Climate Change May Treat Table Grape (*Vitis vinifera* subsp. *vinifera* Hegi) Cultivation and Industry: Niche Modeling and Comparative Phylogenetic Analyses

Mahan Kajkolah¹, Masoud Sheidai^{1* 9}, Fahimeh Koohdar¹

Received: 2024-09-17 Accepted: 2024-11-22

Abstract

Grape (Vitis vinifera subsp. vinifera Hegi) cultivation and its related industry are important sources of income for several regions and countries worldwide. Table grape gains its popularity because of the economic significance of this plant. Global warming and climate change are widely recognized as significant challenges in the 21st century, posing a substantial threat to various aspects of the world. One area in which these phenomena may greatly impact is grape production across different regions. Grape is cultivated in several parts of Iran, ranging from northwest to northeast and southern regions. The present study was performed to predict grape cultivation areas in the present time and future climate changeably in the year 2050. Such studies can provide a clear vision of future cultivation and help us to plan conservation strategies for grape cultivation. We used a combination of different species distribution modeling as well as comparative phylogeny analyses for the present study. Maxent, Dismo, and general linear model analyses of grape plant occurrence showed potential areas of grape cultivation at present and indicated a significant reduction in such areas by the year 2050. The model's result indicated the importance of precipitation and temperature for grape future cultivation. We identified genetic loci with adaptive potentials to climate change, which may be used in conservation and crossing among grape cultivars. The present findings are discussed along with our previous population genetics and landscape genetic studies of the same grape cultivars and suggestions are provided for the conservation of these plants.

Keywords: Dismo, Maxent, GLM, Adaptive loci, Grape

Introduction

Global warming and climate change are widely recognized as significant challenges in the 21st century. The rise in average global temperatures has been notable since the onset of the Industrial Revolution. According to data provided by the Copernicus Climate Change Service, Europe experienced its warmest year on record in 2020. This can be attributed to increased greenhouse gas

1-Department of Plant Sciences and Biotechnology, Faculty of Life Sciences and Biotechnology, Shahid Beheshti University, Tehran, Iran

^{*}The corresponding author's email address: msheidai@sbu.ac.ir Doi: 10.48308/pae.2025.237743.1095



Copyright: © 2025 by the authors. Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

emissions (GHG) from human activities (McIntyre et al., 2014). The global biodiversity is also significantly endangered by climate change. The occurrence of severe ecological ramifications is evident, encompassing recurrent droughts, rampant wildfires, and the emergence of invasive pests. These detrimental consequences have resulted in the depletion of plant species and a decline in productivity. Furthermore, they have led to scarcities in food crops and an escalation in costs for consumers. The genetic diversity and genetic connectivity of plant populations can be negatively impacted by climate change, resulting in a heightened homogeneity in genetic composition and reduced adaptability of species to future environmental changes (McIntyre et al., 2014, Guan et al., 2021).

Species distribution models (SDMs) are utilized to examine the current distribution of species and forecast their future occurrence in response to alterations in climate conditions (Elith and Leathwick, 2009). Species distribution models (SDMs) have the potential to provide valuable insights into the geographical distribution of suitable habitats for species of interest, as well as population demography and genetic diversity (A. Lee-Yaw et al., 2022). By employing computer algorithms, species distribution modeling (SDM), also recognized as environmental niche (ENM), habitat, predictive habitat distribution modeling, and range mapping, can anticipate the geographic and temporal distribution of a species by utilizing environmental data (Elith and Leathwick, 2009). The central concept of species distributions is the niche

theory with the fundamental niche versus the realised niche of a particular species (Hutchins, 1957). Various factors can affect the distribution of species, encompassing both abiotic and biotic environmental conditions. Additionally, the species' capacity to navigate and determine which geographic areas are accessible during the relevant time frame plays a significant role. (Elith and Leathwick, 2009).

Climate data, such as temperature and precipitation, along with other variables like land cover, water depth, and soil type, are utilized by SDMs. Also, these models find application in the fields of conservation biology, evolution, and ecology, aiming to elucidate the impact of environmental factors on the distribution and population size of specific species. Data acquired can be utilized for predictive intentions, such as ecological forecasting. It can also be employed to determine the future distribution of a species under the influence of climate change. Additionally, data can be utilized to assess the past distribution of a species, aiding in the evaluation of evolutionary relationships. Furthermore, data can be used to predict the potential future distribution of an invasive species. Similarly, estimations are formulated regarding the present and/ or forthcoming suitability of the habitat species under consideration. for the These predictions hold significant value for management purposes such as the reintroduction or translocation of species at risk, as well as the strategic placement of reserves in preparation for potential climate alterations (Elith and Leathwick, 2009).

Climate affects plant species in various

ways, influencing different aspects of their biological organization and scale. These impacts can be observed in terms of geographic distribution, genetic composition, and variations in phenotype.

The distributions of species are established by a range of characteristics and the capacity of organisms to adapt to various climatic conditions. These features and physiological tolerances interact to shape the distribution of species across the planet (Woodward and Woodward, 1987).

The population genetic peculiarities of species are similarly influenced by climate. These peculiarities are closely tied to genetic structure, population dynamics, and migration patterns, all of which play a role in shaping the fine-scale distribution patterns of species (Avise, 2000). In recent decades, there has been notable progress in the field of Species Distribution Models (SDM). This advancement can be attributed to the growing demand from scientists for effective methodologies and tools to evaluate the potential effects of climate change on the geographical range of various species or communities of species. Furthermore, the potential impacts of climate change on ecosystems have garnered interest from both the public and private sectors (Hinojos Mendoza et al., 2020).

