Received: 2 February 2022 | Revised: 23 September 2022 | Accepted: 29 September 2022
DOI: 10.1111/mec.16715

ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Evaluating the persistence and utility of five wild *Vitis* species in the context of climate change

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Funding information
National Science Foundation, Grant/Award Number: 1741627; UC-Mexus Conacyt

Handling Editor: Regina S. Baucom

Abstract

Crop wild relatives (CWRs) have the capacity to contribute novel traits to agriculture. Given climate change, these contributions may be especially vital for the persistence of perennial crops, because perennials are often clonally propagated and consequently do not evolve rapidly. By studying the landscape genomics of samples from five *Vitis* CWRs (*V. arizonica*, *V. mustangensis*, *V. riparia*, *V. berlandieri* and *V. girdiana*) in the context of projected climate change, we addressed two goals. The first was to assess the relative potential of different CWR accessions to persist in the face of climate change. By integrating species distribution models with adaptive genetic variation, additional genetic features such as genomic load and a phenotype (resistance to Pierce's Disease), we predicted that accessions from one species (*V. mustangensis*) are particularly well-suited to persist in future climates. The second goal was to identify which CWR accessions may contribute to bioclimatic adaptation for grapevine (*V. vinifera*) cultivation. To do so, we evaluated whether CWR accessions have the allelic capacity to persist if moved to locations where grapevines are cultivated in the United States. We identified six candidates from *V. mustangensis* and hypothesized that they may prove useful for contributing alleles that can mitigate climate impacts on viticulture. By identifying candidate germplasm, this study takes a conceptual step toward assessing the genomic and bioclimatic characteristics of CWRs.

KEYWORDS
climate change, crop wild relatives, genetic offset, genomic load, local adaptation, migration load, species distribution models

1 | INTRODUCTION

Natural populations respond to climate change by adapting to new conditions, by tolerating wider environmental ranges (phenotypic plasticity), by migrating to suitable areas, or by going extinct (Feeley et al., 2012). There is a pressing need to better understand each of these mechanisms to manage and conserve species (Des Roches et al., 2021; Frankham, 2005; Waldvogel et al., 2019). This need is even more pressing for the wild relatives of crop plants (or crop wild relatives, CWRs), because CWRs often contain novel genetic diversity that can contribute to crop improvement (Janzen et al., 2019). The potential loss of CWRs has repercussions beyond biodiversity: they are crucial for breeding crops that meet the climate challenge (McCouch, 2013).

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Given their importance, numerous studies have focused on the geographic distributions, ex situ germplasm collections and in situ conservation of CWRs (e.g., Castañeda-Álvarez et al., 2016). Surprisingly fewer studies have assessed the potential effects of climate change on CWRs (Jarvis et al., 2008), but recent notable exceptions include studies of CWRs in Europe (Aguirre-Gutiérrez et al., 2017) and the United States (US) (Khoury et al., 2020). These and similar studies typically employ species distribution models (SDMs) to infer the climatic niche of CWRs based on the locations where the species is (or is not) found. This niche is then projected into the future, based on the predicted climate. The outcome of SDMs is an estimate of the predicted geographic niche under climate change, which helps inform the fate of species. SDMs are limited, however, because they usually ignore biotic interactions (Lawler et al., 2006), phenotypic plasticity, and the potential for evolutionary adaptation. As a consequence, SDMs probably yield biased predictions about species persistence (Exposito-Alonso et al., 2018; Hällfors et al., 2016; Ikeda et al., 2017; Razgour et al., 2018).

Although the number of climate-based studies of CWRs is growing, fewer studies have assessed the fate of CWRs by integrating climate predictions with landscape genomic data (Aguirre-Liguori et al., 2021, 2019). Genomic data can be used to model how adaptive genetic variation will change in the context of climate predictions. In this way, one can identify species or populations that appear genetically poised to adapt to climatic change and, conversely, populations that may require especially dramatic genetic changes and are thus genetically endangered. This integration of genomic data with climate predictions is relatively new (Capblancq et al., 2020; Fitzpatrick & Keller, 2015), and hence it has been applied to only a handful of taxa (see Capblancq et al., 2020). Studies of poplars, pearl millet and *Arabidopsis* have been especially notable, because they have shown that predicted shifts in allelic variants correlate with components of fitness (Exposito-Alonso et al., 2019; Fitzpatrick et al., 2021; Rhoné et al., 2020), thus arguing for the relevance of the approach.

While genomic data include potential information about the adaptive process, the data also contain information about nonadaptive processes that can provide insights into the potential evolutionary fate of species (Aguirre-Liguori et al., 2021; Waldvogel et al., 2019). Such information includes the history of genetic migration among populations, insights into the history and potential effects of genetic drift, and the magnitude of genomic load, which is a measure of the deviation from an optimal fitness (Frankham, 2005). To incorporate additional genetic and ecological information into species predictions, Aguirre-Liguori et al. (2021) proposed the FOLDS model, a conceptual framework to evaluate potential responses to climate change. The goal of the FOLDS model is to predict which populations are most likely to respond adequately to climate change, based on multiple layers of information. Those layers can include SDMs, information about putative climate-adaptive alleles, phenotypic data and other population genetic information, such as population size and genomic load.

In this study, we employ the FOLDS model to assess potential responses to climate change for samples from five North American (NA) *Vitis* CWRs. We focus on the CWRs of *Vitis* because they are climatically diverse (Callen et al., 2016) and agronomically crucial. *Vitis* CWRs are employed for hybrid scion breeding (between the domesticated species and the wild relative) and also as rootstocks, to the extent that ~80% of viticulture worldwide utilizes rootstocks from NA *Vitis* species (Ollat et al., 2016). Among ~25 NA *Vitis* species (Wan et al., 2013), those from the American Southwest are of particular interest, because some are resistant to important diseases and others grow under abiotic stresses like extreme conditions that may "preadapt" them to some aspects of climate change (Heinitz et al., 2019). As concrete examples, *V. berlandieri* is used as a root-stock especially in limestone soils and hot, dry environments (Heinitz et al., 2019), and *V. arizonica* has been used to create hybrid grape-vine scions that are resistant to Pierce's disease (Riaz et al., 2009), an economically devastating disease caused by a bacterium that infects several economically important crops (Rapicavoli et al., 2018).

We also focus on *Vitis* because climate change is predicted to disrupt the phenology and production of domesticated grapevines (*V. vinifera*) (Morales-Castilla et al., 2020), representing substantial impacts to a crop with a farm gate value >$68 billion worldwide (Alston & Sambucci, 2019). In addition, despite their ubiquitous use, rootstocks have a remarkably narrow genetic foundation. Currently, a collection of ~10 rootstocks are used for 90% of grafted grapevines. The most common rootstocks include hybrid or solo contributions from seven NA Vitis species. However, the contribution from each species is often (and, in fact, usually) a single accession (Marín et al., 2021). These observations underscore the pressing need to identify additional germplasm for rootstock and scion breeding (Heinitz et al., 2019; Riaz et al., 2019), given the pressures of climate change.

With genomic data from samples representing five *Vitis* species, this study had two goals. The first was to employ the FOLDs model to evaluate which sets of individuals in the sample are most likely to persist through climate change at their sampled locations in na-ture. Our evaluation considers climate predictions, the complement of putatively adaptive alleles, resistance to Pierce's disease and aspects of population history. The second goal was to assess whether accessions have adaptive alleles that may allow them to persist in predicted future climates where *V. vinifera* is currently grown in the United States. The motivation for this second goal is to evaluate whether CWRs have combinations of alleles that may make them potentially useful, pending extensive future functional validation, for scion or rootstock breeding. Overall, our study takes a conceptual step toward estimating the climate impacts on CWRs and toward identifying candidate species and accessions that may prove useful for the in situ adaptation of an important crop.

2 | MATERIALS AND METHODS

2.1 | Plant material, resequencing and variant identification

The plant material used in this study consisted of 105 individuals from five American *Vitis* species (*V. arizonica*, $n = 22$; *V. mustangensis*, $n = 24$; *V. berlandieri*, $n = 22$; *V. girdiana*, $n = 18$ and *V. riparia*; $n = 19$), which were described previously in Morales-Cruz et al. (2021)

(Table S1). The 105 accessions were also assayed previously for resistance to *Xylella fastidiosa* (Morales-Cruz et al., 2021; Riaz et al., 2018), the causative agent of PD. Briefly, PD resistance was evaluated using greenhouse experiments in which *X. fastidiosa* was inoculated in different individuals and concentration was evaluated using ELISA tests 10 to 14 weeks after inoculation. Individuals were considered to be resistant to PD if they had concentrations of *X. fastidiosa* <13 least square means of colony forming units (CFUs) per ml (Riaz et al., 2020).

We used the sequencing data generated by Morales-Cruz et al. (2021), which is in the Short Read Archive at NCBI under BioProject ID: PRJNA731597, and their SNP calls. Briefly, they filtered Illumina paired-end reads of 150 base pairs (bp) and mapped them to the *V. arizonica* b40-14 version 1.0 genome (Morales-Cruz et al., 2021) (https://doi.org/10.5281/zenodo.4977234 and www.grapegenomics.com/pages/Vari/). Joint SNP calling was conducted using the HaplotypeCaller in the GATK version 4.0 pipeline following Zhou et al. (2017). The VCF files were split by species, and the raw SNPs were filtered with bcftools version 1.9 (https://samtools.github.io/bcftools/) and vcftools version 0.1.15 (https://vcftools.github.io/). SNPs sites were kept for downstream analyses if they were biallelic, had no missing data, had quality higher than 30, had a depth of coverage higher than five reads, and also had no more than three times the median coverage depth. Additionally, the following expression was applied under the exclusion argument of the filter function in bcftools: "QD<2.0 | FS>60.0 | MQ<40.0 | MQRankSum<−12.5 | ReadPosRankSum<−8.0 | SOR>3.0". These steps resulted in a range of high-quality filtered SNPs from 3.6 million in *V. girdiana* to 5.6 million in *V. riparia* (Table S2).

2.2 | Species distribution models

For each CWR *Vitis* species and for *V. vinifera* we downloaded occurrences from the Global Biodiversity Information Facility (www.gbif.org; 2020; DOI 10.15468/dl.4emr87). We removed duplicated locations and those that were potential misclassifications due to being obvious outliers. We also downloaded 19 bioclimatic variables from Worldclim 2 (Fick & Hijmans, 2017) for a period representing the present, which is an average of observations from 1970 to 2010, and to 54 forecasts of climate change (FCCs). Our rationale for including 54 FCCs was to incorporate uncertainty in climate projections. The forecasts were downloaded at a 2.5 min resolution from Worldclim 2 (last accessed May 2022), based on the CMIP6 project (Eyring et al., 2016). The 54 FCCs corresponded to five circulation mod-els (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL), three time periods (2041–2060 [mean 2050]; 2061–2080 [mean 2070]; 2081–2100 [mean 2090]) and four shared socioeconomic pathways (SSPs) that model different trajectories of greenhouse effects (SSPs 126, 245, 370, 585). We were unable to acquire the data for the GFDL-ESM4 model with SSPS 245 and 585 for any time period, resulting in 54 instead of total 60 FCCs.

