuals of other species. However, including other species was essential to root the overall within-species tree and to estimate clade ages. Divergence times were calibrated by fixing the age of one clade (the ancestor of *S. jarrovii*, *S. insignis*, and *S. torquatus*) based on previous estimates for this clade's age. Details are provided in Appendix S3.

We generated double-digest RADseq data from each individual following the protocol of Peterson, Weber, Kay, Fisher, and Hoekstra (2012). Details of data collection and analysis are provided in Appendix S3. We generated two main datasets, corresponding to the sequencing of individuals in different "batches." One dataset included only individuals from the same batch (Table S3), with 1–14 individuals per mountain range (mean = 4.7). The other incorporated 30 additional individuals from a second batch, with 1–18 per mountain range (mean = 6.6). For each dataset, we estimated a phylogeny among individuals using maximum likelihood (with RAxML; Stamatakis, 2014), and estimated divegence times using treePL (Smith & O'Meara, 2012). The results were generally similar between the two datasets, and we therefore focus primarily on the larger dataset (119 individuals) that combined individuals from the two batches.

Many other approaches are available for analyzing RADseq data. However, concatenated likelihood remains standard for estimating phylogeny. Furthermore, using individuals as terminal taxa allowed us to address monophyly of mountain ranges, relationships among ranges, and divergence times. Species-tree approaches may generally be preferable for inferring phylogeny, but were problematic here. Most importantly, the phylogeny was among individuals and populations, not species. Even if we treated populations in different ranges as different species, short sequence lengths per locus would make it difficult to estimate gene trees for species-tree estimation. The many loci would also be problematic for some approaches. A species-tree approach would also not address monophyly of populations.

Many approaches have also been developed for landscape genetics. However, only some are applicable to RADseq data, and many would not address our questions of interest here. Our estimate of phylogeny and divergence times was also necessary for many other analyses (phylogenetic regression, estimating rates of niche change).

2.4 | Physiological data

Under the hypothesis that *S. jarrovii* failed to adapt to warming conditions in the lowlands in the past, we predicted that there would be little or no physiological adaptation to different climatic conditions among low-elevation populations across different mountain ranges today. We measured two temperature-related physiological variables (field body temperatures: FBT; voluntary thermal maxima: VTM). Specifically, we tested whether these variables were correlated with relevant climatic variables across sites. Although a strong relationship between climate and physiology would not necessarily prove physiological adaptation to different climatic conditions, the lack of a relationship would provide evidence against it. We used the same six climatic variables from the fine-scale climatic analyses above (MAT, MWMT, MAP, MSP, DD_0, CMD), including the two identified as most impoortant from the niche modelling analyses of this dataset (DD_0, CMD).

We considered VTM to be the most relevant physiological variable here, since it should reflect the maximum temperature at which lizards can be active (as opposed to actively seeking shelter). Higher VTM should allow persistence in hotter climates (Camacho et al., 2018). In contrast, critical-thermal maxima (e.g., temperatures at which lizards cannot locomote) may be less relevant, since these are often much higher than VTM, and lizards would likely seek shelter and avoid these temperatures long before they were reached (Camacho et al., 2018). FBT represent body temperatures at which lizards are active, reflecting their preferred temperatures and those locally available (review in Camacho & Rusch, 2017).

We obtained data for *S. jarrovii* at one low-elevation site in each of 10 ranges (FBT: mean = 7.3 individuals/site; range = 3–13; VTM: mean = 7.7 individuals/site; range = 3–10; Datasets S6 and S7). We also obtained limited VTM data for *S. clarkii* at three sites and FBT at one. Each site was close to the lowest elevational limit of *S. jarrovii* for our transect in that mountain range (see Appendix S4 for details). The sites spanned a broad range of lower elevations (1,309–1,889 m) and the latitudinal and longitudinal limits of the study area. We focused on only 10 ranges because road access to sites with *S. jarrovii* in some ranges was difficult, and VTM measurements required a vehicle.

Details of data collection and analysis for FBT and VTM are provided in Appendix S4. In short, FBT was measured immediately after capture. VTM was the body temperature at which an individual exited a gradually warming chamber. For statistical analyses, we pooled data from all individuals in a site and analyzed mean values. Within a site, we used climatic data (from ClimateWNA) from the specific location where most individuals were captured for