The integration of SDM into landscape genetics, also known as ecological niche modeling (ENM), has become increasingly prevalent. This methodology enables the investigation of the connection between genetic variation and environmental gradients, thereby providing insights into the role of gene flow and selection (Ortego et al., 2012, Poelchau and Hamrick, 2012). Model predictions are frequently employed in these studies to depict the suitability of habitat or climate as a unified measure encompassing various intricate environmental factors. Subsequently, the impact of this measure on genetic patterns is evaluated. In the current scenario, multiple methodologies are utilized to estimate the potential consequences of climate change on the distribution and composition of species spatio-temporal various scales. across Several methodologies can be employed, such as the general linear model (glm), Artificial Neural Networks, regression trees, Bayesian approaches, as well as dismo and Mxent (Maximum entropy) methods.

Grape (Vitis vinifera subsp. vinifera Hegi) cultivation and its related industry are important sources of income for several regions and countries throughout the world. These plants have been under cultivation and human consumption since ancient history (Crespan, 2004, This et al., 2004, Emanuelli et al., 2013). Table grape has gained popularity due to their versatility and economic significance. They are utilized in various forms such as wine, juice, fresh consumption, dried fruit, and distilled liquor. As a result, table grapes play a crucial role in the global economy and agricultural sector (Goufo et al., 2020, Parihar and Sharma, 2021, Ekhvaia and Akhalkatsi, 2010). The grape has also played a role in natural medicines with therapeutic potential since ancient civilizations, including Iran (Taskesenlioglu et al., 2022, Naqinezhad et al., 2018).

Managers of grape orchards and the grape

industry as a whole need to take into account several critical factors. These include a comprehensive analysis of the genetic diversity and agronomic characteristics of grape cultivars, the selection of superior genotypes, and the assessment of the adaptability of these cultivars to various adverse environmental conditions in which grape cultivation is intended. However, we should also be cognizant of the consequences of climate change and global warming on the future cultivation of these important plants and the potential restriction of grape production due to these impacts. We suggest that a combination of population genetic study and landscape genetics investigation, along with niche modeling and prediction of future constraints on all important plant crops and ornamentals including grapes, may illustrate a detailed knowledge of genetic diversity, adaptation also the perils related to climate change on the cultivation of economically valuable plant species. The findings obtained from this multi-approach investigation provide us with a detailed dataset for future breeding and conservation plans these plant species.

From our previous preliminary population genetic studies on table grapes of Iran (unpublished data), we learned that, though local cultivars show some degree of genetic distinctness, they have a great magnitude of gene flow and admixture too. Moreover, geographical variables of longitude and latitude have a more profound effect on the local genetic structuring of grape plants compared to altitude and temperature. We could also identify some genetic regions (SCot loci), that are potentially associated with a present geological extension of table grape. This study builds upon our previous research by examining the genetic factors influencing the geographical distribution of table grapes. Additionally, it aims to identify and forecast potential future cultivation areas for these plants within the country, taking into account the impacts of climate change.

Therefore, to fulfill these tasks. the following aims are proposed. Performing different species distribution modelings (SDMs), such as dismo, Maxent (Maximum entropy) and glm (general linear model), as well as comparative phylogenetic analyses to study the significant role of different environmental factors on grape population divergence. Identify the genetic regions or loci that may enhance the cultivation and propagation of table grapes under future climatic conditions. To achieve this, we employed the Bayesian approach utilizing the latent factor mixed model (LFMM). Our comprehensive review of the existing literature indicates that this is the inaugural addressing the aforementioned report objectives concerning grape plants in Iran.

Material and methods

Plant material

A comprehensive assessment was conducted in this research, encompassing a total of 178 accessions derived from 35 cultivated populations of *V. vinifera* L. These cultivated populations were sourced from six provinces, namely Fars, North Khorasan, Kordestan, East Azarbaijan, Hamadan and Zanjan. The detailed information regarding the characteristics of the populations and

NO.	Туре	Name of population	Province	Locality	Longitude	Latitude	Altitude (m)	Number of samples
1	Cultivated	Siah	Kurdistan	Qalee	4780392	351362	1790	3
2	Cultivated	Siah	Kordest An Kurdistan	Marivan	4616667	355166	1310	7
3	Cultivated	Siah	East Azarbaijan	Malekan	461028	371458	1295	3
4	Cultivated	Siah samarghan di	Shiraz	firuzabad	5256388	288395	1467	5
5	Cultivated	Siah bidaneh	Shiraz	firuzabad	5256388	288395	1467	3
6	Cultivated	Fakhri	Kordestan	Qalee	4780392	3513625	1790	7
7	Cultivated	Fakhri	Hamedan	Malayer	488235	342969	1744	7
8	Cultivated	Fakhri	East Azarbaijan	Malekan	461028	371458	1295	4
9	Cultivated	Sefid sahani	Kordestan	Marivan	4616667	3551666	1310	5
10	Cultivated	Asgari	Shiraz	firuzabad	5256388	2883952	1467	5
11	Cultivated	Asgari	Hamedan	Malayer	488235	342969	1744	7
12	Cultivated	Rish baba sefid	Shiraz	firuzabad	5256388	2883952	1467	5
13	Cultivated	Rotabi	Shiraz	firuzabad	5256388	2883952	1467	5
14	Cultivated	Keshmeshi	Shiraz	firuzabad	5256388	2883952	1467	5
15	Cultivated	Keshmeshi	East Azarbaijan	Malekan	461028	371458	1295	5
16	Cultivated	Keshmeshi	East Azarbaijan	Maragheh	4626667	3738333	1472	7
17	Cultivated	Keshmeshi	Zanjan	Khorramdare h	4919296	3621094	1586	7
18	Cultivated	Keshmeshi	North Khoraran	Quchan	5830429	376229	1149	4
19	Cultivated	Keshmeshi Ghermez	Hamedan	Malayer	488235	342969	1744	7
20	Cultivated	Keshmeshi sefid	Hamedan	Malayer	488235	342969	1744	7
21	Cultivated	yaghuti	Shiraz	firuzabad	5256388	2883952	1467	5
22	Cultivated	yaghuti	Hamedan	Malayer	488235	342969	1744	7
23	Cultivated	Lorkosh	Shiraz	firuzabad	5256388	2883952	1467	5
24	Cultivated	Ghazvini	Shiraz	firuzabad	5256388	2883952	1467	5
25	Cultivated	Hoseini	East Azarbaijan	Malekan	461028	371458	1295	4
26	Cultivated	Hoseini	East Azarbaijan	Maragheh	4626667	3738333	1472	8
27	Cultivated	Ghezel ozam	East Azarbaijan	Malekan	461028	371458	1295	4
28	Cultivated	Ghezel ozam	East Azarbaijan	Maragheh	4626667	3738333	1472	7
29	Cultivated	Dorosht daneh dar	Zanjan	Khorramdare h	4919296	3621094	1586	3
30	Cultivated	Ghermez daneh dar	Zanjan	Khorramdare h	4919296	3621094	1586	3
31	Cultivated	Khalili	East Azarbaijan	Malekan	461028	371458	1295	7
32	Cultivated	Shani	East Azarbaijan	Malekan	461028	371458	1295	3
33	Cultivated	Sahebi	East Azarbaijan	Malekan	461028	371458	1295	3
34	Cultivated	Gaznei	KordestanKurdistan	Qalee	4780392	351362	1790	3
35	Cultivated	Kordkosh	KordestanKurdistan	Qalee	4780392	351362	1790	3

