

# A tale of three vines: current and future threats to wild Eurasian grapevine by vineyards and invasive rootstocks

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## Abstract

**Aim:** Eurasian grapevine (*Vitis vinifera*), one of the most important fruit crops worldwide, diverged from its wild and currently endangered relative (*V. vinifera* ssp. *sylvestris*) about 11,000 years ago. In the 19th century, detrimental phylloxera and disease outbreaks in Europe forced grapevine cultivation to use American *Vitis* species as rootstocks, which have now become naturalized in Europe and are starting to colonize similar habitats to the wild grapevine. Accordingly, wild grapevine now faces two additional threats: the expansion of vineyards and invasive rootstocks. Furthermore, climate change is expected to have significant impacts on the distribution of all grapevines in Europe. In this study, we quantified the distributional and bioclimatic overlap between grapevine's wild relative and the taxa associated with viticulture, under current and future climate.

**Location:** Europe, North America.

**Methods:** The distributions of wild Eurasian grapevine, cultivated Eurasian grapevine and five American grapevine species used in rootstock breeding programs were linked to climate variables to model their bioclimatic niches. These ecological niche models were used to quantify the spatial and bioclimatic overlap between these seven *Vitis* taxa in Europe.

**Results:** Niche and spatial overlap is high between the wild, cultivated and rootstock grapevines, suggesting that existing conflicts between vineyards and wild grapevine conservation may be further complicated by naturalized rootstocks outcompeting the wild grapevine, especially under future scenarios of climate change. In the hottest scenario, only 76.1% of the current distribution of the Eurasian grapevine remains in suitable area.

**Main Conclusions:** As wild grapevine may ultimately provide a valuable gene pool for adapting viticulture to a changing world, these findings demonstrate the need for improved management of the wild grapevine and its natural habitat, to counteract the harmful effects of global change on the wild relatives of viticulture.

## KEYWORDS

climate change, ecological niche models, grapevine, invasive, niche overlap, viticulture, *Vitis*

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## 1 | INTRODUCTION

### 1.1 | *Vitis* in Europe: a multidimensional illustration of global change

Rapid global changes induced by human activities in this Anthropocene era have severe impacts on biodiversity (Newbold et al., 2015; Seddon et al., 2016; Storch et al., 2022). The drivers of biodiversity loss include biological invasions, climate change, habitat destruction (particularly for the expansion of agricultural land) and often a combination of these drivers (IPBES, 2019; Ruckelshaus et al., 2020). Rare plant species can be highly threatened by this multidimensional spectrum of global changes (Enquist et al., 2019), yet endangered species can provide useful gene pools for crop breeding (Khoury et al., 2020). Given the increasing 21st century threats to food security and biodiversity (Scherer et al., 2020), the conservation of crop wild relatives (CWR) is a crucial tool to ensure a rich source of novel genetic diversity for crops (FAO, 2013). This becomes especially important in a future marked by climate change, including increased heat, drought, soil degradation, and water and land shortages (Aguirre-Gutiérrez et al., 2017; Cortés & López-Hernández, 2021; McCouch et al., 2013).

### 1.2 | The native view: from wild to cultivated grapevine

Only one *Vitis* species, the Eurasian grapevine (*V. vinifera* L.), is native to Europe, originating in the Mediterranean basin and the Caucasus. Its domestication started in the Near East, between the Black and Caspian Seas, during the early Neolithic period, ~11,000 years ago (Dong et al., 2023; Grassi & De Lorenzis, 2021; Myles et al., 2011). Domestication processes led to cultivated grape varieties (*V. vinifera* ssp. *vinifera* L., hereafter *V. vinifera*) diverging from their wild relative (*V. vinifera* ssp. *sylvestris* (Gmelin) Hegi; hereafter *V. sylvestris*) and presenting numerous genotypical and phenotypical differences (Aradhyia et al., 2003; Cunha et al., 2020; De Andrés et al., 2012; Dong et al., 2023; Grassi & De Lorenzis, 2021; Levadoux, 1956; McGovern, 2003; This et al., 2006; Zecca et al., 2012). Since then, viticulture has rapidly diversified and spread to become one of the most widely distributed and cultivated fruit crops with important economic interests (Arroyo-García and Revilla, 2013; De Mattia et al., 2008; Fraga et al., 2012; Grassi & De Lorenzis, 2021). The world's winegrowing area now represents 7.5 kha across five continents and produces more than 75 million tons of grapes (OIV, 2021).

The historical distribution of wild grapevine (*V. sylvestris*) covered a broad range of habitats, from the Mediterranean basin to the Caucasus (Arnold, 2002; Arroyo-García and Revilla, 2013; Dong et al., 2023; Grassi & De Lorenzis, 2021). Since the beginning of the 19th century, however, its distribution has dramatically declined. Wild grapevine is affected by habitat loss and fragmentation, for example, through the intensification of forest and river management

in Europe, since the 18th century (Arnold, 2002; Arroyo-García et al., 2016; Naqinezhad et al., 2018). It has been frequently eradicated from forests along with other climbing plants (e.g. lianas), considered to be detrimental to the growth of the trees (Finlayson et al., 2022; Smith, 1984). In many countries, clear-cutting practices in silviculture have proven harmful to the regeneration of wild grapevines (Arnold, 2002; Arnold et al., 2005). Along the rivers, construction of dykes had an impact on the frequency and magnitude of flooding, a crucial factor for the germination of the seeds of the Eurasian wild grapevine (Arnold et al., 2010). Furthermore, the resulting loss of alluviality allowed other competitive lianas to develop (clematis or ivy for example; Heuzé et al., 2009). The introduction of pests and diseases like Phylloxera (*Daktulosphaera vitifoliae* Fitch) and powdery and downy mildews (*Erysiphe necator* Schwein and *Plasmopara viticola* (Berk. & M.A. Curtis) Berl. & De Toni) negatively affected both cultivated grapevines and its wild relative (Cantos et al., 2017; Crovetto & Rossi, 1987). Combined together, these factors strongly reduced the distribution of the wild grapevine, which is now mainly restricted to floodplain habitats, sand dune shrublands and screes (Arnold, 2002; Naqinezhad et al., 2018). Similar to many wild varieties of other cultivated plants (Khoury et al., 2020), wild grapevine is now variably threatened depending on the country, and especially on the western side of its distribution (Arnold, 2002; Arroyo-García and Revilla, 2013; Cantos et al., 2017; Di Vecchi-Staraz et al., 2009; Niklfeld, 1999). While *V. vinifera* is classified as Near Threatened (NT) in the European Union (Bilz et al., 2011), it is included in the national Red List of eight countries under various categories, such as Critically Endangered (CR), Endangered (EN), Vulnerable (VU) or Least Concern (LC). Additionally, conservation concerns for this species have been pointed out in at least seven other countries (Table S1).

