RESEARCH ARTICLE

Diversity and **Distributions** WILEY

Forecasting climate change response in an alpine specialist songbird reveals the importance of considering novel climate

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Editor: Dr Chris Burridge

Abstract

Aim: Species persistence in the face of climate change depends on both ecological and evolutionary factors. Here, we integrate ecological and whole-genome sequencing data to describe how populations of an alpine specialist, the Brown-capped Rosy-Finch (*Leucosticte australis*) may be impacted by climate change.

Location: Southern Rocky Mountains in North America.

Methods: We sampled 116 Brown-capped Rosy-Finches from 11 sampling locations across the breeding range. Using 429,442 genetic markers from whole-genome sequencing, we described population genetic structure and identified a subset of 436 genomic variants associated with environmental data. We modelled future climate change impacts on habitat suitability using ecological niche models (ENMs) and impacts on putative local adaptation using gradient forest models (a genetic-environment association analysis; GEA). We used the metric of niche margin index (NMI) to determine regions of forecasting uncertainty due to climate shifts to novel conditions.

Results: Population genetic structure was characterized by weak genetic differentiation, indicating potential ongoing gene flow among populations. Precipitation as snow had high importance for both habitat suitability and changes in genetic variation across the landscape. Comparing ENM and gradient forest models with future climate predicted suitable habitat contracting at high elevations and population allele frequencies across the breeding range needing to shift to keep pace with climate change. NMI revealed large portions of the breeding range shifting to novel climate conditions.

Main conclusions: Our study demonstrates that forecasting climate vulnerability from ecological and evolutionary factors reveals insights into population-level vulnerability to climate change that are obfuscated when either approach is considered independently. For the Brown-capped Rosy-Finch, our results suggest that persistence may depend on rapid adaptation to novel climate conditions in a contracted breeding range. Importantly, we demonstrate the need to characterize novel climate conditions that influence uncertainty in forecasting methods.

1 | INTRODUCTION

Global climate change is dramatically affecting biodiversity, and extinction rates are accelerating across taxonomic groups (Urban, 2015). Alpine organisms that already inhabit the upper elevational reaches can be at particular risk of climate change driving upslope range shifts due to reduced potential to shift their range (Freeman et al., 2018; Sekercioglu et al., 2008); however, this risk may be tempered in regions that provide an abundance of microclimates (Seastedt & Oldfather, 2021). If range shift is not feasible, a species' long-term persistence in the face of climate change will likely depend on evolutionary or behavioural adaptation (Aitken et al., 2008; Forester et al., 2018; Hoban et al., 2016; Hoffmann & Sgró, 2011). Advances in ecological genomics are elucidating the genomic architecture of local adaptation (Hämälä & Savolainen, 2019; Savolainen et al., 2013; Tigano & Friesen, 2016) and providing insight into population-level responses to climate change (Bay et al., 2018; Dauphin et al., 2021; Fitzpatrick et al., 2021; Fitzpatrick & Keller, 2015; Rellstab et al., 2016; Ruegg et al., 2018). While common garden experiments are widely recognized as the best method for identifying signals of local adaptation (de Villemereuil et al., 2016; Kawecki & Ebert, 2004), ecological genomic approaches provide an alternative in species where common garden approaches are infeasible due to constraints related to life history and/or conservation status (i.e. threatened or endangered status).

Ecological niche models (ENMs) are used to assess vulnerability to climate change by forecasting the distribution of climatic conditions that characterize an organism's current range (Guisan & Thuiller, 2005; Pacifici et al., 2015). Given the variety of terminology used in the literature surrounding ENMs, we will follow the guidelines set out by Sillero (2011) that ENMs model an organism's ecological niche and the resulting output maps forecast habitat suitability. Genomic offset is a complementary approach to predicting climate vulnerability and provides a relative measure of the magnitude of evolutionary adaptation required for a population to track changing climate conditions (Capblancq et al., 2020; Fitzpatrick & Keller, 2015; Rellstab et al., 2021). Genomic offset is based on identifying genetic-environment associations putatively underlying local adaptation and predicting future adaptive genetic composition based on the current genetic-environment associations (e.g., with gradient forest models; Fitzpatrick & Keller, 2015). However, genomic offset predictions may ignore key ecological factors (e.g., habitat suitability) that would affect persistence, especially for organisms with ranges that are experiencing drastic environmental changes. While genomic offset has predominantly been assessed independently of ecological factors (Capblancq et al., 2020, Rellstab et al., 2021; but see Chu et al., 2021; Gougherty et al., 2021; Nielsen et al., 2021), vulnerability to climate change is a multifaceted problem that should be

assessed with multiple methodologies and data sources (Dawson et al., 2011). Integrating genomic offset and ecological niche models would provide an understanding of the ecological factors shaping where populations could persist, and the evolutionary factors underlying the amount adaptation required to persist there.

The objective of our study was to combine methods for predicting population-level response to climate-driven disruptions to habitat suitability and genomic adaptation to improve forecasting of climate vulnerability. We addressed this objective using the Brown-capped Rosy-Finch (*Leucosticte australis*), an alpine-obligate species endemic to the Southern Rocky Mountains (Wyoming, Colorado and New Mexico) and part of a broader species complex notable for specializations to alpine sky islands and arctic tundra (Johnson et al., 2020). While climate change broadly results in species shifting distributions poleward and upward in elevation (Chen et al., 2011; Parmesan & Yohe, 2003), the Brown-capped Rosy-Finch has limited potential for poleward range shift given the isolation of the Southern Rocky Mountains from other high-elevation mountain ranges and the presence of congeneric species that already inhabit those mountain ranges. Furthermore, Brown-capped Rosy-Finches already occupy nesting cliffs at the highest elevations (above 3350 m) of the Southern Rocky Mountains, which limits the possibility for major upslope range shifts, although they occupy lower elevations during the winter months (Johnson et al., 2020). Recent genetic studies have suggested that mountain ranges do not function as geographic barriers to dispersal for the North American Rosy-Finch complex (Black Rosy-Finch [*Leucosticte atrata*], Grey-crowned Rosy-Finch [*Leucosticte tephrocotis*], Brown-capped Rosy-Finch) given the level of ongoing gene flow among these species (Drovetski et al., 2009; Funk et al., 2021). Ongoing gene flow among Brown-capped Rosy-Finch populations may be an important component that mitigates genomic offset and prevents genetic isolation.