Table 1. Details of V. vinifera populations used in the study

DNA extraction and PCR details

the number of individuals examined can be found in Table 1.

In this study, we used the information of Kajkolah et al. (in press), genomic DNA was isolated from leaves using a modified extraction protocol known as Cetyltrimethylammonium bromide-activated charcoal (CTAB) method. This procedure was employed to extract the DNA, which was subsequently utilized as the input material for the preparation of DNA samples (Križman et al., 2006). The extraction method utilized activated charcoal, polyvinylpyrrolidone (PVP), and 2-mercaptoethanol to facilitate the binding of polyphenolics during the extraction process. This approach was carried out under gentle extraction and precipitation conditions, ensuring the isolation of high-molecular-weight DNA without any disruptive impurities. To determine the concentration of DNA, aliquots were subjected to electrophoresis on a 1% agarose gel. For the PCR reactions, a total volume of 25 µL was utilized, comprising 14 µL of master mix, 8 µL of water, 1 µL of Primer (SCoT), and 3 µL of DNA. Three different SCoT primers, namely SCoT-1, SCoT-2, and SCoT-36, were employed in this study. The polymerase chain reaction (PCR) was conducted using a total of 45 cycles. The initial denaturation step lasted for 4 minutes at a temperature of 95 °C. Subsequently, the reaction underwent a denaturation step at 94 °C for 1 minute, followed by an annealing step at a temperature range of 54-56 °C for 1 minute. Finally, an extension step was performed at 72 °C for 1 minute. The reaction was finalized through a concluding extension phase lasting 7 minutes at a temperature of 72 °C. The resulting amplification products were subjected to analysis using 2% agarose gel electrophoresis and fluorescence staining on KBC power load, a product of Kowsar Biotech Company located in Iran. To determine the size of the fragments, a 100-bp molecular size ladder was employed (Fermentas, Germany).

Data analysis

Species distribution modeling (SDM)

A variety of techniques were employed to conduct species distribution modeling (SDM) for table grapes in the region, including the utilization of Dismo, Maxent, and glm analyses (1).

The grape cultivar's contemporary speciesclimate relationship was simulated by employing Maxent, a maximum entropy modeling technique specifically designed for presence-only species data, which effectively handles irregularly sampled data (Phillips et al., 2006).

Maxent employs a statistical technique to estimate the distribution that exhibits the highest level of uniformity, commonly referred to as the ,maximum entropy', within the study area. This estimation is subject to the condition that the expected value of each environmental predictor variable, based on this estimated distribution, aligns with its empirical average derived from the collection of species' presence records (Phillips et al., 2006).

Maxent was utilized to conduct model runs incorporating linear, quadratic, and product features. By employing Maxent's logistic output, climatic habitat suitability maps were generated for grape cultivars. These maps offer an estimation of the probability of presence in geographic space, ranging from 0 (indicating low suitability) to 1 (indicating high suitability).

We have determined significant climatic factors by employing Maxent's metrics of variable contribution and permutation importance. Due to the sensitivity of these metrics to correlations among variables, it becomes crucial to consider their impact. In addition, we employed Maxent's jackknife tests to assess the significance of variables. These tests evaluate the (1) predictive capability of individual variables when utilized independently and (2) the distinct impact of each variable by measuring the reduction in predictive capability when a variable is omitted from the model.

In our research, we utilized the dismo package within R version 4.1.2 to perform species distribution modeling (SDM) analysis. The Bioclim algorithm, recognized for its effectiveness in this domain, was applied. This algorithm is often known as the 'climate-envelope-model' and has seen extensive use in the field.

SDMs necessitate the presence of species absence point data, which we acquired through the utilization of pseudo-absences (PAs) techniques, in order to forecast appropriate species habitats. All of the models were developed using 80% of the occurrence data for training purposes, while the remaining 20% was used for testing. The evaluation of the models was conducted using both the threshold method and the determination of the Area Under the Curve (AUC) through the Receiver Operating Characteristic (ROC) curve.

In the dismo model, the initial step involved

estimating the pseudo-absence points, after which the model was evaluated through a post hoc analysis. This was done by partitioning the data into training and test data (80% and20% respectively). The dismo package's k-fold function was employed to To systematically assign each observation to a random group.

By utilizing the group-presence vector alongside the observed data, we successfully segregated our observations into a training data set and a testing data set. Then we performed model testing for both the train data as well as the test data.