### 1.3 | The exotic view: from grapevine diseases to exotic rootstock invasions

In the middle of the 19th century, grapevine diseases and pests from North America were introduced to Europe (Granett et al., 2001), devastating and destroying many European vineyards (This et al., 2006). As a result, since the mid-19th century, many efforts have been dedicated to improving knowledge of wild *Vitis* relatives, with the hope of reviving vineyard through grafting and breeding with wild grapevine relatives capable of resisting introduced diseases and pests, such as *V. labrusca* L., *V. aestivalis* Michx. or *V. riparia* Michx. in America (Arnold & Schnitzler, 2020).

Most of modern rootstocks are the result of intentional interspecific hybridizations between five American *Vitis* species: *V. berlandieri* Planch (syn. *V. cinerea* var. *helleri* (Bailey) M.O. Moore), *V. riparia* Michx., *V. rupestris* Sheele, *V. aestivalis* Michx and *V. acerifolia* Raf. (André et al., 2018; Heinitz et al., 2019; Marín et al., 2021; Millardet, 1885; This et al., 2006). Spontaneous hybridization can also occur among these rootstocks, for example, in fallow vineyards in France (André et al., 2018). In their native ranges, *V. riparia* has a

wide distribution in North America, *V. rupestris* is mainly distributed in the south-eastern part of the United States and *V. berlandieri* is primarily distributed in Texas and Mexico. *V. acerifolia* and *V. aestivalis* have a restricted range in south-central United States (USDA and NRCS, 2021; Figure 1). Taken together, these American *Vitis* are thus adapted to a wide range of climatic conditions and forest structures (André et al., 2020; Arnold & Schnitzler, 2020; Arrigo & Arnold, 2007; Callen et al., 2016; Heinitz et al., 2019; Marín et al., 2021; Morano & Walker, 1995).

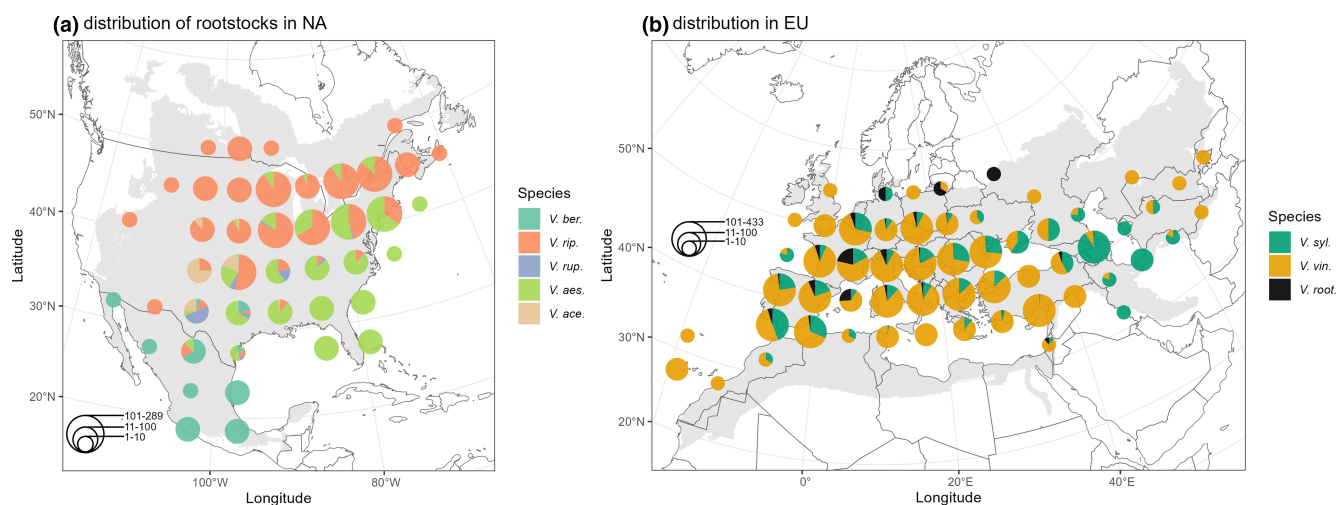
#### 1.4 | Arising spatial conflicts: three groups of grapevines with the same habitat preferences?

There is now growing evidence of rootstock cultivars escaping vineyards and colonizing novel habitats (André et al., 2020; Ardenghi et al., 2015; Arnold et al., 2017; Arrigo & Arnold, 2007; Bodor et al., 2010; Laguna, 2004; Meléndez et al., 2016; Stinca, 2019; Zecca et al., 2010). Featuring interspecific genomes, these selected rootstocks exhibit high adaptability and stronger propagule pressure (André et al., 2020). As a result, they have become pervasive invaders, covering hundreds of kilometres of transportation structures, ravines, as well as shrub and woodland communities in Spain, France, Italy and Georgia (Ardenghi et al., 2015; Laguna, 2004; Ocete Rubio et al., 2012; Stinca, 2019). All five American species from which the rootstocks are hybridized belong to the inventory of alien invasive species in Europe (Roy et al., 2020) or to the Global Register of Introduced and Invasive Species (Pagad et al., 2018). These American *Vitis* have been naturalized in the same locations and habitats as the wild Eurasian grapevine, particularly in the alluvial forests where they are serious competitors (Arrigo & Arnold, 2007; Cantos et al., 2017; Meléndez et al., 2016). Furthermore, within these

mixed populations, hybridization between *V. sylvestris* and escaped rootstocks is leading to genetic pollution (André et al., 2020; Arnold et al., 2017; Bodor et al., 2010).

The assessment of ecological niche overlap between escaped rootstocks has been conducted in various case studies at the regional scale (Arrigo & Arnold, 2007; Laguna, 2004; Meléndez et al., 2016). However, to the best of our knowledge, no previous attempts have been made to assess the niche overlap at a global scale encompassing the entire distribution of these taxa. Such analyses are crucial for assessing future areas of wild grapevine conservation, grape production and rootstock invasions, particularly in the context of rapid climatic change. Indeed, these distribution changes may have enormous economic and cultural implications, and thus require investigation (Fraga et al., 2016; Hannah et al., 2013; Jones et al., 2005; Kenny & Harrison, 1992; Morales-Castilla et al., 2020; Tóth & Végvári, 2016; Van Leeuwen et al., 2019; White et al., 2006).