To build an SDM for each species, we used previously published scripts (Aguirre-Liguori et al., 2021) that performed four steps. First, the script removed correlated bioclimatic variables ($r > 0.8$) with the highest variance inflation factor, to moderate multicollinearity between variables. Second, it identified a calibration or background area, which corresponded to the migration layer in the biotic, abiotic and migration (BAM) model (Peterson et al., 2011; Soberón, 2010) and to terrestrial ecoregions of the world (Olson et al., 2001). Third, the script employed the BIOMOD2 package in R (Thuiller et al., 2009) and the Maxent algorithm (Phillips et al., 2006; Phillips & Dudík, 2008) to build and project the models. Finally, we performed 20 bootstrap replicates per model. For each replicate we used 70% of occurrences to train the model and 30% to test the model with True Skill Statistics for ten-fold internal cross-validation.

Based on the present-day SDMs, we projected the potential distribution of species to the 54 FCCs. For each species and each FCC we estimated how the geographic distribution (i.e., the number of pixels in the projection) was expected to change from the present. Ultimately, we evaluated the mean change and the dispersion across the FCCs in each of the three projected time-periods. We also estimated whether each of the 105 accessions was expected to persist in a given FCC. That is, for each individual at a given time period, we counted how many times FCCs predicted the persistence of the individual's sample location. If the location was predicted to be outside the species' estimated niche for all 20 FCC models at a specific time-period, we coded that population as extinct by that time period and into the future.

2.3 | Investigating patterns of local adaptation

2.3.1 | Identification of outlier SNPs

For each CWR species sample, we used Baypass (Gautier, 2015) to identify outlier loci that had significant associations with the first four principal components (PC) of bioclimatic variables (Figure S1). Figure S1 provides a schematic overview of methods that incorporated genomic and environmental data, as applied to the FOLDS model. The PCs were determined with the *prcomp* function in R, based on the 19 bioclimatic variables from the present-day. Baypass analyses patterns of covariation among accessions to account for population structure and then analyses the correlation between a variable (in this case each PC) and the allelic frequencies of individual SNPs across individuals. A SNP was deemed an outlier if it had a significant correlation with a variable that was not explained by the covariance between populations. Following Jeffreys' rule (Gautier, 2015), we characterized outlier SNPs as those that had a Bayes Factor (BF) >20.

2.3.2 | Genetic offsets

To calculate genetic offsets, we used gradient forest (GF; Figure S1) (Ellis et al., 2012), a machine learning method that models the turnover in genetic composition across the landscape (Fitzpatrick

& Keller, 2015). GF identifies which bioclimatic variables contribute importantly to the construction of the model, the SNPs that are associated with bioclimatic variables, and the adaptive genetic composition across the predicted climate (Capblancq et al., 2020; Fitzpatrick & Keller, 2015; Waldvogel et al., 2019). When applied to bioclimatic data from both the present and the future, GF also estimates the genetic offset, reflecting the expected amount of genetic change necessary to adapt in the future at the same local-ity (Capblancq et al., 2020; Fitzpatrick & Keller, 2015). The genetic offset depends on the genetic composition of populations and the magnitude of the environmental change that is expected to occur; populations with higher genetic offsets are expected to be more vulnerable to climate change (Fitzpatrick & Keller, 2015).

For each species, we obtained the GF model using the gradient forest package in R (Ellis et al., 2012) for all the outlier SNPs identified by Baypass (Table 1), based on allelic frequencies within individuals (Figure S1). These frequencies were either 0 or 1 for homozygotes or 0.5 for inferred heterozygotes. The genetic offset was then calculated as the Euclidian distance of the genetic compositions between the present and different time periods (Fitzpatrick & Keller, 2015) (Figure S1). We used the GF models to predict how genetic compositions were expected to change in each of the 54 FCCs.

GF is traditionally applied to allele frequencies across populations, but here we applied it to individual genotypes. To investigate whether results were applicable for individuals, we performed two tests. First, we transformed allelic frequencies within individuals to pseudo-population frequencies, using a probabilistic model, and reanalysed the data (see Methods S1). Our simulations suggest that the sampling of individuals, instead of populations, had little impact on the construction of the GF model, the estimation of genetic offsets and the identification of important bioclimatic variables (see Methods S1 and Figure S2). Second, we used a population data set that had been used to calculate genetic offsets previously (Aguirre-Liguori et al., 2021) and evaluated the effect of subsampling from 1 to 11 individuals per population on the estimation of genetic offsets (see Methods S1). We found that using individuals instead of allelic frequencies reduced the estimated genetic offsets across populations but also that the rank correlation among genetic offsets was >0.99. This high correlation indicated that the relative magnitude and order of genetic offsets remained similar across locations and sampling strategies (Figure S3), further suggesting that use of individuals in GF is a suitable for our comparisons.

2.3.3 | Calculating the adaptive score

In addition to genetic offsets, we calculated other parameters from the data to help summarize genetic information that can be used to evaluate climate persistence. For example, to summarize information about adaptive alleles we calculated an adaptive score (S_a). S_a measured the proportion of alleles across all candidate SNPs that were preadapted to climate, based on climate projections (Figure S1). As used here, S_a is modelled after the population adaptive index (PAI) of Bonin et al. (2007). The PAI measured the proportion of loci that have a selective signal within populations—that is, the proportion of loci that were outliers due to high allelic frequency deviations among populations. In our case, we identified the alleles that, according to turnover functions from GF analyses, were predicted to be adaptive in future climates (Figure S4).

To identify preadapted alleles, we assessed the projected direction of environmental change for important bioclimatic variables (i.e., change across the x-axis in Figure S4) by identifying preadapted individuals that, according to turnover functions, require small change in their genetic composition in the future (i.e., small changes across the y-axis, Figure S4). After identifying preadapted individual(s), for each candidate SNP we built a linear model (using "lm" in R) to confirm that the genotypic state correlated significantly with the expected bioclimatic variable. Significantly correlated alleles were deemed adaptive, and the high frequency allele was categorized as the adaptive state. Given adaptive alleles, we calculated S_a as the total number adaptive alleles per individual across all candidate SNP sites, divided by 2x the number of candidate SNPs (the factor of 2x reflected the diploid state). Thus S_a reflected the proportion of adaptive alleles that were present in an individual across all candidate SNPs. It ranged from 0 to 1, where 0 indicates an individual with no adaptive alleles and 1 indicates homozygosity of adaptive alleles at all candidate SNPs.

TABLE 1 Five *Vitis* CWR samples, with summary statistics

Species	N_{ind}[a]	N_e (95% CI)[b]	N_{Bay}[c]	N_{GF}[d]	BIO[e]
V. arizonica	22	35,448 (33,658–37,237)	13,531	5792	3, 15, 2, 9
V. berlandieri	22	40,112 (37,008–43,215)	8425	3371	4, 7, 3, 10
V. mustangensis	24	74,839 (59,722–89,957)	8787	2730	18, 5, 10, 4
V. girdiana	18	53,666 (47,065–60,267)	5650	5254	4, 7, 3, 11
V. riparia	19	49,279 (45,454–53,105)	10,626	8720	10, 4, 8, 1

[a] N_{ind} is the number of samples per species.

[b] The mean effective population size estimated across six samples with 95% confidence intervals.

[c] N_{Bay} refers to the number of outlier SNPs identified with Baypass.

[d] N_{GF} refers to the number of outlier SNPs identified with gradient forest.

[e] BIO includes the list of the four top bioclimatic variables identified with GF, in decreasing order of importance.

For each species, we calculated S_a for each of the four bioclimatic variables that had the strongest contribution to building the GF model and then calculated the mean across the four variables (Figure S1). Further details, tests for potential biases and rationale for S_a are provided in the Methods S1. We note that S_a overlaps with, but differs from, genetic offsets in two ways. First, high genetic offsets can be caused either by strong predicted environmental shifts or by extensive expected genetic shifts. In contrast, S_a focuses solely on genetic composition by counting whether an inferred adaptive allele is present at each position. Second, genetic offsets cannot be compared across species (Láruson et al., 2022), but S_a can because it reports a proportion—that is, of adaptive alleles across candidate climate-related SNPs.

2.4 | Additional population genetic parameters

2.4.1 | Demographic history

To incorporate information about genetic drift into the FOLDS model, we estimated the effective population (N_e) size of each species using MSMC2 version 2.1.1 (Mallick et al., 2016) with unphased SNPs. To include only the most informative genomic regions, we created a mappability mask and a coverage mask. We created the mappability mask for the *V. arizonica* b40-14 version 1.0 genome using the software SNPable (http://lh3lh3.users.sourceforge.net/snpable.shtml). We generated 150 bp mers moving in 1 bp increments across the genome, mapped the sequences back to the genome with BWA version 0.7.8-r455 (Li & Durbin, 2009) and identified "mappable" genomic regions where the majority of sequences mapped uniquely without mismatches. To include only the regions with sufficient sequencing coverage, we calculated the coverage from the alignment file of each sample with the bedcov program from the Samtools (version 1.10) package, supplying a bed file of 10 kb nonoverlapping windows across the genome. We then created a mask per sample that only included regions with sequencing coverage higher than 5x. We then used unphased SNPs from the six samples per species with the highest average coverage as input for the run in MSMC2. For analyses, we assumed a mutation rate of 5.4e-9 (Liang et al., 2019) and a generation time of 3 years (Zhou et al., 2017). In addition to MSMC2 with unphased data, we applied MSMC2 to phased data and also used SMC++ as another source for N_e estimation (see Methods S1). The results of the most recent time index from SMC++ and MSC2-unphased were highly similar (Figure S5). The results were also very consistent among individual MSMC2 runs (Figure S6), and so we showed the average per species (Figure S5).

2.4.2 | Genomic load

In theory, genomic load is a measure of deviation from a fitness optimum; in practice, it is measured by the number of predicted deleterious alleles in an individual (Do et al., 2015). To identify putatively deleterious alleles, we first determined the functional context (exonic, intronic, and intergenic) of SNPs based on *V. arizonica* B40-14 genome annotations (Morales-Cruz et al., 2021, https://doi.org/10.5281/zenodo.4977234 and www.grapegenomics.com/pages/Vari/). Exonic SNPs were annotated to be synonymous, nonsynonymous or frameshift mutations using SnpEff version 5.0e (Cingolani et al., 2012). Nonsynonymous SNPs were predicted as deleterious or tolerated using the SIFT score (Ng & Henikoff, 2003), as computed in the program SIFT 4G (Vaser et al., 2016). SIFT scores ≤0.05 were interpreted as deleterious and SIFT scores >0.05 were considered to be tolerant. Because the reference genome biases the distribution of missing data (Lohmueller et al., 2008), we only used polymorphic sites without missing data that were predicted across all five wild grape species, resulting in a set of 397,723 SNPs.