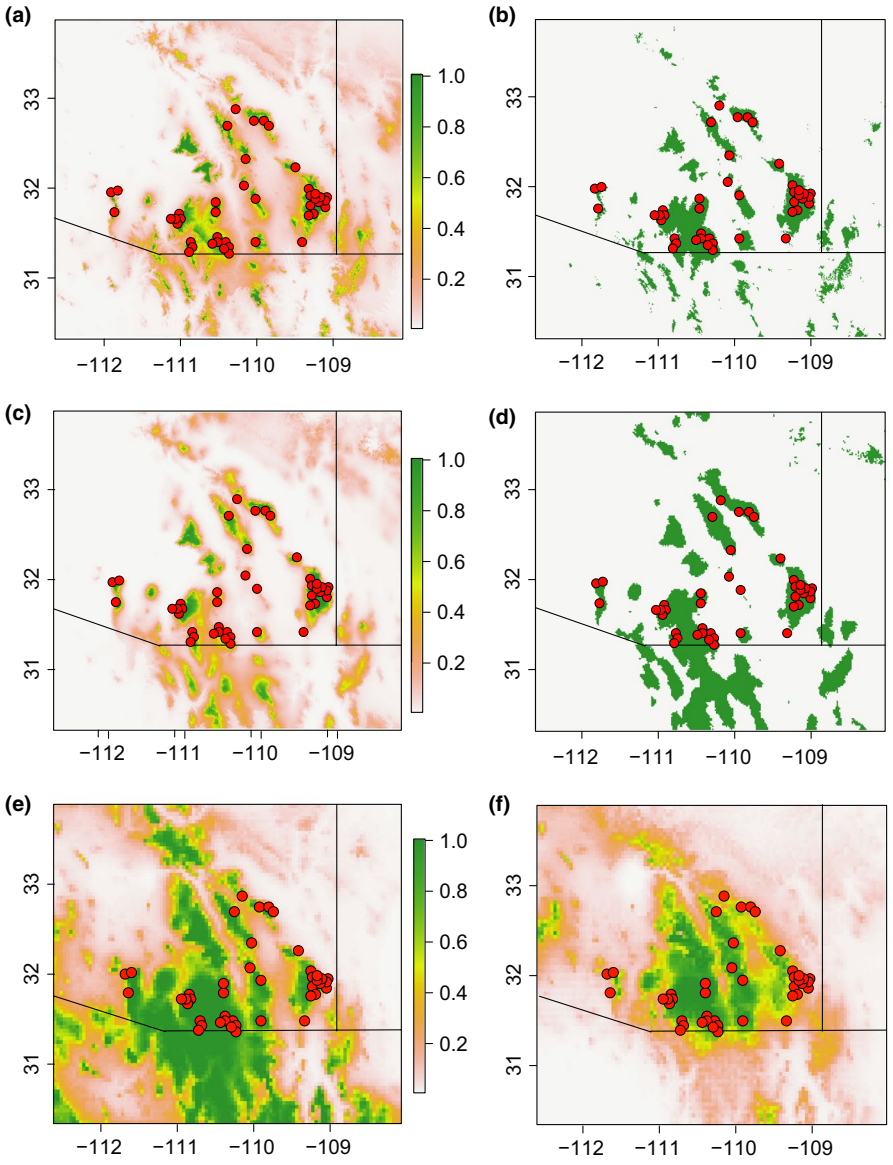

FIGURE 2 Visualization of habitat suitability for *Sceloporus jarrovii* in southeastern Arizona based on climatic niche models. Red dots indicate localities used to build the models (only including those localities within the study area). Models for current climate were built using Maxent and the Wordclim (a, b) and ClimateWNA (c, d) climatic datasets. The models were visualized using logistic probability values (a, c) and converted to presence-absence maps (b, d) using the equal training sensitivity and specificity threshold (green indicating suitability). Models for the Last Glacial Maximum climate (e, f) were built using the CCSM model (e) and the MIROC model (f). These models were also visualized using logistic probability values. Note that *S. jarrovii* actually occurs in several mountain ranges in southwest New Mexico and northern Mexico where it is predicted to be present, but these are outside the study area. The Rincon and Santa Catalina mountains are also considered outside the study area (Appendix S1). Note also that not every part of every mountain range with *S. jarrovii* has been surveyed for this species (i.e., given limited road access)

physiological measurements, or one with an intermediate elevation within the site. Physiological data are given in Datasets S7 and S8.

We tested for significant relationships between the two physiological variables and each of the six climatic variables. Given the strong phylogenetic patterns among ranges (see Section 3), we conducted analyses using phylogenetic-generalized least-squares regression (PGLS; Martins & Hansen, 1997) with the R package CAPER (Orme, 2013). Details are provided in Appendix S4 and trees in Dataset S9.

We also combined our climatic, physiological, and phylogenetic data to infer rates of change in climatic and physiological variables among populations (following Quintero & Wiens, 2013; Jezkova & Wiens, 2016). We compared rates of change estimated among populations here to estimates in these two previous studies, for comparable climatic variables (MAT, MAP). We also compared rates of change in physiological variables and temperature-related climatic variables. Details are given in Appendix S5.

3 | RESULTS

3.1 | Biogeographic patterns

We surveyed a total of 31 mountain ranges in southeast Arizona (Figure 1; Appendix S1). *Sceloporus jarrovii* was present in 18, and apparently absent in the other 13. In many ranges surveyed (n = 16), both *S. jarrovii* and *S. clarkii* were present. However, in two ranges, we did not find *S. clarkii* on our transects (Dos Cabezas, Perillas), despite repeated searches. *Sceloporus clarkii* was present in the other 29 ranges.

Niche-modelling analyses (Appendix S2) showed that all 31 mountain ranges surveyed should be climatically suitable for *S. jarrovii* (Figure 2a–d). Thus, most ranges with Madrean woodland were considered suitable for *S. jarrovii*, even though *S. jarrovii* is apparently absent in 13 of these. Nevertheless, the best-fitting niche models for each dataset had excellent fit to the data (WNA: AUC = 0.92;

Worldclim: AUC = 0.96). In general, most intervening lowlands between ranges were climatically unsuitable for *S. jarrovii*. However, some nearby ranges were connected by areas predicted to be climatically suitable for *S. jarrovii* (especially the Canelo Hills, Huachucas, Patagonias, Santa Ritas, and Whetstones). Suitable climatic conditions for *S. jarrovii* were more widely distributed during the LGM, connecting many currently isolated Sky Islands (Figure 2e,f).

The niche-modelling analyses also identified the climatic variables that seem to be most important in determining the large-scale distribution of *S. jarrovii* in the region (Appendix S2). The relatively precise WNA data suggest that fewer frost-free days (DD_0) and higher values of Hargreave's climatic moisture deficit index (CMD) at lower elevations explain the absence of *S. jarrovii*. Analyses of the coarser WorldClim data support mean diurnal temperature range (Bio2) and mean temperature of the coldest quarter (Bio11) as most important, both with increasing values at lower elevations. For both datasets, warm winter temperatures were more important than hot summer temperatures.