A simple and efficient way to model species niches and distributions is to use ecological niche models (ENMs; also called species distribution models or habitat suitability models), which relate species occurrences to environmental variables (Elith & Leathwick, 2009; Guisan et al., 2017). Generally, at a broad continental scale, abiotic environmental factors related to climate are considered to determine plant distribution range (Barceló et al., 2019; Grace, 1987; Huang et al., 2021; Thuiller et al., 2004). If environmental variables are spatially explicit, it is then possible to project fitted ENMs into geographical space, resulting in a spatial prediction of the species' potential distribution, and further allowing assessment of how current distributions may be affected by climate change (Guisan et al., 2013; Guisan & Thuiller, 2005). These models and related multivariate analyses make it possible to compare niches, through statistically testing niche similarity between different species or ranges (Broennimann et al., 2012; Guisan



**FIGURE 1** Study areas and distributions used for ecological niche modelling. In North America (NA, a), rootstocks' wild relatives *V. berlandieri* (*V.ber.*), *v. riparia* (*V.rip.*), *V. rupestris* (*V.rup.*), *V. aestivalis* (*V.aes.*), *V. acerifolia* (*V.ace.*) are represented by distinct colours nested in pie charts. In Europe (EU, b), pie charts represent the distribution of *Vitis sylvestris* (*V.syl.*), *Vitis vinifera* (*V.vin.*) and exotic rootstocks related to the American taxa (*V.root.*). Size of the pie charts indicates the number of occupied 13 by 13 km cells in the area covered by the pie charts. Grey areas indicate the background, or 'study area', used to calibrate ENMs in NA and EU.

et al., 2014; Warren et al., 2008). Modelling the niches and spatial distributions of the wild and cultivated grapevines and exotic rootstock relatives can therefore provide a better understanding of current and future potential conflict areas, and accordingly provide support for improved land use and conservation planning aimed at safeguarding the wild grapevine, mitigating rootstock invasions and favouring the development of sustainable vineyards (Arnold et al., 2005; Arnold & Schnitzler, 2020).

## 1.5 | Study aim: assessing current and future spatial conflicts between three groups of grapevines

Here, we aim to assess the risk of wild grapevine being threatened by the expansion of viticulture and the naturalization and invasion of rootstock species in its climatically suitable habitats, under current and future conditions. We do this by quantifying the degrees of modelled niche and distribution overlap between the wild grapevine, cultivated grape varieties and American *Vitis* species used as rootstocks, offering a measure of potential threat at a global continental scale. To date, such an assessment has never been conducted comprehensively, especially at a broad enough scale to capture full species' niches, including rootstocks' native niches. To our knowledge, this is also the first attempt at using spatial modelling to address and combine the following aspects of global change within one genus (here *Vitis*): rare and endangered species, land use change, spread of exotic species and climate change.

## 2 | METHODS

### 2.1 | Species occurrences

Species distribution data were gathered using several databases. For all species, the GBIF database (GBIF.org, 2020) was screened in November 2020. Only georeferenced data with accuracy finer or equal to the resolution of the environmental data (13km) were kept for further analyses. Additionally, we included information for every *V. sylvestris* specimen obtained from the herbaria of Geneva, Lausanne, Zürich and Berlin, where georeferences were available. We also included distribution data from the AgroAtlas database (Afonin et al., 2008) for *V. sylvestris* and *V. vinifera* in Eastern Europe, thus compiling the most exhaustive distribution database for *V. sylvestris* to date. For distribution of the cultivated grapevine *V. vinifera* in Western Europe, we used the category 'vineyards' in the CORINE land cover dataset (Copernicus, 2018), complemented with maps from Johnson and Robinson (2002) and Tarapatskyy et al. (2019) for south-eastern Europe and Poland, respectively. For Europe, GBIF observations of *V. riparia*, *V. rupestris*, *V. berlandieri*, *V. aestivalis* and *V. acerifolia* were pooled into one rootstock group. Additional information about escaped rootstocks came from personal communications (Rafael Ocete, Claire Arnold) and literature review (Arrigo & Arnold, 2007; Naqinezhad et al., 2018; Figure 1). Observations were

carefully checked to remove aberrant occurrences, and the dataset was thinned to keep only one observation per analytical unit, that is, keeping a minimal average distance of 13km between observed occurrences. The map of species distribution was referenced at a 0.167° resolution raster and then transformed to an equal area projection system (EPSG:3035) to estimate the geographical overlap between the different distributions. Reference to the full dataset is available in the Appendix S1.

### 2.2 | Environmental data

Environmental data were gathered from the CliMond database (Kriticos et al., 2012), which is an environmental dataset composed of 35 variables at a resolution of 0.167°, grouped into four categories: temperature, precipitation, moisture and solar radiation. However, we excluded the eight variables related to solar radiation as this information was already used in the calculation of soil moisture variables. Soil moisture is a more proximal factor to predict plant species distribution at this scale. Consequently, we calibrated the principal component analysis on 27 variables (as explained the next section). From this set of variables, we selected only eight variables to build ENMs to predict species potential distributions (see below) because the use of a reduced set of variables mitigates model overfitting. These specific eight variables have consistently demonstrated the ability to enhance the transferability of ENMs across various geographic regions, enabling accurate predictions for naturalized species. (Figure S1; Petitpierre et al., 2017).

### 2.3 | Study area and spatial extent

The delimitation of the spatial extent used in ENMs can severely impact measures of niche overlap and geographic predictions and should thus correspond to a biogeographically relevant area for the studied species (Barve et al., 2011; Rödder & Engler, 2011). The two study areas were therefore defined as the union of the ecoregions covered by the five rootstocks species in North America (NA) and the ecoregions covered by wild grapevines and vineyards in Europe (EU; Figure 1). We used ecoregions from Olson et al. (2001), defined as relatively large units of land, where each contains a distinct assemblage of natural communities, yet shares a large majority of species and environmental conditions.

### 2.4 | Comparing bioclimatic niches among *Vitis* species

A principal component analysis (PCA) was calibrated on 27 climate variables covering the pooled extents of NA and EU. We then used the first two components to depict the environmental space and assess niche overlap. This approach (referred to as PCA<sub>env</sub>) was shown to be accurate in assessing species niche overlap in Holarctic

climates (Broennimann et al., 2012). Species occurrences and background extents were then projected into a gridded environmental space (resolution  $R=100$ ) and smoothed by a simple kernel function to calculate species occupancies per cell (Broennimann et al., 2012). Occupancies reflect the density of a species distribution in environmental space, corrected by the general availability of the different environments, thus allowing robust niche comparisons (Broennimann et al., 2012). Additionally, we pooled occurrences of the five American rootstocks and considered them as an aggregated taxon. Overlap was assessed as the Schoener's  $D$  between the occupancies of two taxa at one time. The overlap ( $D$ ) can vary between 0 (no overlap) and 1 (complete overlap). Additionally, we tested if the overlap was significantly higher than random through a one-tailed similarity test in environmental space based on Schoener's  $D$  (Broennimann et al., 2012; Warren et al., 2008).