Here, we outline a process to assess climate vulnerability that considers evolutionary (e.g. genomic offset) and ecological factors (habitat suitability; Figure 1). We aim to answer the question: How can estimates of genomic offset and habitat suitability be combined to improve forecasts of climate vulnerability? Using genome-wide sequence data, we assessed population genetic structure and estimated levels of inbreeding and genetic diversity to describe spatial genetic variation and appropriately inform subsequent genetic-environment association (GEA) analyses (Forester et al., 2018; Funk et al., 2019). We performed environmental variable selection to identify a subset of uncorrelated predictors for use in the GEAs and ENMs. We developed ecological niche models (ENMs) using the environmental predictor data and presence-absence data from the citizen-science database eBird (Sullivan et al., 2009). Additionally, we identified a subset of genomic variants associated with the environmental data and used
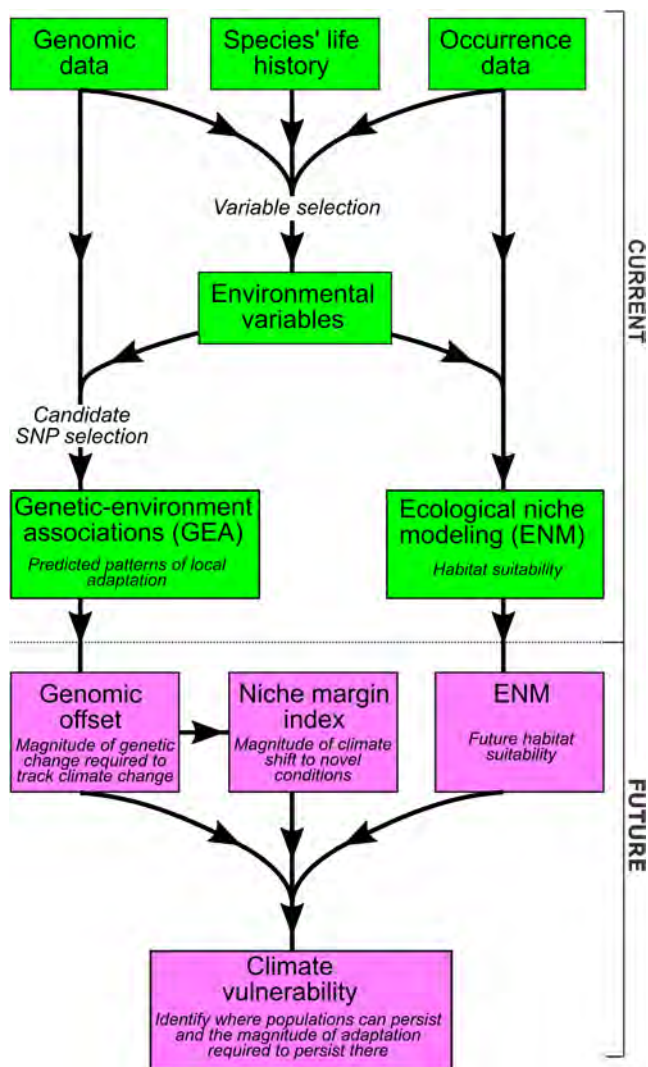
FIGURE 1 Workflow for combining ecological niche modelling and genomic offset for determining populationlevel climate vulnerability. Genomic data and occurrence data inform environmental variable selection by providing the geographic points for which environmental correlation is calculated. Species' life history information informs which variables are selected from correlated pairs, resulting in an uncorrelated set of environmental variables. Candidate adaptive SNPs are obtained through genetic-environment association outlier analyses using the environmental variables and genomic data. The resulting candidate SNPs are the input into gradient forest models which predict adaptive genetic composition across the landscape. The subset of environmental variables are also used with occurrence data in ecological niche models to habitat suitability. Gradient forest models are used to predict adaptive genetic composition to future climate and the distance with the baseline environment provides the measure of genomic offset. Additionally, the niche margin index is calculated to quantify the extrapolation to novel climate. Ecological niche models are also projected to future climate to provide a measure of future habitat suitability. The integration of these models provides a description of where populations are most likely to persist in the future and the magnitude of genetic change required to persist there. Furthermore, regions of novel climate are depicted to highlight uncertainty in the forecasting method

these data to model allelic turnover across the landscape with gradient forest (Ellis et al., 2012; Fitzpatrick & Keller, 2015). Using ensembles of global climate models for two time periods, 2041–2070 and 2071–2100 (AdaptWest Project, 2021), we then forecast climate vulnerability in relation to genomic offset and habitat suitability. We demonstrate a novel application of the niche margin index (Broennimann et al., 2021) to highlight uncertainty in genomic offset predictions due to novel climate conditions.

Specifically, this study aimed to (1) characterize the magnitude of genetic change required to track climate change and where populations could persist to minimize genomic offset; (2) predict climate-driven habitat suitability shifts into the future and (3) compare the underlying climatic drivers of, and spatial vulnerability to, genomic offset and habitat suitability. The integration of these approaches will provide a better understanding of evolutionary and ecological factors underlying species response to climate change and improve our ability to forecast climate change impacts on biodiversity.

2 | METHODS

2.1 | Field sampling and sequencing

We sequenced feather and blood samples from 116 individuals spanning 11 sites across the Brown-capped Rosy-Finch breeding distribution (Table 1). Samples were collected during the breeding season of 2017 and 2018. Individuals from the Lost Man Lake and Independence Lake sites were combined as a single sampling unit for subsequent analyses based on their proximity (<1 km) and the low sample sizes (5 and 1 individuals, respectively). Engineer Mountain and Horseshoe Basin sites were also in close proximity (<5 km), but we retained them as separate sampling units due to the larger number of individuals per site (8 and 18 individuals, respectively).

We extracted DNA from blood samples using the standard protocol for Qiagen DNEasy Blood and Tissue Kits and we modified the protocol to maximize DNA yield from feathers. Whole-genome sequencing libraries were prepared following modifications of Illumina's Nextra Library Preparation protocol. Pooled libraries were sequenced on HiSeq 4000 lanes at Novogene Corporation Inc. All sequence data were quality filtered (GATK: McKenna et al., 2010; BCFtools: Li, 2011; Samtools: Li et al., 2009) and aligned (Burrows-Wheeler Aligner software; Li & Durbin, 2009) to a high-quality Brown-capped Rosy-Finch reference genome that was created by Dovetail Genomics through 10x de novo assembly and HiRise Scaffolding. The reference genome was created from liver samples of the Brown-capped Rosy-Finch (Denver Museum of Nature and Science samples DMNS52416 and DMNS52417). The reference genome was annotated with the most recent zebra finch annotations available (NCBI GCA_008822105.2) using the program Liftoff (Shumate & Salzberg, 2021). For the input into all subsequent analyses, we extracted high-quality single-nucleotide polymorphisms (SNPs; Supporting information).

TABLE 1 Sample location information with environmental data (1991–2020 period) and population genetic parameters

Location	ID	Latitude	Longitude	Sample size	MWMT	PAS	SHM	Elevation	Pi	F	Ne
Devil's Causeway	DECA	40.032	−107.167	15	11.28	954.8	32.9	3508.6	0.00053	0.10293	403.1
Emma Burr Mountain	EBMO	38.751	−106.417	3	10.59	413.8	39.9	3743.9	0.00047	0.24599	-
Engineer Mountain	ENMO	37.967	−107.578	8	9.73	783.2	29.4	3825.7	0.00053	0.09071	-
Horseshoe Basin	HOBA	37.947	−107.554	18	9.34	820.3	28.1	3891.4	0.00056	0.02001	236.5
Independence Lake	LMIN*	39.140	−106.567	1	9.55	603.4	33.4	3937.2	0.00053*	0.13024*	-
Lake Agnes	LAAG	40.473	−105.895	15	10.16	927.0	27.1	3586.2	0.00055	0.04249	-
Lost Man Lake	LMIN*	39.148	−106.570	5	9.55	603.4	33.4	3937.2	0.00053*	0.13024*	-
Mt. Maxwell	MOMA	37.249	−105.147	7	10.04	598.7	25.2	3825.3	0.00053	0.15346	-
Mt. Evans	MTEV	39.588	−105.644	11	8.25	543.7	22.4	4163.8	0.00051	0.18759	108.3
Pike's Peak	PIPE	38.833	−105.041	21	8.8	407.5	17.0	4066.0	0.00052	0.02067	217.0
Snowy Range	SNRA	41.368	−106.303	12	11.5	943.4	35.1	3406.7	0.00052	0.11167	140.2

Note: ID = four letter abbreviation for sample locations used in the manuscript. Latitude and longitude specify the coordinates for sampling site locations and sample size specifies the number of individuals captured at these locations. MWMT is the mean temperature of the warmest month (°C), PAS is the annual amount of precipitation as snow (mm), SHM is the summer heat moisture index (calculated by dividing MWMT by the mean summer precipitation), and the last column is the elevation of the sampling site (m).