2.5 | Applying the FOLDS model

To assess the potential effects of climate change, we employed the FOLDS model (Aguirre-Liguori et al., 2021), based on six layers of genomic, phenotypic and climate information described above (Figure S1). We used UpsetR (Conway et al., 2017) to plot intersections among the six layers of information for each of the 54 FCCs. For each UpsetR model, we evaluated which accessions passed specific filters for the six layers. As described below (see Results), we selected different thresholds and filters for inclusion and synthesis. For example, accessions were included based on SDMs if the sampling location was predicted to be in the species' niche in the future and also when they were resistant to *X. fastidiosa* (i.e., had concentrations <13 least square means of CFUs/ml). We also selected accessions as persistent if they had genetic offsets and genomic load values below 90, 50 and 25% of their distribution across species. Since genetic offsets are not comparable between species (Láruson et al., 2022), the thresholds for genetic offsets were considered only within species. Finally, accessions were included when they had S_a or N_e above the 10%, 50% and 75% of the distributions across species.

2.6 | Migration load

The FOLDS model defined a set of CWR accessions that were best situated to persist in the face of climate change. We focused on these accessions to evaluate their genetic offset at locations where *V. vinifera* is currently cultivated in the United States. This measure of genetic offset, which has been called either the "forward offset" (Gougherty et al., 2021) or the "migration load" (Rhoné et al., 2020), estimates whether an accession has the allelic complement to persist when moved to a different location. Thus, the migration load is the genetic offset for an individual calculated between its present-day sampling site and for predicted climates at other locations. In this case, the other locations represent current locations of viticulture. The migration load is a tool to evaluate whether CWR accessions might be useful in future climates where grapevines are currently cultivated.

We estimated migration load for accessions that passed the FOLDs threshold for each of the 54 FCC models at the 1278 United States locations of *V. vinifera* cultivation available from gbif.org. Following previous studies (Aguirre-Liguori et al., 2021; Rhoné et al., 2020), the migration load was calculated as the Euclidian distance of the genetic composition between the present location of an accession and the future estimate in the projected climate of *V. vinifera* cultivation. We identified locations where the migration load was within the current range of the species' predicted genetic offsets over the same FCC period. Finally, for each *V. vinifera* location, we counted how many times an accession had a migration load within the range of its genetic offsets. We interpreted these accessions as candidates for having climate-related alleles that could be useful to viticulture in the face of climate change.

3 | RESULTS

3.1 | Species sampling and data

In this study, we used previously published resequencing data from 105 individuals representing five North American *Vitis* species: *V. arizonica*, *V. mustangensis* (synonym *V. candicans*), *V. berlandieri*, *V. girdiana* and *V. riparia* (Morales-Cruz et al., 2021). These species are either currently used as rootstocks, represent the parents of hybrid rootstocks and scions, or have phenotypic properties that make them potentially valuable to viticulture (Heinitz et al., 2019). The two most closely related species in this study (*V. girdiana* and *V. arizonica*) split at least 10 million years ago (Wan et al., 2013) and perhaps even earlier (Morales-Cruz et al., 2021), so they have not diverged especially recently.

For each of the five species, 18 to 24 accessions were resequenced (Table 1). We employed the previously determined SNPs (Morales-Cruz et al., 2021), which were used previously to explore the divergence dynamics among species and their history of hybridization. Here, however, we focused on a subset of SNPs that had no missing data within each species. The resulting number of SNPs ranged from 3.6 million in *V. girdiana* to 5.6 million in *V. riparia* (Table S2). The accessions, sampling locations, and SNPs provided the basis for evaluating species' persistence under projected climate change.

3.2 | Evaluating the persistence of wild *Vitis* under predicted climate change

To assess the potential effects of climate change, we combined six layers of genomic and climate information within the FOLDS framework (Aguirre-Liguori et al., 2021). The six layers were chosen to include different types of information including (i) SDMs to incorporate niche information; (ii) patterns of local adaptation and predicted allelic responses to climate change; (iii) insights into genetic drift and genomic load, both of which may affect evolvability and persistence; and (iv) phenotypic characterizations of resistance to PD. Below we describe each of the six layers before synthesizing information within FOLDS framework.

3.2.1 | Layer 1—species distribution models

We estimated SDMs to examine expected changes in the geographic distribution of the five wild *Vitis* species over 54 climate models (FCCs), focusing on four time periods (present-day, 2050, 2070 and 2090), five circulation models and four shared socioeconomic pathways (see Methods). For each of the five species, we projected the SDM onto the 54 FCCs. Then, for each SDM we measured the projected habitable area of each species (Figure 1a), as has been done previously for wild *Vitis* (Callen et al., 2016; Heinitz et al., 2019) but also the predicted trends over time (Figure 1b). Strikingly, the average amount of habitable area was predicted to increase over time for all species, but with a marginal reduction for *V. girdiana* after 2050 (Figure 1b, Table S3).

Although the overall expansion of niche area is promising, there was substantial variation in the details across the 54 FCCs. For example, the dispersion across models increased as a function of time, and the SSPs that predicted higher greenhouse gas emissions predicted larger CWR distributions (Figure 1b). The SDMs predicted many *V. arizonica*, *V. mustangenis* and *V. berlandieri* locations were likely to persist until 2090 (Figure 1c, Table S3). However, persistence varied substantially among species, because from 20% to 43% of sampling localities (depending on the species and climate models), were predicted to disappear from species' niches by 2090. Overall, SDMs predict that distribution of the wild *Vitis* species is expected to increase in the future, but the results also suggest that many populations represented by the samples in our study will need to either adapt or migrate to survive.

3.2.2 | Layers 2 and 3—genetic offsets and adaptative variation

We used GF to estimate the genetic offsets of *Vitis* individuals within each species. Following common practice (Capblancq et al., 2020; Fitzpatrick et al., 2018), we ran GF with a subset of outlier SNPs that were associated with environmental variables. To identify these outlier SNPs, we performed genome environment associations (GEA) with Baypass (Gautier, 2015), identifying SNPs correlated to the first four principal components (PCs) of 19 present-day bioclimatic variables (Figure S1). The first four principal components explained 99.9% of bioclimatic data for *arizonica*; 97.3% for *berlandieri* 97.3%; 92.9% for *mustangensis*; 98.8% for *girdiana* 98.8% and 97.4% for *riparia* 97.4%. Our GEA detected from 5650 to 13,531 outlier SNPs within each species (Table 1). We applied GF to the set of outlier SNPs from the GEA, yielding a subset of 2730 to 8720 candidate SNPs within each species that had significant nonlinear associations across samples (Table 1), based on present-day bioclimatic data.

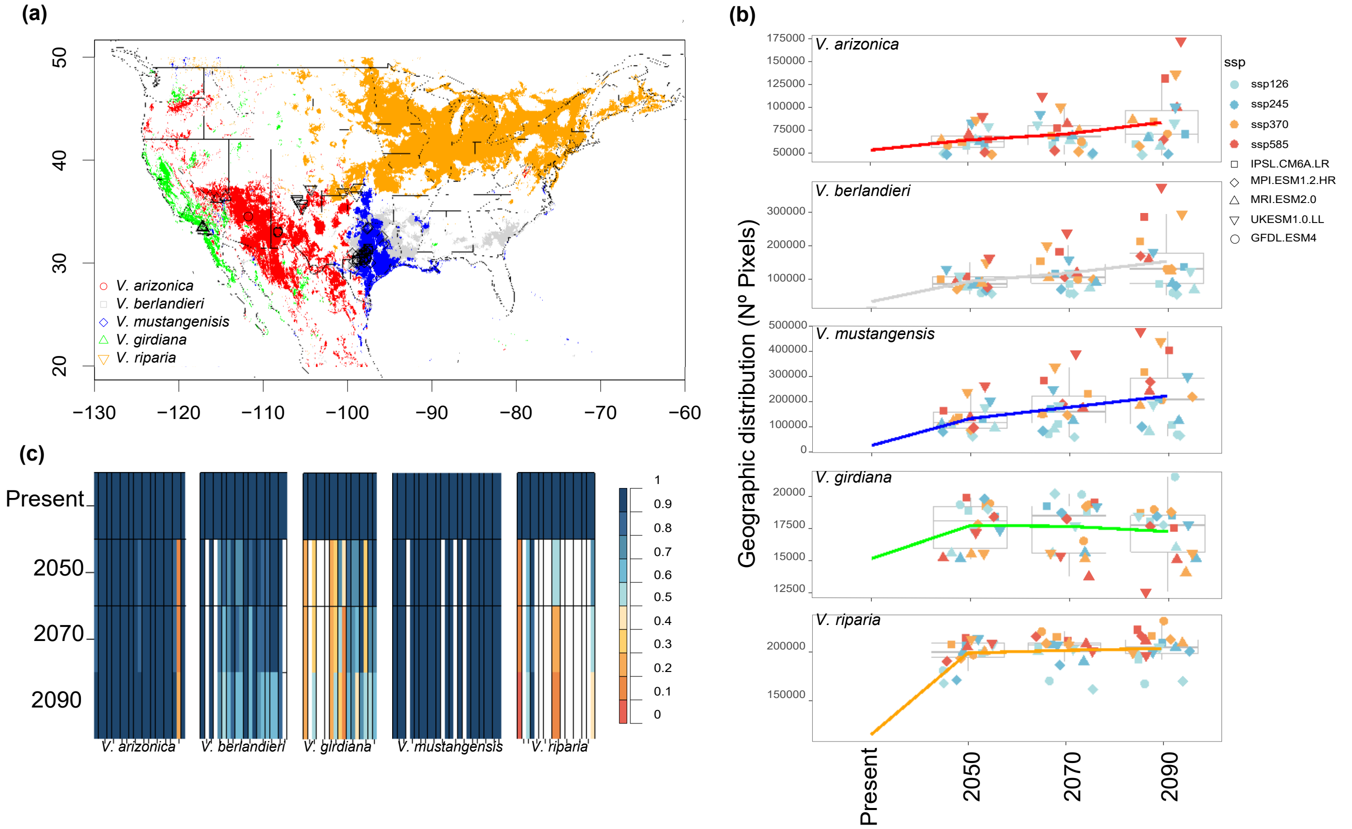

FIGURE 1 Results based on SDMs of the five *Vitis* species in this study. (a) Present-day SDMs showing the estimated bioclimatic niche of each of the five species. Species are coloured according to the key. The map also provides the sampling locations of the 105 accessions, with shapes and colours of different species provided by the key. (b) The geographic area of the niche for each species graphed into the future for 54 future climate change (FCC) models and their mean. The symbols and colours represent the estimated geographic size for different circulation models and shared socioeconomic pathways, respectively. The central line and symbols across the years 2050, 2070 and 2090, represents the mean of SDMs based on the different FCC models. The colours represent the species, as indicated in the key of (a). (c) Each column represents one of the 105 accessions in this study. The colour in the column indicates the proportion of times that an accession was predicted to exist for a given time period across the 18 FCC models. If the location of sampled individual did not fall within the future niche for all FCC models for a given time period, as defined by the SDM, then it is no longer represented in the figure (white column). Hence, by 2090, SDMs predict that most *V. arizonica* and *V. mustangensis* samples will be able to persist in their current locations, as will a few *V. berlandieri*. In contrast, most *V. riparia* in our sample are not predicted to persist.