## 2.5 | ENMs and geographical predictions

We used an ensemble modelling approach (Araújo & New, 2007) to average three statistical techniques commonly used in ENMs: gradient boosting machines (GBM; Friedman, 2001; also called boosted regression trees), maximum entropy regression (MaxEnt; Phillips et al., 2006) and general additive models (GAM; Hastie, 2017). 10,000 pseudo-absences were sampled in the study area and weighted such that presences and pseudo-absences had the same prevalence across ENMs. Species distribution modelling was performed with custom codes using the R software (version 4.0.3; R Core Team, 2020). GAMs were fitted with the mgcv package (version 1.8.33; Wood, 2011) with a smoothing parameter  $k=3$ . GBMs were computed with the libraries gbm (version 2.1.8; Greenwell et al., 2020) and dismo (version 1.3–3; Hijmans et al., 2020), using the function gbm.step to simplify the initial gbm. Learning rate, bag fraction and the maximum number of trees was set to 0.005, 0.5 and 5000, respectively. The dismo package was also used to fit the MaxEnt models. The beta multiplier was set to 1.8, and only linear, quadratic and product terms were used to limit overfitting (Merow et al., 2013). The whole dataset was repeatedly split into a 70% partition for calibrating ENMs and a 30% partition for evaluating them. ENMs were evaluated using four indices: Area Under the Curve of a Receiver Operating Characteristics (AUC; Fielding & Bell, 1997; Swets, 1988), maximized True Skill Statistics ( $TSS_{max}$ ; see Allouche et al., 2006 for TSS, and Guisan et al., 2017 for the maximization) and two 'presence-only' evaluators, the continuous Boyce index (B; Hirzel et al., 2006) and the sensitivity corresponding to the threshold of the  $TSS_{max}$  (Se; Liu et al., 2018). For rarer species limited in their dispersal, such as *V. sylvestris*, presence-only evaluators can be particularly relevant as they do not include the rate of false positive in the evaluation. AUC and Se were scaled between  $-1$  and  $+1$  so that all selected indices could then be averaged into one consensus index varying between  $-1$  (perfect counter prediction) and  $+1$  (perfect prediction), with 0 representing random predictions. Variable importance was assessed through randomization (in a similar way as

the package biomod2, Thuiller et al., 2009). Predictions from each technique were evaluated with this consensus index, so that one can average them with a weight proportional to each technique's accuracy. The final ensemble model thus consisted of a weighted average prediction of these three techniques (Hao et al., 2019). The projections were derived from a final model including 100% of the occurrences and background data.

ENMs were calibrated on the native extent of each taxon and projected onto present day NA and EU. Additionally, ENMs were projected to 2050 and 2100, using two global climate circulation models (GCM, CSIRO-MK3-0 and MIROC-H) for two climate change scenarios based on the fourth assessment of the Intergovernmental Panel on Climate Change: A1B (+2.8°C) and A2 (+3.4°C; IPCC, 2007). To estimate the overlap between potential distributions, continuous predicted suitability values need to be binarized, but it was previously shown that the thresholding strategy chosen can affect the results (Liu et al., 2013). Therefore, we estimated the overlap using six thresholding strategies and averaged the results across the following strategies: maximizing the sum of the sensitivity and specificity, maximizing Kappa, maximizing TSS, minimizing the distance of the ROC curve from the y axis, fixing a sensitivity rate at 0.9 and fixing a sensitivity rate at 0.95.

## 2.6 | Projecting potential distributions

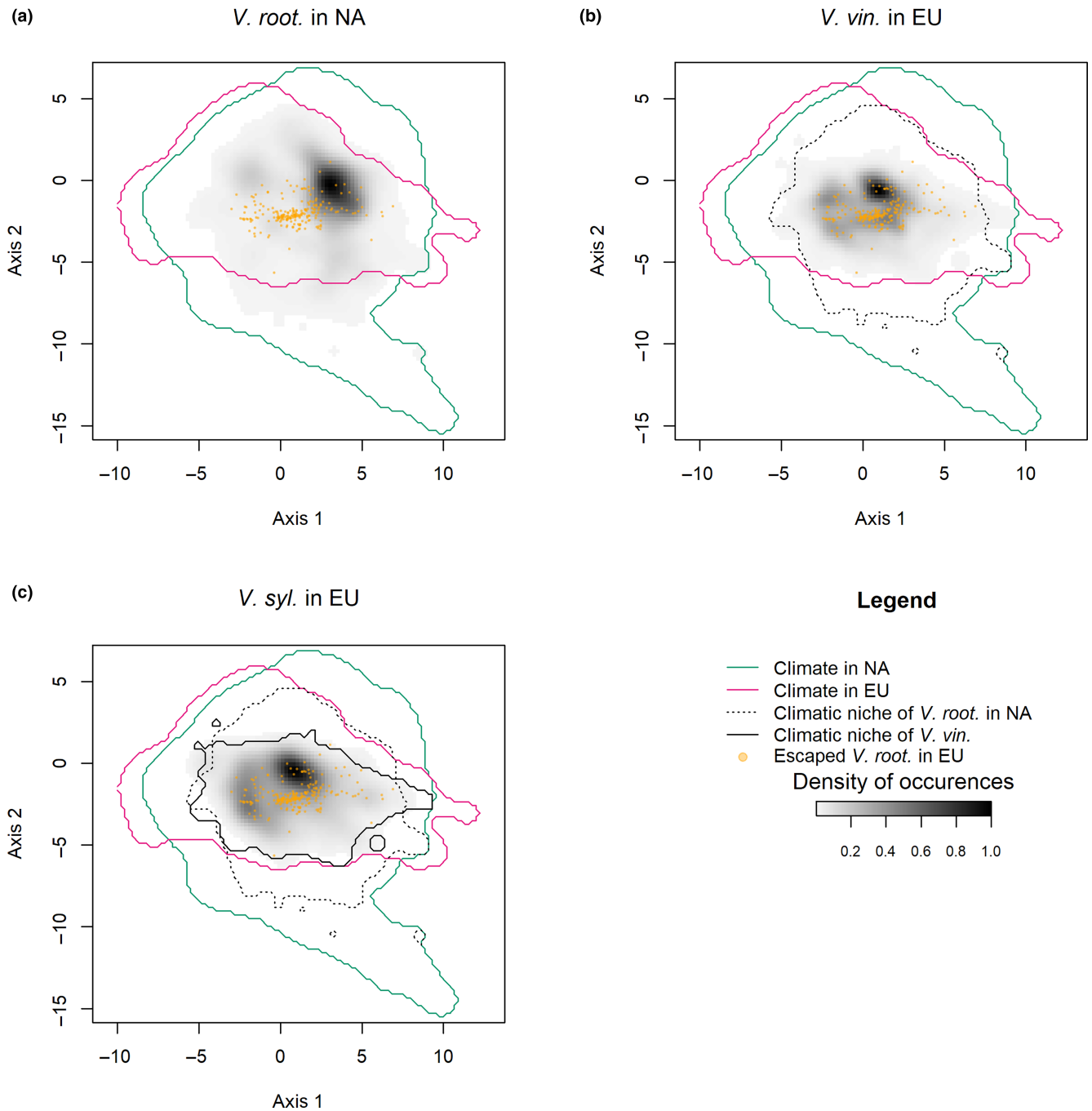
We built a map of the potential distribution of American rootstock species in EU by projecting the binarized distribution of the five American species and retaining every site where at least one of the five species was predicted as present. ENMs extrapolation to future climates that are currently non-existent in the calibration range are highly hazardous (Fitzpatrick & Hargrove, 2009). Therefore, we performed a MESS analysis (multivariate environmental suitability surface; Elith et al., 2011) to estimate the proportion of these non-analogue climates in the predicted distributions. Maps of observed and potential distributions were projected using the EPSG:3035 projection system and resampled at a 1 km resolution, to obtain 'equal area' maps.