The threshold function was employed in our study, providing various options for determining the threshold cutoff based on the state parameter. In this particular case, we opted for "spec_sens", which establishes the threshold at the point where the combined values of sensitivity (true positive rate) and specificity (true negative rate) are maximized. The threshold was employed to create a visual representation of the projected distribution of *V. vinifera* on a map. The same was done for forecasting data in 2050.

By utilizing the BIOCLIM algorithm, the similarity of a given location is determined by evaluating the environmental variable values at that particular location in relation to a percentile distribution of values observed at known occurrence sites, also known as 'training sites'. The location that exhibits a closer proximity to the 50th percentile (the median) is regarded as being more suitable (Hijmans and Graham, 2006). The R version 4.1.2 was utilized to conduct a glm analysis in a similar manner.

In the field of species distribution modeling, we employed climate data layers that were projected for two distinct periods: the current period spanning approximately 1950 to 2000, and the future period of the year 2050 (averaging data from 2061 to 2050). These projections were based on 19 bioclimatic variables, and the spatial resolution of the data was set at 5 minutes, equivalent to approximately 9 km at the equator.

The WorldClim database served as the source for the data acquisition process. These data were specifically downloaded to investigate the implications of climate change. To evaluate the potential impacts, projections were made for future climate variables in the year 2050, employing the Representative Concentration Pathways (RCP) scenario of 2.6.

Bioclimatic variables were employed in our study, which were obtained from the monthly temperature and rainfall data. The coding scheme for these bioclimatic variables is as follows:

BIO1 = Annual Mean Temperature

BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))

 $BIO3 = Isothermality (BIO2/BIO7) (\times 100)$

 $BIO4 = Temperature Seasonality (standard deviation \times 100)$

BIO5 = Max Temperature of Warmest Month

BIO6 = Min Temperature of Coldest Month BIO7 = Temperature Annual Range (BIO5-BIO6)

BIO8 = Mean Temperature of Wettest Quarter

BIO9 = Mean Temperature of Driest Quarter BIO10 = Mean Temperature of Warmest Quarter

BIO11 = Mean Temperature of Coldest Quarter

BIO12 = Annual Precipitation

BIO13 = Precipitation of Wettest Month

BIO14 = Precipitation of Driest Month

BIO15 = Precipitation Seasonality (Coefficient of Variation) BIO16 = Precipitation of Wettest Quarter

BIO17 = Precipitation of Driest Quarter

BIO18 = Precipitation of Warmest Quarter

BIO19 = Precipitation of Coldest Quarter The methodology adopted in this scheme closely resembles that of ANUCLIM, with the exception being the treatment of temperature seasonality. In contrast to ANUCLIM, which employs the coefficient of variation, this scheme utilizes the standard deviation. This alteration is necessary due to the lack of meaningful interpretation when applying the coefficient of variation to temperatures ranging between -1 and 1.

Phylogenetic comparative analyses

The phylogenetic signal of the environmental variables under investigation was evaluated using Blomberg's K and lambda parameters, as implemented in the phytools package in R. These parameters provide insights into the influence of environmental variables on the divergence and similarity of grape populations.

Pagel's λ is a mathematical transformation applied to phylogenetic data in order to optimize the alignment of trait data with a Brownian Motion model (Pagel, 1999).

Blomberg's K can be characterized as the quotient of two distinct ratios. The initial ratio, referred to as the observed ratio, is obtained by dividing the Mean Squared Error of tip data by the Mean Squared Error of data computed using the variance-covariance matrix derived from the phylogeny. On the other hand, the second ratio, known as the expected ratio, is derived from the same procedure but employs data from a model assuming the Brownian motion of trait evolution (Blomberg et al., 2003).

Blomberg's K quantifies the phylogenetic signal's potency by comparing the mean squared error of the tip data (MSE0) obtained from the phylogenetic corrected mean with the mean squared error calculated using the variance-covariance matrix derived from the provided phylogeny, assuming Brownian motion (BM) (Blomberg et al., 2003).

The estimation is calculated in the following manner:

Disparity analyses

To visualize how phylogeny relates to the distribution of populations in terms of their traits, we devised a 'phylomorphospace'. This innovative method involves projecting the branches of a phylogenetic tree onto a two-dimensional morpho-space, thereby representing the diversity of traits among different species or populations (Revell, 2012). A phylomorphospace was established to encompass the analyzed variables, including the PCA-axes corresponding to these variables.

Identification of adaptive genetic regions

Association between SCoT loci and temperature and precipitation of the current time and also in 2050 data was performed by LFMM (Latent factor mixed model) as perfumed in lfmm package in R ver.4.1 (Frichot et al., 2013). LFMM utilizes a Bayesian approach in its methodology which considers both genetic data and environmental / climate variables and other confounding population genetics factors.

Results

Species distribution modeling Dismo results

According to the dismo package's model, the probability of grape cultivars occurring is at its highest, reaching 0.8. This finding implies that our collection of these plants from areas where they are known to occur is quite extensive. However, it is important to acknowledge that there are still potential areas that have not been included in our collection of plant materials.

Following the estimation of pseudo-absence points, a post hoc evaluation of the model was performed, as outlined in the material and methods section. Ultimately, the threshold was utilized to create a map depicting the projected distribution of table grapes (Fig. 1). The distribution area map that has been predicted provides valuable insights into the regions where grapes have the potential to thrive and should be contemplated for planning and conservation purposes to protect this species.

Based on the analysis of climate data for the year 2050, it is anticipated that grape plants will show a diminished presence in the southern areas of Iran (Fig. 2). The findings reveal a notable decline in the prevalence of these plants when compared to earlier periods. The model used for this analysis achieved an AUC value of 0.98, indicating its high accuracy and reliability.