GF analyses provided three additional outcomes (Figure S1). The first was a set of bioclimatic variables that were important for building the model, as measured by the contribution of the variable to the construction of the model ($R^2 > 0$). For simplicity, we focused on the four most important variables for each species, some of which (Table 1) were shared across species. For example, BIO10 (the mean temperature of the warmest quarter) had a strong contribution to the building of GF models in *V. berlandieri*, *V. mustangensis* and *V. riparia*, whereas BIO4 (temperature seasonality) was a top contributor for all species but *V. arizonica* (Table 1).

The second outcome was estimates of genetic offsets, which we computed for each individual in each species based on contrasts between present-day climate and each of 54 FCC models (see Methods), resulting in 5670 (=54 models × 105 individuals) estimates. We compared rank correlations among genetic offsets between all FCC models to determine if there was a consistent genetic offset signal. Pairwise comparison revealed that >95% of pairs had rank correlations of Rho >0.5, suggesting that different climatic models generally showed similar genetic offset trends (Figure S7). For simplicity, in Figure 2a we show the genetic offsets in each species for a single model (IPSL-CM6A-LR_ssp585_2061–2080), because this model had the highest average rank correlation (mean Rho = 0.83) compared to the remaining 53 models. The corresponding results for the remaining models are presented in Table S1.

Genetic offsets cannot be compared quantitatively across species (Láruson et al., 2022) because they are estimated with different SNPs and bioclimatic information. They do, however, help predict whether specific alleles are expected to be adaptive in future climates. To build a metric for cross-species comparison, we utilized genetic offsets to inform a measure, S_a, that measures the proportion of adaptive alleles within each individual and that can be compared across individuals and species (see Methods). For each species, we calculated the mean adaptive score (S_a) (see Methods and Figure S1). Like genetic offsets, S_a varied within species (Figure 2b, Table S1); comparing S_a across species indicated that our *V. girdiana* and *V.*

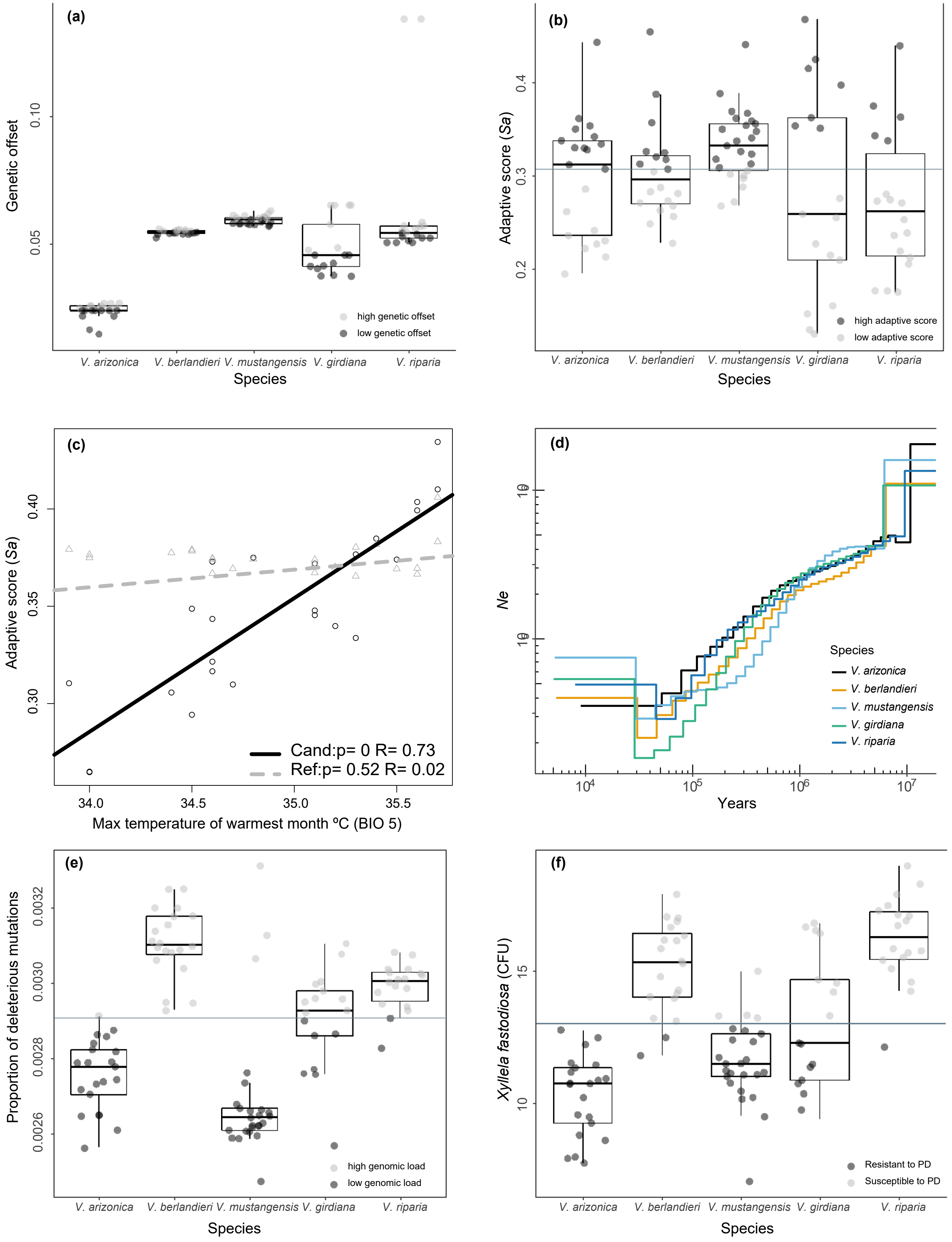
(a)
Genetic offset
0.10
0.05
high genetic offset
low genetic offset
V. arizonica
V. berlandieri
V. mustangensis
V. girdiana
V. riparia
Species
(b)
Adaptive score (Sa)
0.4
0.3
0.2
high adaptive score
low adaptive score
V. arizonica
V. berlandieri
V. mustangensis
V. girdiana
V. riparia
Species
(c)
Adaptive score (Sa)
0.40
0.35
0.30
Cand:p= 0 R= 0.73
Ref:p= 0.52 R= 0.02
34.0
34.5
35.0
35.5
Max temperature of warmest month ºC (BIO 5)
(d)
Ne
Species
V. arizonica
V. berlandieri
V. mustangensis
V. girdiana
V. riparia
10^4
10^5
10^6
10^7
Years
(e)
Proportion of deleterious mutations
0.0032
0.0030
0.0028
0.0026
high genomic load
low genomic load
V. arizonica
V. berlandieri
V. mustangensis
V. girdiana
V. riparia
Species
(f)
Xyllela fastodiosa (CFU)
15
10
Resistant to PD
Susceptible to PD
V. arizonica
V. berlandieri
V. mustangensis
V. girdiana
V. riparia
Species

FIGURE 2 Layers of information used in the FOLDS model. (a) Distribution of genetic offset for each species for future climate change (FCC) model IPSL–CM6A–LR_ssp585_2061–2080. We darkened circles based on their status above and below the median within each species. (b) Variation in the adaptive scores (S_a) across species. Each circle represents a sampled accession. The dashed line shows the median of S_a across all accessions; circles are darkened if they have S_a above the median. (c) An example of correlations between S_a and bioclimatic variables, in this case the maximum temperature of the warmest month (BIO 5) for *V. mustangensis* samples. The dashed line shows the correlation for reference SNPs. For all results and test for potential biases see Figure S8. (d) Change in effective population size across time for each species. The colour of each species is indicated by the key. (e) The measure of genomic load—That is, the proportion of predicted deleterious SNPs per genome across a shared set of SNPs—Plotted for each accession and species. Note that the proportion of deleterious SNPs is equivalent to the number of deleterious SNPs per genome, since all inferences were based on a shared set of SNPs. The dashed line represents the median of the genomic load. Darker circles are below the median. (f) Distribution of the concentration of *X. fastidiosa* in different wild *Vitis* species after exposure to the bacterium. The dashed line represents the value 13 CFUs, which has been the boundary between resistance and susceptibility. Darker circles represent accessions with CFUs <13.

riparia samples had preadaptive alleles in lower proportions than the other species (Figure 2b).

Because S_a had not been applied previously, we performed tests to evaluate whether S_a was biased by geographic, demographic or climatic variables. As expected, S_a was strongly and significantly correlated with at least one of the four most important bioclimatic variables identified by GF (Figure 2c); in fact, it was correlated with all four for three of five species (Figure S8). As also expected, S_a was more highly correlated to bioclimatic variables than a similar score (S_{ref}) calculated from a set of reference SNPs (Figure S8; see Methods), suggesting it contained additional information. The notable exception was for *V. girdiana* samples, where S_{ref} was strongly correlated with all four of the top four associated bioclimatic variables (Figure S8), probably reflecting genetic structure (Morales-Cruz et al., 2021) or other features that complicate interpretation of S_a in this species.

3.2.3 | Layer 4—effective population size

The efficacy of selection depends on adaptive diversity but also on population factors, like genetic drift and genomic load, that are typically ignored in climate studies (Aguirre-Liguori et al., 2021; Brady et al., 2019; Nadeau & Urban, 2019). To assess the potential influence of genetic drift, we estimated historical effective population sizes (N_e) over time, using MSMC2 (Schiffels & Wang, 2020). For all species we found that N_e decreased from the distant past until ~20,000 years ago, followed by recent moderate recoveries (Figure 2d). From these analyses, we retrieved the current estimate of $N_{e,}$ which ranged from ~35,000 individuals in *arizonica* to ~75,000 in *V. mustangensis* (Table 1); *V. mustangensis* also yielded the highest N_e estimate based on another method, SMC++ (Terhorst et al., 2017) (Figure S5) and the results were consistent among individual MSMC2 runs (Figure S6). The relatively high N_e for *V. mustangensis* was surprising, because it currently has a narrow geographic distribution (Figure 1a), but it nonetheless suggests that it may be less prone to drift effects than other species.

3.2.4 | Layer 5—genomic load

Genomic load, the accumulation of deleterious mutations in a population, can predict fitness (Frankham, 2005). We estimated genomic load within and between species by measuring the number of putatively deleterious alleles per accession (see Methods). To account for differences in the number of SNPs between species and potential reference biases, we focused only on SNPs shared between species, with no missing data. Overall, genomic load indicated that *V. mustangensis*, *V. arizonica* and *V. riparia* individuals had relatively low genomic load among species, but there was also notable variation among individuals within species (Figure 2e).

3.2.5 | Layer 6—resistance to Pierce's disease

Biotic interactions between species can play a key role in shaping population's responses to climate (Bascompte et al., 2019; Zamora-Gutiérrez et al., 2021). As a case study for including such information, we included data about resistance to the bacterium *X. fastidiosa* (Morales-Cruz et al., 2021; Riaz et al., 2020). We plotted CFU counts for each individual, revealing variation in PD resistance among individuals and species (Figure 2f), for example, 100% of *V. arizonica* and 87% of *V. mustangensis* accessions were PD resistant while the *V. girdiana* distribution was notably bimodal, with ~50% of accessions resistant (CFU < 13). In contrast, only one *V. riparia* and two *V. berlandieri* accessions were resistant.