## 3 | RESULTS

### 3.1 | Niche overlap in environmental space

The first two axes of the PCA explain 50% and 24% of the total climate variation within the pooled NA and EU calibration extents (Figure 2). The first axis corresponds to an aridity gradient, whereas the second axis relates to temperature variation and coldness (Figure S1).

The niches of wild (*V. sylvestris*) and cultivated (*V. vinifera*) Eurasian grapevine show a high and significant overlap (Table 1). Both are centred in similar climate conditions and share the same niche limits (Figure 2). The pooled native niche of the five American rootstock



**FIGURE 2** Environmental space depicted by the two first axes of a PCA calibrated on climate variables distributed in NA and EU study areas. Species distribution in the environmental space is represented by the cloud densities for (a) the pooled American rootstock species in North America (*V.root.* in NA), (b) the cultivated grapevine in Europe (*V.vin.* in EU) and (c) the Eurasian wild grapevine in Europe (*V.syl.* in EU). The distribution of the escaped American rootstock species in Europe is represented with orange points. Climates of the whole study area in NA and EU are delineated with a green and purple line, respectively. Niche margins of the pooled native distribution of the five American rootstock species (*V.root.*) in NA and *Vitis vinifera* (*V.vin.*) in EU are delineated with a black dashed and continuous lines, respectively.

species also shows a significant overlap with both cultivated and wild Eurasian *Vitis* taxa (Table 1, niche similarity test  $p$ -value <.05).

This pooled native niche of the American rootstock species is wider along the extremities of axis 2, meaning higher temperature variations and lower minimum and arises in more tropical conditions (i.e. hot and wet) than the *Vitis* distributions in EU (Figure 2, Figure S1 for the correlations between the variables and the axes of

the PCA). Interestingly, the niche of the rootstock species in EU is completely nested within the niches of the three vine groups, wild (*V.syl.*), cultivated (*V.vin.*) and American rootstocks (native *V.root.*) (Figure 2). This shows that the EU rootstocks did not expand into novel climates beyond their native range, nor beyond climates occupied by wild and cultivated grapevine in EU. Furthermore, the niche of the invasive rootstocks in EU shows a significant overlap with the

niche of the cultivated grapevine, and a marginally significant overlap with the niche of the wild grapevine (niche similarity test  $p$ -value  $<.05$  and  $p$ -value = .06, respectively, Table 1).

When the native niches of the five American rootstock species are considered individually, they occupy distinct subniches of the pooled rootstock niche. *V. riparia* occupies the cold and continental half, *V. rupestris* occupies median climates, *V. berlandieri* occurs in hotter and wetter climates, *V. aestivalis* in the wettest conditions and *V. acerifolia* is restricted to a small drier and cooler part of the niche. Among these five American rootstocks, *V. aestivalis* and *V. riparia*

**TABLE 1** Niche overlap (Shoener's  $D$ ) between the pooled native niche of the five American rootstock species ( $V. root_{NA}$ ), the invasive niche of the five American rootstock species ( $V. root_{EU}$ ), wild and cultivated grapevine in EU ( $V. syl.$  and  $V. vin.$ , respectively). The significance of the niche similarity test is also provided. When two niches are compared, the niche similarity test randomizes only one of the two niches at the same time. A significant (or marginally significant) value indicates that the overlap is higher than expected by a null model (\*\*, \* and ' shows that the  $p$ -value is comprised between .001 and .01, between .01 and .05 or between .05 and .1, respectively).

	$V. root_{NA}$	$V. root_{EU}$	$V. vin.$
$V. root_{EU}$	0.29*		
$V. vin.$	0.38*	0.5*	
$V. syl.$	0.40**	0.41'	0.71*

have the highest overlap with the native niche of the pooled rootstocks. Consequently, these two American taxa are the main drivers of the pooled rootstock niche ( $D=0.64$  and  $0.53$ , respectively, Figure S2, Table S2).

### 3.2 | Geographical overlap with the wild grapevine

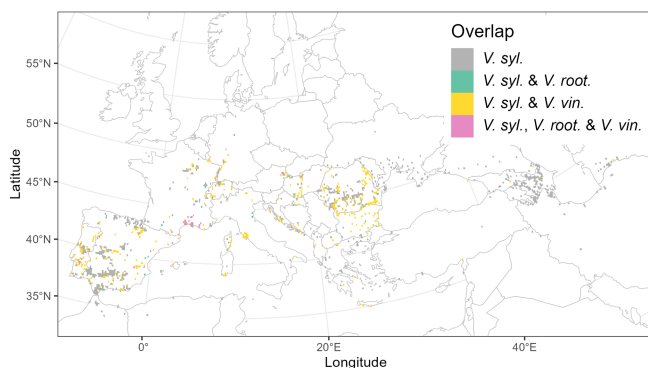
When recorded at a resolution of  $0.167^\circ$ , the distribution of wild grapevine covers  $286,476 \text{ km}^2$ , cultivated grapevine covers  $33.5\%$  ( $95,927 \text{ km}^2$ ) of the wild grapevine distribution and rootstock species are present in  $4.4\%$  ( $12,727 \text{ km}^2$ ) of wild grapevine's geographical distribution (Figures 1 and 3a). Note that  $2.9\%$  ( $8414 \text{ km}^2$ ) of the distribution of wild grapevine is shared with both cultivated grapevine and the rootstock species (Figure 3a).