Pi = mean nucleotide diversity across 25000 base pair windows. F = individual inbreeding statistics. Ne = effective population size for locations with sufficient sample size for the linkage disequilibrium method of calculation.

*Two sampling sites (Engineer Mountain and Horseshoe Basin) from which individuals were combined as a unit for analyses due to close proximity of the sites.

2.2 | Population genetic structure

We performed several analyses to describe geographic patterns of genetic variation. The presence of closely related individuals can skew signatures of population structure, so we used KING (Manichaikul et al., 2010) to identify and remove individuals with up to second-degree relationships (kinship > 0.0884). PCA provides an efficient nonmodel-based method for assessing population structure in high-dimensionality data sets (Patterson et al., 2006). We implemented principal components analysis (PCA) using the R package SNPrelate (Zheng et al., 2012) in R version 3.6.2 (R Core Team, 2019). Additionally, we estimated individual ancestry coefficients with the snmf function in the R package LEA (Frichot et al., 2014; Frichot & François, 2015), and tested a range of clusters from K = 1 to 6 with 100 iterations each. Finally, we tested for effects of isolation by distance (linearized FST versus log10 geographic distance) with a Mantel test in the R package adegenet (Jombart, 2008). Pairwise FST was calculated in VCFtools version 0.1.13 (Danecek et al., 2011). Pairwise FST provides an estimate of genetic divergence between populations where higher FST values indicate higher divergence. Genetic divergence can increase through genetic drift but is homogenized by gene flow between populations. Thus, any patterns of high FST between sites can be used to identify potential barriers to gene flow. The interaction between levels of gene flow and effective population size can result in different patterns of nucleotide diversity and inbreeding. We calculated nucleotide diversity across 25,000 base-pair windows and individual inbreeding coefficients using VCFtools (Danecek et al., 2011). We estimated contemporary effective population size using the LD method from NeEstimator (Do et al., 2014).

2.3 | Bioclimatic variables

Snow is a major component of weather that shapes alpine communities. Snow cover can insulate soils from extreme cold air temperatures (Neuner, 2014) and also dictate the length of the growing season (Jonas et al., 2008; Keller et al., 2005). In some alpine plant species, reductions in snow cover can result in increased frost damage and decreased plant production (Abeli et al., 2012; Baptist et al., 2010; Inouye, 2000). The Brown-capped Rosy-Finch feeds on a variety of seeds throughout the year and on insects during the breeding season (Johnson et al., 2020; Martin et al., 1961; Packard, 1968; Warren, 1916). Elevation is an important component of the Brown-capped Rosy-Finch breeding range in relation to the presence of high-elevation nesting cliffs (Johnson et al., 2020). To encapsulate the range of bioclimatic factors that may influence Brown-capped Rosy-Finch alpine breeding habitat, we obtained 32 bioclimatic variables and elevation from the AdaptWest Project at a 1 km resolution (AdaptWest Project, 2021; Wang et al., 2016). Variable selection involved removing correlated variables (Pearson correlation coefficient > 0.75) and using

expert opinion to select the most likely biological relevant predictor from correlated sets. To best represent the current time period that corresponds to our sampled data, we obtained the bioclimatic variables as means across the time period of 1991–2020, and we obtained the dataset at an appropriate resolution for Brown-capped Rosy-Finch breeding movements (1 km).

2.4 | Identifying putative adaptive variants

We used two genetic-environment association (GEA) approaches to identify a set candidate SNPs that are associated with environment. First, we implemented the multivariate approach of redundancy analysis (RDA) as it performs well for detecting weak, multilocus signatures of selection (Forester et al., 2018). We performed RDA using environmental and elevation data from individual sampling locations as the predictor variables and individual genotypes as the response variables. To account for isolation by distance, we created Moran Eigenvector Maps (MEMs) from the geographic locations of sampling data and conditioned the RDA model on the MEMs. All RDAs were conducted with the R package vegan (Oksanen et al., 2013), and step-wise model selection was performed using the ordistep function. Multicollinearity in the model was checked with variance inflation factors (VIF) and predictors with a VIF greater than 10 were removed (Zuur et al., 2010). RDA component contribution was used to determine the number of components included for identifying candidate SNPs. Candidate SNPs underlying local adaptation were identified by having p-values outside a three standard deviation cutoff (two-tailed p-value = .0027).

Second, we used latent factor mixed models (LFMM) as a univariate regression model to identify candidate SNPs associated with each of the predictor variables (Frichot & François, 2015). We set the number of K latent factors based on the results from the individual ancestry coefficient results. For each model, we set the false discovery rate to 0.05 and calibrated the p-values by setting the genomic inflation factor to achieve a flat p-value distribution with a peak at 0 (François et al., 2016). LFMM analysis was conducted in R using the LEA package (Frichot & François, 2015). SNPs identified in both RDA and LFMM were used as the candidate SNP set putatively underlying local adaptation. We identified chromosomal position and gene information of the candidate SNPs using the Bedtools "closest" function (Quinlan & Hall, 2010) with the annotated *Leucosticte australis* genome. We identified candidate genes by selecting SNPs within 10,000 bases from genes of known function and tested for gene ontology enrichment with the chicken (*Gallus gallus*) genome using the Gene Ontology resource (Ashburner et al., 2000; Carbon et al., 2021; Mi et al., 2019).

Importantly, GEA analyses rely on the assumption that current allele frequencies are at equilibrium with the environment (Capblancq et al., 2020; Lasky et al., 2018). However, populations may experience an adaptational lag associated with historical environmental conditions (Browne et al., 2019). To test the influence

of this assumption, we created two candidate SNP sets based on two temporal periods: one that temporally encompassed our sample period (1991–2020) and one based on potential adaptational lag (1961–1990).

2.5 | Geographic distribution of putative adaptive variation

We used the gradient forest algorithm to describe the associations of spatial, environmental and genetic variables (Ellis et al., 2012; Fitzpatrick & Keller, 2015). Gradient forest is a machine learning method developed to model ecological community turnover in relation to environmental gradients by creating separate random forest models for each species (Breiman, 2001; Ellis et al., 2012). Community turnover is then identified by aggregating environmental predictor importance for each species. This concept has been extended to landscape genetics by substituting allele frequencies at genetic loci for species and modelling adaptive genetic composition across the landscape (Fitzpatrick & Keller, 2015). The turnover functions in gradient forest allow for inference of the environmental predictors driving observed changes in allele frequency (Fitzpatrick & Keller, 2015). We fit gradient forest models to environmental and spatial data as predictors for the nine sampling sites with at least six individuals using the package gradientForest (Smith & Ellis, 2013). We modelled adaptive genetic variation turnover on the landscape using the candidate SNP set as the response variable. Model tuning was performed on the parameters *mtry* (random subset of predictors used in random forest) and *ntree* (number of trees grown in each forest; Hastie et al., 2009). We evaluated model performance with prediction accuracy calculated from the out-of-bag samples (Ellis et al., 2012). We tested model performance of the candidate SNPs against a randomized model of candidate SNP allele frequencies and a SNP set that included putatively neutral loci (Supporting information). Using the top gradient forest model, we interpolated genetic composition across the remaining 1 km^2 cells from the breeding range for which we did not sample genetic data.