The lower-elevational limits of *Sceloporus jarrovii* in our transects (Figure 3) varied considerably across mountain ranges, from 1,275 m (Dos Cabezas) to 1,867 m (Winchesters). The average across the 17 adequately surveyed ranges was 1,630 m. Across ranges, there were strong relationships between lower limits of *S. jarrovii* (independent variable) and most climatic variables (dependent variable) at

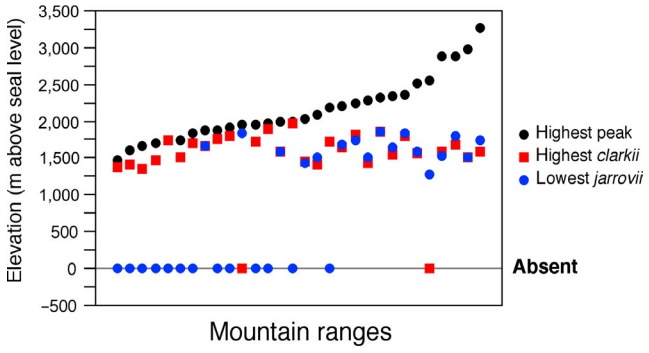

FIGURE 3 Elevational distribution of *Sceloporus clarkii* and *Sceloporus jarrovii* among 30 mountain ranges in southeastern Arizona. Black circles indicate the maximum elevation (i.e., highest peak) for each range. Red squares indicate the highest elevation where *S. clarkii* was recorded on our transect. Blue circles indicate the lowest elevation where *S. jarrovii* was recorded on our transect. Note that elevational distributions could vary from these patterns outside of our transects due to slope and other factors. A symbol for a given species at 0 elevation indicates that it is apparently absent from that mountain range. Mountains are listed from left to right, generally in order of increasing maximum elevation as follows: Pozo Verde, Muleshoe Ranch Hills, Grosvenor Hills, Empire, Johnny Lyon Hills, Tumacacori, San Cayetano, Canelo Hills, Sierrita, Northern Santa Rita Foothills, Perilla, Atascosa, Mustang, Coyote, Pedregosa, Little Dragoon, Quinlan, Swisshelm, Patagonia, Mule, Dragoon, Winchester, Galiuro, Baboquivari, Santa Teresa, Dos Cabezas, Santa Rita, Huachuca, Chiricahua, Pinaleno. Raw data are given in Table S1. Transects from the Whetstones were excluded (see Appendix S1), but they nevertheless fit the overall pattern (presence of *S. jarrovii* in a higher elevation range)

those locations (with lower temperatures and higher precipitation at higher elevations; MAT: $r^2 = 0.283$, $p = 0.0280$*; MWMT: $r^2 = 0.438$, $p = 0.0038$; MAP: $r^2 = 0.476$, $p = 0.0022$; MSP: $r^2 = 0.309$, $p = 0.0205$*; CMD: $r^2 = 0.408$, $p = 0.0058$; *not significant after Bonferroni correction), except for days-below-zero (DD_0: $r^2 = 0.184$, $p = 0.0855$). These results are consistent with the idea that similar tolerances to DD_0 determine their lower elevational range limits across these ranges (as indicated by the niche-modelling analyses), despite variation in other variables.

Both species were present in 16 mountain ranges. In many ranges (Figure 3), the maximum elevation of *S. clarkii* we recorded was either just below the lowest elevation for *S. jarrovii* ($n = 11$ ranges) or slightly overlapping ($n = 4$ ranges; Whetstones excluded).

Analyses of six climatic variables showed no significant differences between the lowest-elevation *jarrovii* sites ($n = 17$) and those highest-elevation *clarkii* sites ($n = 13$) in *clarkii*-only mountain ranges (MAT: $p = 0.0536$; MWMT: $p = 0.2717$; MAP: $p = 0.5829$; MSP: $p = 0.1488$; CMD: $p = 0.8976$), except for number-of-days-below-zero (DD_0: $p = 0.0278$, greater for *jarrovii* sites). Again, DD_0 strongly predicts the distribution of *S. jarrovii* based on niche modelling (Appendix S2). For MAP and MSP, precipitation values were higher in *clarkii*-only sites. In fact, mean elevation was higher for *S. clarkii* than *S. jarrovii* (1,647 vs. 1,630 m). Despite the similar climatic distributions between highest *S. clarkii* sites and lowest *S. jarrovii* sites among mountain ranges, we found that in all mountain ranges with both species present and 10 or more sites overall, the climatic distributions of each species were significantly different, with *S. jarrovii* in cooler and wetter climates (Table S4). These results support the niche-modelling analyes, suggesting that the lower elevational limits of *S. jarrovii* are set by unsuitable climatic conditions, not species interactions.

We next explicitly tested whether the highest-elevation site for *S. clarkii* was higher in mountain ranges without *S. jarrovii*. We tested the 28 ranges with both species or *clarkii* only (Figure 3), but excluding the six lowest ranges (below 1,750 m; Empire, Grosvenor Hills, Johnny Lyon Hills, Muleshoe Ranch Hills, Pozo Verde, Tumacacori). We found that *S. clarkii* extends to significantly higher sites in ranges where *S. jarrovii* is absent (mean = 1,795 m) rather than present (mean = 1,611 m; $p = 0.0047$; unpaired *t*-test).

In contrast, there was no significant difference between the lower elevational range limits of *S. jarrovii* in mountain ranges with ($n = 15$) and without ($n = 2$) *S. clarkii* (mean elevation with = 1640, without = 1554; $p = 0.5036$). Among the two mountain ranges without *S. clarkii*, *S. jarrovii* extends to low elevations in the Dos Cabezas, but was found only at high elevations (above average for the species) in the Perillas (Figure 3). If both *jarrovii*-only ranges had the same lower elevational limits as the Dos Cabezas, then the difference would be significant ($p = 0.0024$, unpaired *t*-test, or $p = 0.0253$ for a nonparametric Mann–Whitney *U* test). Thus, a nonsignificant result was not inevitable. Overall, these results are consistent with the hypothesis that *S. jarrovii* limits the upper elevational range of *S. clarkii*, but *S. clarkii* does not constrain the lower elevational range of *S. jarrovii*. We describe the results of the climatic analyses in Appendix S6.