### 3.3 | ENMs and overlap of the potential distributions

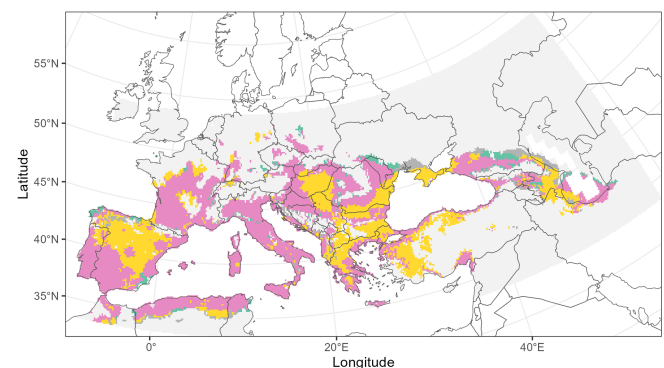
Based on a consensus index (summarizing  $TSS_{max}$ , AUC, Boyce index and sensitivity of  $TSS_{max}$ ), the accuracy of ENMs prediction ranges between  $0.73 \pm 0.01$  (fair; for *V. vinifera*) and  $0.93$  (excellent; for *V. rupestris*, *V. acerifolia* and *V. riparia*; Table S3).

The distribution of wild grapevine appears to be particularly driven by the mean temperature of the coldest quarter. Interestingly,

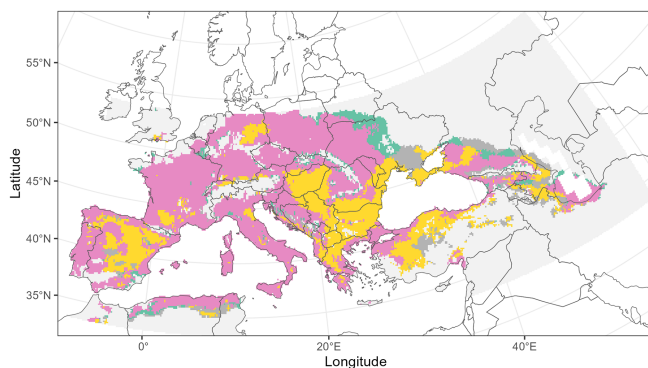
(a) observed current



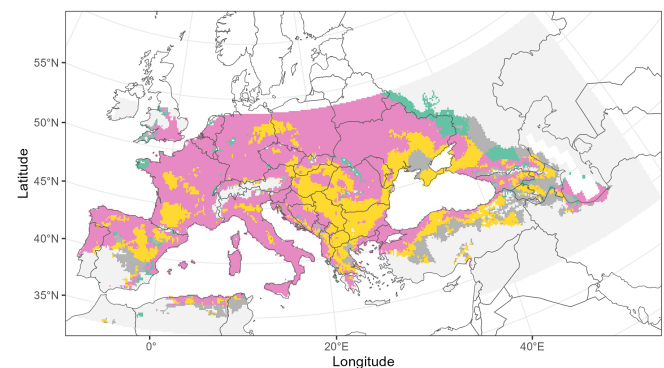
(b) potential current



(c) potential 2050 A1B



(d) potential 2100 A1B



**FIGURE 3** Overlap of the distribution of *Vitis sylvestris* (*V. syl.*) with *Vitis vinifera* (*V. vin.*) and the American rootstock species (*V. root.*) in the current observed (a), current potential (b) and future potential distribution (b and c) with the scenario A1B.

all taxa have their own response to the different climate variables, even in the case of two closely related taxa such as *V. sylvestris* and *V. vinifera* (Figure S3).

Across all climate scenarios, the maximum proportion of potential distributions located in non-analogue climates was 1.3%, 2.4% and 0.4% for wild grapevine, cultivated grapevine and the pooled rootstock species, respectively. Therefore, uncertainty due to extrapolation to non-analogue climates should have a null or minimal impact on our predictions and subsequent analyses. When habitat suitability is reclassified into potential presences and absences using six different thresholding approaches,  $87.7 \pm 10.1\%$  of the observed distribution of wild grapevine is included in its current potential distribution (thresholds for each approach and taxon are provided in Table S4).

Under the assumption of a no dispersal limitation, this proportion is expected to drop to  $76.1 \pm 5.6\%$  in the hottest climate scenario (Figure 4). The southern distribution of wild grapevine (in Morocco, Algeria, southern Spain and southern Greece) is predicted to become climatically unsuitable in future climates (Figure 3, Figures S4 and S5). Under the assumption of a possible dispersal for *V. sylvestris*, climatic suitability is predicted to increase in Europe from 18,886 to more than 24,000 sites (at a resolution of 13 km; Figure 3). This trend for an expansion of the potential distribution in EU also exists for cultivated grapevine and all the rootstocks in Europe, except for *V. riparia* (Table S5).

The niche overlap illustrated in the PCA of the environmental space is also translated at geographical level, with the mapped potential distributions (Figure S5). Under current conditions,  $90 \pm 4.2\%$  of the potential distribution of wild grapevine is shared with cultivated grapevine, and  $63.1 \pm 3.9\%$  is shared with the pooled rootstock species (Figure 3). More than half of the potential distribution of the wild grapevine ( $59.1 \pm 5.1\%$ ) overlaps with both cultivated grapevine

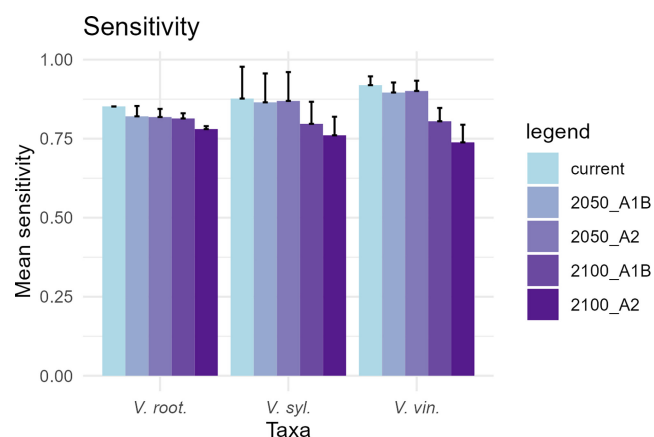
and the rootstock species (Figures 3 and 5). However, proportion of overlap is predicted to decrease with climate warming, falling to  $79.1 \pm 9\%$  (with *V. vinifera*),  $50.3 \pm 10.6\%$  (with rootstock species) and  $46.2 \pm 2.2\%$  (with *V. vinifera* and the rootstock species combined) under the warmest climate scenario (Figures 3 and 5).