2.6 | Habitat suitability under climate change

We created ENMs using the ensemble modelling approach in the R package *biomod2* (Thuiller et al., 2016; Supporting information). Presence-absence data were obtained from the eBird Basic Dataset (Sullivan et al., 2009) using the R package *ebirdst* (Strimas-Mackey et al., 2021). We used the same uncorrelated set of environmental predictor variables as in the GEA analyses. Models were trained on random subsets of 80% of the data with 10 replications for five algorithms (regression based methods: generalized linear model (GLM; McCullagh & Nelder, 2019)), multiple adaptive regression splines (MARS; Friedman, 1991), and machine learning methods: gradient boosting trees (GBM; Elith et al., 2008), maximum entropy (Maxent; Phillips et al., 2006), artificial neural networks (ANN; Lek &

Guégan, 1999). Given the focus of our subsequent analyses on temporal forecasting, we aimed to use a set of algorithms with balanced biases and avoided models that tend to project extreme outcomes (Beaumont et al., 2016). Model performance was based on total area under the receiver operator and the relation of specificity and sensitivity (true skills statistic, TSS). Only the top performing algorithms were included in the final ensemble model. Binary rasters of suitable/unsuitable habitat were created based on a TSS threshold that maximized the sum of specificity and sensitivity since this has been shown to effectively represent presence (Jiménez-Valverde & Lobo, 2007).

Future distribution was modelled for two time periods (2041–2070 and 2071–2100) and for four different shared socioeconomic pathways (SSPs). The SSPs vary in the possible climate change challenges global socioeconomic policy will produce (O'Neill et al., 2016): SSP126 (low challenges), SSP245 (medium challenges), SSP370 (high challenges) and SSP585 (high challenges). Given that the SSP585 scenario most closely tracks the recent climate predictions from the Intergovernmental Panel on Climate Change report (IPCC, 2021), we used the SSP585 results for all figures in the main body of the article and provided details of the other scenarios in the Supporting information. For all possible combination of time period and SSPs (8 combinations), we obtained 1 km resolution bioclimatic data from 13 general circulation models provided by AdaptWest (AdaptWest Project, 2021; Wang et al., 2016). We test for upward elevational shifts in habitat suitability between current and future projections using a two-sample t-test for the elevation values in the suitable habitat binary rasters.

2.7 | Genomic offset to climate change

Genomic offset estimates the magnitude of evolutionary adaptation needed for a population to keep pace with climate change (Capblancq et al., 2020; Rellstab et al., 2021). When using gradient forest models, genomic offset is calculated by the Euclidean distance between current genetic composition with the predicted genetic composition based on future environment (Fitzpatrick & Keller, 2015). We calculated the mean genomic offset for each cell across the different SSP and time period combinations of future climate. In gradient forest models, environmental values outside the range of the provided trained values from sampling sites result in extrapolation of genetic composition. We used the default method of linear extrapolation from the non-linear turnover functions in the gradientForest package (Smith & Ellis, 2013; Supporting information).

2.8 | Quantifying uncertainty in genetic-environment associations

The niche margin index (NMI) is a metric that characterizes the distance from niche margins with 0 representing the margin, 1 being the maximum value within the niche, and decreasing negative values

representing distance outside the niche (Broennimann et al., 2021). We use this concept to quantify the niche margins of the observed environmental data from our sampling sites and then measure NMI for all raster cells in the genomic offset predictions of future climate. In our usage of NMI, negative values represent regions with novel future climate conditions in relation to the current observed genetic-environment associations (i.e. at the sampling sites). Positive NMI values represent regions with future climate conditions that are currently experienced on the breeding range. Thus, genomic offset predictions in regions with positive NMI are based on the space-for-time assumption in the gradient forest models (Capblancq et al., 2020), while genomic offset predictions in regions with negative NMI indicate higher model uncertainty due to extrapolation in the gradient forest models.

3 | RESULTS

3.1 | Population genetic structure

Whole-genome sequencing produced genomic data with an average 6x depth of coverage and variant filtering resulted in 429,442 SNPs for subsequent genetic analyses. We removed 12 individuals from the dataset due to relatedness. Visualizing PCA results revealed weak clustering of Pike's Peak individuals from other sampling sites (Figure S1). The weak PCA clustering of individuals suggests low genetic differentiation among the sites, which was also supported by low pairwise FST values ranging from 0 to 0.042 (mean FST = 0.012; Table S1). The Mantel test did not identify associations between genetic and geographic distance ($r = -0.003$, p-value = .42), but visualization of these pairwise comparisons revealed the Pike's Peak population had elevated genetic differentiation compared with other site comparisons (Figure S2). Individual ancestry coefficients had the lowest cross-entropy values for K = 1 clusters (cross-entropy = 0.870; Figure S3). Results for K = 2 had only slightly higher cross-entropy (0.872) and revealed separation of Pike's Peak individuals (Figure S3), similar to PCA results. Nucleotide diversity was similar across sampling locations (pi mean = 0.00053, range = 0.00047–0.00056; Table 1). The per-individual F inbreeding statistic was also similar across sampling locations (F mean = 0.11, range = 0.02–0.25; Table 1). Effective population size for the five sampling locations that had sufficient sampling size ranged from 108 to 403 (Table 1).

### 3.2 | Identifying putatively adaptive variants

The final uncorrelated environmental variable set consisted of mean temperature of the warmest month (MWMT), precipitation as snow (PAS) and summer heat moisture index (SHM; mean summer temperature divided by summer precipitation), as well as elevation. For RDA, we retained the first MEM (MEM1) spatial predictor for accounting for population structure as it was uncorrelated with the other predictor

variables and explained 42.4% of the spatial variation. Model selection in the RDA retained all predictor variables. RDA outlier SNPs putatively associated with climate were identified by loadings on the first constrained axis (Figure S4). We identified 2040 and 2045 candidate SNPs from the 1961–1990 and 1991–2020 environmental predictor datasets, respectively. In LFMM, we used a lambda of 0.7 to achieve the optimal distribution of p-values for each of the four predictor tests (Figure S5). With K = 2 latent factors, we identified 4844 and 4502 candidate SNPs from the 1961–1990 and 1991–2020 environmental predictor sets, respectively. Intersecting the RDA and LFMM datasets identified 501 and 436 candidate SNPs for the 1961–1990 and 1991–2020 environmental predictor sets, respectively. Gene ontology enrichment analysis identified 12 genes associated with the biological process glutamatergic regulation of synaptic transmission (Gene Ontology ID: 0051966, p-value = 2.69e-6, false discovery rate = 3.67e-2) and six genes associated with regulation of small GTPase mediated signal transduction (Gene Ontology ID: 0051056, p-value = 2.73e-6, false discovery rate = 1.86e-2; Table S2).