The results we obtained in our previous study concerned with landscape genetic analysis of



Fig. 1. A = Distribution map of grape cultivars studied, and B = Cover-land of Iran



Fig. 2. Distribution map of grapes in the present time and in the year 2050



Fig. 3. Gain plot of the bio-climate variables (tA), and ROC curve(B), from Maxent package, showing importance of the variables and good fit of the model obtained (Bioclim data bio1-bio19, are as given before)

the same grape cultivars also demonstrated the existence of genetic structuring of grapes through the identification of several genetic clines situated in the north-eastern region in the north-west of the country which extends to some parts of Southern Iran as also produced by predicted presence area presented here. The anticipated climate change in 2050 may result in the potential loss of grape cultivation areas in both genetic cline regions. Therefore, we should plan for this great loss ahead of time, as will be suggested in the following paragraphs.

Maxent results

The results from the Maxent modeling produced distribution maps that closely resembled those created with the dismo package. The importance and significance of bioclimatic variables are illustrated in Figure 3. Variables associated with precipitation are essential in influencing the current distribution of grape plants. This finding holds true when forecasting the distribution of grape plants for the year 2050. The performance of the Maxent model was found to be highly accurate based on the AUC and ROC curves, both in the present time and in the forecast for the year 2050 (Fig. 3). Both the AUC for the present time and the year 2050 demonstrated a score of 1, signifying an impeccable model. The glm analyses of both multiple general linear methods and logistic regression also produced a significant correlation (p<0.001), between longitude and latitude as well as precipitation. Both R-squared and AUC = 0.80, showed a high accuracy of the models obtained.

Comparative phylogenetic analyses

Phylogenetic signal determined for environmental variable longitude, produced a significant K = 0.04 (P-value calculated by performing 1000 randomizations = 0.001), and lambda = 0.52 (P-value calculated using the LR test = 1.44907e-07 for), respectively. Similar results were obtained for latitude (K



Fig. 4. Significant Pagals' lamda obtained for all environmental variables studied

= 0.14, P = 0.001), and longitude (K = 0.06, P = 0.002), as well as temperature (K = 0.14, P = 0.001).

We also obtained significant Pagals' lambda value (> 0.6), for these variables (Fig. 4). Therefore, all these environmental and climatic variables play a role in the

differentiation and distribution of grape populations.

The findings are corroborated by the development of a two-dimensional phylomorphospace that demonstrates the differentiation and distribution of population groups within the space (Figs. 5 and 6).



Fig. 5. Morpho-space diagram of longitude and latitude separating different grape population groups



Fig. 6. Morpho-space diagram of temperature and altitude separating different grape population groups

accurately forecasting the reactions of intricate species to environmental influences.

The Maxent program incorporates various computational techniques, rendering it a

highly proficient tool for addressing diverse

data collection strategies. In the current study, we utilized 178 plant specimens

gathered from 35 occurrence data points.All



Fig. 7. Manhattan plot showing significantly associated SCoT loci with environmental variables in 2050

SCoT loci with adaptive potentials to future climate change

LFMM analysis followed by FDR (False detection rate), identified SCoT loci numbers 9, 13, 23, 28, and 29, as potentially adaptive to the temperature in the year 2050 (Fig. 7). Previously, we had identified SCoT loci 7 and 23 as potentially adapted to the present time temperature.

Discussion

Species distribution model analysis

We reported the predicted distribution of table grapes both in the present time as well as in the year 2050, with climate change in the course of time. The predication models showed a reduced geographical extent of grape cultivation in the future time, which should be tackled properly and conserve the cultivation level of this important crop plant. We obtained almost similar results from different species models utilized and irrespective of different computational methods used in these models. The Maxent model offers a thorough methodology for feature types, including interactions among predictors, are utilized in Maxent when there are a minimum of 80 occurrences (Elith and Leathwick, 2009). In instances where the occurrences fall between 15 and 79, the Maxent model incorporates linear, quadratic, and hinge features. In contrast, when the occurrences are between 10 and 14, it utilizes only linear and quadratic features. Furthermore, for cases with 10 occurrences or fewer, the Maxent model depends exclusively on linear features. The 'jackknife' contributions plot we obtained in the present study, to account for the dependencies between predictor variables, the models are developed in two ways: one model focuses solely on a particular feature, while the other model incorporates all features except for the one under consideration. The x-axis represents the measure of the models' predictive ability, which can be assessed using either 1) training gain, 2) test gain, or 3) AUC on test data. We obtained AUC = 1, which shows perfect predictive accuracy of the model.

The dark blue bars illustrate the performance of a model that relies exclusively on a particular feature, contrasted with the maximum performance of the model, represented by the red bar. Currently, in species distribution, the BIOCLIM variable, primarily associated with precipitation, emerges as a significant feature. Conversely, the light blue bars indicate the model's performance when the influence of that specific feature is excluded. Consequently, the omission of the bio18 and bio3 variables from the model may lead to a decrease in accuracy. In general, the BIOCLIM variables studied in grape cultivars showed the presence of both dark blue colored and light blue colored bars in the gain plot. The significant factors can exhibit either 1) substantial dark blue bars, signifying a robust (yet potentially non-exclusive) impact on presences; 2) brief light blue bars, indicating that no other factor possesses comparable information; or 3) both, suggesting that the factor independently predicts the global suitability of the red bar model (Elith and Leathwick, 2009, Kearney and Porter, 2009). The geographical distribution of a species is shaped by a variety of factors that stem from both evolutionary and ecological processes (Riordan et al., 2016). This distribution can be influenced by abiotic factors, such

as large-scale climate conditions, as well as biotic interactions that occur on a more localized level. The distribution of species is affected by a range of abiotic factors, including climatic elements such as the atmosphere, sunlight, temperature, salinity, and humidity. Additionally, edaphic agents like soil characteristics, including local geology, coarseness, aeration, and soil pH play a significant role. Furthermore, social factors, such as land use patterns and water availability, also contribute to species distribution (Elith et al., 2006, Booth et al., 2014).