## 4 | DISCUSSION

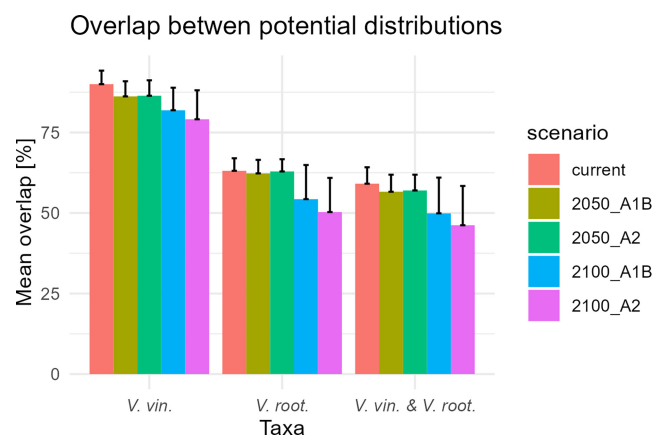
By comparing the climatic conditions of wild grapevine's geographic range with cultivated grape varieties and potentially invasive American rootstock species, we show that substantial bioclimatic niche overlap exists between wild, cultivated and rootstock grapevines (especially between the first two), which also translates into geographical overlap in Europe, both now and in the future. This highlights that the threatened wild grapevine (*V. sylvestris*) competes for the same climatic conditions as its cultivated relatives across most of its global distribution. These findings serve as an indication of potential further endangerment. Conservation of wild grapevine will thus require active consideration in future agricultural developments of cultivated grapevine and rootstock species, especially under future scenarios of climate change.

### 4.1 | Sharing similar niches

The bioclimatic overlap between wild and cultivated grapevines is not surprising, as the divergence of *V. sylvestris* and *V. vinifera* only occurred in recent human history (Dong et al., 2023). Vineyards are established under suitable climates for wild grapevines acting as direct and indirect environmental stressors for *V. sylvestris*. First, this high niche overlap between wild and cultivated grapevine supports the fact that viticulture was established in regions where



**FIGURE 4** Proportion of the observed distribution of *Vitis sylvestris* (*V. syl.*), *Vitis vinifera* (*V. vin.*) and the American rootstock species (*V. root.*) included in the current and future potential distributions with scenarios A1B and A2 for the years 2050 and 2100 in Europe. Under current conditions,  $87.7 \pm 10.1\%$  of the distribution of *Vitis sylvestris* is predicted to be suitable by the ENMs. In future climate conditions, this proportion is predicted to drop (e.g. down to  $76.1 \pm 5.6\%$  for the A2 scenario in 2100).



**FIGURE 5** Proportion of the potential distribution of *Vitis sylvestris* covered by the potential distribution of *Vitis vinifera* only (*V. vin.*), the rootstock species only (*V. root.*) and *Vitis vinifera* and the rootstock species together (*V. vin. & V. root.*). The potential distributions were projected under current climate and scenarios A1B and A2 for the dates of 2050 and 2100.



wild grapevines used to grow in the past. Favourable forests for the Eurasian wild grapevine have been replaced by vineyards (Arnold et al., 2005). Secondly, diseases and pests can spread from vineyards to wild populations, so as American rootstocks species, which are more resistant to these stresses (Hannah et al., 2013; Heinitz et al., 2019; Ocete Rubio et al., 2012). These escaped rootstocks can outcompete the Eurasian wild grapevine in their natural habitats. For instance, between 1995 and 2014 along the Ega river in Spain, the number of rootstocks and hybrids increased up to 28%, while 73% of the wild Eurasian grapevine disappeared (Meléndez et al., 2016). At this continental scale, it has been shown that the potential distribution of the insect pest *Daktulosphaira vitifoliae*, which causes phylloxera, overlaps with most of the distribution of the Eurasian wild grapevine (Ji et al., 2021). Under the most severe climate change scenarios, its presence is predicted to increase in Europe (Ji et al., 2021). Additionally, the spread and prevalence of (pseudo-) fungal diseases such as powdery and downy mildews are predicted to be favoured in a globalized viticulture (Anderson et al., 2004; Fisher et al., 2012; Fontaine et al., 2021; Ristaino & Records, 2020).

Interestingly, temperature is the most important driver in the distribution of cultivated grapevine, whereas the distribution of wild grapevine depends more on precipitation and moisture seasonality (Figure S3). The human mitigation of water stress in viticulture may explain the observed difference, combined with the selection of drought resistant varieties through breeding programs (Carbonell-Bejerano et al., 2016; Chaves et al., 2010; Wang et al., 2021). However, an important difference in the niches of wild and cultivated Eurasian grapevines occurs at a finer level, one not considered in this study. The habitats where wild grapevine populations currently remain are alluvial and colluvial forests. These areas are neither suitable for viticulture nor conducive for the development of grape pests (Arnold, 2002; Ocete Rubio et al., 2012). This difference in habitats at a finer resolution may explain the contrast between the very high overlap of potential distributions and the moderate overlap of observed distributions.

In North America, each of the five rootstock species occupies different environmental conditions while they are partially overlapping. Our study shows the same climatic differences between *V. riparia*, *V. rupestris*, *V. acerifolia* and *V. aestivalis* as in Callen et al. (2016), that is, cold and dry climates for *V. riparia*, a larger climatic width for *V. rupestris*, warm and dry conditions for *V. acerifolia*, and warm and wet climates for *V. aestivalis*. When the native bioclimatic niches of the American rootstock species are pooled together from the hot, dry climates of *V. berlandieri* to the cold, continental climates of *V. riparia* (Figure 2), they largely overlap with the niche of both wild and cultivated Eurasian grapevine. The macroclimatic differentiations between American rootstocks correspond to species' ecology at the finer habitat scale, often on sandy soils, where *V. berlandieri* has the widest niche and grows in the driest conditions compared to *V. rupestris* and *V. riparia* (Callen et al., 2016; Morano & Walker, 1995). Together, the five American rootstock species occupy a broader range of climatic conditions

than both wild and cultivated Eurasian grapevine, suggesting a high climatic suitability for naturalized rootstocks in Europe. Moreover, all observations of the naturalized rootstock species are nested within their native niche and show no niche expansion towards novel climates, supporting climate matching between native and exotic ranges, and therefore, a broad potential invasive range in Europe.