3.3 | Geographic distribution of putative adaptive variation and habitat suitability

Our evaluation of tuning parameters in gradient forest models identified the out-of-bag testing accuracy to reach convergence with 100 trees ($ntree = 100$). Using all predictors in each tree ($mtry = 5$) achieved the highest proportion of variance explained across the predictors (Figure S6). The comparison of the two time period predictor sets, with the corresponding candidate SNPs, revealed similar relative predictor importance (Figure S7). Therefore, we continued all subsequent analyses with the 1991–2020 predictor set and candidate SNPs. With the candidate SNP set, raw predictor importance was ranked in descending order of precipitation as snow (PAS), mean temperature of the warmest month (MWMT), summer heat moisture index (SHM), elevation and MEM-1 (Figure 2a). The order and magnitude of importance in the top predictor variables was not reflected in the randomized candidate SNP set or the reference SNP set that included neutral variation (Figure 2a). Turnover functions for the predictors revealed mostly stepwise patterns of allelic turnover, except for sharp turnover between precipitation as snow values of 500–600 mm (Figure 2b-f). Sampling sites were most strongly separated in genetic composition turnover driven by precipitation as snow (Figure 3a).

Filtering eBird data resulted in 192 presence points and 4973 absence points in the ENMs. The Maxent and GLM algorithms were used for the ensemble ENM as they had the strongest ability in discerning species presence with high mean true skills statistic across runs (Maxent: 0.86 ± 0.03 standard deviation, GLM: 0.86 ± 0.03) and area under the receiver operator curve (AUC; Maxent: 0.97 ± 0.01, GLM: 0.95 ± 0.02). Environmental variable importance was similar among the algorithms with MWMT, PAS, and elevation as the most important variables (Table S3). Binary rasters were created using a habitat suitability threshold of 0.03 derived by maximizing the specificity and sensitivity of the model. The highest values for habitat
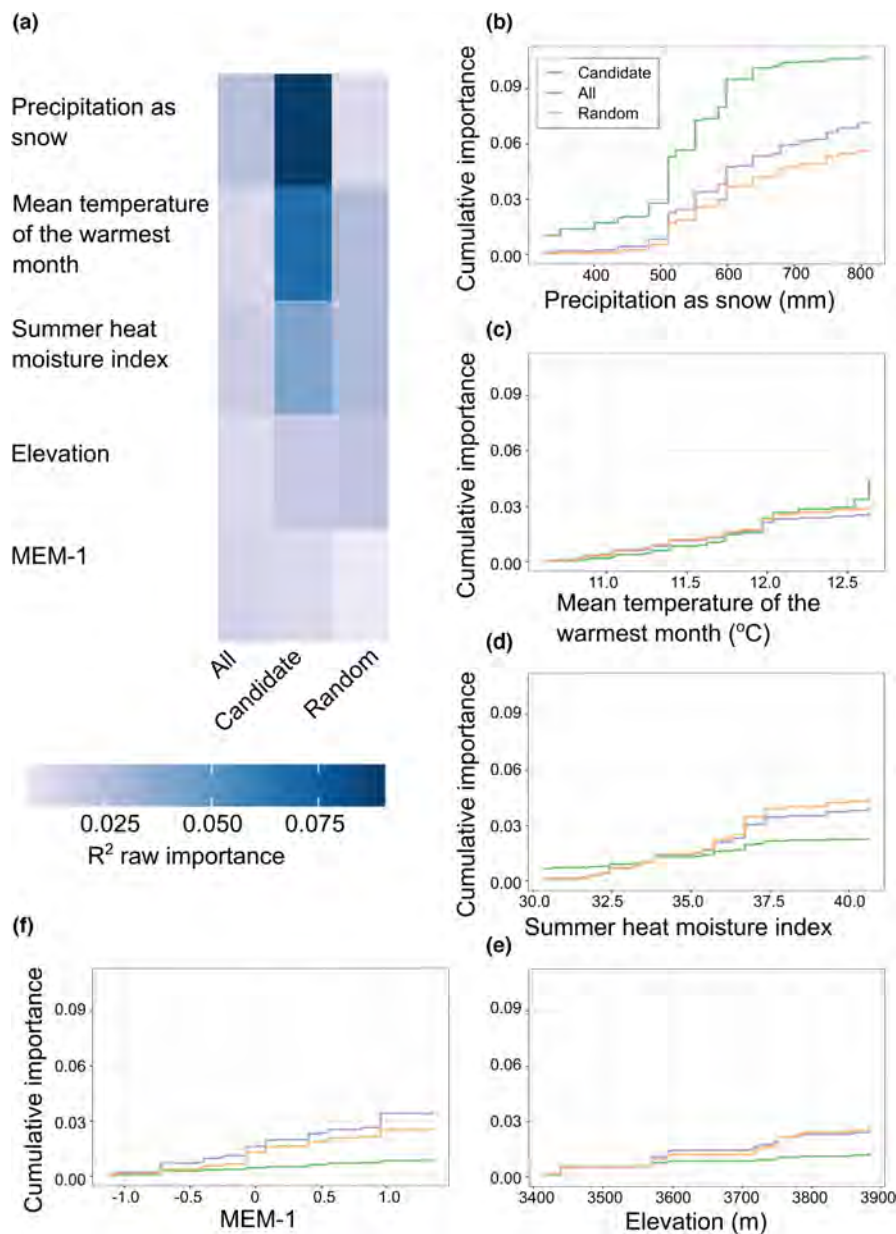
FIGURE 2 Performance of gradient forest models. (a) Raw R2 importance values for variables used as predictors in gradient forest model for three different datasets, which are: "All" is the total genomic variant set of 429,442 SNPs, "candidate" is the 436 candidate SNPs associated with the 1991–2020 baseline environment, and "random" is randomized genotypes of the candidate SNPs among the sampling locations. Using the candidate SNPs, larger raw importance values were obtained with the environmental predictors (precipitation as snow, mean temperature of the warmest month, and summer heat moisture index) than in the other two SNP sets. (b-f) the turnover functions from gradient forest model show the weighted cumulative importance values, which represent the relative importance of a variable in explaining changes in allele frequency. Here, only (b) precipitation as snow reveals consistently higher importance in the candidate SNP set than the other two datasets

suitability were produced for the highest elevation portions of the breeding range with lower habitat suitability in the north-western portions of the Rocky Mountains (Figure 3b).

3.4 | Genomic offset and habitat suitability under climate change

The magnitude of genomic offset was highly variable across the breeding range with some of the lowest values in the southwestern mountains (Figure 3c). Some of the eastern mountain ranges had the largest concentration of high genomic offset values (Figure 3c). While the magnitude of genomic offset increased with climate scenario and time period, the spatial patterns of the relatively low and high genomic offset remained the same (Figure S8). The ENM models revealed that

future suitable habitat broadly became more fragmented in the 2041–2070 time period (Figure 3d). Future suitable habitat shifted upward in elevation from baseline habitat suitability projections by a mean of 178 m (3367 m to 3545 m) across all raster cells ($t = -74.6$, $df = 35,378$, p-value $< 2.2e-16$, 95% CI: 173.3, 182.7). Less severe climate scenarios showed reduced range contraction, and range contraction increased when forecasted to the 2071–2100 time period (Figure S9).