3.3 | The FOLDS framework

Ideally, assessing the response of populations to climate change should be based on multiple layers of information (Razgour et al., 2018; Waldvogel et al., 2019); we relied on the preceding six layers to surmise whether an accession is relatively well situated to adapt to climate change. Such accessions should have low genetic offsets, low genomic loads, high S_a values, high N_e (low drift), PD resistance and predicted persistence based on SDMs.

We applied the FOLDS (Aguirre-Liguori et al., 2021) using different thresholds (Figure S1). For example, we first filtered accessions based on all six layers, with thresholds defined by: PD resistance (CFU < 13), SDM persistence, among the lowest 25% of genetic offset and genomic load within a species, and among the highest 25% of N_e and S_a within a species. We illustrated the intersection of layers for the IPSL-CM6A-LR_ssp585_2061–2080 climatic model (Figure 3a), based on the set of summary statistics (Table S4). The

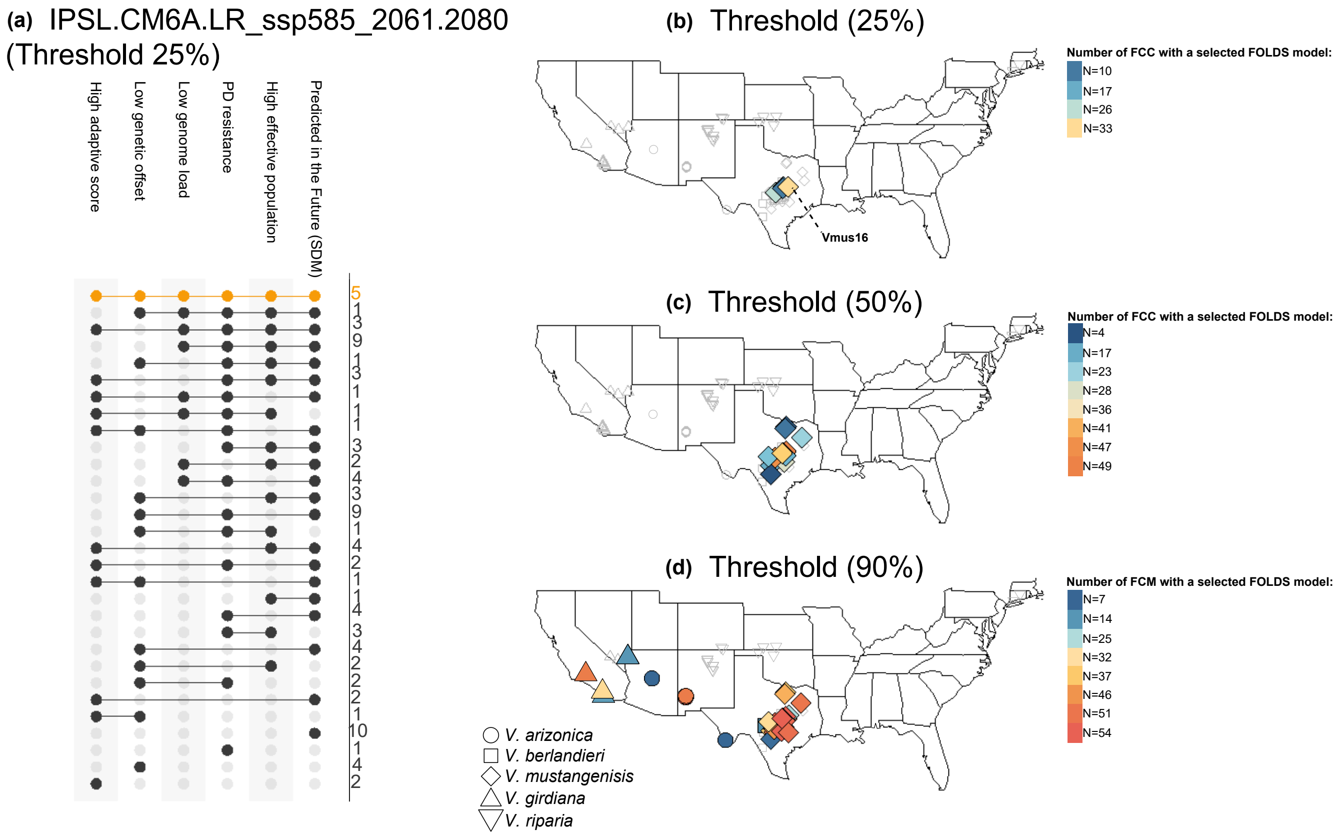

FIGURE 3 The FOLDS model applied to wild *Vitis*. (a) The upsetR plot shows the intersection across all 105 individuals that pass thresholds (at the strictest 25% threshold) for the six layers of information and for future climate change model IPSL–CM6A–LR_ssp585_2061–2080. Black dots joined by a line indicate that individuals pass the threshold for those layers of information. The number of individuals presenting different intersections are at the right side of the plot. The orange line at the top, indicated that five individuals pass the thresholds for six layers of information. (b–d) The maps plot the individuals that remained after applying each of the three thresholds (25%, 50%, 90%). The colour of the symbols indicate the number of times an individual passes the six layers of information based on the 54 FCC models. The symbols indicate the different species, as shown in the legend at the end of (b). Table S7 reports the number of times an individual passed the FOLDS test for different thresholds FCC models.

figure shows some of the combinations of layers, and the number of accessions that pass that combination of filters. We can see, for example, that five accessions passed all six layers, suggesting that they are best poised to contribute alleles to adapt climate change, based on location, climate and genomic data. In addition, results for the model in Figure 3a, we provided the complete set of summary statistics used for the UpsetR analyses, with results for the additional 53 climate models (Table S1). These additional tables can be used to determine which accessions are suited to respond adequately to climate change for a particular FCC model.

Since we examined 54 FCCs, we calculated the number of times an accession passed the threshold for all six layers for each FCC model (Figure 3b,c). Overall, we found that for the conservative thresholds (0.25 and 0.5), only accessions of *V. mustangensis* passed all six filters for at least one climate model (Figure 3b,c). For the 25% threshold, four *V. mustangensis* accessions (Vmus02, Vmus03, Vmus14 and Vmus16) passed all filters for at least 48% of the 54 climate models. Based on this information, we predict that *V. mustangensis* accessions are relatively well situated to persist to predicted shifts in climate or to contribute adaptive variation in the future.

We also relaxed the thresholds, so that (for example) accessions remained when they retained among the lowest 90% of genetic offset and genomic load within a species, and among the highest 10% of N_e and S_a within a species (Figures 3c,d). At these threshold levels, a few accessions of *V. girdiana* and *V. arizonica* passed the filters. Importantly, the exercise also provided potential insight into relative risks among taxa. For example, only one *V. riparia* accession remained, even after applying 90% thresholds, for most models (Figure 3d). These results suggest that this species is particularly susceptible to population extinction within our sampled areas.

3.4 | Assessing the potential of wild *Vitis* to mitigate climate change in viticulture

Given insights into the potential persistence of wild species, our next task was to evaluate their potential to aid viticulture in the face of climate change. To evaluate which CWRs might be best suited for in situ adaptation of the crop, we relied on the concept of migration load (Rhóné et al., 2020), which is the genetic offset for an individual calculated between its present-day sampling site and other locations. In this case, the "other locations" were all of the 1278 *V. vinifera* locations in the United States identified in GBIF (Figure 4a, Table S5).

The approach and results are perhaps most easily represented by examples. *V. mustangenesis* accession vmus16 was one of six accessions that passed the FOLDS criteria at the strictest threshold level (Figure 3). As an illustration, we calculated the migration load for this accession in one FCC model (IPSL-CM6A-LR_ssp585_2061–2080) (Figure 4a). We then asked: which, if any, of the migration loads fell within the range of genetic offsets for the wild species? If the migration load fell within the range of genetic offsets, we surmised that vmus16 is a potential bioclimatic fit for crop adaptation at that location. Altogether, vmus16 had low migration load in many locations of the Northeastern USA and in one location in the Northwest for this single FCC model (Figure 4a). These are, then, candidate regions for the use of this CWR, where it may have climate alleles that could contribute to agricultural applications.

We extended these analyses to the six *V. mustangenesis* accessions that passed the filters of the FOLDs model (Figure 4b), calculating the migration load for each accession and each FCC model at all 1278 *V. vinifera* locations. After assessing whether the migration load fell within the range of genetic offsets for each FCC model, we counted the proportion of times the *V. mustangenesis* accessions passed the assessment at each location. The resulting map illustrates the potential suitability of *V. mustangensis* at each location (Figure 4b). Overall, *V. mustangensis* was projected to be more suitable for predicted climates in the Northeast US than in the Western US.

We expanded these analyses to all 48 accessions that passed filters for all six layers of the FOLDS model across the three threshold levels. We found 2630 instances in which an accession passed the FOLDS model for at least one FCC model and one threshold level, including 2096 cases for 90% FOLDS threshold, 391 cases for the 50% threshold, and 143 cases for strictest (25%) threshold (Figure 3b–d). From these, we estimated 2630 x 1278 = 3,361,140 migration loads. Tables S5 and S6 provide the calculated migrations loads and indicates whether they fell within the range of genetic offsets. These tables thus provide a preliminary evaluation of the potential climate adaptability of wild *Vitis* accessions in regions of *V. vinifera* cultivation.