The distribution of species may be affected by a range of biotic factors, including predation, disease, and competition for essential resources such as water, food, and mates. Notably, human activities, such as continuous industrialization and construction projects, play a significant role in altering species distribution.(Booth et al., 2014, Elith et al., 2006).

The response of various populations within a species to climate can differ significantly. For instance, species with extensive distributions spanning multiple climatic regions may display distinct associations with climate when analyzed at regional levels compared to species-wide scales (Rehfeldt et al., 2002). Therefore, it has been suggested that it is more suitable to concentrate geographical variations in species on distribution while investigating the impact of climate on various biological processes, particularly in regions characterized by considerable environmental heterogeneity. (Riordan et al., 2016).

The climatic variables that play a role in

grape populations distribution models are precipitation and eco-physiological limiting factors, namely temperature and water availability, that can impose constraints survival and ecological performance on of a species. (Guisan and Thuiller, 2005). However, we can't overlook the additional environmental agents that have a significant impact on ecological and evolutionary processes, including biotic interactions and soil composition as a landscape genetic study showed the presence of genetic clines at both the North-East of the country as well as the North-Western regions, which may differ in land cover features.

These models used in our study revealed an enormous reduction in the cultivation areas by the year 2050. The remaining suitable areas would be mostly confined to the North-West of Iran and to a lesser extent in the North-Eastern region.

In a similar study, Mendoza, et al. (2020), aimed to evaluate the appropriate regions in France for growing grapes (Vitis vinifera) under current and future climate conditions. They employed the Climate Data Science (CDS) Toolbox and Species Distribution Model (SDM) to accomplish this task. The model was constructed by incorporating 23 variables that were readily accessible online. Assumptions were made regarding the interconnections between these variables and the spatial distribution of species. The research indicated that the area's most conducive to grapevine cultivation are anticipated to undergo a substantial decline, estimated between 41% and 83%, by the year 2070, taking into account the current locations of vineyard parcels. The

findings highlight a possible relocation of the appropriate regions in the northern section of the French land. Additionally, they indicate a potential displacement of the most favorable regions in terms of altitude, with an average increase of 60 meters for the RCP6.0 scenario (Hinojos Mendoza et al., 2020).

Genetic structure and variability concerning geographical species distribution

In this present study, we identified some genetic loci with potential adaptive value with future climate change, and particularly with precipitation and temperature. Some of these loci have been elected by local environmental conditions too. Our previous research in population genetics and landscape genetics (unpublished data) revealed that Iranian table grapes exhibit considerable genetic variation and are genetically organized in response to both local and global environmental factors. These cultivars reveal a remarkable genetic admixture and contain a low to moderate within cultivar / or population. Genetic variability ranging from 5. 71% to 60%. Genetic patterns at a regional level are determined by two main factors: restricted gene flow, leading to isolation by distance (IBD), and isolation by environment (IBE). By which, gene flow is more prevalent among comparable environments due to selective forces or ecological barriers that impede movement (Wang and Bradburd, 2014, Soularue and Kremer, 2014).

The occurrence of adaptive genetic loci related to both geographical variables of longitude and latitude, or altitude, and those related to precipitation and temperature is of great significance in all plants. Species including grape, as these adaptive loci can help the plants during movement, migration, or artificial introduction to new habitats and cultivation areas. The immigrants who are not well-suited to the prevailing climatic conditions of the local area may face negative consequences, leading to a positive relationship between adaptive divergence and genetic differentiation, which is commonly referred to as isolation by adaptation (IBA) (Andrew et al., 2012, Nosil et al., 2008).

The environmental conditions in vineyards worldwide are being modified as a result of climate change. While some grapegrowing regions may benefit from positive impacts on grape production, the quantity and quality of wines produced can be adversely affected in regions experiencing hotter or drier conditions (Duchêne, 2016). The process of adapting to new climatic conditions encompasses adjustments in the cultivation areas, alterations in vineyard or cellar practices, and the use of new combinations of rootstock and scion. The grape industry has the potential to respond to climatic changes by relocating cultivation zones and altering the characteristics of the wines produced, leveraging the inherent small-scale variability that already exists. (Duchêne, 2016).

Vegetative propagation is the method by which grape plants are reproduced. Accidental modifications in the DNA during cell division can lead to the emergence of new characteristics in a bud. These inherent and unplanned occurrences may not always have significant impacts, but

when they do, the newly formed plant can showcase fascinating traits, including a white coloration, a fragrance reminiscent of Muscat grapes, or an upright growth habit, for instance. The process of genetic variability remains in progress, giving rise to what is referred to as "clonal variation". This entails the identification of slightly different plants within a particular variety and transmitting their unique characteristics through vegetative propagation (Duchêne, 2016). Moreover, the exploration of the available grape clone collections can reveal any phenotypic variations that hold the potential for aiding in the adjustment to climate change.

We reported a high magnitude of genetic admixture among grape cultivars of Iran, probably due to some events of sexual reproduction. The genome of the grapevine exhibits a significant level of heterozygosity, suggesting that the crossbreeding of two different grapevine varieties can produce an infinite variety of diverse offspring. This observation highlights the pivotal role of sexual reproduction, whether influenced by random events or human intervention, genetic diversity identified in cultivated grapevines(Duchêne, 2016).

Genetic diversity plays a crucial role in adapting to climate change and for adjusting cultivation zones and training systems. By utilizing various genotypes for both scion and rootstock, including new ones, the potential for adaptation is significantly enhanced (Duchêne, 2016).