3.5 | Quantifying uncertainty in genetic-environment associations

For the baseline time period, the majority of the geographic region for which we interpolated genetic composition was within or close to the niche margins derived from our sampling sites (Figure 4a). For

FIGURE 3 (a) Mapping of genetic composition from the candidate SNP gradient forest model with colours based on the biplot of environmental variable contribution to allele frequency change. Similar colours represent regions predicted to contain populations with similar genetic composition based on environment. Sampling sites represented by grey triangles. (b) Habitat suitability from the ENM for the current time period had the highest habitat suitability values in the highest elevation portions of the breeding range (bright yellow). The northwestern mountain ranges (e.g. snowy range and Devil's causeway) had some of the lower values of habitat suitability (darker colours). Using the future time period of 2041–2070 and the SSP 585 scenario we predicted genomic offset and habitat suitability. (c) Genomic offset was highly variable across the breeding range with some of the lowest values (blue) in the southwestern mountains and highest (red) in the eastern mountain ranges. (d) Habitat suitability decreased across the range with isolated patches of high suitability (bright yellow)
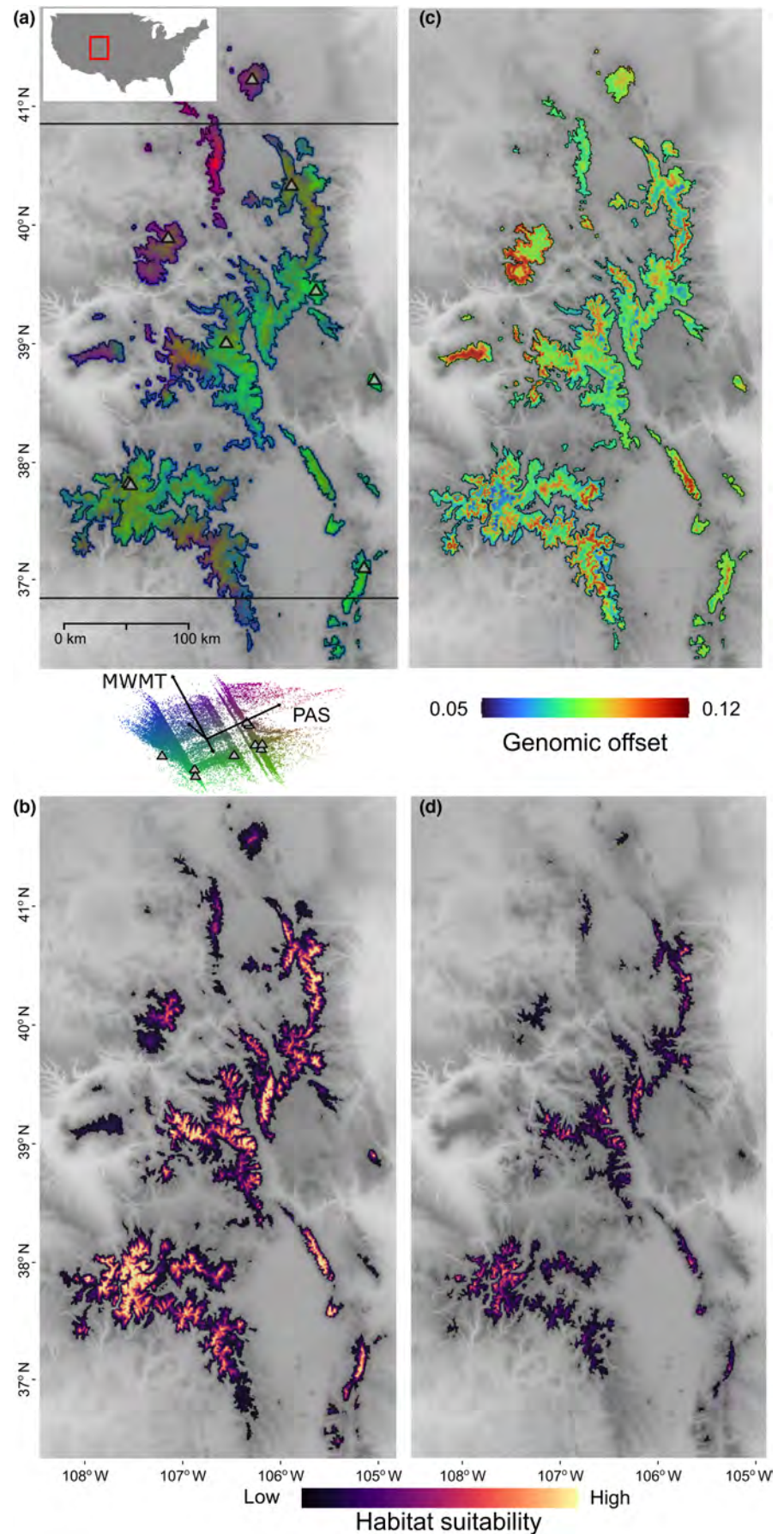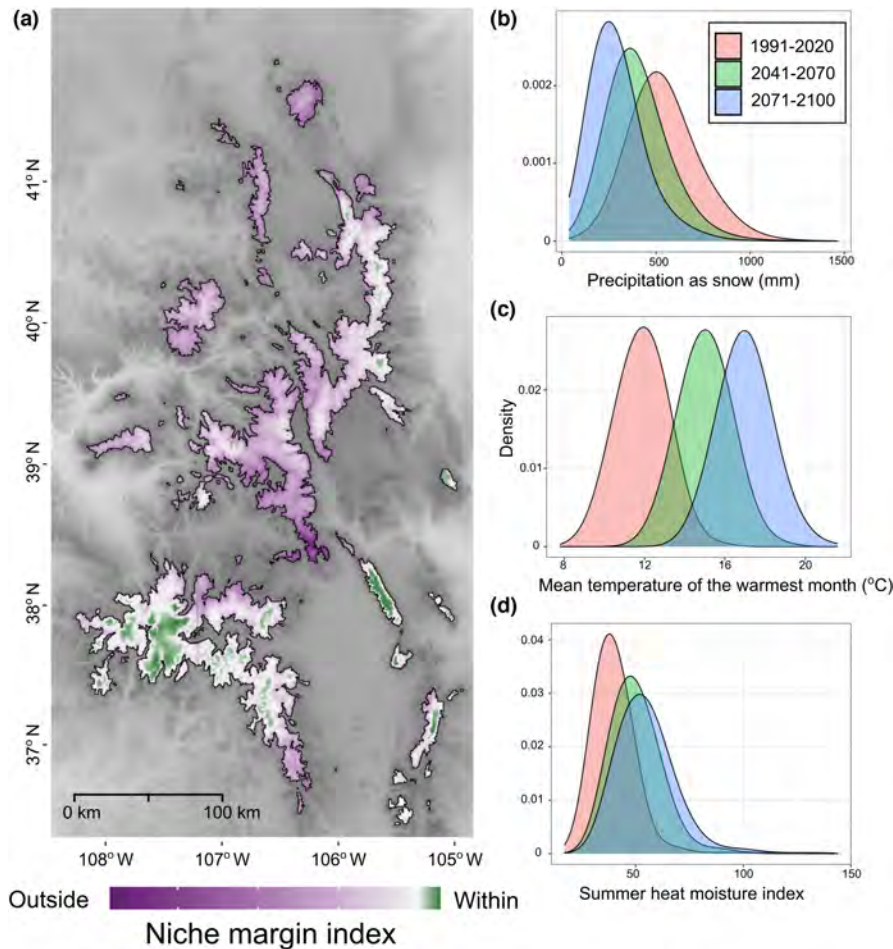
FIGURE 4 Identifying the magnitude of climate shift to novel conditions. (a) Calculating the niche margin based on our sampling sites and the niche margin index to future climate revealed large portions of the breeding range shifting to novel climate conditions (purple). The southern portions of the breeding range had the largest geographic areas retaining similar climate conditions (green) to the sampling sites. (b–d) of the three environmental variables in the gradient forest model that change temporally (i.e. excluding elevation), the largest shifts to novel conditions are present in the mean temperature of the warmest month

the 2041–2070 time period, a larger portion of the range shifted outside the niche margins, broadly indicating a shift to novel climate conditions. Comparing the environmental data among time periods showed in overall decrease in future precipitation as snow (Figure 4b) and increases in mean temperature of the warmest month (Figure 4c) and summer heat moisture index (Figure 4d). The largest shift to novel climate conditions occurred with the temperature of the warmest month (Figure 4c). Combining visualizations of genomic offset, habitat suitability, and NMI showed that the central portion of the breeding range had the most uncertain genomic offset predictions due to climate shifts (Figure 5).