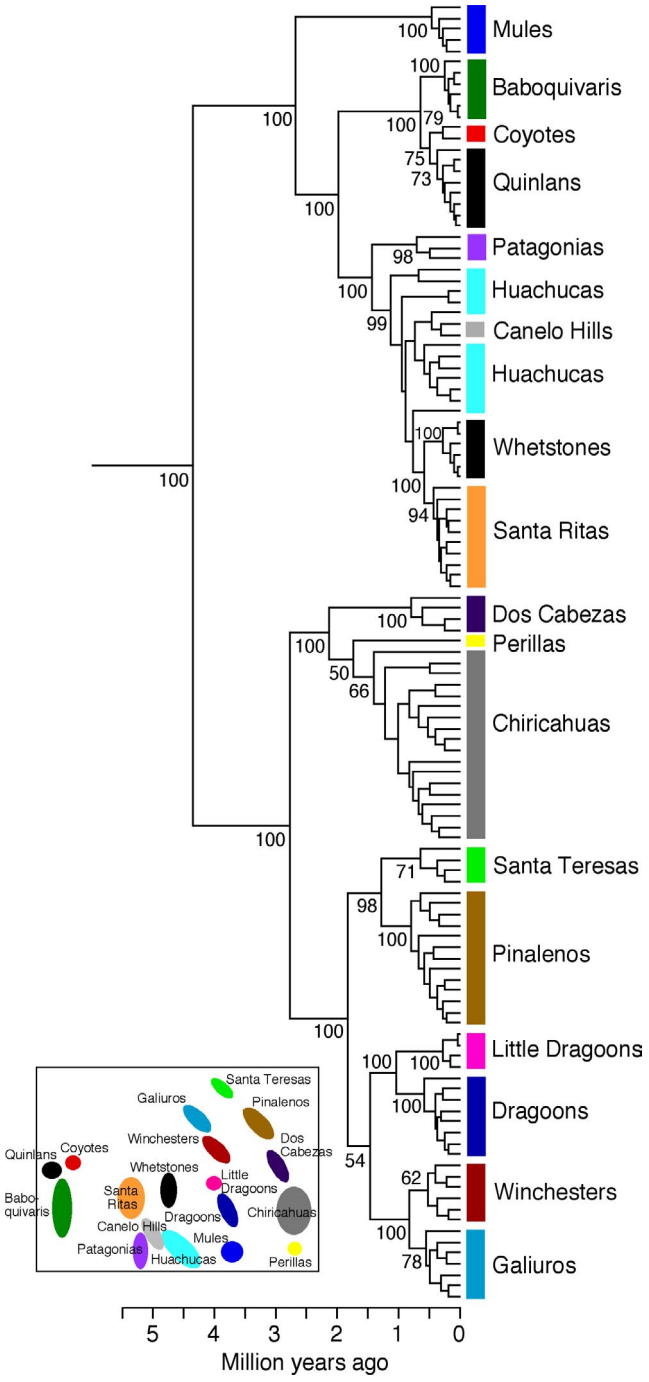

FIGURE 4 Time-calibrated maximum-likelihood tree estimated using the RADseq dataset with all 119 individuals of *Sceloporus jarrovii*. Outgroup taxa are not shown. A diagrammatic map of the included mountain ranges is inset. Bootstrap support values are indicated on nodes showing relationships among mountain ranges or indicating the monophyly of mountain ranges (values for nodes within mountain ranges are not shown, nor are values <50%). An analysis including only 90 individuals from the same batch, yielded similar results (summary in Figure S3). Individuals sampled and all support values for the full tree of 119 individuals are shown in Figure S4, and the time-calibrated tree is available in newick format in File S19. Results of other alternative analyses are shown in Figures S1, S2, S5–S7

Logistic regression showed that the maximum elevation of each mountain range predicts the presence of *S. jarrovii* among ranges (p = 0.0097; pseudo-r^2 = 0.716). As seen in Figure 3, almost all ranges with maximum heights >2,000 m have *S. jarrovii* (except the Swisshelms at 2,190 m), whereas most ranges with peaks <2,000 m lack *S. jarrovii*, except the Canelo Hills (1,881 m), Coyotes (1,991 m), and Perillas (1,947 m).

3.2 | Population genomic analyses

The first RADseq dataset (single batch) included 90 individuals, 1,683 loci, 481,104 sites, and 5,489 variable sites. The second (incorporating individuals from a second batch) included 119 *S. jarrovii*, 1,495 loci, 428,203 sites, and 4,491 variable sites. Both are available on Dryad (https://doi.org/10.5061/dryad.dp13668), as Datafiles S1 and S2. Phylogenetic analyses of both datasets yielded similar results. Therefore, we focus primarily on the second, larger dataset. The time-calibrated tree and branch-support values are summarized in Figure 4. Many relationships among populations in different ranges were strongly supported (bootstrap support > 95%). Furthermore, *S. jarrovii* samples in most ranges were monophyletic, often with strong support. Divergence times were relatively old, with most splits among populations in different ranges occurring between ~4.5 and 0.5 million years ago.