4 | DISCUSSION

Climate change is a threat to all biodiversity (Parmesan, 2006; Parmesan & Yohe, 2003), but the fate of CWRs is particularly important. A growing literature has predicted the fate of CWRs under climate change, based on SDMs, but without explicit consideration

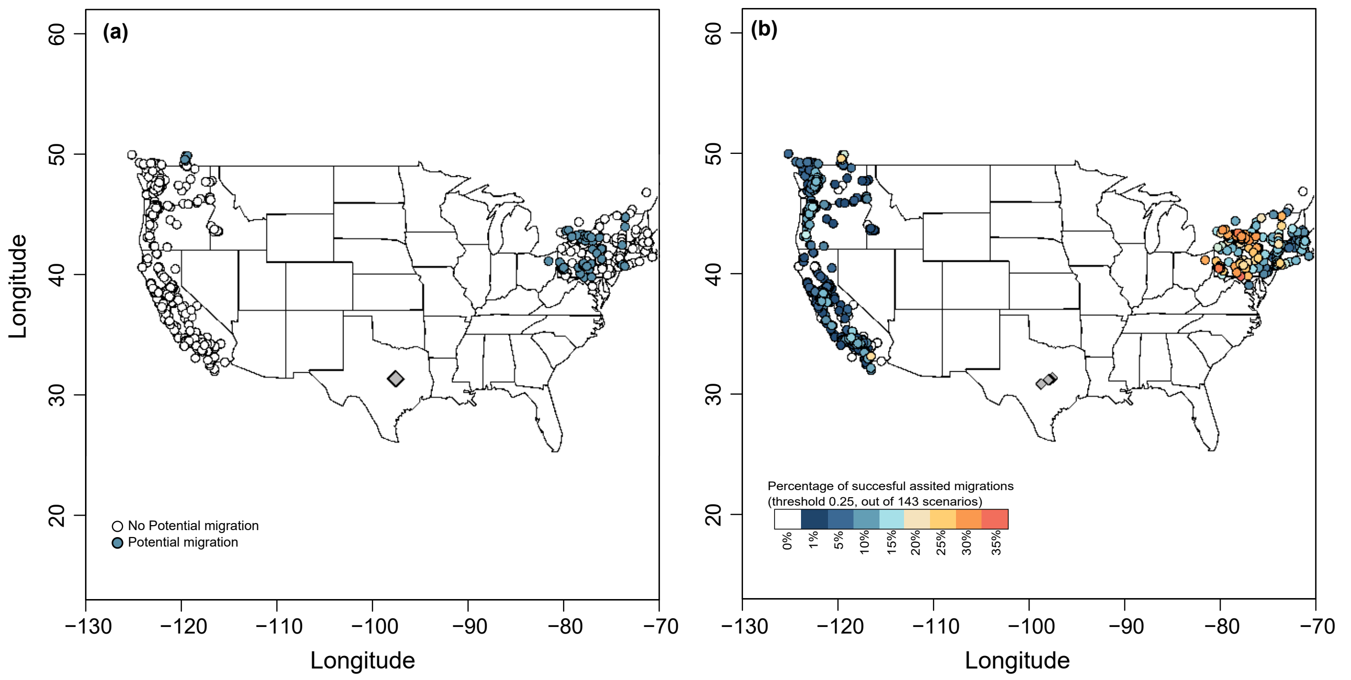

FIGURE 4 Climate change and in situ adaptation of *V. vinifera*. (a) An example of the locations where the migration load of *Vmus16* (see Figure 3) would be higher (white circles) or lower (blue circles) than the genetic offset of *V. mustangesis* if it was moved to locations where *V. vinifera* currently grow. This was performed using the future climate change (FCC) model IPSL-CM6A-LR_ssp585_2061-2080. Based on this analysis, *Vmus16* is more likely to be a suitable candidate for in situ adaptation of grapevine in the NE of the distribution. (b) Percentage of times that the migration load for 6 *V. mustangensis* individuals identified by the FOLDS model at a 0.25 threshold (Figure 3b) is lower than the genetic offset of *V. mustangensis* across the 54 (FCC) models. The colours of the symbols indicate, from all the possible events, the percentage of times than assisted migration could potentially be used for in situ adaptation (out of 143 possible events).

of evolutionary change, evolutionary history, or phenotypes. Here, we focused on five *Vitis* CWRs as exemplars to address three goals. The first has been to incorporate genomic data to assess the relative potential of CWRs to persist under climate change. The second has been to assess which CWRs, if any, have bioclimatic and genomic profiles that are of potential agronomic interest, pending further experimental evaluation. Finally, we offer this study as a framework to apply to other CWRs and crop systems.

4.1 | Evaluating CWR persistence: insights and caveats

Predicting how populations and species will respond to climate change is not a simple task because multiple factors, including evolutionary, human, and ecological processes, impact the response of populations to climate change (Waldvogel et al., 2019). We have combined individual measures, including SDMs and measures of genomic variability, to assess the relative ability of CWRs to respond to climate change. To our knowledge, no formal statistical framework exists to perform this task; instead, we relied on the existing FOLDS framework (Aguirre-Liguori et al., 2021).

We recognize that this approach is not complete for many reasons. For example, myriad additional biotic and abiotic phenomena probably affect the ability of populations to evolve in the face of climate change, but not all have been (or can be) measured. In theory, an advantage of the FOLDS approach is that it can incorporate unlimited layers of information, including additional biotic interactions, genetic and environmental data, and potential human impact data (e.g., urbanization or human-mediated fire threats) (Aguirre-Liguori et al., 2021). However, a corresponding shortcoming is that individual layers are weighted equally and treated independently, which may be inaccurate. For example, we have found that N_e and genomic load are correlated across NA *Vitis* accessions ($r = -0.41$, $p < .001$; Figure S9). While this correlation is not unexpected—because selection is less efficient in small populations—it implies that information from the two layers is partially redundant. We have also unexpectedly found that genomic load and PD resistance are negatively correlated ($r = -0.26$; $p < .01$; Figure S9). Perhaps the simplest explanation for the correlation is that less-fit plants (as measured by genomic load) are more susceptible to disease, but it again demonstrates that two seemingly unrelated layers may not provide fully independent information. One important extension of the FOLDS (or similar) models will be the ability to weight the contribution of individual layers to maximize predictive power. This may not be possible, however, without experimental data from climate experiments that can empirically test the accuracies of predictions. Such experiments are an obvious and important next step.

Additional shortcomings of our analyses relate to our treatment of the *Vitis* data set. For example, genetic offsets are typically calculated on estimated allele frequencies within populations (Fitzpatrick & Keller, 2015), but we have applied it to diploid frequencies within individuals. While this may decrease predictive power, and is probably conservative for that reason, both simulations and resampling analyses suggest that our conclusions based on single genotypes are robust (see Methods S1). We have also ignored the potential for natural migration, which may also impact opportunities to adapt to climate change.

Nonetheless, our synthesis provides a framework to begin to evaluate the relative risk among CWRs to predicted climate change that goes beyond SDMs and niche modelling. By considering evolutionary information, we predict that *V. mustangensis* accessions are the most apt to persist in the face of predicted climate change. The *V. mustangensis* accessions have good persistence in SDMs, high N_e, low genomic load, low genetic offsets and PD resistance. The framework also provides additional information for conserving other wild *Vitis* species. For example, some individuals scored well for five of six layers but have either low N_e or low adaptive scores (Figure 3a). Based on this information, it may be necessary to aid management of source populations by adding genetic diversity from different populations or species. Finally, we accentuate again that any predictions should, and can, be validated experimentally (Kardos & Shafer, 2018), for example, by growing suitable wild *Vitis* accessions in common gardens that simulate climate change and testing for fitness effects.

4.2 | Crop adaptation and climate change

Given genomic information from CWRs, we have used the GF framework to assess the potential of specific accessions to grow in the projected climates where domesticated grapevines are currently grown in the United States. The motivation for this approach is that viticulture is under climate risk. For example, Morales-Castilla et al. (2020) have used phenological data to estimate that 56% of current, worldwide growing locations will be lost under 2°C of warming, although this value decreased to 24% when they considered intraspecific variety in phenology among grapevine cultivars. Similarly, Hannah et al. (2013) projected a 25% to 73% decrease in suitable land for viticulture by 2050 among major wine producing regions. Hence, we view our analyses as a step toward assessing whether CWRs have alleles that can help mediate the effects of climate change on viticulture.

An important question is how best to counteract climate threats to crops. Generally, there are three nonexclusive strategies. One is human-assisted migration that shift the locations of cultivation for a specific crop (Sloat et al., 2020). A second is to develop new agricultural regions, that is, to expand arable land. However, land availability is limited, and the ecological and economic costs of this strategy is especially large (Fita et al., 2015). The third strategy is in situ adaptation, that is, breeding cultivars that tolerate stresses associated with climate change in their current locations of cultivation (Sloat et al., 2020). This is a strategy that has been advocated previously for *Vitis* rootstocks (Callen et al., 2016) and one for which genomic data may be helpful. In fact, genomic data have been used to inform this strategy, as illustrated in a landmark study of pearl millet (Rhoné et al., 2020). In that study, Rhoné et al. (2020) generated genomic data from landraces across the African continent, identified geographic regions where cultivation was at risk due to climate change, and then determined the migration load to determine which landraces have genomic profiles that may thrive if moved to at-risk regions.

Using a similar approach, we have asked which of our sampled CWRs have genetic and bioclimatic profiles that may make them suitable for growing in viticulture locations within the United States. Our CWR sample from the Southwestern U.S. may be particularly suitable for this study, because the accessions are adapted to warm and dry environments and hence may be needed for future breeding programmes (Heinitz et al., 2019). Since the FOLDS model predicted that six *V. mustangensis* accessions are particularly likely to persist under climate change, we focused on estimating their migration loads across a range of climate models. Migration load was often within the range of genetic offsets for that species (Figure 4). Based on these results, we hypothesize that some of these wild accessions may prove useful for in situ adaptation of cultivated grapevine and specifically that *V. mustangensis* may prove vital agronomically.

It is important, however, to discuss this hypothesis critically. First, we recognize that *V. mustangensis* is not currently used as a rootstock or for scion breeding. In fact, it may not even be the best candidate CWR for in situ adaptation at vulnerable sites, given that we have studied only five of ~30 species and 105 accessions. In this context, it is worth noting that *V. riparia* is commonly used as a rootstock but none of the *V. riparia* accessions in our sample fared particularly well in the FOLDS model. We suspect this reflects the fact that our sample is taken from the geographic limits of the species, where genomic load is often higher and fitness may be lower (Willi et al., 2018).

Second, our analyses are clearly only a first step, because many additional features of wild germplasm must be characterized before assessing agronomic utility. For example, although our study is rare for including one potential biotic interactor, there are many more other potential biotic interactors (Griggs et al., 2021), especially resistance to phylloxera, that are crucial for agricultural use. We also are not considering important complexities about viticulture, like irrigation and soil type. It is also an open question whether in situ adaption to climate change in grapevine will be better achieved by identifying new rootstocks or by using CWRs for hybrid scion breeding. The latter has already been shown to be effective for discrete traits that are governed by a few major loci, such as disease resistance. Indeed, PD resistance at the *Pdr1* locus (Krivanek et al., 2006) has been backcrossed into various varieties to introduce PD resistance. Bioclimatic adaptation is polygenic, however, as evidenced by the thousands of SNPs associated with bioclimatic variables in each of these species (Table 1) and by the fact that associated SNPs are distributed throughout the chromosomes (Morales-Cruz et al., 2021). Given, the polygenic nature of bioclimatic adaptation, we suspect that *Vitis* CWRs will typically be more effective as rootstocks. That said, rootstocks can have a multitude of effects on the scion, including yield, phenology and drought tolerance that may also display environmental interactions (Warschefsky et al., 2016). Moreover, potential rootstock and scion combinations can be incompatible, for reasons that are not yet well understood genetically (Gaut et al., 2019).

Finally, we have assumed that the climate models are accurate. Although we see no way around this assumption, we have tried to represent uncertainty in climate predictions by including 54 FCC models representing different time scales, circulation models and SSPs. Some accessions have low migration loads in some locations across most climate models, providing some consistency to the hope that these can be sources for climate-related alleles that may prove useful. Altogether, we have applied a unique combination of both climate and genomic information to identify potential and unexpected candidates for priority evaluation. We believe that this methodological approximation could be valuable for identifying CWRs of other crop for conservation or improvement in the future.

AUTHOR CONTRIBUTIONS

All authors contributed to the ideas of the study; Jonas A. Aguirre-Liguori and Abraham Morales-Cruz performed analyses; all authors wrote the manuscript.