4 | DISCUSSION

In this study, we evaluate climate change consequences related to disruptions of climate conditions putatively underlying local adaptation and habitat suitability on the breeding range of an alpine specialist, the Brown-capped Rosy-Finch. Persistence of Brown-capped Rosy-Finch populations in the face of climate change may depend on rapid adaptation in a contracted region of suitable habitat. We broadly demonstrate genomic offset predictions by themselves can be problematic for inferring vulnerability to climate change when (1) changes in habitat suitability preclude a population from persisting

in a region of forecasted low genomic offset and/or (2) when there are widespread regions forecasted to experience novel climate conditions.

4.1 | Comparing climate drivers of habitat suitability and local adaptation

For the Brown-capped Rosy-Finch, precipitation as snow, mean temperature of the warmest month, and elevation were the strongest predictors of habitat suitability. Our results forecast that the lowest elevational limits of suitable habitat for Brown-capped Rosy-Finches will contract to higher elevations. Similar forecasts of suitable habitat loss at lower elevations have been made for another alpine-obligate species complex (avian genus *Lagopus*; Scridel et al., 2021). Importantly, the upward elevational shift of predicted high habitat suitability may not necessarily correspond to a similar scale of actualized range contraction. A key factor that may mitigate climate change risks for alpine species, especially in the Rocky Mountains, is the highly heterogeneous topography of the alpine landscape (Seastedt & Oldfather, 2021). Alpine microtopography can result in thermal refugia along short horizontal distances that mimic air temperature changes of hundreds of meters upslope (Scherrer & Körner, 2010). The American Pika (*Ochotona princeps*)

FIGURE 5 Population-level vulnerability to future climate of 2041–2070. Colours represent genomic offset and the niche margin index (NMI). Genomic offset ranges from 0.05 (blue) to 0.12 (red), and the transparency of the colours reflects NMI. Bright colours represent NMI within the niche margins (between 0 and 1), while decreasing negative NMI values (novel climate) are represented by the darkening of the colours. Genomic offset predictions are shown for the predicted future suitable breeding range from the ecological niche model. The current ENM projection (1991–2020) is shown with shaded black lines. The central and northwestern portions of the range have the largest concentration of regions shifting to novel climate, and therefore uncertain forecasting predictions
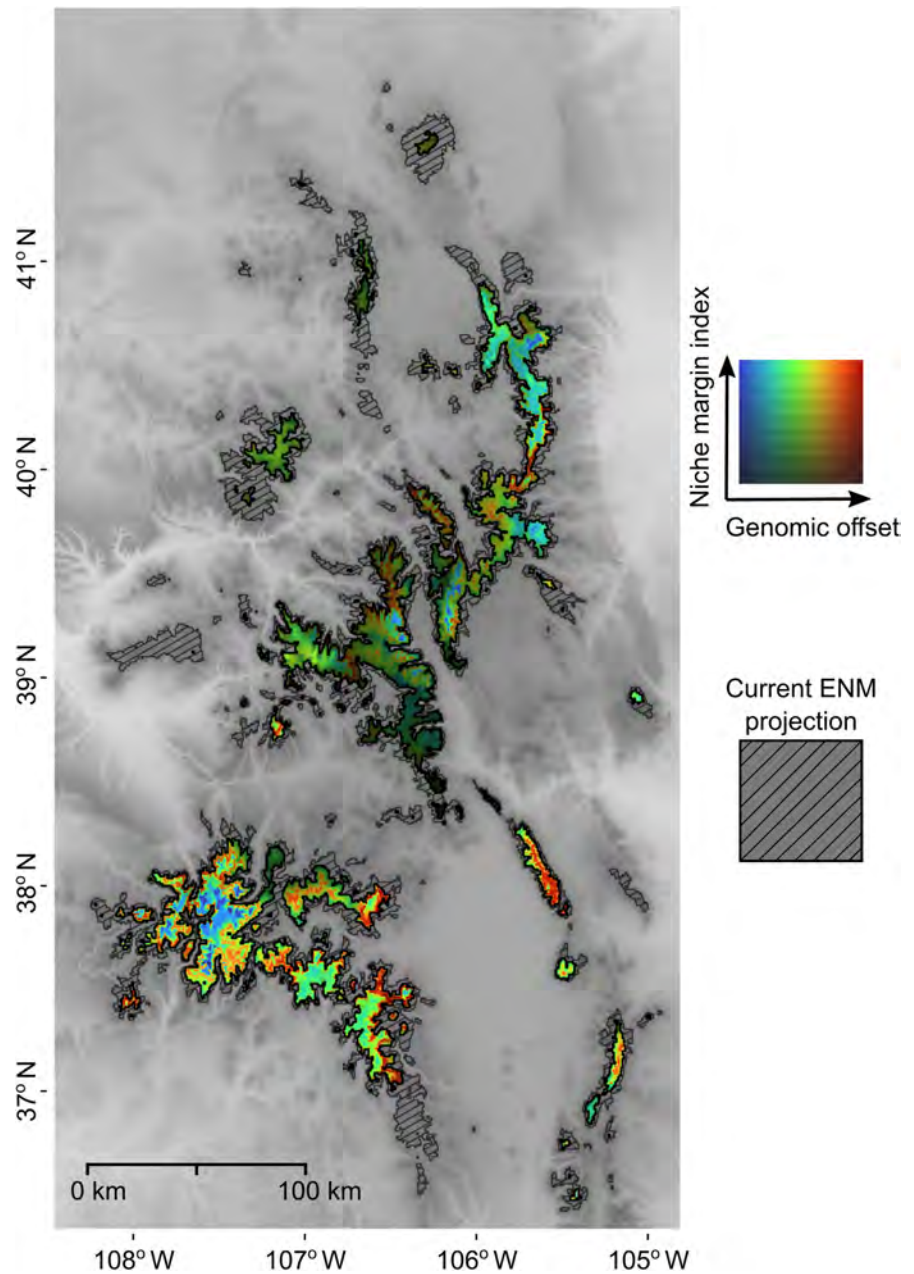
is an example of a small alpine species that can behaviourally adapt to suboptimal thermal regimes using different microhabitats (Millar et al., 2018; Rodhouse et al., 2017). While the thermal tolerance of the Brown-capped Rosy-Finch is unknown, behavioural adaptation to microhabitat use may be an important component of their climate change response. Given that Brown-capped Rosy-Finches nest in cliffs (Hendricks, 1977; Packard, 1968; Sclater, 1912), small changes in nesting site selection (e.g. cliff aspect) could provide dramatic differences in the microhabitat climate. Research into Rosy-Finch microhabitat usage and physiology would provide much needed additional information regarding predicted response to climate change.