In addition to our study and reporting genetic loci related to climate change, several studies have been undertaken to analyze and compare the behaviors of diverse grapevine genotypes under water restriction conditions (Duchêne, 2016). In a recent investigation conducted by Coupel-Ledru et al. (2014), the genetic foundation of this particular attribute was explored through the utilization of a QTL methodology. The study involved an analysis of 186 genotypes, derived from a reciprocal cross between Syrah and Grenache. This comprehensive examination yielded significant findings regarding the hereditary patterns associated with this trait, thereby offering valuable insights into its inheritancemechanisms(Coupel-Ledruetal., 2014). The authors of this study successfully recognized quantitative trait loci (QTLs) associated with various traits, including specific hydraulic conductance, minimal daytime leaf water potential, and specific transpiration rate. However, achieving the most favorable blend of alleles from various loci, which results in optimal behavior in situations characterized by a lack of water resources in natural environments, remains a complex and arduous process (Tardieu, 2003). Rootstocks exhibit significant diversity in their capacity to tolerate water stress among available grape cultivars, which can be monitored and employed in the process of regenerating incompatible selections. The environmental conditions in numerous grape orchards worldwide will experience significant alterations due to climate change, which will consequently have a profound effect on grape production and the industry as a whole... We reported here that a reduction in water precipitation and an increase in temperature by the year 2050 could significantly reduce the

agricultural land available for cultivation in Iran. Consequently, it is essential to develop various conservation and selection strategies to safeguard grape production within the nation. These strategies should encompass the evaluation of germplasm for tolerance to water stress, the identification of genetic loci associated with adaptation to climate change, as well as the implementation of artificial selection and inter-varietal crossing techniques.

References

- A. Lee-Yaw, J., L. McCune, J., Pironon, S. and N. Sheth, S., 2022. Species distribution models rarely predict the biology of real populations. *Ecography*, 2022(6), p.e05877. DOI: https://doi. org/10.1111/ecog.05877
- AAndrew, R.L., Ostevik, K.L., Ebert, D.P. and Rieseberg, L.H., 2012. Adaptation with gene flow across the landscape in a dune sunflower. *Molecular ecology*, 21(9), pp.2078-2091. DOI:
- https://doi.org/10.1111/j.1365-294X.2012.05454.x Avise, J.C., 2000. Phylogeography: the history and formation of species. Harvard University Press. DOI: https://doi.org/10.1093/ icb/41.1.134
- Blomberg, S.P., Garland Jr, T. and Ives,
 A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution, 57(4), pp.717-745. DOI: https://doi.org/10.1111/j.0014-3820.2003.tb00285.x
 Booth, T.H., Nix, H.A., Busby, J.R. and Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modelling

package, its early applications and relevance to most current MAXENT studies. *Diversity and distributions*, 20(1), pp.1-9. DOI: https://doi. org/10.1111/ddi.12144

Coupel-Ledru, A., Lebon, É., Christophe, A., Doligez, A., Cabrera-Bosquet, L., Péchier, P., Hamard, P., This, P. and Simonneau, T., 2014. Genetic variation in a grapevine progeny (Vitis vinifera L. cvs Grenache× Syrah) reveals inconsistencies between maintenance of daytime leaf water potential and response of transpiration rate under drought. *Journal of Experimental Botany*, *65*(21), pp.6205-6218. DOI: https://doi. org/10.1093/jxb/eru228

- Crespan, M., 2004. Evidence on the evolution of polymorphism of microsatellite markers in varieties of *Vitis vinifera* L. *Theoretical and Applied Genetics*, *108*(2), pp.231-237. DOI: https://doi. org/10.1007/s00122-003-1419-5
- Duchêne, E., 2016. How can grapevine genetics contribute to the adaptation to climate change?. *Oeno One*, *50*(3), pp.113-124. DOI: https://doi. org/10.20870/oeno-one.2016.50.3.98
- Ekhvaia, J. and Akhalkatsi, M., 2010.
 Morphological variation and relationships of Georgian populations of Vitis vinifera L. subsp. sylvestris (CC Gmel.) Hegi. *Flora-Morphology, Distribution, Functional Ecology of Plants, 205*(9), pp.608-617. DOI: https://doi.org/10.1016/j.flora.2009.08.002
- Elith, J., Graham, C.H., Anderson, R.P., Dudık, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F.,

Leathwick, J.R., Lehmann, A. and Li, J., 2006. Townsend Peterson, Steven J. Phillips, Karen Richardson, Ricardo Scachetti-Pereira, Robert E. Schapire, Jorge Soberón, Stephen Williams, Mary S. Wisz, and Niklaus E. Zimmermann. Novel methods improve prediction of species' distribution from occurrence data. Ecography, 29(2), pp.129-151. DOI: https://doi.org/10.1111/j.2006.0906-7590.04596.x

- Elith, J. and Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics, 40*(1), pp.677-697. DOI: https://doi.org/10.1146/ annurev.ecolsys.110308.120159.
- Emanuelli, F., Lorenzi, S., Greskowiak,
 L., Catalano, V., Stefanini, M., Troggio,
 M., Myles, S., Martinez-Zapater, J.M.,
 Zyprian, E., Moreira, F.M. and Grando,
 M.S., 2013. Genetic diversity and
 population structure assessed by SSR
 and SNP markers in a large germplasm
 collection of grape. *BMC Plant Biology*, *13*, pp.1-17. DOI: https://doi.
 org/10.1186/1471-2229-13-39.
- Frichot, E., Schoville, S.D., Bouchard,
 G. and François, O., 2013. Testing for associations between loci and environmental gradients using latent factor mixed models. *Molecular biology and evolution*, 30(7), pp.1687-1699. DOI: https://doi.org/10.1093/molbev/mst063.
- GGoufo, P., Singh, R.K. and Cortez, I., 2020. A reference list of phenolic compounds (including stilbenes) in grapevine

(Vitis vinifera L.) roots, woods, canes, stems, and leaves. *Antioxidants*, *9*(5), p.398. DOI: https://doi.org/10.3390/antiox9050398.