Most relationships were consistent with expectations given a widespread ancestral population in the region that was split by extinction in the lowlands as climates warmed (Figure 4). First, many clades of populations correspond with elevated groups of mountain ranges (isolated by gaps below 1,400 m–1,500 m). These included clades consisting of populations from (a) the Chiricahuas, Dos Cabezas, and Perillas, (b) the Pinalenos and Santa Teresas, and (c) and the Galiuros, Winchesters, Dragoons, and Little Dragoons. There is also an elevated group of mountain ranges (isolated from others by gaps below 1,400–1,500 m) that in Arizona includes the Mules, Huachucas, Canelo Hills, Patagonias, Santa Ritas, and Whetstones. This group of mountains largely corresponds to a strongly supported clade of *S. jarrovii* populations, but this clade also includes populations from the three ranges at the western edge of the study area (Baboquivaris, Coyotes, Quinlans). Overall, *S. jarrovii* populations in southeastern Arizona were divided into an eastern clade and western clade, with populations from this latter set of 9 ranges forming the western clade.

Also consistent with predictions from lowland extinction, most individuals sampled from each mountain range formed a monophyletic group (Figure 4), and most ranges were separated from each other by lowland habitat. There were two exceptions to the overall pattern of monophyly: (a) Perillas, having data for only a single individual (and thus inconclusive), and (b) Huachucas. Individuals from the Huachucas and Canelo Hills were interspersed, but these two ranges were not separated by low-elevation habitats (lowest elevation separating > 1,800 m). Individuals from the Huachucas were also paraphyletic with respect to individuals from the nearby Santa Ritas and Whetstones (which were each supported as monophyletic). In

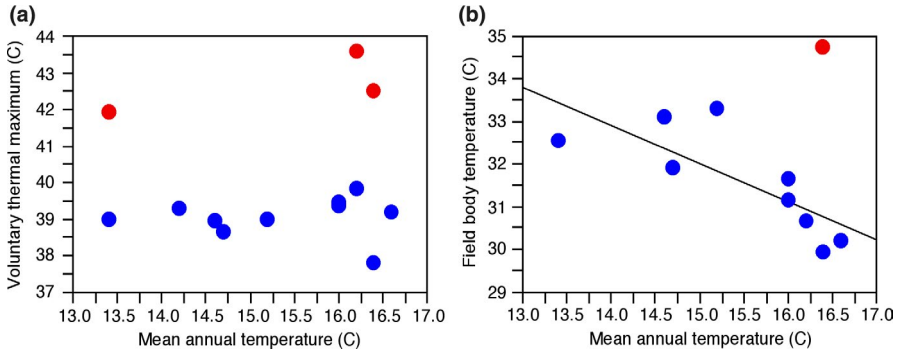

FIGURE 5 Relationships between physiological and climatic variables among low-elevation populations of *Sceloporus jarrovii*. (a) Mean values of voluntary thermal maxima (VTM) among individuals in 10 populations of *S. jarrovii* (in blue) plotted againt values of mean annual temperature for the same sites. There is no significant relationship (r^2 = 0.002, p = 0.9881) nor for other climatic variables. (b) Relationship between mean values of field body temperature (FBT, both sexes) among individuals in nine populations of *S. jarrovii* (in blue) and values of mean annual temperature for the same sites (r^2 = 0.597, p = 0.0081). The relationship shown is for nonphylogenetic regression, but PGLS yields an identical relationships. Other temperature-related climatic variables also show significant relationships. Red dots are values for *S. clarkii*, which were not included in the statistical analyses. Full statistical results (based on PGLS) are in Table S6

summary, there was support for monophyly for 16 of 17 mountain ranges in which monophyly could be tested. Almost all ranges were isolated from each other by low-elevation habitats (Figure 1), except the two that were not were not supported as reciprocally monophyletic (Canelo Hills-Huachucas).

3.3 | Physiology and climate

We obtained data on voluntary thermal maxima (VTM) from 77 individuals of *S. jarrovii* from 10 sites. Mean VTM values among individuals within a site (Figure 5; Table S5) were broadly similar across sites (mean among sites = 39.10°C; range = 37.80–39.83°C). There were no significant relationships between mean values of VTM and any of the six climatic variables (from PGLS, r^2 = 0.00–0.13; p = 0.35–0.99; Table S6). However, these climatic variables were strongly related to differences in elevation among these 10 sites (CMD: r^2 = 0.662, p = 0.0042; MAT: r^2 = 0.491, p = 0.0239; MWMT: r^2 = 0.681, p = 0.0033; MAP: r^2 = 0.697, p = 0.0026; MSP: r^2 = 0.673, p = 0.0036) except for days below zero (DD_0: r^2 = 0.272, p = 0.122; Table S6). Thus, we found no evidence for physiological adaptation to different climatic conditions in different low-elevation populations across the region.

Obtaining physiological data for *S. clarkii* was not our primary goal. Nevertheless, the few individuals measured differed strongly from syntopic *S. jarrovii* (Figure 5). VTM for *S. clarkii* was similar among the three localities sampled (mean = 42.68°C; range = 41.95–43.60°C) and much higher than values for *S. jarrovii* (mean of population means = 39.10°C). This difference is highly significant (p < 0.0001, unpaired t-test). The single field body temperature (FBT) of *S. clarkii* was also higher (34.80°C) than among *S. jarrovii* (29.97–33.33°C), especially at the locality where FBT data for both species were collected (Texas Canyon: 29.97°C vs. 34.80°C).

FBTs were obtained for *S. jarrovii* from 66 individuals from 9 sites (Table S5). Results here are for all individuals combined (sex-specific results in Table S6). Mean values among individuals within a site were similar across sites (mean = 31.63°C; range = 29.97–33.33°C; Figure 5). There was no relationship between mean values of VTM and FBT across the nine sites (r^2 = 0.010; p = 0.9315). FBT values were negatively related to temperature-related climatic variables among sites (MAT: r^2 = 0.597, p = 0.0081 [Figure 5]; MWMT: r^2 = 0.599, p = 0.0079) and positively related to the number-of-days-per-year-below-zero (DD_0: r^2 = 0.494, p = 0.0226*). FBT values were related positively but nonsignificantly to precipitation variables (MAP: r^2 = 0.337, p = 0.0860; MSP: r^2 = 0.304, p = 0.1108). Overall, individuals at cooler, higher elevations seemed to have higher FBT, whereas those at hotter, lower elevations had lower FBT. This result also contrasts with the expectation that populations adapt physiologically to warmer conditions.