The amount of precipitation as snow appears to have biological importance for both local adaptation and the realized niche for the Brown-capped Rosy-Finch (Figure 2b; Table S3). In alpine plant communities, snow cover can have a large effect on flower abundance and the evolution of adaptive traits to reduce frost damage (Inouye, 2000). In turn, this could affect Brown-capped Rosy-Finches foraging in the breeding season as they feed on available insects and seeds from a wide-range of plant species and families (Johnson et al., 2020; Packard, 1968). Our findings of candidate SNPs having enriched gene ontology categories—synaptic transmission (GO:0051966) and GTPase-mediated signal transduction (GO:0051056)—provide an avenue for future research to understand environmental selective pressures. Of the 18 genes we identified in these gene ontology categories, eight genes (*CDC42SE2*, *RASA3*, *ITGB1*, *SLIT2*, *RASGEF1A*, *GRIK2*, *GRM3* and *NRXN1*) are associated with cognitive function, three with high-altitude adaptation (*GRM5*, *NRXN1* and *HCN1*) and two with feather colour and morphology (*KITLG* and *GRM8*; Table S2). The cognitive-associated genes *SLIT2*

and *GRM3* have been identified as being important to the foraging and food-caching habits of a montane bird, the Mountain Chickadee (*Poecile gambeli*; Branch et al., 2022). White-tailed Ptarmigan (*Lagopus leucura*) is another alpine specialist with low genetic differentiation and range-wide adaptive divergence potentially associated with diet (Fedy et al., 2008; Zimmerman et al., 2021). For Brown-capped Rosy-Finch, further elucidating the connections between gene functions and local adaptation (e.g. linking genotypes and phenotypes) is an important next step in understanding the effects of climate change.

4.2 | Geographic patterns of climate vulnerability

Our integrative forecast of range shift and genomic offset in the Brown-capped Rosy-Finch shows that climate vulnerability from decreased habitat suitability and increased genomic offset do not necessarily align spatially. For example, some of the northern mountain ranges had low-to-medium values of genomic offset (Figure 3c) but were not forecasted to have suitable habitat in the future (Figure 3d). However, some southwestern regions with the highest genomic offset (Figure 3c) also showed high vulnerability to loss of suitable habitat in the future (Figure 3d). Broadly, these results show that interpretation from genomic offset predictions alone leave out important considerations of climate vulnerability. Furthermore, these results underscore the importance of using multiple measures of vulnerability for informing conservation and management (Dawson et al., 2011; Rellstab et al., 2021). For organisms that inhabit regions experiencing large climate shifts, even the lowest genomic offset values may indicate relatively large allelic shifts required for a population to retain optimal genetic-environment associations.

Alpine climate conditions are changing dramatically in the Southern Rocky Mountains, especially in relation to snowpack (Pederson, Gray, Ault, et al., 2011; Pederson, Gray, Woodhouse, et al., 2011) and summer temperature increases (Pepin et al., 2022). In our study, NMI results suggest that the central and northwest portion of the Brown-capped Rosy-Finch breeding range are shifting to novel climate conditions (Figure 4a). Of the bioclimate variables most tied to habitat suitability and putative adaptive variation, the amount of precipitation as snow is decreasing across the breeding range in the future (Figure 4b), and the mean temperature of the warmest month is dramatically increasing (Figure 4c). However, our characterization of change in these specific bioclimate variables is based on the ecological niche model predictions of range from eBird citizen science data. Importantly, citizen science data for this organism may be more likely to be collected at lower elevations that are more accessible to observers than the higher elevation portions of the breeding range. This sampling bias could over- (or under-) estimate the current distribution of the breeding range, as well as the distributions of climate values across future time periods (Figure 4b–d). Nonetheless, our NMI measures, which were solely based on climate distance from the climate niche defined by our sampling sites,

reveal large climate shifts across high-elevation portions of the range (Figure 4a).

4.3 | Considerations in forecasting genomic offset

Recent reviews have highlighted a number of key assumptions and limitations that need to be addressed in the ongoing development of genomic offset methods for effective use in conservation (Capblancq et al., 2020; Rellstab et al., 2021). Genomic offset approaches assume that similar future conditions will result in similar genetic composition (space-for-time assumption). While this assumption may be problematic (e.g. multiple genetic architectures underlying an adaptive optimum), novel future conditions further increase the uncertainty of population response due to predicted genetic composition from unobserved environmental conditions. To address part of the uncertainty temporal extrapolation, we used the niche margin index highlight these regions of extrapolation to future climate conditions (Figure 4a). Given the reliance of gradient forest methods on temporal extrapolation from non-linear turnover functions, potentially to novel conditions, we strongly recommend future studies to provide some measure of this uncertainty. Another similar assumption is that populations are at adaptive equilibrium with the temporal period during which genetic-environment associations are being tested. Long-lived species (e.g. trees) are particularly prone to violate this assumption given that populations may have been established centuries ago with different selection pressures (Rellstab et al., 2021). For the shorter-lived Brown-capped Rosy-Finch, we tested for the potential influence of adaptational lag by comparing environmental predictors between two baseline environmental periods. While our results suggested limited differences in genetic-environment associations with these two periods, additional study into the role of effective population size and genetic drift in adaptive (non)equilibrium in this this system may be insightful (Láruson et al., 2022).

Furthermore, incorporating factors of evolutionary adaptation into genomic maladaptation forecasting methods could further refine these predictions. Large populations with gene flow and minimal genetic drift are expected to have higher adaptive potential than small, isolated populations (Funk et al., 2019). Our results show that Brown-capped Rosy-Finches have relatively high genetic connectivity and previous studies have showed that there is introgression within the Rosy-Finch complex (Drovetski et al., 2009; E. R. Funk et al., 2021). Gene flow can promote the rapid spread of beneficial alleles among populations and also maintain standing genetic variation for novel selection pressures (Bernatchez, 2016; Tigano & Friesen, 2016; Yeaman, 2015). Given that genomic offset does not account for gene flow, estimates of genomic offset may overestimate or underestimate future maladaptation (Exposito-Alonso et al., 2017). In the case of the Brown-capped Rosy-Finch, understanding the influence of gene flow on adaptation to a changing environment is an important next step for incorporating these results into management decisions.

5 | CONCLUSIONS

Here, we show that the Brown-capped Rosy-Finch faces climate threats across their breeding range from changing habitat suitability and disruptions of genetic-environment associations. Future persistence may depend on rapid adaptation to novel climate conditions in a contracted breeding range. Expanding future research to forecast climate threats across the fall and wintering range would facilitate an assessment of climate vulnerability across the full annual cycle. We also note the importance of identifying the potential for behavioural adaptation to alpine microrefugia that may mitigate climate change threats. The results of this study highlight the importance of combining multiple methods to characterize climate vulnerability in a more nuanced manner than provided by any of the methods alone.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://doi.org/10.5061/dryad.stqjq2c4r. The analysis scripts are available at https://github.com/mgdesaix/bcrf-climate.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13628.

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BIOSKETCH

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Author contributions: M.D. and K.R. conceptualized the study. K.R., A.S. and G.S. acquired funding and K.R., L.G., G.S. and A.S. facilitated sample collection. M.D. performed developed the methodology and performed all analyses. M.D. wrote the original manuscript draft and all authors participated in the review process.

SUPPORTING INFORMATION

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