ACKNOWLEDGEMENTS

The authors thanks Yongfeng Zhou, Summaira Riaz, Andrew Walker and Dario Cantu for sharing data from previous manuscripts. This study was improved by the comments of three anonymous reviewers and was supported by National Science Foundation grant no. 1741627 to B.S.G. J. A-L was supported in part by a UC-Mexus postdoctoral fellowship.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Sequence data that supports the findings of this study were downloaded from the Short Read Archive at NCBI under BioProject ID: PRJNA731597.

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REFERENCES

Aguirre-Gutiérrez, J., van Treuren, R., Hoekstra, R., & van Hintum, T. J. L. (2017). Crop wild relatives range shifts and conservation in Europe under climate change. *Diversity and Distributions*, *23*(7), 739–750. https://doi.org/10.1111/ddi.12573

Aguirre-Liguori, J. A., Ramírez-Barahona, S., & Gaut, B. S. (2021). The evolutionary genomics of species' responses to climate change Jonás. *Nature Ecology & Evolution*, *5*(10), 1350–1360. https://doi.org/10.1038/s41559-021-01526-9

Aguirre-Liguori, J. A., Ramírez-Barahona, S., Tiffin, P., & Eguiarte, L. E. (2019). Climate change is predicted to disrupt patterns of local adaptation in wild and cultivated maize. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1906), 20190486. https://doi.org/10.1098/rspb.2019.0486

Alston, J. M., & Sambucci, O. (2019). Grapes in the world economy. In D. Cantu & M. A. Walker (Eds.), *The Grape Genome* (p. 24). Springer Nature.

Bascompte, J., García, M. B., Ortega, R., Rezende, E. L., & Pironon, S. (2019). Mutualistic interactions reshuffle the effects of climate change on plants across the tree of life. *Science Advances*, *5*(5), 1–9. https://doi.org/10.1126/sciadv.aav2539

Bonin, A., Nicole, F., Pompanon, F., Miaud, C., & Taberlet, P. (2007). Population adaptive index: A new method to help measure intraspecific genetic diversity and prioritize populations for conservation. *Conservation Biology*, *21*(3), 697–708. https://doi.org/10.1111/j.1523-1739.2007.00685.x

Brady, S. P., Bolnick, D. I., Angert, A. L., Gonzalez, A., Barrett, R. D. H., Crispo, E., Eckert, C. G., Fraser, D. J., Fussmann, G. F., Guichard, F., Lamy, T., McAdam, A. G., Newman, A. E. M., Paccard, A., Rolshausen, G., Simons, A. M., & Hendry, A. P. (2019). Causes of maladaptation. *Evolutionary Applications*, *12*(7), 1229–1242. https://doi.org/10.1111/eva.12844

Callen, S. T., Klein, L. L., & Miller, A. J. (2016). Climatic niche characterization of 13 north American vitis species. *American Journal of Enology and Viticulture*, *67*(3), 339–349. https://doi.org/10.5344/ajev.2016.15110

Capblancq, T., Fitzpatrick, M. C., Bay, R. A., Exposito-Alonso, M., & Keller, S. R. (2020). Genomic prediction of (mal)adaptation across current and future climatic landscapes. *Annual Review of Ecology, Evolution, and Systematics*, *51*, 245–269. https://doi.org/10.1146/annurev-ecolsys-020720-042553

Castañeda-Álvarez, N. P., Khoury, C. K., Achicanoy, H. A., Bernau, V., Dempewolf, H., Eastwood, R. J., Guarino, L., Harker, R. H., Jarvis, A., Maxted, N., Müller, J. V., Ramirez-Villegas, J., Sosa, C. C., Struik, P. C., Vincent, H., & Toll, J. (2016). Global conservation priorities for crop wild relatives. *Nature Plants*, *2*(4), 1–6. https://doi.org/10.1038/NPLANTS.2016.22

Cingolani, P., Platts, A., Wang, L. L., Coon, M., Nguyen, T., Wang, L., Land, S. J., Lu, X., & Ruden, D. M. (2012). A program for annotating and predicting the effects of single nucleotide polymorphisms, SnpEff: SNPs in the genome of Drosophila melanogaster strain w1118; iso-2; iso-3. *Fly*, *6*(2), 80–92. https://doi.org/10.4161/fly.19695

Conway, J. R., Lex, A., & Gehlenborg, N. (2017). UpSetR: An R pack-age for the visualization of intersecting sets and their properties. *Bioinformatics*, *33*(18), 2938–2940. https://doi.org/10.1093/bioinformatics/btx364

Des Roches, S., Pendleton, L. H., Shapiro, B., & Palkovacs, E. P. (2021). Conserving intraspecific variation for nature's contributions to people. *Nature Ecology and Evolution*, *5*(5), 574–582. https://doi.org/10.1038/s41559-021-01403-5

Do, R., Balick, D., Li, H., Adzhubei, I., Sunyaev, S., & Reich, D. (2015). No evidence that selection has been less effective at removing deleterious mutations in Europeans than in Africans. *Nature Genetics*, *47*, 126–131.

Ellis, N., Smith, S. J., & Roland Pitcher, C. (2012). Gradient forests: Calculating importance gradients on physical predictors. *Ecology*, *93*(1), 156–168. https://doi.org/10.1890/11-0252.1

Exposito-Alonso, M., Burbano, H. A., Bossdorf, O., Nielsen, R., & Weigel, D. (2019). Natural selection on the Arabidopsis thaliana genome in present and future climates. *Nature*, *573*(7772), 126–129. https://doi.org/10.1038/s41586-019-1520-9

Exposito-Alonso, M., Vasseur, F., Ding, W., Wang, G., Burbano, H. A., & Weigel, D. (2018). Genomic basis and evolutionary potential for extreme drought adaptation in Arabidopsis thaliana. *Nature Ecology and Evolution*, *2*(2), 352–358. https://doi.org/10.1038/s41559-017-0423-0

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. E. (2016). Overview of the coupled model Intercomparison project phase 6 (CMIP6) experimental design and organization. *Geoscientific Model Development*, *9*(5), 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016

Feeley, K. J., Rehm, E. M., & Machovina, B. (2012). Perspective: The responses of tropical forest species to global climate change: Acclimate, adapt, migrate, or go extinct? *Frontiers of Biogeography*, *4*(2), 69–84. https://doi.org/10.21425/f5fbg12621

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Fita, A., Rodríguez-Burruezo, A., Boscaiu, M., Prohens, J., & Vicente, O. (2015). Breeding and domesticating crops adapted to drought and salinity: A new paradigm for increasing food production. *Frontiers in Plant Science*, *6*(NOVEMBER), 1–14. https://doi.org/10.3389/fpls.2015.00978

Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, *18*(1), 1–16. https://doi.org/10.1111/ele.12376

Fitzpatrick, M. C., Chhatre, V. E., Soolanayakanahally, R. Y., & Keller, S. R. (2021). Experimental support for genomic prediction of climate maladaptation using the machine learning approach gradient forests. *Molecular Ecology Resources*, *21*(8),1–17. https://doi.org/10.1111/1755-0998.13374

Fitzpatrick, M. C., Keller, S. R., & Lotterhos, K. E. (2018). Comment on "Genomic signals of selection predict climate-driven population declines in a migratory bird". *Science*, *361*(6401), 1–2. https://doi.org/10.1126/science.aat7956

Frankham, R. (2005). Genetics and extinction. *Biological Conservation*, *126*(2), 131–140. https://doi.org/10.1016/j.biocon.2005.05.002

Gaut, B. S., Miller, A. J., & Seymour, D. K. (2019). Living with two genomes: Grafting and its implications for plant genome-to-genome interactions, phenotypic variation, and evolution. *Annual Review of Genetics*, *53*, 195–215. https://doi.org/10.1146/annurev-genet-112618-043545

Gautier, M. (2015). Genome-wide scan for adaptive divergence and association with population-specific covariates. *Genetics*, *201*(4), 1555–1579. https://doi.org/10.1534/genetics.115.181453

Gougherty, A. V., Keller, S. R., & Fitzpatrick, M. C. (2021). Maladaptation, migration and extirpation fuel climate change risk in a forest tree species. *Nature Climate Change*, *11*(2), 166–171. https://doi.org/10.1038/s41558-020-00968-6

Griggs, R. G., Steenwerth, K. L., Mills, D. A., Cantu, D., & Bokulich, N. A. (2021). Sources and assembly of microbial communities in vineyards as a functional component of winegrowing. *Frontiers in Microbiology*, *12*(April), 836. https://doi.org/10.3389/fmicb.2021.673810

Hannah, L., Roehrdanz, P. R., Ikegami, M., Shepard, A. V., Shaw, M. R., Tabor, G., Zhi, L., Marquet, P. A., & Hijmans, R. J. (2013). Climate change, wine, and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(17), 6907–6912. https://doi.org/10.1073/pnas.1210127110

Heinitz, C. C., Uretsky, J., Dodson Peterson, J. C., Huerta-Acosta, K. G., & Walker, M. A. (2019). Crop wild relatives of grape (*Vitis vinifera* L.) throughout North America. In *North American Crop Wild Relatives* (Vol. *2*, pp. 329–351). Springer.

Hällfors, M. H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G. C.& Hellmann, J. J. (2016). Addressing potential local adaptation in species distribution models: Implications for conservation under climate change. *Ecological Applications*, *26*(4), 1154–1169. https://doi.org/10.1890/15-0926

Ikeda, D. H., Max, T. L., Allan, G. J., Lau, M. K., Shuster, S. M., & Whitham, T. G. (2017). Genetically informed ecological niche models improve climate change predictions. *Global Change Biology*, *23*(1), 164–176. https://doi.org/10.1111/gcb.13470

Janzen, G. M., Wang, L., & Hufford, M. B. (2019). The extent of adaptive wild introgression in crops. *New Phytologist*, *221*(3), 1279–1288. https://doi.org/10.1111/nph.15457

Jarvis, A., Lane, A., & Hijmans, R. J. (2008). The effect of climate change on crop wild relatives. *Agriculture, Ecosystems and Environment*, *126*(1–2), 13–23. https://doi.org/10.1016/j.agee.2008.01.013

Kardos, M., & Shafer, A. B. A. (2018). The peril of gene-targeted conservation. *Trends in Ecology and Evolution*, *33*(11), 827–839. https://doi.org/10.1016/j.tree.2018.08.011

Khoury, C. K., Carver, D., Greene, S. L., Williams, K. A., Achicanoy, H. A., Schori, M., León, B., Wiersema, J. H., & Frances, A. (2020). Crop wild relatives of the United States require urgent conservation action. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(52), 33351–33357. https://doi.org/10.1073/PNAS.2007029117

Krivanek, A. F., Riaz, S., & Walker, M. A. (2006). Identification and molecular mapping of PdR1 a primary resistance gene to Pierce's disease in Vitis. *Theoretical and Applied Genetics*, *112*(6), 1125–1131. https://doi.org/10.1007/s00122-006-0214-5