Rates of climatic-niche change among populations (Table S7, Appendix S5, Dataset S10) were similar to those estimated for comparable variables in previous studies among species (Quintero & Wiens, 2013) and populations (Jezkova & Wiens, 2016), and thus much lower than projected rates of future climate change. Specifically, among the 18 populations, MAT and MWMT changed at ~0.90°C/Myr and MAP changed at 67 mm/Myr. For paired populations, rates of change in the two physiological variables were similar to those for the climatic-niche variables (Appendix S5), and not significantly different. FBT changed at a faster mean rate than VTM (VTM: ~0.30°C/Myr, FBT: 0.66°C/Myr), but the difference was not significant (p = 0.08–0.09).

4 | DISCUSSION

In this paper, we combine data from field surveys, niche modelling, population genomics, and thermal physiology to address the origin of the Sky Island distribution of a montane species. Overall, our results support the hypothesis that the distribution of the Mountain Spiny Lizard (*Sceloporus jarrovii*) in southeastern Arizona was largely shaped by widespread lowland extinctions related to past climate change. Our phylogenomic results are consistent with

the idea that this species was once broadly distributed in lowlands across the region, but underwent local extinction, becoming restricted to higher ridges and mountain ranges over time. Niche-modelling analyses show that lower elevations between most ranges are now climatically unsuitable for the species. Results of distributional analyses are consistent with the hypothesis that *S. jarrovii* excludes a lower-elevation congener (*S. clarkii*) where they are sympatric, rather than *S. jarrovii* being excluded from low elevations by *S. clarkii*. A thermal physiological variable (voluntary thermal maximum; VTM) shows similar values among low-elevation populations across the region (with little evidence for adaptation to different climates), but significantly lower values relative to a sympatric congener occurring at lower elevations (*S. clarkii*). We suggest that this and other Sky Island species may offer insights into whether species will adapt or go extinct (locally or globally) in response to future, anthropogenic climate change. Our results from *S. jarrovii* suggest that Sky Island distributions are shaped by extinction stemming from the failure to adapt to climate change. Nevertheless, even though our results generally support this scenario, we also find many unexpected patterns, many of which remain difficult to explain. In the sections that follow, we address these surprising aspects of our results and implications for future climate change.

4.1 | Surprising results

Our results differed in several surprising ways from simple expectations. First, we found *S. jarrovii* appears to be absent in several medium-elevation mountain ranges inferred to be climatically suitable based on niche modelling (Figures 1, 2), and located between ranges where the species presently occurs. These include the Atascosas, Mustangs, Pedregosas, Sierritas, and Swisshelms. We found that the distribution of *S. jarrovii* among mountains is predicted by the overall height of these ranges (Figure 3), not their current climate. One potential explanation for these patterns is that *S. jarrovii* was driven to extinction in these lower ranges during periods that were warmer than today (i.e. "pushed off the top"). Our results do not directly address when this might have happened, but climates were considerably warmer during some periods from ~400,000–100,000 years ago (Hansen, Sato, Russell, & Kharecha, 2013; Lisiecki & Raymo, 2005). We also acknowledge that we have not proven that *S. jarrovii* was ever present in these ranges, nor that it is currently absent. However, the strong relationship between range height and presence of *S. jarrovii* would be difficult to explain based on random failure to find this species in some ranges (see also "Methodological concerns" in Appendix S1). Another alternative explanation is that these five mid-elevation ranges are not climatically suitable today because of their fewer days-below-zero (DD_0), which significantly differs between comparable sites in mountains with and without *S. jarrovii* (contrasting with the niche-modelling results). Under this hypothesis, the populations in these ranges may simply have gone extinct when other lowland populations did. Finally, it is possible that *S. jarrovii* was excluded from these mountain ranges by *S. clarkii*. However, our results do not necessarily support this hypothesis, as we discuss below.

We also found that populations of *S. jarrovii* in different Sky Island ranges diverged long before the Last Glacial Maximum (LGM) at ~18,000 years ago (Figure 4), despite the potential for recent dispersal and gene flow among many ranges during that period (Figure 2). Many divergences among populations in different ranges occurred ~4.5–0.5 million years ago (Mya). The surprisingly ancient divergence times among these Sky Island populations do have precedents in some earlier studies. For example, a study of *S. virgatus* in four Sky Islands at the eastern edge of the study area (Animas, Chiricahua, Peloncillo, San Luis) inferred divergence dates of ~1–5 Mya among populations in different mountain ranges (using very different data and methods; Tennessen & Zamudio, 2008). They also found no evidence of recent gene flow among ranges during the LGM. Studies of other organisms have also inferred possible divergence times among some Madrean Sky Islands of ~1 Mya or more (e.g., spiders: Masta, 2000; beetles: Smith & Farrell, 2005; scorpions: Bryson, Riddle, Graham, Smith, & Prendini, 2013). Other studies found deep divergence among ranges, but without estimating dates (e.g., frogs: Barber, 1999). In contrast, another set of studies inferred much more recent divergence times among these ranges (e.g., birds: McCormack et al., 2008; beetles: Ober et al., 2011), and limited genetic differentiation (e.g., insects: Downie, 2004; amphibians: Streicher et al., 2014). We suggest that these different results reflect different patterns in different taxa, not methodological artifacts. Our results may provide the most comprehensive and strongly resolved hypothesis of biogeographic relationships among Madrean Sky Islands so far, especially since most previous studies sampled fewer ranges and relationships among ranges were often obscured by nonmonophyly of individuals from each range (see references above). At the same time, our biogeographic results may not be relevant to groups with younger histories or different distributions in the region. Overall, our genetic results show a striking counterexample to the idea that current distributions and diversity patterns in the region were shaped solely by responses to Pleistocene climatic cycles. Studies in other Sky Island systems have also found divergence times among populations in different ranges that predated the LGM, often by 1 Myr or more (e.g., Eastern Arc mountains of Africa: Bowie, Fjeldså, Hackett, Bates, & Crowe, 2006; Voelker, Outlaw, & Bowie, 2010; Mexican highlands: Ornelas et al., 2013; review in Mastretta-Yanes, Moreno-Letelier, Pinero, Jorgensen, & Emerson, 2015).