- Guan, B., Gao, J., Chen, W., Gong, X. and Ge, G., 2021. The effects of climate change on landscape connectivity and genetic clusters in a small subtropical and warm-temperate tree. *Frontiers in plant science*, *12*, p.671336. DOI: https:// doi.org/10.3389/fpls.2021.671336.
- Guisan, A. and Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecology letters*, 8(9), pp.993-1009. DOI: https://doi.org/10.1111/j.1461-0248.2005.00792.x..
 Hijmans, R.J. and Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global change biology*, *12*(12), pp.2272-2281. DOI: https://doi.org/10.1111/j.1365-2486.2006.01256.x.
- HHinojos Mendoza, G., Gutierrez Ramos, C.A., Heredia Corral, D.M., Soto Cruz, R. and Garbolino, E., 2020. Assessing suitable areas of common grapevine (Vitis vinifera L.) for current and future climate situations: The CDS Toolbox SDM. *Atmosphere*, *11*(11), p.1201. DOI: https://doi.org/10.3390/atmos11111201.
 Kearney, M. and Porter, W., 2009.
 Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology letters*, *12*(4), pp.334-350. DOI:
- https://doi.org/10.1111/j.1461-0248.2008.01277.x.

KRIŽMAN, M., Jakše, J., Baričevič,

D., Javornik, B. and Prošek, M., 2006. Robust CTAB-activated charcoal protocol for plant DNA extraction. *Acta Agriculturae Slovenica*, *87*(2), pp.427-433. DOI: https://doi.org/10.14720/ aas.2006.87.2.15122.

- McIntyre, N.E., Wright, C.K., Swain, S., Hayhoe, K., Liu, G., Schwartz, F.W. and Henebry, G.M., 2014. Climate forcing of wetland landscape connectivity in the Great Plains. *Frontiers in Ecology and the Environment*, *12*(1), pp.59-64. DOI: https://doi.org/10.1890/120369.
- NNaqinezhad, A., Ramezani, E., Djamali, M., Schnitzler, A. and Arnold, C., 2018.
 Wild grapevine (Vitis vinifera subsp. sylvestris) in the Hyrcanian relict forests of northern Iran: an overview of current taxonomy, ecology and palaeorecords. *Journal of Forestry Research*, 29, pp.1757-1768. DOI: https://doi. org/10.1007/s11676-017-0549-6.
- Nosil, P., Egan, S.P. and Funk, D.J., 2008. Heterogeneous genomic differentiation between walking-stick ecotypes:"isolation by adaptation" multiple roles divergent and for selection. Evolution, 62(2), pp.316-336. https://doi.org/10.1111/j.1558-DOI: 5646.2007.00299.x.
- Ortego, J., Riordan, E.C., Gugger, P.F. and Sork, V.L., 2012. Influence of environmental heterogeneity on genetic diversity and structure in an endemic southern Californian oak. *Molecular Ecology*, 21(13), pp.3210-3223. DOI: https://doi.org/10.1111/j.1365-294X.2012.05591.x.

Pagel, M., 1999. Inferring the historical

patterns of biological evolution. *Nature*, 401(6756), pp.877-884..

- Parihar, S. and Sharma, D., 2021. A brief overview on Vitis Vinifera. *Sch Acad J Pharm*, *12*(12), pp.231-9. DOI: 10.36347/sajp.2021.v10i12.005.
- Phillips, S.J., Anderson, R.P. and Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological modelling*, 190(3-4), pp.231-259. DOI: https://doi.org/10.1016/j. ecolmodel.2005.03.026.
- Poelchau, M.F. and Hamrick, J.L., 2012. Differential effects of landscape-level environmental features on genetic structure in three codistributed tree species in C entral A merica. Molecular Ecology, 21(20), pp.4970-4982. DOI: https://doi. org/10.1111/j.1365-294X.2012.05755.x. Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. and Milyutin, L.I., 2002. Intraspecific responses to climate in Pinus sylvestris. Global Change Biology, 8(9), pp.912-929. DOI: https://doi. org/10.1046/j.1365-2486.2002.00516.x. Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution, (2), pp.217-223. DOI: 10.1111/j.2041-210X.2011.00169.x.
- Riordan, E.C., Gugger, P.F., Ortego, J., Smith, C., Gaddis, K., Thompson, P. and Sork, V.L., 2016. Association of genetic and phenotypic variability with geography and climate in three southern California oaks. *American journal of botany*, 103(1), pp.73-85. DOI: https:// doi.org/10.3732/ajb.1500135.

- Soularue, J.P. and Kremer, A., 2014. Evolutionary responses of tree phenology to the combined effects of assortative mating, gene flow and divergent selection. *Heredity*, *113*(6), pp.485-494. DOI: https://doi.org/10.1038/hdy.2014.51.
- Tardieu, F., 2003. Virtual plants: modelling as a tool for the genomics of tolerance to water deficit. *Trends in plant Science*, 8(1), pp.9-14. DOI: 10.1016/s1360-1385(02)00008-0.
- Taskesenlioglu, M.Y., Ercisli, S., Kupe, M. and Ercisli, N., 2022. History of grape in Anatolia and historical sustainable grape production in Erzincan agroecological conditions in Turkey. *Sustainability*, *14*(3), p.1496. DOI: https://doi. org/10.3390/su14031496.
- This, P., Jung, A., Boccacci, P., Borrego, J., Costantini, L., Crespan, M., Eisenheld, C., Grando, M.S., Lacombe, T., Lacou, V. and Meredith, C.P., 2004. Development of a common set of standard varieties and standardized method of scoring microsatellites markers for the analysis of grapevine genetic resources. *Theoretical* and Applied Genetics, 109, pp.1448-1458. DOI: 10.1007/s00122-004-1760-3. Wang, I.J. and Bradburd, G.S., 2014. Isolation by environment. *Molecular* ecology, 23(23), pp.5649-5662. DOI: https://doi.org/10.1111/mec.12938.
- Woodward, F.I., 1987. Climate and plant distribution. Cambridge University Press. DOI: https://doi.org/10.1007/BF00038700.

20