## 4.2 | Distribution overlap now and in the future

Currently, only a small proportion of the wild Eurasian grapevine distribution overlaps with American rootstocks, but according to the predicted suitability maps, this overlap could be multiplied by 11–14 times, depending on the degree of climate warming. This means that successful colonization of naturalized rootstocks in the habitats of the Eurasian wild grapevine observed in Spain, France, Italy and Georgia (Arrigo & Arnold, 2007; Laguna, 2004; Meléndez et al., 2016; Ocete Rubio et al., 2012; Zecca et al., 2010) could occur over a large portion of remaining wild grapevine habitats.

When applied to future climatic scenarios, ENMs predictions show an overall increase in the suitable area for wild and cultivated grapevines in Europe, with novel suitable areas appearing in the northern part of the projection extent (Figure 3, Figures S4 and S5). Our predictions for cultivated grapevine in 2050 corroborate previous results from global studies on the potential future distribution of viticulture in Europe (Fraga et al., 2016; Hannah et al., 2013; Morales-Castilla et al., 2020; Tóth & Végvári, 2016; Van Leeuwen et al., 2019). The high geographical overlap between wild and cultivated Eurasian grapevine is not predicted to change substantially in the future (Figure 3), except if their ecological niches would change due to novel biotic interactions or niche evolution (Pearman et al., 2008). The proportion of wild grapevine's potential distribution that is shared with that of cultivated grapevine or American rootstock species is predicted to slightly decrease with climate warming (Figure 3), despite the absolute area of overlap being predicted to increase (Figure 3, Figure S5). Potential suitable habitats for *V. sylvestris* – but not *V. vinifera* or rootstock species – are predicted to appear in Russia and Turkey under future climate warming. However, it is highly unlikely that these novel areas can be naturally colonized by wild grapevine due to its low dispersal ability, especially in the fragmented and senescent population of its western distribution (Di Vecchi-Staraz et al., 2009). Accordingly, assuming a 'no dispersal' hypothesis, only  $76.1 \pm 5.6\%$  of the current distribution of the wild grapevine is predicted to remain suitable under the hottest climate scenario A2. This corresponds to a loss of 13.5% of its distribution due future climate change (Figure 4). On the contrary, because of its economic viability, viticulture is expected to benefit from new opportunities offered by climate change, as recently shown by emerging viticulture in Belgium (Delval et al., 2021) and Scandinavia (Gustafsson & Mårtensson, 2005). Therefore, cultivated Eurasian grapevine and American rootstock species are likely to expand their range in northern and eastern Europe (Marin et al., 2021),

potentially posing additional threats to already endangered wild grapevine populations.

The high niche overlap between wild grapevine and its competitors, such as cultivated grapevine and naturalized rootstock, combined with the potential decline of its distribution due to climate warming, strongly support the need to establish active conservation programs for *V. sylvestris* (Arnold et al., 2005). Having a higher genetic diversity than cultivars, viticulture sustainability depends upon the protection of the wild grapevine as a valuable genetic resource (Arroyo-García and Revilla, 2013; De Andrés et al., 2012; Garfi et al., 2013; Myles et al., 2011), calling for the conservation of high genetic diversity within the wild relative (Kell et al., 2012). Homogenization through pollen-mediated gene flow between rootstocks and cultivated and wild grape varieties has already been documented and could contribute to the risk of extinction and inbreeding depression in wild grapevines (Arnold et al., 2017; Arnold & Schnitzler, 2020; Bodor et al., 2010; Di Vecchi-Staraz et al., 2009). This gene flow may become more prominent under future warming scenarios with increased carbon dioxide levels that would favour a growth response in lianas (Allen, 2015; Schnitzler & Bongers, 2011). Mapping suitable habitats for wild Eurasian grapevine, where *V. sylvestris* could grow with less pressure from viticulture, would allow for more efficient preservation (e.g. grey area in Figure 3; see Bradley et al., 2012). Our results highlight four areas where ENMs suitability predictions are more favourable to the endangered wild relatives: the Iberic peninsula, the northern Maghreb, central Europe and the Caucasus. Interestingly, these areas represent distinct gene pools for wild grapevine (Dong et al., 2023; Myles et al., 2011). The southern distribution of wild grapevine in Maghreb is forecasted to become climatically unsuitable under future climate conditions. The wild grapevine populations in this region are among the least researched. While they are described as small and fragmented, they likely harbour the best-adapted resources to cope with climate warming due to their extreme meridional location (Bounab & Laiadi, 2019; Slimane et al., 2010; Zoghalmi et al., 2002). In addition to the three other regions, this is where the species' conservation should be prioritized.

Future research should model grapevine niches and distribution at a finer scale, where other relevant factors such as soil quality (e.g. see Ocete et al., 2015), landcover (e.g. NDVI in Rahimi et al., 2021) or light availability may be included. Because they are more limited in availability, such fine-scale information can pose challenges related to the 'niche truncation' when modelling species distribution, as it may limit the generalizability of the modelling across the species' entire distribution (Chevalier et al., 2021, 2022). To better incorporate the influence of scale-dependent drivers on species distribution, our comprehensive coarse-scale dataset and predictions can now be combined with fine-grained regional environmental factors using hierarchical data integration methods. Such approaches can enhance the accuracy and robustness of the predictions by capturing the complexity of species-environment relationships across different scales (Adde et al., 2023; Fletcher et al., 2019; Mateo et al., 2019).

## 4.3 | Conclusion

The bioclimatic niches and geographic distributions of three grapevine groups –wild, cultivated, American rootstocks – were modelled and compared. These grapevine groups represent three corners of a global change story, characterized by high niche overlap between the wild Eurasian grapevine and its cultivated relatives. As a result, the already endangered wild grapevine – *V. sylvestris* – faces increased potential threats under future scenarios of climate change. While its distribution is predicted to drop, the cultivated Eurasian grapevine and five American naturalized rootstock species may increasingly colonize its natural habitats in Europe, especially with climate warming and the expansion of viticulture. Our findings support the need for more active conservation measures for wild grapevine populations, which are foundational to sociocultural heritage and contribute valuable genetic resources for the maintenance and development of cultivated grape varieties under changing environmental conditions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13780>.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo: [10.5281/zenodo.8330781](https://doi.org/10.5281/zenodo.8330781).

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#### BIOSKETCH

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#### SUPPORTING INFORMATION

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

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