Consideration of global temperatures over time makes our results seem even more surprising. Global mean-annual temperatures (Hansen et al., 2013; Lisiecki & Raymo, 2005) were generally warmer than baseline Holocene temperatures from 5 to ~2.5 Mya (and before), and then became cooler than the Holocene baseline, but with some brief, rapid spikes of much warmer temperatures (~400,000–100,000 years ago). Clearly, the observed patterns in *S. jarrovii* would be far easier to explain if temperatures were instead cooler than today before 4.5 Mya (i.e., allowing *S. jarrovii* to disperse in the lowlands between mountain ranges) and then became as warm as

today (or warmer) from 4.5 Mya to the present (i.e., isolating populations in each mountain range). Detailed paleoclimate maps from the region for these time periods (i.e., 5–0.5 Mya) would be helpful but are not yet available. However, it seems unlikely that they would overturn these global-scale trends.

The monophyly of sampled individuals from most mountain ranges (Figure 4) is consistent with the hypothesis that climate-driven local extinction caused their isolation, but is surprising given the potential for recent dispersal among ranges during the Last Glacial Maximum (LGM), especially in the western clade (Figure 2e,f). There is also fossil evidence that pine-oak woodlands (where *S. jarrovii* commonly occurs today) were widespread in the lowlands during this time period (Betancourt et al., 1990). We acknowledge that we have not extensively tested for recent gene flow among ranges, and limited gene flow could be somewhat independent of the monophyly of sampled individuals from a mountain range for concatenated data (i.e., the concatenated estimates presumably reflect the majority of informative loci sampled, whereas gene exchange may occur in fewer loci). Nevertheless, it is clear that the overall pattern in our data is of relatively ancient splits among ranges that are still maintained today (Figure 4).

Many factors might explain the surprising monophyly of most mountain ranges. One potential explanation is that populations failed to disperse into the lowlands during the LGM because of non-climatic factors, such as competitors or microhabitat. Yet, our results are consistent with the hypothesis that the most likely lowland competitor (*S. clarkii*) is displaced by *S. jarrovii* in cooler habitats, not vice versa (although conditions may have been different in the past). Based on our observations, there are no other lizards of similar size utilizing similar microhabitats at the relevant elevations in the region (see also Brennan & Holycross, 2006). Another potential explanation is that there is a reduction in the rocky microhabitat utilized by *S. jarrovii* at lower elevations. However, we have found some individuals of this species using trees and logs for basking sites and shelter in some locations (e.g., Scotia Canyon), suggesting that rocks are not strictly necessary. Furthermore, *S. virgatus* shows similar patterns among the Madrean Sky Islands where it occurs, and is a ground dweller (Tennessen & Zamudio, 2008).

The results of our niche-modelling analyses are surprising in the variables that they identify as setting the distribution of *S. jarrovii* (Appendix S2). Rather than being limited by high summer temperatures in the lowlands as one might expect, our analyses imply that the absence of *S. jarrovii* at lower elevations is explained largely by the scarcity of cold winter temperatures (i.e., number-of-days-below-zero; DD_0). It is unclear why *S. jarrovii* would require cold winter temperatures, but it might be related to their life cycle, which involves mating in the fall, gestation over the winter (during which they remain active), and live birth in the spring (Ruby, 1977). Thus, higher winter temperatures might interfere with their normal reproductive cycles. In contrast, many lizards in the lowlands, like *S. clarkii*, are inactive during winter and mate and lay eggs in spring and summer (Tinkle & Dunham, 1986). We acknowledge the possibility that some methodological error may explain why we infer DD_0 as being important, but it is not clear what that error would be. Instead, multiple lines of evidence support its importance. In the finescale analyses, DD_0 is the only climatic variable that distinguishes *clarkii*-only mountain ranges from those with *S. jarrovii*. For well-sampled elevational transects, localities for *S. jarrovii* and *S. clarkii* differ significantly for this variable (Table S4). Moreover, niche-modelling analyses with a different set of climatic variables (WorldClim) also suggested that warm winter temperatures help explain the distribution of *S. jarrovii* (Appendix S2). Overall, further work is needed to determine the specific mechanisms that limit the distribution of *S. jarrovii* at lower elevations, and if other montane species are limited by warm winter temperatures at lower elevations.

Some of our physiological results are also unexpected. As predicted, we found little evidence that voluntary thermal maxima (VTM) covary with different temperature regimes at different low-elevation sites (Figure 5, Table S6). However, our analyses of field body-temperatures (FBT) suggest that individuals at sites with hotter climates maintain cooler body temperatures (at least during the time period of our analyses). A tendency to avoid higher temperatures in warmer climates might reduce the ability of this species to adapt physiologically to hotter temperatures at lower elevations (e.g., Huey, Hertz, & Sinervo, 2003), and might help explain the limited variability in VTM among populations. Our niche-modelling analyses (Appendix S2) also suggest that these physiological variables are not the most relevant for explaining the low-elevation range limits of *S. jarrovii*. We also found that mean population VTM values (37.8–39.8°C) were consistently higher than maximum annual temperatures (Bio5, maximum = 35.1°C; Dataset S2), both for these low-elevation populations of *S. jarrovii* and for all our *S. clarkii* localities (many well below those of *S. jarrovii*). The observation that maximum annual temperatures remain below the VTM can be interpreted as indicating that the highest summer temperatures do not set the lower-elevational range limits of *S. jarrovii* (following Camacho et al., 2015).