Lawler, J. J., White, D., Neilson, R. P., & Blaustein, A. R. (2006). Predicting climate-induced range shifts: Model differences and model reliability. *Global Change Biology*, *12*(8), 1568–1584. https://doi.org/10.1111/j.1365-2486.2006.01191.x

Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with burrows-wheeler transform. *Bioinformatics*, *25*(14), 1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Liang, Z., Duan, S., Sheng, J., Zhu, S., Ni, X., Shao, J., Liu, C., Nick, P., Du, F., Fan, P., Mao, R., Zhu, Y., Deng, W., Yang, M., Huang, H., Liu, H., Ding, Y., Liu, X., Ding, Y., … Dong, Y. (2019). Whole-genome resequencing of 472 Vitis accessions for grapevine diversity and demographic history analyses. *Nature Communications*, *10*(1), 1–12. https://doi.org/10.1038/s41467-019-09135-8

Lohmueller, K. E., Indap, A. R., Schmidt, S., Boyko, A. R., Hernandez, R. D., Hubisz, M. J., Sninsky, J. J., White, T. J., Sunyaev, S. R., Nielsen, R., Clark, A. G., & Bustamante, C. D. (2008). Proportionally more deleterious genetic variation in European than in African populations. *Nature*, *451*(7181), 994–997. https://doi.org/10.1038/nature06611

Láruson, Á. J., Fitzpatrick, M. C., Keller, S. R., Haller, B. C., & Lotterhos, K. E. (2022). Seeing the forest for the trees: Assessing genetic offset predictions from gradient forest. *Evolutionary Applications*, *15*(3), 403–416. https://doi.org/10.1111/eva.13354

Mallick, S., Li, H., Lipson, M., Mathieson, I., Gymrek, M., Racimo, F., Zhao, M., Chennagiri, N., Nordenfelt, S., Tandon, A., Skoglund, P., Lazaridis, I., Sankararaman, S., Fu, Q., Rohland, N., Renaud, G., Erlich, Y., Willems, T., Gallo, C., … Reich, D. (2016). The Simons genome diversity project: 300 genomes from 142 diverse populations. *Nature*, *538*(7624), 201–206. https://doi.org/10.1038/nature18964

Marín, D., Armengol, J., Carbonell-Bejerano, P., Escalona, J. M., Gramaje, D., Hernández-Montes, E., Intrigliolo, D. S., Martínez-Zapater, J. M., Medrano, H., Mirás-Avalos, J. M., Palomares-Rius, J. E., Romero-Azorín, P., Savé, R., Santesteban, L. G., & de Herralde, F. (2021). Challenges of viticulture adaptation to global change: Tackling the issue from the roots. *Australian Journal of Grape and Wine Research*, *27*(1), 8–25. https://doi.org/10.1111/ajgw.12463

McCouch, S. (2013). Feeding the future. *Nature*, *499*, 13–17.

Morales-Castilla, I., Cook, B. I., Lacombe, T., Parker, A., Van Leeuwen, C., Nicholas, K. A., & Wolkovich, E. M. (2020). Diversity buffers winegrowing regions from climate change losses. *Proceedings of the National Academy of Sciences*, *117*(6), 2864–2869. https://doi.org/10.1073/pnas.1906731117

Morales-Cruz, A., Aguirre-Liguori, J. A., Zhou, Y., Minio, A., Riaz, S., Walker, A. M., Cantu, D., & Gaut, B. S. (2021). Introgression among north American wild grapes (Vitis) fuels biotic and abiotic adaptation. *Genome Biology*, *22*(1), 1–27. https://doi.org/10.1186/s13059-021-02467-z

Nadeau, C. P., & Urban, M. C. (2019). Eco-evolution on the edge during climate change. *Ecography*, *42*(7), 1280–1297. https://doi.org/10.1111/ecog.04404

Ng, P. C., & Henikoff, S. (2003). SIFT: Predicting amino acid changes that affect protein function. *Nucleic Acids Research*, *31*(13), 3812–3814. https://doi.org/10.1093/nar/gkg509

Ollat, N., Peccoux, A., Papura, D., Esmenjaud, D., Marguerit, E., Tandonnet, J. P., Bordenave, L., Cookson, S. J., Barrieu, F., Rossdeutsch, L., Lecourt, J., Lauvergeat, V., Vivin, P., Bert, P.-F., & Delrot, S. (2016). Rootstocks as a component of adaptation to environment. *Grapevine in a Changing Environment: A Molecular and Ecophysiological Perspective*, 68–108. https://doi.org/10.1002/9781118735985.ch4

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change. *Nature*, *421*, 37–42. https://doi.org/10.1038/nature01286

Peterson, A. T., Soberón, J., Richard, G. P., Robert, P. A., Martínez-Meyer, E., Nakamura, M., & Araújo, M. B. (2011). Ecological niches and geographic distributions.

Phillips, S. J., Anderson, R., & Schapire, R. (2006). Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S., & Dudík, M. (2008). Modeling of species distributions with axent: New extensions and comprehensive evaluation. *Ecography*, *31*, 161–175. https://doi.org/10.1111/j.2007.0906-7590.05203.x

Rapicavoli, J., Ingel, B., Blanco-Ulate, B., Cantu, D., & Roper, C. (2018). Xylella fastidiosa: An examination of a re-emerging plant pathogen. *Molecular Plant Pathology*, *19*(4), 786–800. https://doi.org/10.1111/mpp.12585

Razgour, O., Taggart, J. B., Manel, S., Juste, J., Ibáñez, C., Rebelo, H., Alberdi, A., Jones, G., & Park, K. (2018). An integrated framework to identify wildlife populations under threat from climate change. *Molecular Ecology Resources*, *18*(1), 18–31. https://doi.org/10.1111/1755-0998.12694

Rhoné, B., Defrance, D., Berthouly-Salazar, C., Mariac, C., Cubry, P., Couderc, M., Dequincey, A., Assoumanne, A., Kane, N. A., Sultan, B., Barnaud, A., & Vigouroux, Y. (2020). Pearl millet genomic vulnerability to climate change in West Africa highlights the need for regional collaboration. *Nature Communications*, *11*(1), 5274. https://doi.org/10.1038/s41467-020-19066-4

Riaz, S., Huerta-Acosta, K., Tenscher, A. C., & Walker, M. A. (2018). Genetic characterization of Vitis germplasm collected from the southwestern US and Mexico to expedite Pierce's disease-resistance breeding. *Theoretical and Applied Genetics*, *131*(7), 1589–1602. https://doi.org/10.1007/s00122-018-3100-z

Riaz, S., Pap, D., Uretsky, J., Laucou, V., Boursiquot, J. M., Kocsis, L., & Andrew Walker, M. (2019). Genetic diversity and parentage analysis of grape rootstocks. *Theoretical and Applied Genetics*, *132*(6), 1847–1860. https://doi.org/10.1007/s00122-019-03320-5

Riaz, S., Tenscher, A. C., Graziani, R., Krivanek, A. F., Ramming, D. W., & Walker, M. A. (2009). Using marker-assisted selection to breed pierce's disease-resistant grapes. *American Journal of Enology and Viticulture*, *60*(2), 199–207.

Riaz, S., Tenscher, A. C., Heinitz, C. C., Huerta-Acosta, K. G., & Andrew Walker, M. (2020). Genetic analysis reveals an east-west divide within north American Vitis species that mirrors their resistance to Pierce's disease. *PLoS One*, *15*(12 December), 7–10. https://doi.org/10.1371/journal.pone.0243445

Schiffels, S., & Wang, K. (2020). MSMC and MSMC2: The multiple sequentially Markovian coalescent. In *Statistical population genomics* (pp. 147–166). Humana. https://doi.org/10.1007/978-1-0716-0199-0

Sloat, L. L., Davis, S. J., Gerber, J. S., Moore, F. C., Ray, D. K., West, P. C., & Mueller, N. D. (2020). Climate adaptation by crop migration. *Nature Communications*, *11*(1), 1–9. https://doi.org/10.1038/s41467-020-15076-4

Soberón, J. M. (2010). Niche and area of distribution modeling: A population ecology perspective. *Ecography*, *33*(1), 159–167. https://doi.org/10.1111/j.1600-0587.2009.06074.x

Terhorst, J., Kamm, J. A., & Song, Y. S. (2017). Robust and scalable inference of population history from hundreds of unphased whole genomes. *Nature Genetics*, *49*(2), 303–309. https://doi.org/10.1038/ng.3748

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography*, *32*(3), 369–373.

Vaser, R., Adusumalli, S., Leng, S. N., Sikic, M., & Ng, P. C. (2016). SIFT missense predictions for genomes. *Nature Protocols*, *11*(1), 1–9. https://doi.org/10.1038/nprot.2015.123

Waldvogel, A., Rellstab, C., Bataillon, T., Feldmeyer, B., Rolshausen, G., Exposito-alonso, M., Rellstab, C., Kofler, R., Mock, T., Schmid, K., Schmitt, I., Bataillon, T., Savolainen, O., Bergland, A., Flatt, T., Guillaume, F., & Pfenninger, M. (2019). Evolutionary genomics can improve prediction of species' responses to climate change. *Evoution Letters*, 1–15. https://doi.org/10.1002/evl3.154

Wan, Y., Schwaninger, H. R., Baldo, A. M., Labate, J. A., Zhong, G. Y., & Simon, C. J. (2013). A phylogenetic analysis of the grape genus (Vitis L.) reveals broad reticulation and concurrent diversification during neogene and quaternary climate change. *BMC Evolutionary Biology*, *13*(1), 1–20. https://doi.org/10.1186/1471-2148-13-141

Warschefsky, E. J., Klein, L. L., Frank, M. H., Chitwood, D. H., Londo, J. P., von Wettberg, E. J. B., & Miller, A. J. (2016). Rootstocks: Diversity, domestication, and impacts on shoot phenotypes. *Trends in Plant Science*, *21*(5), 418–437. https://doi.org/10.1016/j.tplants.2015.11.008

Willi, Y., Fracassetti, M., Zoller, S., & Van Buskirk, J. (2018). Accumulation of mutational load at the edges of a species range. *Molecular Biology and Evolution*, *35*(4), 781–791. https://doi.org/10.1093/molbev/msy003

Zamora-Gutiérrez, V., Rivera-Villanueva, A. N., Martínez Balvanera, S., Castro-Castro, A., & Aguirre-Gutiérrez, J. (2021). Vulnerability of bat-plant pollination interactions due to environmental change. *Global Change Biology*, *27*(14),1–16. https://doi.org/10.1111/gcb.15611

Zhou, Y., Massonnet, M., Sanjak, J. S., Cantu, D., & Gaut, B. S. (2017). Evolutionary genomics of grape (Vitis vinifera ssp. vinifera) domestication. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(44), 11715–11720. https://doi.org/10.1073/pnas.1709257114

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How to cite this article: Aguirre-Liguori, J. A., Morales-Cruz, A., & Gaut, B. S. (2022). Evaluating the persistence and utility of five wild *Vitis* species in the context of climate change. *Molecular Ecology*, *31*, 6457–6472. https://doi.org/10.1111/mec.16715