Our results also show a surprising pattern that is potentially relevant to species interactions. We found that *S. clarkii* and *S. jarrovii* occur parapatrically in many mountain ranges in the region, with *S. clarkii* generally occurring at lower elevations (Figure 3). Thus, one might be tempted to conclude that *S. clarkii* prevents *S. jarrovii* from occurring in lower-elevation habitats. Surprisingly, we found that *S. clarkii* occurs at significantly higher elevations when *S. jarrovii* is absent (when low mountain ranges are excluded). These results are consistent with the idea that *S. jarrovii* is the superior competitor, and that it prevents *S. clarkii* from extending its range to higher elevations in the many ranges where they are both present. We think that this is plausible given that both species have similar diets (i.e., generalist insectivores: Simon, 1975; Degenhardt, Painter, & Price, 1996) and use similar microhabitats in sympatry, and show only limited elevational overlap in sympatry (Figure 3). However, we acknowledge that we have not proven that competition explains these patterns. Furthermore, *S. jarrovii* might not be a superior competitor in all contexts. Instead, *S. clarkii* might become superior in low-elevation habitats, such that the lower elevational limits are explained

by a combination of lowland climate and competition. Interestingly, the climatic variable that best explains the absence of *S. jarrovii* relates to fewer winter days with subfreezing temperatures (DD_0), but *S. clarkii* is not active in winter (Tinkle & Dunham, 1986). Thus, it is unclear how a combination of this variable and competition with *S. clarkii* would explain the lower elevational range limits of *S. jarrovii*.

If *S. jarrovii* does exclude *S. clarkii* at higher elevations, then how might this happen? We speculate that this might be related to the bolder behaviour of *S. jarrovii*. We found evidence that *S. clarkii* is significantly shyer than *S. jarrovii* where these species occur together (Appendix S7; Dataset S11), and previous authors have mentioned the relatively bold behaviour of *S. jarrovii* (e.g. Schwalbe, 2009). More cautious behaviour may be advantageous in lower-elevation habitats if those habitats have higher predation, but might be disadvantageous in higher-elevation habitats where they occur together. There is evidence that juvenile *S. jarrovii* experience higher predation pressure near their lower-elevational range limits than at higher elevations (Ballinger, 1979). Finally, we note that there is a precedent for the idea that more aggressive montane species may exclude their lowland relatives from higher-elevation habitats (e.g., Arif, Adams, & Wicknick, 2007). Clearly, more work is necessary to establish whether competitive interactions help explain the distribution of these species in the region, the mechanisms involved, and whether their relative boldness is even relevant. Nevertheless, we believe that our results justify future work along these lines.

4.2 | Implications for future climate change

Overall, our results suggest that the distribution of *S. jarrovii* in the region is shaped by the failure to adapt to a warming climate in the past. Although this species appears to be relatively robust to the limited anthropogenic climate change that has occurred so far (Appendix S1), lower-elevation populations may be unable to adapt rapidly enough to the much more extensive warming predicted in the future. This species is also absent from many lower mountain ranges where it presumably had to either adapt or perish (Figure 3), assuming it was formerly present in these ranges. Its apparent absence in these ranges implies that it was unable to adapt rapidly enough. Fortunately, the range of *S. jarrovii* in southeastern Arizona includes many very tall mountain ranges (>3,000 m; Figure 3), and the species occurs across a broad range of elevations. Thus, it may persist in the highest ranges, even if it is lost from the lowest ranges, such as the Canelo Hills and Perillas. Other regions with highly diverse, endemic Sky Island biotas may be less fortunate, particularly in tropical mountain systems with lower maximum elevations (Western Ghats of India, coastal ranges of northeast Australia, Atlantic Forests of Brazil). We suggest that examining Sky Island distributions in general might be relevant to predicting species responses to climate change in the future. Our results from *S. jarrovii* suggest that Sky Island distributions may be shaped by the inability of montane-adapted species to survive in warmer climates.

5 | CONCLUSIONS

In this paper, we demonstrate how analyses of the distribution of Sky Island species may offer insights into the resilience of species to global warming. Sky Island species are particularly important, because they are relevant to how species may respond specifically to warming climates, not just changing climates in general. Our results for *Sceloporus jarrovii* supported our general expectations for a species that was formerly widespread in the lowlands but experienced widespread local extinction in response to a warmer climate. However, many aspects of our results were unexpected, including the specific climatic variables that limit its distribution, its absence from many climatically suitable mountain ranges, the timeframe of its genetic divergence among mountain ranges (especially in relationship to past climates), the negative relationship between body temperatures and climatic temperatures, and a surprising pattern potentially related to species interactions. Overall, these findings may be relevant to many other Sky Island systems.

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AUTHOR CONTRIBUTIONS

J.J.W. designed the study, analyzed ecological and physiological data, and wrote the main paper. A.C. and J.J.W. collected physiological data. R.L.W. and J.J.W. performed field surveys and collected behavioural data. A.G. compiled museum locality data. T.J. performed niche modelling analyses and analyzed niche rates. M.E.K. provided samples. E.C.M., S.M.L., and J.W.S. generated molecular data. S.M.L. analyzed molecular data. Most authors helped collect samples and contributed to manuscript revisions.

DATA AVAILABILITY

Data archiving: nonmolecular data are included as Supplementary Materials. These and the molecular datasets are available on Dryad (https://doi.org/10.5061/dryad.dp13668).

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SUPPORTING INFORMATION

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

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